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Electrophysiological Correlates of Reversal Processes in Ambiguous Figure Perception

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Declaration

The research presented in this thesis was conducted at the School of Psychology, University of Kent, whilst the author was a full-time postgraduate student, supported by the University of Kent's Postgraduate Research Bursary for two terms, under the supervision of Dr. Joseph Brooks. The data reported in this thesis was collected at the Brain Electrophysiology and Perception Laboratory at Keele University. Chapter 3 of this thesis is under review for publication (please see below). The data reported in Chapters 3 & 4 have been presented at numerous conferences.

Peer-reviewed journal articles:

- Abdallah, D., Brooks, J.L. Response dependence of reversal related ERP components in perception of ambiguous figures. *Psychophysiology.* https://doi.org/10.1111/psyp.13685

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- Abdallah, D., Brooks, J.L. (August 2018). Task dependence of reversal related ERP components in perception of the Necker Lattice. Poster presented at the European Conference on Visual Perception, Trieste, Italy.

Abstract

Ambiguous figures provide an opportunity to study fluctuations in perceptual experience without corresponding changes in sensory input. Researchers have taken great interest in the mechanisms that generate them using electrophysiology because of the potential to track these processes across time as perceptual reversals of these figures unfold. This work has highlighted brain activity both before and after perceptual reversals involving a wide range of mechanisms. Some of the known electrophysiological correlates of perceptual reversals, like the Reversal Negativity (RN) and Reversal Positivity (RP), have the potential to be explained by demands of the tasks used to elicit them. In addition, many findings on perceptual reversals and ambiguous figure interpretation originate from studies using univariate analyses that do not take full advantage of the multivariate nature of EEG data. In four experiments, I used psychophysics, ERP, and multivariate pattern analysis (MVPA) of EEG data to address the interpretation of two reversal-related ERP components and to identify new multivariate correlates of perceptual reversals. First, I found that the reversal-related RP only appears when reversals are response targets. This result suggests that the RP is not a pure correlate of perceptual processing of endogenous perceptual reversals but rather may reflect response-related monitoring processes. Second, using MVPA, I found that activity linked to perceptual reversals in the post-stimulus period is an ongoing process that involves a wide range of frequency bands (1-30Hz) and spans over a substantial amount of time (~550 ms). Finally, I found that I was able to isolate in time and frequency pre-stimulus activity that is predictive of the upcoming subjective interpretation of the ambiguous stimulus and of perceptual reversals. Overall, these results provide a new

interpretation for some extant reversal-related electrophysiological markers as well as identify a set of new phenomena to guide neural theories of perceptual reversals going forward.

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Table of Contents

Chapter 1: Introduction

1.1. A Brief History of Multistable Perception

We rely on our visual system to produce a single and presumably veridical representation of the outside world. However, the optical projection of the three dimensional world is incomplete and provides us with sensory information that is often ambiguous. Current theories of perception suggest that the brain performs statistically optimal inferences about the structure of the external world based on limited sensory information (Knill and Pouget, 2004; Pastukhov, 2017).

The visual system has direct access only to the proximal stimulus (e.g., the retinal image). The proximal stimulus is the physical stimulation (i.e. the patterns of the physical stimuli) that can reach and be measured by the observer's sensory apparatus. The proximal stimulus changes with changes in the properties (e.g. position or lighting) of the physical (distal) stimulus. Therefore, perception is sometimes described as the process of constructing mental representations of distal stimuli (i.e. the state of the objects in the world around us) using the information available in the proximal stimuli. For instance, when an individual sees a piece of cake, it is because the piece of cake (the distal stimulus) created a retinal image (the proximal stimulus) that was interpreted as a piece of cake by the person's visual system. The proximal stimulus is the stimulus that the observer can measure directly. However, measuring the distal stimulus is not as straight forward and the relationship between these two types of stimuli is generally complex. It is clear that the process will involve an inference and may not always produce veridical results.

A comprehensive understanding of the precise nature and neural implementation of perception and more specifically perceptual inference is still underway. In order to develop this comprehensive understanding of the underlying brain mechanisms behind our visual experiences, researchers have focused on clarifying the dynamic between top-down and bottom-up processes between and within the neural structures involved (Park & Friston, 2013). This means understanding the relationship between low-level cognitive functions usually observed in early visual areas (e.g. occipital cortex; Kosslyn et al., 1995; Slotnick et al., 2005; Thirion et al., 2006) and high-level cognitive functions from the higher-level areas (e.g. parietal and frontal cortex; Ishai et al., 2000; O'Craven and Kanwisher, 2000; Mechelli et al., 2004). Previous and recent research suggests that during perception, bottom-up influences such stimulus presentation mode (i.e. manipulation of the stimulus parameters; e.g intermittent presentation of the stimulus; Orbach et al., 1963; Kornmeier et al., 2002; Leopold et al., 2002; Long & Toppino, 2004; Maier et al., 2003; Noest et al., 2007), neural fatigue (e.g. Köhler, 1940; Orbach et al., 1963; Toppino and Long, 1987) and passive adaptation (e.g. Long & Moran, 2007; Orbach et al., 1963; Toppino and Long, 1987) influence the activation level of visual representations. However, other work suggests that top-down projections from fronto-parietal areas are heavily involved in perceptual inference (Mechelli et al., 2004; Dentico et al., 2014). Perception, in studies focused on understanding the top-down mechanisms, is seen as an active process in which a representation of our environment is constructed based on external information and internal factors including past experience (e.g. Long et al., 1992), current goals (i.e. intention; e.g. Pitts et al., 2008), task demands, attention (e.g. Leopold & Logothetis, 1999), prediction (e.g. Heekren et al., 2008; Bar, 2009) and assumptions about the nature of the world (Gregory, 1980). There is a growing body of research positing that these mechanisms play a central and predictive role in perception (Buschman & Miller, 2007; Friston, 2010; Muckli, 2010). This is in line with the 'predictive coding' approach which suggests that the brain continuously generates and updates a prediction of the sensory environment. The actual sensory input (i.e. the incoming information) is then compared against internally generated predictions of the world and the prediction mechanism is updated to reflect any conflicts (Rao and Ballard, 1999).

Researchers have also started to take a more holistic approach, combining both top-down and bottom-up mechanisms. 'Visual experience [and perception] is a product of the reciprocal exchange of bottom-up and top-down influences throughout the neuronal hierarchy' (Dijkstra et al., 2017, Bastos et al., 2012; Mumford, 1992). The bottom-up and top-down mechanisms listed above are explained in more detail later in this chapter (section 1.2).

Ambiguous figures, such as Rubin's Face-Vase (Figure 1C; Rubin, 1915) or the Necker Cube (Figure 1A; Necker, 1832), have been used in order to study mechanisms of perceptual inference. When viewing these images, our perceptual interpretations of them are only temporarily stable and often spontaneously fluctuate between different interpretations of the stimulus despite no corresponding changes in the sensory input. This spontaneous fluctuation between two or more different interpretations of an ambiguous image is often referred to as bistable (two) or multistable perception (two or more). These figures have been used in experiments investigating perceptual organization (i.e., Pomerantz & Kubovy, 1981), object representation, and conscious awareness (i.e., Blake & Logothetis, 2002; Crick & Koch, 1998; Dehaene & Changeux, 2011). Ambiguous figures have been suggested to offer a unique window into perceptual inference mechanisms (Long & Toppino, 2004) because any changes in our interpretation of them usually cannot be attributed to changes in the sensory input itself. Instead, changes seem to arise from internal processes and how they interact with the sensory input. Furthermore, perception of ambiguous figures has been found 'to engage a distributed network of occipital, parietal, and frontal cortical areas' (Tong et al., 2006; Sterzer et al., 2009; Hramov et al., 2017). Thus, there is a clear basis for questions of whether the moment-to-moment fluctuations in ambiguous figure perception are driven by bottom-up mechanisms, top-down mechanisms, or both.

Figure 1. Examples of ambiguous figures. (A) The Necker Cube (Necker, 1832). (B) Boring's Old-Young Woman figure (Boring, 1930). (C) Rubin's Face-Vase illusion (Rubin, 1915).

1.1.1. Multistabe Perception

Ambiguous figures provide a unique opportunity to study the neural correlates of conscious change without corresponding changes in sensory input (Kornmeir & Bach, 2014). Thus, comparisons of neural activity associated with different interpretations of the same image (e.g., face vs. vase for Rubin's image, Figure 1C) are not confounded by differences in sensory input, assuming that viewing conditions (e.g., eye movements/position, lighting conditions) are equated. Perception of ambiguous figures involves spontaneous switching between alternative percepts of the stimulus (e.g., Andrews, Schluppeck, Homfray, Matthews & Blakemore, 2002). These switches are known as perceptual reversals. For instance, the Necker Cube image (see Figure 1A) can be interpreted as either left-oriented or right-oriented (Borsellino et al., 1972). The juncture of the two faces that are parallel to the observer forms a rectangle, and the lines that join on the square form a "y-junction" at the two diagonally opposite sides. If an observer focuses on the lower "y-junction", the upper right face will appear to be in front (see Figure 1Aa). However, if the focus is on the higher junction, the lower left face will appear to be in front (see Figure 1Ab). The human perceptual system picks an interpretation of the features of the image and thus, an orientation, making the whole stable for a short period before switching to the other interpretation. This switch in perceived orientation is known as a perceptual reversal. Another well-known ambiguous stimulus that illustrates this reversal behaviour is Rubin's (1915) Faces-Vase stimulus (see Figure 1C). It is alternately perceived as either two profile faces with a space between them or a vase in the centre of the image due to the figure-ground ambiguity of the two edges bounding the regions (Leopold and Logothetis, 1999; Peterson, 2014; Rubin, 1915).

There are two types of reversals that have been identified. Endogenous reversals occur spontaneously during observation of ambiguous stimuli without any corresponding change in the stimulus or its viewing conditions. In contrast, exogenous reversals are induced by changes in the ambiguous stimulus itself (e.g., presenting different unambiguous variants sequentially; e.g., face-biased then vase-biased) or in changes to the viewing conditions. Furthermore, reversals can occur both when we observe an ambiguous figure continuously as well as when it is viewed intermittently with blank intervals between discrete presentations. Most research on ambiguous stimuli focuses on endogenous reversals. However, comparing results between the two types of reversals can be important because it can reveal whether changes in neural activity are uniquely related to creating reversals of ambiguous stimuli or generally activated by any change in perception.

On exogenous reversal trials, different variants of the unambiguous stimulus are presented (e.g., face-biased Rubin-vase followed by a vase-biased Rubin vase). For exogenous stable trials, the same unambiguous variant will be presented sequentially and thus there is no change in perceptual experience. Presumably, the neural representation does not change significantly from one stimulus to the next if the same unambiguous variants of the ambiguous stimulus are presented successively. For endogenous reversals, on the other hand, the same ambiguous visual input can activate two mutually exclusive neural representations, each underlying one of the two perceptual interpretations. The reversal from one interpretation to the other is not related to a change in the stimulus properties. Presumably the reversal arises from an unstable brain state in response to the ambiguous stimulus input. These differences between the two types of reversals (exogenous and endogenous reversals) lead to some differences in the latencies of their corresponding electrophysiological correlates (see Kornmeier & Bach, 2012 for a review; these differences will be detailed in section 1.3.2 of this Chapter). Moreover, there are some correlates that are observable for endogenous reversals but not for exogenous ones.

1.2. The Bottom-Up vs. Top-Down Controversy

Several factors come into play to account for perceptual reversals. Numerous psychophysical studies have resulted in the two explanatory approaches mentioned previously that view perceptual switching as either a cognitive, top-down process or a bottom-up process (Blake, 1989; Leopold and Logothetis, 1999; Long and Toppino, 2004). Several authors, however, have taken a more integrative approach to explain this phenomenon by incorporating both approaches (Kornmeier & Bach, 2012; for review see Peterson, 2014).

In short, the bottom-up approach (explained in more detail in section 1.2.1.) assumes that activity in the early visual areas (i.e. the sensory cortex) plays the dominant role in producing perceptual reversals (Andrews, Schluppeck, Homfray, Matthews & Blakemore, 2002). This approach suggests that factors (explained in more detail below) such as adaptation (e.g., Köhler, 1940; Long et al., 1992; Long and Olszweski, 1999; Toppino and Long, 1987), stimulus features (e.g. size of the stimulus; Washburn et al., 1931; Ammons & Ammons, 1963), and presentation mode (e.g. intermittent versus continuous presentation of the stimulus; Orbach et al., 1963; Kornmeier et al., 2007) are the dominant forces that influence the reversal dynamics of ambiguous figures (e.g. the rate of reversals; Kornmeier & Bach, 2012).

Other studies have found that top-down modulation from high-level regions such as the frontal/parietal cortices influence perceptual reversals (Brascamp, Blake & Knapen, 2015; de Graaf, de Jong, Goebel, van Ee & Sack, 2011; Pitts, Martínez, Stalmaster, Nerger & Hillyard, 2009; see section 1.2.2.). This approach assumes that perceptual reversals are the result of active high-level/cognitive factors like attention, expectation, decision-making, and learning (Gregory, 1974; Rock et al., 1994; Leopold and Logothetis, 1999) among others (Kornmeier & Bach, 2012). Below I describe the bottom-up and top-down processes that have been suggested as underlying mechanisms of ambiguous figure perception and perceptual reversals.

1.2.1. Bottom-Up Influence

Several studies designed to investigate the influence of low-level factors on perceptual reversals have demonstrated that the factors detailed below influence the reversal dynamics of ambiguous figures. In the following, I will define these factors and detail the findings in the literature that support them.

1.2.1.1. Presentation Mode and Inter-Stimulus Interval (ISI).

Presentation mode (i.e. the manner in which the stimulus is presented - continuously vs. intermittently; see detail in Chapter 2) is considered to be a bottom-up factor (Long and Toppino, 2004) that can affect reversal dynamics of ambiguous figures (e.g., Orbach et al., 1963; Kornmeier et al., 2002; Leopold et al., 2002; Maier et al., 2003; Noest et al., 2007). One way of presenting stimuli to examine the underlying mechanisms of perceptual reversals is to present the stimulus intermittently/discontinuously. This involves presenting the ambiguous stimulus for short periods separated by blanks rather than continuously. Orbach et al. introduced this presentation mode with the Necker cube (Orbach, Ehrlich, & Heath, 1963). The reversal rates of ambiguous figures can vary as a function of the ISI between presentations of the stimulus (Orbach et al., 1963; Kornmeier et al., 2002; Leopold et al., 2002; Maier et al., 2003; Kornmeier et al., 2007).

Kornmeier et al. (2007), in an attempt to study the effect of varying ISIs on reversal rates, presented the Necker stimulus intermittently and found that randomly varying ISIs within the same session led to strong modulations of the reversal rates (Orbach et al., 1963). In their experiment, the Necker Lattice (a variant of the Necker Cube; see Figure 5A in Chapter 2) was presented for 800ms and each presentation was followed by one of four randomly chosen ISIs between 14 and 390ms (Kornmeier et al., 2007). The results from this experiment, coupled with results from other experiments revealed that short ISIs (up to 400 ms), compared to the continuous presentation method, can increase reversal rates (Kornmeier et al., 2007; Kornmeier et al., 2002, Orbach et al., 1963) and concurrently decrease stability durations. With longer ISIs (>400 ms), reversal rates noticeably drop to as low as zero reversals (i.e., complete stabilization; Leopold et al., 2002, Maier et al., 2003, Sterzer and Rees, 2008; see Figure 2). However, this is only the case if presentation times are shorter than the individual average stability duration. For presentation times below a certain threshold, Kornmeier et al. (2007) described the relationship between stimulus presentation duration and ISI as an inverted-U-shaped function (Figure 2; Kornmeier et al., 2007).

Orbach et al. (1963) explained their findings as evidence for a bottom-up influence: interplay between adaptation and recovery of neural populations representing the competing percepts. Kornmeier et al. (2007) interpreted the existence of an ascending and a descending part of the function as evidence for two different neural processes underlying perceptual reversals. In addition to their behavioral results, Kornmeier et al. (2007) found that ISIs also modulated the amplitude of ERP components that have been found to be related to perceptual reversals (e.g., the Reversal

Negativity, RN, and Reversal Positivity, RP; Kornmeier & Bach, 2004, 2005; see section 1.3 and Chapter 3). They found that the amplitude of the short latency reversal positivity (RP) was reduced with increased ISI compared to the shorter ISIs where amplitude was not affected. In contrast, the reversal negativity (RN) increased in amplitude when ISIs were reduced. Kornmeier and Bach (2012) suggested that for short ISIs, the underlying processes could be similar to presenting a stimulus continuously, whereas for ISIs above 400ms, the reversal dynamics observed are due to a kind of perceptual decision about the representation of the ambiguous stimulus appearing and then disappearing on a blank screen (this is discussed in Chapter 2, section 2.2.2.). This means that for the longer ISIs (>400ms), perceptual reversals may be separate percepts (choice events) and are not spontaneous.

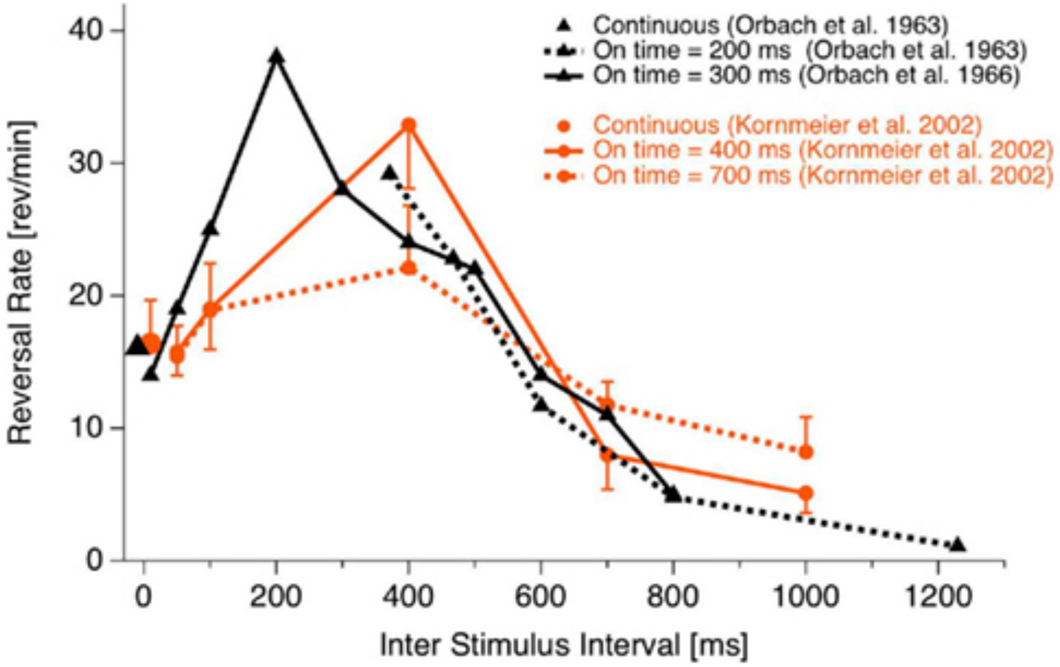


Figure 2. Reversal Rates during Continuous and Discontinuous presentation of ambiguous stimuli (Kornmeier et. al, 2007). Reprinted from Figure 3 in "Ambiguous Figures – what happens in the brain when perception changes but not the stimulus" by Kornmeier, J. & Bach, M., 2012, *Frontiers in Human Neuroscience*, 6, 51.

1.2.1.2. Satiation Theory, Adaptation and Neural Fatigue.

Bottom-up theories often describe perceptual reversals as a result of fatigue followed by recovery cycles of the adaptation and recovery (Köhler, 1940; Orbach et al., 1963; Toppino and Long, 1987). Psychophysical and physiological evidence from cortical regions that have been thought to be 'selectively tuned' to certain properties (e.g., spatial frequency or orientation) has been used in an attempt to explain perceptual reversals in ambiguous figures as a result of neural adaptation. This means in terms of satiation or fatigue of low-level mechanisms (e.g. the selective processing of stimulus features; Babich & Standing, 1981; Blakemore & Campbell, 1969; De Valois, 1977; Hochberg, 1950; Maffei, Fiorentini, & Bisti, 1973).

Satiation theory, originally proposed by Kohler (1940) and later advanced by Hock et al (1996), provides an explanation for perceptual reversal of ambiguous figures as an automatic, bottom-up process involving neural fatigue and/or adaptation. Adaptation effects on perception of ambiguous stimuli typically occur after prolonged (i.e., from ~60 to ~150 s) exposure to an unambiguous version of the stimulus (Long and Moran, 2007; Long and Olszweski, 1999; Long et al., 2002; Long et al., 1992; Orbach et al., 1963; Toppino and Long, 1987, 2014). For instance, after prolonged viewing of face stimuli, an ambiguous Rubin Faces-Vase stimulus would be more likely to be reported as a vase than as a face. In general, adapting to one unambiguous version of a stimulus increases the likelihood of a reversal (i.e., seeing the opposite interpretation) when viewing a subsequent ambiguous stimulus.

These results have been explained using the neural adaptation framework. The neural units corresponding to the interpretation of the unambiguous version initially presented become adapted, leading to a reversal and the alternative version of the ambiguous figure becomes dominant. The idea of the neural fatigue approach is that there are separate (or at least partially separate) populations of neurons associated with each of the different perceptual interpretations of an ambiguous stimulus. Critically, these populations have mutually inhibitory connections. As one population gains activation through either supporting sensory input or top-down strategic factors (e.g., attention or previous experience), it actively inhibits the activity of the other and vice versa. This process continues until one of the populations “wins” in a winner-takes-all process. The percept associated with the winning population is then consciously perceived.

Reversals in this system arise from an additional factor present in the system, the neural fatigue element. It is hypothesised that there is an element of neural fatigue, which builds up in the active population as they remain active. This fatigue reduces their activity and this causes a shift in competitive weights toward the other population of neurons representing the other percept. While these other neurons are ‘winning’, the population of neurons representing the percept that was initially perceived recover. If this second population is sufficiently satiated again, with the neural population representing the second percept being fatigued enough, competitive weights are once again shifted in favor of the first population and the other percept will be then be perceived until its satiation results in further reversal, etc. This process has been extensively studied using computational models (e.g. on binocular rivalry; Lago-Fernández & Deco, 2002; Moreno-Bote, Rinzel, & Rubin, 2007; Shpiro, Moreno-Bote, Rubin, & Rinzel, 2009; Wilson, 2003).

Behavioral work by Long & Moran (2007) has suggested that adaptation influences on bistable perception only occur after extended exposure to an unbiased stimulus. In this study, participants viewed an unambiguous prime stimulus followed by an ambiguous stimulus and had to report the identity of the ambiguous stimulus. The results of this study showed an adaptation effect (i.e., perception of ambiguous stimulus was opposite of the identity of the unambiguous prime stimulus) but only for extended (150 seconds) unambiguous prime durations. In contrast, a priming effect was found for brief prime durations. When observers were presented with the unambiguous stimulus for 2 seconds before, a priming effect occurred. That is, observers were more likely to report a perceptual interpretation consistent with the unambiguous version, which they had just seen (e.g., face prime leads to face perception of the ambiguous Rubin faces-vase; Long, Toppino, & Mondin, 1992).

Recent research shows that adaptation is attached to specific object features. In order for adaptation to occur, both adapting (unambiguous figure) and testing (ambiguous figure) stimuli have to share configural properties such as stimulus orientation (upright vs. inverted), size, and location (Long & Moran, 2007; Spitz & Lipman, 1962; Webster & MacLeod, 2011) and can only differ in their level of ambiguity. If a Necker cube is viewed for a prolonged period of time (i.e. several minutes) but then moved to a different location in the visual field, the rate of reversals decreases meaning that the adaptation effect is no longer applicable to this situation (Spitz & Lipman, 1962). Similarly, Toppino and Long (1987) used the rotating Necker cube figure and demonstrated that a change in retinal location produces a decrease in the rate of reversals.

Toppino and Long (1987) also found that the reversal rates reported during adaptation to a figure of one size and then viewing a cube of a different size is similar to when participants did not obtain any adaptation experience. Other studies have also shown that the adaptation effect is brief, sensitive to the inter-trial intervals between adapting and test stimuli and to the presentation period of the adapting stimulus (Intaite et al., 2013). Research shows that it is possible to reduce it significantly by prolonging the ITI to approximately 10 s (Long & Moran, 2007). If any of these conditions is modified (i.e., the unambiguous adapting stimulus is viewed for a shorter period, adapting and test stimuli are presented at different retinal locations, or the delay between the stimuli is too long), then a priming effect is obtained. In that case, the participant's interpretation of the subsequent ambiguous figure is the same as the previously presented unambiguous adapting stimulus (Long and Moran, 2007, Long and Olszweski, 1999, Long et al., 1992). This effect, however, does not seem to extend to binocular rivalry stimuli (Pearson & Clifford, 2005). Regardless of the duration of presentation of the 'adapting' image presented to one eye followed by the rivalrous image, perception has been found to flip to the second image (flash suppression; Pearson & Clifford, 2005; Wolfe, 1984).

1.2.2. High-Level Factors Influence

In addition to the passive bottom-up theory, another approach has been used to explain perceptual reversal and ambiguous stimulus perception, based on more active, top-down or cognitive processes (e.g., learning, decision making, attention, familiarity or knowledge, expectations, etc.). There are several theories supporting a top-down approach in explaining the nature of perceptual reversals and percept choice in ambiguous figures. The top-down mechanisms that have been attributed to these phenomena are attention, intention, voluntary control, past experience, context and more recently, working memory load.

1.2.2.1. Attention, Intention and Voluntary Control.

Attention is often directed 'covertly', even though it takes the form of discrete and spontaneous actions. Both psychophysical and physiological experiments have found that the processing of sensory input can be strongly influenced by attention.

Attention improves the capacity to process and discriminate attended objects, particularly in cluttered environments. This effect has been shown to result from a modification of sensory processing where improvements in sensitivity were found (Jehee et al., 2011; Pratte et al., 2013). These are brought about by orienting attention towards a particular stimulus. Neurophysiological studies in both monkeys (single-unit) and humans (fMRI) have suggested that enhanced widespread activation of neurons throughout the extrastriate visual cortical and subcortical areas is associated with spatially directed attention to a target stimulus (Treue & Maunsell, 1996; Kastner, 1998).

According to Leopold and Logthetis (1999) attention is similar to multistable perception in that it is an active process that could be influenced by and is subject to a great degree of voluntary control. Just as voluntary processes can create a motor output (e.g. a finger movement) or influence behavior that is stimulus dependent (e.g. the likelihood of an express saccade; Fischer & Webber, 1993), researchers have found that these processes can also control which stimuli/stimulus features are attended to. In the case of ambiguous images, the intention of the observer plays an important role in perceptual reversals (Peterson & Hochberg, 1983). Although voluntary control has been found to be weaker in binocular rivalry than in other multistable stimuli (George, 1936), research shows that the subject’s intention nevertheless plays an important role in perceptual switching and dominance (Meredith & Meredith, 1962). Participants with no past experience with multistable stimuli, for instance, can increase their perceptual switches by a factor of three if they intentionally attempt to see ‘fast’ fluctuations rather than ‘slow’ fluctuations. Moreover, control over the rate of perceptual reversals improves with exposure and practice. In one study by Lack (1978), for instance, the results showed that control over the rate of rivalry switches was found to improve after a training period of 10 days.

In terms of ambiguous images such as the Necker Cube (Necker, 1832) and more recently, Pitts, Gavin and Nerger (2008) investigated attention as an underlying mechanism of bistable perception by introducing conditions involving voluntary control to their experimental paradigm as well. This is in line with numerous previous behavioral studies that found that reversals can be influenced by observers' intentions. For example, van Ee et al. (2005) measured changes in reversal rates of various bistable stimuli under conditions involving voluntary control. Observers were asked in one condition to increase the rate of reversals ('speed up reversals') and in another condition to decrease it ('hold one percept stable for as long as possible') (van Ee et al., 2005). van Ee et al. (2005) asked their participants to engage in 3 different control-exertion tasks. In the first task, they were asked to passively view the stimulus without controlling reversal rate. In the second task, they were asked to passively view the stimulus for 6 min and then try to hold the same stimulus interpretation for 3 min. And in the third task, they were asked to passively view the stimulus for 3 min and then attempt to maximize the rate of reversals. Their results show that participants were able to voluntarily control and alter the rate of reversals, for the Necker Cube (and the other ambiguous stimuli used), depending on what they were instructed to do and significantly increased or decreased it (Washburn & Gillette, 1933). In line with previous research (e.g. Long and Toppino, 2004; Meng and Tong, 2004; Rock et al., 1994; Struber and Stadler, 1999;

Toppino, 2003; van Ee et al., 2005; Windmann et al., 2006), these findings suggest that some degree of voluntary control over Necker cube reversal rates is attainable.

To further these findings and to have a more physiological understanding of the underlying mechanisms behind the relationship between attention and voluntary control in experiments involving bistable and multistable perception, Pitts et al. (2008) compared ERPs associated with voluntary (intentional; top-down) perceptual reversals to those associated with involuntary (unintentional; bottom-up) reversals. For the voluntary perceptual reversals, participants were instructed in separate experimental blocks, to either increase reversals as much as possible or to hold their perception stable as long as possible. For the involuntary condition, participants were asked to remain passive and allow reversals to occur naturally. Pitts et al. (2008) found an increase in the reversal negativity component (RN) for the intentional/voluntary reversal conditions (see section 1.3 and Chapter 3). They explained their findings by suggesting that selective attention plays a critical and early (~150ms) role in bistable perceptual reversals.

Involuntary shifts in selective attention have been previously indicated in the mediation of perceptual reversals (Pitts et al., 2007). Selective attention involves a salience increase of certain visual features such as location, color, motion, or form (Sperling, Reeves, Blaser, Lu, & Weichselgartner, 2001). In some theories, attention to location is suggested to influence attention to features in those locations by determining which features can be attended to and integrated into a coherent percept (Anllo-Vento and Hillyard, 1996; Treisman and Galade, 1980). In the context of ambiguous figures, attending to certain locations within this type of figure, may allow features at those locations to be preferentially processed, and therefore interpreted by mechanisms at later stages in the visual system as ‘nearest’, which in turn would bias the interpretation of the bistable image. Recent fMRI studies have provided evidence supporting the view that attention facilitates voluntary reversals of bistable stimuli (Slotnick & Yantis, 2005). In a study conducted by Slotnick and Yantis (2005) in which they compared the pattern of activity during voluntary Necker cube reversals vs. simple spatial (left-right) attention shifts, their results showed similar areas of neural activation for the two tasks. There were brief increases of activation of the superior parietal lobule and intraparietal sulcus for both voluntary shifts in spatial attention as well as voluntary reversals of the Necker cube. Slotnick and Yantis (2005) as well as Pitts et al. (2008) suggest that when observers attempt to control the rate of perceptual reversals of bistable stimuli, they are tapping into this normally automatic, exploratory, perceptual-refresh mechanism. This leads to a change in the features being attended to (a change in selective attention) and in turn a reorganization of their perceptual interpretation of the stimulus.

According to Pitts et al. (2008), this is in line with Leopold and Logothetis (1999)’s ‘environment exploration’ theory. Drawing from a wide variety of perceptual rivalry research, Leopold and Logothetis (1999) proposed this theory to explain how and why perceptual reversals occur. They put forth a view in which perceptual reversals are the consequences of a generalized high-level “exploratory” mechanism that directs selective attention in a way that forces lower-level perceptual systems to periodically “refresh”. Pitts et al. (2008) suggest that the exploratory mechanism described by Leopold and Logothetis (1999) is neither purely sensory nor purely motor, but rather a mechanism in which the ultimate purpose is to “use” and “act upon” information present in the surrounding environment. According to this theory, continuously reorganizing and refreshing perceptual processing improves accurate interpretation of visual input. In this model, with regards to our interaction to our surrounding environment, visual attention is most easily controlled through eye movements, (using the frontal eye fields) and objects of interest are usually disambiguated early on (Pitts et al., 2008). However, in bistable perception experiments, observers are usually required to fixate on a central location (unlike in everyday situations that require a continuous exploration of the visual scene through eye movements). This does not change the effect proposed in the 'environment exploration' approach. Covert attention (without eye movements) may still be changed by this central exploratory mechanism.

Due to the ambiguity of the stimuli, the visual scene requires ongoing exploration, and perceptual reversals consistently occur. This idea is supported by the study by van Ee et al. (2005). In this study, they investigated the role of both eye movements and blinks during perception of the slant rivalry stimulus, which is a type of ambiguous stimulus. Van Ee et al. (2005) found that microsaccades (i.e. small involuntary eye movements)/saccades (i.e. rapid eye movements that change the point of fixation) and blinks are not essential to voluntarily experience a perceptual reversal. Moreover, van Ee et al. (2005) found that blinks and saccades, but not microsaccades, are inhibited while subjects induced a perceptual reversal. Although a study by Ellis and Stark (1978) found that there is a correlation between the position of the eye and reversals of the Necker Cube, other studies have also suggested that voluntary control of reversal rates is not solely attributable to eye movements (e.g. Washburn & Gillette, 1933; Pritchard, 1958). For instance, Washburn and Gillette (1933) used the Necker

Cube and its after image (participants were asked to close their eyes after looking at the Necker Cube) to study the effect of voluntary control of the reversal rates of the after image of the Necker Cube. They found that participants were able to voluntarily induce and maintain one of the orientations of these after images when instructed to do so. This type of voluntary control does not involve eye movements. Although the central exploration theory is based on the assumption that this mechanism works largely in an unconscious, automatic fashion (Leopold & Logothetis, 1999), voluntary control over bistable perceptual reversals may work through this same mechanism. For instance, Leopold and Logothetis (1999) note the similarities between control over bistable perception and other voluntary behaviors, specifically with regards to the improvement over time with practice and learning.

Thus, mechanisms of selective attention and multistability might indeed be closely related. However, there are some key differences that suggest they are not one and the same. First, voluntary control in orienting attention is generally greater than in multistable vision. It is a lot easier to voluntarily control what you are attending to but it is not as easy to voluntarily control the rate of reversals of an ambiguous figure (Leopold & Logothetis, 1999; Meng & Tong, 2004). This is supported by findings that reveal that although perceptual reversals can be slowed down or decreased in number, they cannot be entirely stopped. Perceptual reversals continue regardless of the intent of the participant. This was reported in Slotnick and Yantis (2005)'s study where in the hold condition (maintaining one perceptual interpretation of the ambiguous figure through voluntary control) participants still experienced involuntary switches in their interpretation of the ambiguous image. This was not the case when participants voluntarily controlled shifts in selective attention. Their behavioral results showed that the task difficulty across both conditions (voluntary control of reversals vs. voluntary control of attention shifts) was the same. However, this is due to the design of the experiment whereby the researchers, based on the results of a pre-training session, calibrated the features of the stimulus so as to yield an accuracy value that would ensure that task difficulty was well matched between conditions.

In multistability, top-down influences are not limited simply to enhancing the visual processing of a particular object (or features of that object) or spatial location. Instead top-down attentional influences spur organizational mechanisms to change perception completely, and thereby possibly feed into the neural fatigue mechanism described previously to enhance one representation over the other (i.e. by shifting the balance between mutually exclusive neural representations in the visual system itself; Mathes et al., 2006; Slotnick & Yantis, 2005). Finally, attentional shifts can proceed with a speed that is considerably faster than even the most rapid perceptual reversals. Attention can shift as fast as several times per second (Duncan, Ward, & Shapiro, 1994; Egeth & Yantis, 1997), whereas the transition between rivaling percepts may take seconds or even tens of seconds to complete (Pastukhov & Braun, 2007).

1.2.2.2. Past Experience and Learning.

Several adaptation and priming studies (e.g., Long et al., 1992) support the idea that our perceptual system uses (amongst other processes) past perceptual experiences (on various time scales) to disambiguate and interpret ambiguous information (Leopold et al., 2002; Maier et al., 2003; Pearson and Brascamp, 2008) and its neural processing (Kornmeier and Bach, 2006; de Jong et al., 2012b; Pitts and Britz, 2011). Previous evidence suggests that often, ambiguous stimuli do not automatically generate perceptual reversals until participants are told that reversals can occur and are therefore 'learned' (Girgus, Rock & Egatz, 1977; Leopold et al., 2002; Maier et al., 2003; Orbach et al., 1963; Pearson and Brascamp, 2008; Rock & Mitchener, 1992). In other words, prior knowledge of the different percepts in Rubin's Face-Vase illusion, for instance, makes it easier and in some cases even possible for the subject to perceive the different interpretations (faces or vase) and experience perceptual switches. Recent studies have suggested that this dependence however is not only limited to the immediate, short-term exposure to the different interpretations of a multistable image. It is also observed longer-term (Pastukhov and Braun, 2008; Pearson and Brascamp, 2008; Brascamp et al., 2009; de Jong et al., 2012a).

At short timescales, perception of a bistable stimulus can either reverse or remain the same from that of the preceding unambiguous version of the stimulus. The aftereffect of previous brief unambiguous stimulus presentation is found to be suppressive, leading to a perceptual reversal (i.e. the interpretation of the current ambiguous stimulus is different from the unambiguous version preceding it; Long and Toppino, 2004; Pearson and Clifford, 2005; Thompson and Burr, 2009). This depends on the length of the inter-stimulus interval and the presentation time of the unambiguous stimulus (Nawrot and Blake, 1993; Kanai and Verstraten, 2005; Long and Moran, 2007). This effect is also perceived when ambiguous stimuli are presented intermittently, whereby stimulus presentation durations and ISIs influence the occurrence of perceptual reversals. Several researchers (Orbach et al., 1963; Leopold et al., 2002; Maier et al., 2003; Brascamp et al., 2009) found that very brief stimulus presentations of ambiguous stimuli lead to stabilization (i.e. the interpretation of the ambiguous image remains the same for each presentation). The latter is assumed to be related to short-term perceptual memory traces that accumulate over a very short period of time (in the span of seconds) with an effect that lasts several minutes (Brascamp et al., 2009; Pastukhov and Braun, 2008; Pearson and Brascamp, 2008; De Jong et al., 2012b).

Behaviorally, the effect of long-term perceptual history can be seen as a facilitator, leading to the interpretation that was primarily perceived in the recent past to be favoured over the other interpretation (Pearson and Brascamp, 2008). Longer-term experiences have been linked to associative learning (Murphy, Leopold & Welchman, 2014). In contrast to conventional notions of associative learning however, recent findings suggest that the resolution of perceptual ambiguity seems to be more important than unambiguous stimulus presentation for learning to occur (Harrison and Backus, 2010; Van Dam and Ernst, 2010). Learning therefore appears to be driven by past perceptual experiences - internally generated interpretations of ambiguous sensory input. Similarly, prior presentations of unambiguous stimuli can be used to explicitly “train” a long-lasting association between a percept and a retinal location (de Jong et al., 2014). This is known as perceptual association (de Jong et al., 2014).

In addition to that, other studies have suggested that instrumental learning shapes perceptual inference of an ambiguous stimulus. For instance, Fleming et al. (2010) found that participants often reported perceiving a house in the ambiguous face-house images (overlaid images of a face and a house that could be perceived as one of the two) when they were told that they would lose money (Tversky & Kahneman, 1979) if they interpreted the ambiguous image as being a face. Moreover, Wilbertz et al. (2014) conducted a study in which they used a binocular rivalry stimulus that was evoked by two orthogonal grating stimuli presented to the two eyes that resulted in perceptual reversals between the two gratings. In this study, they conducted two experiments, one in which participants won money whenever they reported one of the interpretations of the rivaling stimuli and the other where they lost money whenever they reported it. Before beginning the experiment, participants underwent some training on the target detection task with the rivaling stimuli. They found that an increase in stable durations of the percept associated with reward in comparison to the non-reward percept. They also found that same increase for the non-punishment perception compared to a decrease in the punishment percept. Wilbertz et al. (2014) accounted for general changes in task performance (e.g. learning with regards to target detection or higher task motivation during conditioning – when they performed the task and there was condition associated with it) as well as potential baseline differences between the two percepts. They did this by comparing the two percepts during conditioning (i.e. receiving an award or punishment during task completion) corrected by the corresponding difference during baseline in paired t-tests. The baseline corresponded to the portion of the task where they had to report their interpretation of the ambiguous stimulus but there was no reward or punishment associated with it. Their findings suggest that perceptual inference is an adaptive process that is shaped by its consequences, similar to instrumental/reinforcement learning.

Using a rotating Necker Cube stimulus, Murphy et al. (2014) found long-lasting perceptual biases that were expressed from the outset and remained stable for up to 40 min (i.e. perceptual stability; Brascamp et al., 2009) that were specific to certain retinal location (i.e. retinotopically specific). In their study, Murphy et al. (2014) investigated whether long-term associative learning can emerge naturally from repeated instances of short-term perceptual memory in the absence of explicit training. They did this by conducting two experiments. In the first experiment, they intermittently presented a rotating Necker-Cube during an extended initial training period. The training period involved presenting the unambiguous variant of their ambiguous stimulus at the start of the session (for a couple of trials) at two different retinal locations and investigating their influence on the subsequent presentation of the ambiguous stimulus (for the rest of the trials). The latter also varied in their retinal locations (same locations as the unambiguous trials). They compared the results from the training session to results from participants who did not undergo any training. The participants that did not undergo training completed the same task as the training group but did not receive any training (no unambiguous stimuli). Murphy et al. (2014) found that perceptual biases emerged in both trained and untrained groups. Their results revealed that the subjective interpretation of the first stimulus at each retinal location biased the subsequent interpretation of the following trials presented at that location for the untrained participants. This suggests an association between the interpretation of the ambiguous stimulus and its initial retinal location presentation. Murphy et al. (2014)'s results show that there was no significant effect of the training trials on the magnitude of the bias. Moreover, they found that the bias in both conditions emerged at the start of the session and lasted for the entirety of the experiment (20 minutes). These results reveal that although biases can emerge during training, similar perceptual biases emerge without any training. This suggests that associative learning results from associations formed between the different perceptual interpretations of the ambiguous stimulus and retinal locations rather than between the actual physical stimulus and retinal locations.

In their second experiment (completed by the same set of participants that took part in the first experiment), Muphy et al. (2014) examined whether periods of spontaneous reversals would affect recently acquired perceptual biases, and whether they would do so in a retinotopically specific manner. They did this by modifying the previous paradigm from their first experiment and instead of presenting an unambiguous variant of their ambiguous stimulus; they interposed 5 minutes of continuous ambiguous rotating Necker Cube at one of the two retinal locations into a training block (the other retinal location remained blank). Participants reported their perceptual experiences for both the continuous and intermittent presentations. The results of this experiment showed that the continuous presentation effects abolished the trained perceptual biases at the retinal location where the stimulus was presented but not at the blank location. Moreover, participants expressed significant biases that were nearly equally divided between the two different interpretations of the stimulus at the corresponding retinal location that the continuous stimulus was presented in. On the other hand, the blank retinotopic location maintained its previous bias from the unambiguous training experiment. They found that during intermittent presentation, participants reported the interpretation that was mostly reported during continuous presentation at its corresponding retinal location.

These results suggest that perceptual biases can arise naturally and may principally reflect the brain's tendency to favour recent perceptual interpretation at a given retinal location. Further, they suggest that an association between retinal location and perceptual state, rather than a physical stimulus, is sufficient to generate long-term biases in perceptual organization based on the individual's past experiences with the given ambiguous stimulus (de Jong et al., 2014).

1.2.2.3. Working Memory Load.

Top-down influences are often based on our goals and expectations (e.g., Kumar, Soto & Humphreys, 2009). For instance, Duncan and Humphreys (1989) suggested that 'the attentional template' of a certain visual stimulus (i.e. its properties and description) held in working memory (WM), is used to bias percept selection with properties that match the 'template' held in memory (Downing, 2000; Hodsoll & Humphreys, 2001; see Soto et al., 2008 for a review). The relationship between visual selection and WM has been studied in several lines of research. For example, neuroimaging studies have found that attention and WM show patterns of activity with overlapping networks, including regions around the intraparietal sulcus and frontal eye fields (e.g. McCarthy, 1995; LaBar et al., 1999; Pollmann & von Cramon, 2000). Behaviorally, researchers found that WM seems to play an important and central role in the suppression of distractors and maintaining focus on the relevant information for the current task (de Fockert, 2001; Woodman et al., 2007; Woodman & Luck, 2004).

Recently, working memory has been studied in experiments investigating the underlying mechanisms behind ambiguous figure perception. These studies suggest that working memory plays a role in the rate of reversals and percept choice. For instance, although not explicitly stated, Paffen, Alais, and Verstraten (2006) found that manipulating working memory and attentional resources in a motion-detection task reduced the rate of perceived binocular rivalry reversals. They wanted to investigate the role of attention on binocular rivalry and therefore manipulated working memory by manipulating task difficulty. They presented a concurrent task while participants were presented with a binocular rivalry stimulus containing random dot motion. Paffen et al. (2006) manipulated task difficulty through the motion coherence of the dots (i.e. whether the dots presented to each eye moved in the same direction or in opposite direction). Participants were required to report which rival target was perceptually dominant indicated by a cue following presentation of the stimulus. They were also instructed to indicate whether each cue was preceded by a burst of coherent motion. The motion-detection task demands did not prevent the participants' ability to track perceptual reversals, as participants were capable to correctly track the perceptual changes of the rivalrous percepts (coherent versus incoherent motion) while completing the motion detection task. The motion-detection task demands did reduce the rate of reversals. However, none of the reported manipulations eliminated reversals. Therefore, Paffen, Alais, and Verstraten (2006) suggested that perceptual ambiguity involves more than an allocation of attentional resources.

Intaite, Koivisto and Castelo-Branco (2014) found that previous studies using ambiguous stimuli did not manipulate the level of working memory load, leaving open the possibility that the reductions of perceptual reversals were due to the requirement to perform two tasks simultaneously. Therefore, in their study, they investigated how perceptual decision making is affected by the recruitment of attentional resources. They also investigated the possible effects of working memory load on perceptual reversals of the Necker cube. Thus they chose a secondary working memory load task (e.g., mental arithmetic) that is known to exhaust the available attentional resources (Kumar, Soto, & Humphreys, 2009; Singhal & Fowler, 2004). In their experiment, Intaite et al. (2014) had two types of stimuli. They had ambiguous Necker Cube stimuli that were presented at the center of the screen that were preceded by memory stimuli that appeared that the same location. The memory stimuli consisted of a memory prime (sham – load condition: 4 asterix; letter-load condition: four to seven capital consonant letters) and a memory probe that consisted of two arrows (either pointing to the left or to the right) in the sham-load condition or of one letter in the letter-load condition. On every trial, the memory prime was presented followed by the ambiguous Necker Cube and then the memory probe was presented. The latter consisted of the sham-load condition arrows or of one letter that had either been part of the memory set (positive probe) or had not been part of it (negative probe) in the letter-load conditions. Participants had to discriminate between the direction of the arrows presented and the positive versus negative probes. They found that increasing working memory load (increasing the number of letters presented) delayed the latency and the rate of reversals. However, reversals continued to occur. This suggests that there are shared mechanisms that are responsible for working memory maintenance and for perceptual reversals or at least are tightly linked in terms of top-down control.

Other research manipulating working memory load has also shown that performing secondary tasks that require working memory load increases the time for the report of (Reisberg & O’Shaughnessy, 1984; Wallace, 1986) and decreases the rate of (Reisberg & O’Shaughnessy, 1984; Wallace & Priebe, 1985; Wallace, 1986) perceived reversals in an ambiguous figure and their interpretation of it (Resiberg, 1983).

In a further study investigating the relationship between working memory load and ambiguous images, Intaite, Duarte and Castelo-Branco (2016), used fMRI to explore the neural activity patterns in response to perceptual reversals under differing amounts of working memory load using the same dual-task design. Their findings suggest that there is an overlap in the brain regions activated during perceptual reversals and the fronto-parietal attention network (Knapen et al., 2011; Lumer et al., 1998, Lumer and Rees, 1999, Sterzer and Kleinschmidt, 2007, Weilnhammer et al., 2013). Previously, Sterzer and Rees (2008) reported activations in visual cortex along with activity in prefrontal and parietal regions for percept-specific signals in response to binocular rivalry stimuli. They also discussed comparable BOLD signal changes over visual and fronto-parietal regions in response to voluntary engagement of facial WM (Courtney et al., 1997; Haxby et al., 2000). The authors suggested a possible influence of higher-level mechanisms on perceptual durations that share a common activation network with WM. Moreover, Intaite, Duarte and Castelo-Branco (2016) found that the right posterior Superior Parietal Lobule (pSPL) showed differences in response to perceptual reversals under different load levels, and was stronger in response to perceptual reversals than stimulus changes. The Superior Parietal Lobule (SPL) also had been found to be involved in perception of reversals in previous studies (e.g. Baker et al., 2015; Carmel et al., 2010; Kanai et al., 2010; Kanai et al., 2011). Stimulating the right anterior SPL with transcranial magnetic stimulation (TMS) increased the rate of reported reversals whereas stimulating the right posterior SPL decreased it (Carmel et al., 2010). Right SPL seems to be also activated when participants perform WM manipulation of stimulus content (Champod and Petrides, 2007). Moreover, anterior Prefrontal (where activation is suppressed by the highest loads) and Dorsolateral Prefrontal (where deactivation is reduced by highest loads) cortices exhibited differential BOLD signal changes in response to perceptual reversals under working memory load (Intaite, Duarte & Castelo-Branco, 2016). These findings (enhanced BOLD response in SPL) have been previously suggested by other fMRI studies (e.g. Knapen et al., 2011, Lumer et al., 1998, Lumer and Rees, 1999, Weilnhammer et al., 2013). The suggested modulatory role of the anterior Prefrontal and Dorsolateral Prefrontal cortices, showing a significant interaction between rate of reversals and load levels, suggest a more direct role of the anterior Prefrontal Cortex in reversal generation.

1.2.3. Spontaneous Fluctuations in Patterns of Neural Activity

Research shows that trial by trial cortical responses to the same stimulus vary. This type of variability, however, was initially viewed as ‘noise’ in task-response studies and was usually minimized through averaging or sometimes discarded during processing. However, an increasing number of studies show that this type of activity is far from being just noise. In fact, this type of spontaneous activity has been found to be time-locked to a certain neural event (e.g. firing or synaptic inputs from other neurons even without a sensory input; Arielli et al., 1995, 1996) or cognitive state (e.g. perceptual interpretation of Rubin’s Face-Vase; Hesselmann et al., 2008) and is not an independent process. For instance, spontaneous BOLD fluctuations measured in the left somatomotor cortex are specifically correlated with spontaneous fluctuations in the right somatomotor cortex and with medial motor areas in the absence of overt motor behavior (Fox & Raichle, 2007). These linked mechanisms suggest that this type of observed activity cannot be attributed to random noise and relate to anatomical mechanisms.

Moreover, ongoing spontaneous fluctuations in patterns of neural activity have been found to influence numerous types of processing (e.g. near-threshold stimulus detection, reaction times, etc… Busch et al., 2009; Dustman & Beck, 1965; Hanslmayr et al., 2013; Nunn & Osselton, 1974) including stimulus processing signatures such as ERPs (Jansen & Brandt, 1991; Gruber et al., 2014). Arieli et al. (1996)'s findings suggest that trial-to-trial variations in the neural response to identical stimuli correlate with fluctuations in pre-stimulus activity. This means that the amplitude of evoked responses can be partially explained by the activation pattern at the moment of the onset of the stimulus. This correlation was also found with perceptual responses and variations in pre-stimulus activity (Super et al., 2003; Hesselmann et al., 2008; Coste et al., 2011). Recent views, in functional imaging studies, on the origin of spontaneous activity fluctuations suggest that these fluctuations group together neural processes occurring at several layers. These range from intrinsic activity patterns that are also observed in sleep or anesthesia (Beckmann et al., 2005; Kiviniemi et al., 2003) to conscious mental processes involving thoughts that in turn can be unrelated to the stimulus (mind-wandering) (Macey et al., 2004) or stimulus-related (context-oriented) (Fox et al., 2005). This suggests that ongoing fluctuations are an inherent property of the brain and that they are not induced by unconstrained mental activity (e.g. daydreaming; Fox & Raichle, 2007).

One approach taken to understand these variations is by using multistable stimuli. This is because, when looking at an ambiguous image, the brain is unstable and switches between multiple possible interpretations of the visual input. Recently, researchers have found that ongoing spontaneous fluctuations contribute a functionally relevant signal that may affect the subsequent perceptual interpretation of an ambiguous image (e.g. Hesselmann et al., 2008; Rassi et al., 2019; Ronconi et al., 2017). For example, Hesselmann et al. (2008) used Rubin's Faces-Vase in their experiment and found that ongoing slow activity fluctuations influenced whether participants perceived a face or a vase. Their results showed that face percepts, compared to vase percepts, were associated with higher pre-stimulus activity levels in the right FFA. This effect was found to arise during periods that have been previously suggested to belong to prolonged periods of rest or "baseline" (Fox & Raichle, 2007). The inter-trial intervals (ITIs) used were random but they are commonly used for baseline epochs separating experimental blocks (>=20s). These long ITIs were used in order to reduce any overlapping effects between stimuli and allow the development of spontaneous activity between trials.

Hesselmann et al. (2008) also found that stimulus presentation resulted in the deactivation of the brain regions that are known to be more active during these baseline periods (i.e. the precuneus and ventral medial prefrontal cortex). They found no differences in activation of these regions between the faces and vase trials. This suggests that the effect they found arises from task-unrelated spontaneous activity variations in the right-FFA rather than strategic, top-down effects from higher order areas. Hesselmann et al. (2008) also found that the FFA activity in the pre-stimulus period carries as much information about the upcoming reported interpretation as the time window that contains the evoked response (i.e. higher FFA activity on face reported trials in the post-stimulus period; Grill-Spector et al., 2004; Kleinschmidt & Cohen, 2006) and the subjects' manual response. In addition to that, they found that the post-stimulus FFA activity was higher during face reported trials when elevated activity in this region was observed in the pre-stimulus period. These results corroborate the idea that the observed ongoing pre-stimulus fluctuations cannot be attributed to noise seeing as this activity is linked to an evoked response. Moreover, they contribute significantly to the perceptual interpretation of the ambiguous image. According to Hesselmann et al. (2008) the effects measured can only be attributed to ongoing activity because nothing else in their experiment differentiates activity at the time point where the pre-stimulus effect was found from that at earlier time points. This effect observed varies between trials and cannot be found at earlier pre-stimulus time points.

Interestingly, the difference in activity between faces and vase trials was found to differ across the pre-stimulus period. Hesselmann et al. (2008) found that the difference in activity in the FFA is greatest before stimulus onset, reduces for a few seconds, and then increases again at the evoked peak response in the post-stimulus period. This change over the peristimulus time is consistent with a modulation of evoked responses (Arieli et al., 1996). Moreover, Hesselmann et al. (2008) suggest that this indicates an interaction between pre-stimulus activity and the evoked response. According to Hesselmann et al. (2008), this observed effect differs from a simple additive effect of the evoked component, which would produce faces-vase differences that are conserved throughout peristimulus time. Put more simply, it was not merely a higher baseline signal that was propagated all of the way to the response peak that decided how the stimulus would be perceived. The interaction that was measured suggests that there are independent and complementary contributions to whether trials were reported as faces vs. vase. All of these results suggest that the source of variability in interpretation of an ambiguous stimulus is linked to the initial state of the system before stimulus presentation (Hesselmann et al., 2008). They reveal that this initial state is subject to slow ongoing spontaneous fluctuations separated from evoked responses. The fluctuations are considered to be slow because they were detected by hemodynamic signals. Previous research has suggested that slow fluctuations contribute to the formation of a meaningful structure (Gilden, 2001).

The precise role of these fluctuations remains unclear. However, Hesselmann et al. (2008) suggest that their results are in line with Fox and Raichle (2007)'s idea that they might reflect dynamic predictions (Fox & Raichle, 2007). It is important to note that fluctuations at different frequencies and pre-stimulus time points could also contribute to the perceptual interpretation of ambiguous stimuli and these could differ between different types of ambiguous stimuli. For instance, Ronconi et al. (2017) presented results that suggest that the interpretation of an ambiguous stimulus depends on the ongoing phase of pre-stimulus oscillations at different frequency bands. Their results suggest that ongoing oscillations at certain frequency bands are related to trial-by-trial fluctuations in cortical sensory responses. This is in line with previous findings (e.g. Busch et al., 2009; Fiebelkorn et al., 2013; Hanslmayr et al., 2013; Mathewson et al., 2009). They also found that the ongoing fluctuations at these frequency bands are predictive of the interpretation of visual stimuli over time. In their experiment, Ronconi et al. (2007) presented participants with two bistable stimuli. One comprised of two distinct flashes in the same retinal location and separated by an ISI of 40 ms (two-flash fusion). The other comprised of two distinct flashes appearing in different retinal locations and separated by an ISI of 120 ms (apparent motion trials). Their results suggest that differences in activity between the subjective interpretations of the two flash fusion stimulus (one flash vs. two flashes perceived – integration vs. segregation) could be detected in the phase of the ongoing oscillation within the alpha band in the pre-stimulus period at around 400/300ms before stimulus onset. On the other hand, when participants were presented with apparent motion stimulus, the difference in activity between the two perceptual interpretations (motion vs. alternation – integration vs. segregation) could be detected in the phase of the ongoing oscillation within the theta band at around 500/400ms before stimulus onset. These results suggest that trial-by-trial fluctuations at different frequencies contribute to the interpretation of different ambiguous stimuli. Ronconi et al. (2017) suggest that the way in which ongoing neural oscillations determine whether ambiguous visual information is temporally interpreted does not depend on a single, general sampling rhythm. This in line with Hesselmann et al. (2008) that suggest that these fluctuations do not contribute to the perceptual interpretation of an ambiguous in a simple additive manner. On the contrary, different ongoing oscillatory rhythms determine the temporal perceptual interpretation of stimuli over time.

Other findings in the literature using Multivariate Pattern Analysis (MVPA; briefly described in section 1.4 of this Chapter and described in detail in section 2.3.2 in Chapter 2; e.g. Ronconi et al., 2017) have also furthered the findings that ongoing spontaneous fluctuations in the pre-stimulus period are linked to post-stimulus activity linked to the perceptual interpretation of an ambiguous figure. In short, MVPA refers to a set of methods that analyze neural responses as patterns of activity that are associated with different cognitive/perceptual states. The most popular application of MVPA is decoding. The goal of decoding analysis is to test whether one can predict what the participant was viewing based on the pattern of activity in the brain. This type of analysis outputs a value known as the prediction accuracy that indicates to what degree the patterns of activity associated with the different perceptual states are significantly distinguishable from one another.

One such study by Rassi et al. (2019) presented results whereby increased information flow from the FFA (suggested to be a category-selective brain region) to the V1 (primary visual cortex) in the pre-stimulus period predicted subsequent interpretation of Rubin's Face-Vase. They found that the strength of the pre-stimulus feedback connectivity from FFA to V1 was correlated with post-stimulus neural activity strength as well as the accuracy of predicting the upcoming percept. They found that this connectivity is concentrated in the alpha and theta bands. Their findings suggest that connectivity of neural activity in the pre-stimulus period can predict the perceptual interpretation of an ambiguous image. In their experiment, Rassi et al. (2019) adopted the same experimental paradigm as Hesselmann et al. (2008).

All the results of these experiments reveal that ongoing spontaneous fluctuations are not independent mechanisms but are linked to a certain evoked potentials and behavioral responses. Moreover, these fluctuations, in the pre-stimulus period, seem to contribute significantly to the perceptual interpretation of ambiguous figures. However, as was mentioned previously, the functional role of these fluctuations remains unclear. Independent mechanisms have been identified to try to explain the neural bases of these spontaneous ongoing fluctuations. Although, their functional origin remains to be clarified, as well as their cognitive connotation. Functional magnetic resonance imaging (fMRI) experiments on anaesthetised monkeys have found temporally coherent fluctuations in haemodynamic activity across widely distributed functional architectures, indicating that resting-state fluctuations are an intrinsic physiological trait persisting even after loss of consciousness (Vincent et al., 2007). However, resting-state fluctuations can also reflect ongoing cognitive processes such as conscious thought (Mason et al., 2007). It has been argued that variations in ongoing activity support predictive coding (Sadaghiani et al., 2010; Fox and Raichle, 2007). In support of this claim, it has been suggested that the slow fluctuations in ongoing activity as measured through fMRI have meaningful structure, perhaps contributing to the formation of representations (Gilden, 2001). Although detailed mechanisms are unclear, all of the above data suggest that perceptual experience and the neural response to stimuli depend not only on their physical characteristics but also critically upon the pre-existing state at many levels of the neural system when the stimulus is received.

1.2.4. When Bottom-Up and Top-Down Coincide

Attempts to explain the fluctuating, multistable character of ambiguous figures, traditionally, have attributed reversals to either bottom-up (stimulus-driven) or top-down (goal-driven) processes. These processes were seen as functioning independently of one another. However, many researchers have been arguing for a hybrid model in which both types of processes contribute to perceptual reversals (e.g. Long & Toppino, 2004; Toppino & Long, 2005).

In a series of experiments conducted by Long and Toppino (1981, 2004) and some of their colleagues (1983, 1992) (for a review see Long & Toppino, 2005), the findings provided strong evidence that perceptual reversals are influenced by both bottom-up processes (e.g. adaptation or fatigue) and by top-down processes (e.g. learning, attention and intention). For instance, in the study described previously in section 1.2.1.3. of this chapter (Chapter 1), Toppino and Long (1987) found that the reversal rate was high (i.e., adaptation occurred) when the test stimulus was similar to the adapting stimulus and low when the location and size of the test stimulus changed from the adapting one. These findings suggest that rotating Necker Cube reversals are mediated by fatigue and recovery of multiple independent neural channels. Altering the size or the retinal location of the rotating cube changes the neural channels mediating its perception and nullifies the adaptation effect.

However, toward the end of each experimental session, Toppino and Long (1987) noted a significant increase in reversal rates. Long et al. (1983) explored this effect in a previous experiment. They had participants view the rotating Necker Cube for an extended period of time, using a similar paradigm, over a period of 4 weeks (Long et al., 1983). Participants were presented with two rotating Necker Cubes on both sides of the centered fixation cross and were randomly assigned to different viewing conditions. Participants had to report if they experienced a reversal of the stimulus on the left (condition 1), on the right (condition 2) or both cubes (condition 3). Long et al. (1983) also added a control condition whereby a different set of participants completed the same conditions but they were only presented with one rotating Necker Cube on either side of the fixation cross. The experiment consisted of six 2-minute blocks with 2 minute rest periods in between each block to allow for potential satiation effects from the initial viewing period to dissipate. This was repeated over four weeks for all participants. Long et al. (1983) found a significant steady increase in the rate of reversals across the four weeks. They even found that the rate of reversals increases between each 2 minute block within the same experimental session. They suggest that, in addition to neural fatigue and adaptation, a top-down effect in the form of learning may be taking place across sustained perceptual reversals of the same stimulus. This is potentially because if a fatigue process alone was the basis for the reversals occurring, then the rate of reversals observed should be nearly identical across the experimental blocks and sessions.

Moreover, Toppino (2003) found, once again, in an experiment studying the role of intentional control on reversal rates, that there is simultaneous influence of top-down and bottom-up processes. In their study, Toppino (2003) conducted two experiments where subjects were presented with an ambiguous Necker Cube at the center of the screen. In the first experiment, participants were directed to maintain their gaze at a specified focal point of the cube: either the Y-junction at the top-right of the cube (described earlier; see Figure 1Ab), or the Y junction on the bottom left (see Figure 1Aa). Half of them were instructed to hold one of the interpretations of the cube (hold condition) and the other half were asked to passively view it (no-hold condition). In both cases participants reported whenever they experienced a perceptual reversal. They found that the total time for which an interpretation of the Necker Cube was reported was significantly determined by the focal point that the participants directed their gaze to. In addition to that, there was a significant effect of the hold vs. no-hold instructions factor. Compared to the passive observation of the cube (i.e., no hold), instructing observers to hold an orientation led to a significant increase in the percentage of time that a certain orientation was perceived. This means that participants were able to voluntarily control their perceptions of the cube. However, Toppino (2003) found no interaction between fixation location and hold conditions. Toppino (2003) suggests that the findings of their first experiment show that intentional control over perception of an ambiguous image can be employed by means of direct, top-down priming or activation of the desired interpretation.

In their second experiment, Toppino (2003) used the same experimental paradigm as the first experiment but varied the cube size. They found no effect of cube size on the hold conditions. The pattern of findings from both experiments was suggested to show that processes other than focal-feature processing mediate the effect of intentional control. However, Toppino (2003) also found that reversals cannot be prevented regardless of hold condition suggesting that there seems to be processes at work that cannot be suppressed volitionally. They suggest that a low-level process, such as neural fatigue, produces reversals that participants cannot prevent. This is consistent with previous pre-existing findings in the literature on intentional control (Babich & Standing, 1981; Liebert & Burk, 1985; Suzuki & Peterson, 2000). Toppino (2003) suggests an additive effect of adaptation and priming that influences the perception of the Necker Cube.

Kornmeier et al. (2009) also observe this influence of the additivity of effects in a study where their results suggest that there is an additive effect of volitional control (considered top-down mechanism) and discontinuous stimulus presentation (considered bottom-up mechanism) that influenced the rate of reversals. In their study, Kornmeier et al. (2009) conducted two experiments. Their first experiment was similar to the first experiment conducted by Toppino (2003) but with no focal points (i.e. participants maintained their gaze at the center of the cube) and found the same results at Toppino (2003). In their second experiment, Kornmeier et al (2009) used the same experimental paradigm as their first experiment but they presented their ambiguous stimulus discontinuously. They also varied the length of the Inter-Stimulus Interval and the presentation time of the stimulus. They found that volitional control with discontinuous stimulus presentation lead to full additivity of effects (i.e. discontinuous stimulus presentation and volitional control) where the rate of reversals observed in the discontinuous paradigm was higher than the continuous presentation paradigm.

In summary, several studies tried to reconcile the on-going debate regarding the function of bottom-up versus top-down processes in ambiguous figure perception (e.g. Hochberg & Peterson, 1987; Leopold & Logothetis, 1999; Long et al., 1983) and the additivity of their effects (e.g. Kornmeier et al., 2009; Long & Moran, 2007; Long & Toppino, 2004; Toppino, 2003). Recently, researchers have been exploring multistable perception as a result of changes in the attractor states of a neural network (Lehky, 1988; Noest et al., 2007; Wilson, 2003). Kornmeier and Bach (2012) used this model in order to investigate the integrative relationship between top-down and bottom-up processes.

1.2.4.1. An Integrative Theory? (Kornmeier & Bach, 2012).

Kornmeier and Bach (2012) put forward a perspective that integrates both bottom-up and top-down findings. Their approach assumes two separate processes involving both bottom-up and top-down factors. They claim that reversals involve an initial process of ‘destabilization’ followed by a ‘restabilization/disambiguation’ process. These two processes work on different time scales (5-6 seconds on average for the destabilization period and milliseconds for the restabilization/disambiguation period). In this perspective, Kornmeier and Bach (2012) use terminology and an approach based in non-linear dynamics to describe the mechanisms underlying perceptual reversals (Braun and Mattia, 2010). Representations of objects in the brain are modeled as attractors (i.e., representations in the brain of a physical stimulus) and their depth as a measure of the stability of the current pattern of activity corresponding to the percept. For instance, both the Necker cube and Rubin's Face Vase would have two attractors each that belong to the different interpretations. One interpretation is perceived whenever its representation is activated and therefore the state of the perceptual system is located with the attractor that belongs to that interpretation. A perceptual reversal occurs if the perceptual system escapes from one attractor state and jumps into the alternative one if the depth of the attractor is shallow enough.

The authors assume that during prolonged observation of an ambiguous stimulus (i.e., for several minutes) a transiently stable percept gets destabilized (i.e., it changes from one available percept to the other) in a slow and constant manner. Once the percept gets 'destabilized', a fast restabilization (disambiguation) takes place. This results in a change in interpretation of the ambiguous stimulus. This integrative theory suggests that different bottom-up and top-down processes work either together or against one another leading to a perceptual reversal.

This theory is supported by electrophysiological evidence. For instance, the Reversal Positivity (RP – Figure 3A) is suggested to be a marker of the disambiguation/restabilization process. There are other correlates that have been identified in the both the pre-stimulus and post-stimulus periods that are suggested to be linked to the destabilization and disambiguation/restabilization mechanisms of this theory. These physiological bases will be described in section 1.3.

1.2.4.1.1. Destabilization.

According to Kornmeier and Bach (2012), both top-down and bottom-up processes are involved in the destabilization process. This can be modeled as a slow reduction in the activation of the attractor in which the state is located leading to a more unstable perceptual state. The shallower the attractor, the easier it is for endogenous spontaneous fluctuations or exogenously induced fluctuations (e.g., by blinks and/or eye movements, visual transients, like short interruptions (Orbach et al., 1963) of stimulus presentation or light flashes (Kanai et al., 2005)) to influence a perceptual reversal.

In terms of top-down processes, effects of volitional control on reversal rates fit within the attractor model in terms of possibly causing an a priori change in the level of activation of specific attractors. This means that this effect could have an influence on the baseline activity or the threshold of activation or destabilization of the attractor. This in turn would prolong or shorten the destabilization time and increase or decrease the influence of fluctuations on the probability of a perceptual reversal.

In summary, a neural representation can be modeled as a brain state, located as an attractor within a state space. The depth of the attractor depends on the quality of the visual input (amongst others). For instance, the activation of an attractor is higher when the visual input is the unambiguous variant of the ambiguous figure presented. However, its activation is shallower if the stimulus presented is ambiguous. In other words, if the input is ambiguous, the attractor will be shallower. Thus, the more sensitive the representation is to spontaneous fluctuations and the more probable is a reversal between attractors. Kornmeier and Bach (2012) assume that in the case of ambiguous input, the activated attractor, is initially shallow and slowly flattens over time. Different bottom-up (e.g., discontinuous stimulus presentation, Kornmeier et al., 2009) as well as top-down factors (like volitional control, Toppino, 2003) may be able to alter attractor depth and/or increase the noise level (Braun & Mattia, 2010; Moreno-Bote et al., 2007) and thus influence both the rate of perceptual reversals and stability duration times, even simultaneously in an additive manner (Braun and Mattia, 2010; Kornmeier et al., 2009). Thus, bottom-up and top-down processes are no longer mutually exclusive with this idea.

1.2.4.1.2. Restabilization/Disambiguation.

Each reversal from one stable percept to another passes through a point of maximal instability when the perceptual state is on top of the barrier between the two related attractors. As was mentioned at the start of this thesis, our brain performs statistically optimal inferences about the structure of the external world and is structured to disambiguate and interpret the ambiguous visual information as fast as possible. This is based on limited sensory information that our brain receives (Knill and Pouget, 2004; Pastukhov, 2017). This is necessary for evolutionary reasons and our brain tries to keep the unstable brain state as short as possible and thus to achieve a fast stable percept of whatever sensory information is available (Kornmeier & Bach, 2012).. Therefore, after this maximum period of instability, an attractor is activated for a certain period of time (period of stability – dwell times) and the process is repeated all over again.

In summary, in terms of this theory, jumping from one attractor (destabilization) and arriving at another (disambiguation/restabilization) are different processes, working on different time scales (seconds vs. milliseconds; Borsellino et al., 1972; Kornmeier et al., 2009; Orbach et al., 1963, Struber & Stadler, 1999). Given a brain state of maximal instability, either at the onset of an ambiguous figure or as a result of the previously described slow destabilization process during prolonged observation, our perceptual system tries to find as fast as possible a more stable state. As was mentioned previously, according to Kornmeier and Bach (2012), the early RP ERP component (explained in more detail below) and the Beta band deactivation may be related to the fast disambiguation/restabilization of ambiguous visual input. Destabilization, however, starts immediately after the new percept has been established and is much slower (Kornmeier & Bach, 2012). It can take from seconds to minutes and its dynamic can be changed in different ways and perhaps at different time points by, for instance, new stimulus inputs or changes in goals (e.g. through volitional control). Some EEG correlates and activity have also been identified and linked to the destabilization process. These are correlates found to take place before the onset of the stimulus in experiments using the Onset Paradigm (paradigm explained in detail in Chapter 2). For instance, there is an increase in lower gamma-band activity (26–40 Hz) at the right-hemispheric central and parietal electrodes roughly 200 ms before onset of a reversal trial compared to a stable that does not have a reversal (Ehm et al., 2011). Ehm et al. (2011) suggest that these gamma modulations are indicative of an upcoming perceptual reversal. This means that these pre-stimulus/pre-reversal gamma modulations could be indicative of a transient brain state of maximal instability reached in the period before the onset of the stimulus. This suggests that these modulations could be a marker for the destabilization process explained earlier. There are also correlates that have been identified before the manual indication of a perceived reversal in experiments using the Manual Response Paradigm (this paradigm is explained in detail in Chapter 2) (e.g. gamma-band activity in right-hemispheric positions roughly 1000ms before response; Basar-Eroglu et al., 1996; Lumer et al. 1998; Nakatani & van Leeuwen, 2006; VanRullen et al., 2006; Roeber et al., 2008).

1.3. Physiological Bases of Ambiguous Stimulus Perception

The bottom-up and top-down mechanisms described previously, along with the integrative theory proposed by Kornmeier and Bach (2012) have been found to be consistent with several neurophysiological correlates. For instance, as was mentioned previously, Kornmeier and Bach (2012) suggest that the Reversal Positivity (described below), which is an ERP component suggested to be linked to perceptual reversals, is a marker of the disambiguation process. Moreover, another signature identified to support the integrative theory are the pre-onset gamma modulations linked to the destabilization process. There are several neurophysiological correlates that have been identified and linked to ambiguous figure perception and perceptual reversals. In this section, I discuss these correlates and their suggested significance in the literature. I have mentioned some of these correlates in the previous sections but will go over them again in more detail in this section. These signatures have been identified in both the pre- and post-stimulus periods and have been linked to several factors.

1.3.1. Pre-Stimulus

Several studies have explored the nature of pre-stimulus brain activity in an attempt to understand if this could bias observers' subsequent perception of an ambiguous figure using brain imaging techniques. Some studies have also investigated whether activity in the pre-stimulus period is predictive of the upcoming percept.

1.3.1.1. Functional Magnetic Resonance Imaging (fMRI) findings.

In one such study, conducted by Hesselmann, Kell, Eger and Kleinschmidt (2008), using fMRI to study the relationship between pre-stimulus brain activity and visual perception in Rubin's face-vase illusion, results showed a high pre-stimulus activation of the right Fusiform Face Area (rFFA) when the subjects subsequently reported perceiving faces compared with the activation of that area when they reported perceiving vase percepts. Moreover, an analysis of the baseline activity before and after presentation of the stimulus (pre-stimulus vs. post-stimulus) showed a non-linear interaction. The results from Hesselmann et al. (2008)'s study suggest two separable but complementary contributions to perceptual decisions, one related to ongoing activity, the other to stimulus-driven processes. Moreover, the results of this study suggest the initial state of the stimulus is subject to fluctuations that are slow enough to be detected by hemodynamic signals. Their results however do not show any activity in the higher frequency bands, which could be due to the low temporal sensitivity of BOLD signals. The full results of this study are described and discussed previously in this chapter (Chapter 1) in section 1.2.3.

1.3.1.2. Electroencephalography (EEG) findings.

In line with these findings, the results from Britz et al. (2009) were also suggested to be indicative of ongoing spontaneous fluctuations in the pre-stimulus period that influence subsequent percept. Britz, Landis and Michel (2009) used high resolution (256 – channel) EEG to see if pre-stimulus spontaneous fluctuations were predictive of an upcoming perceptual reversal using the Necker Cube and found a period of activity 50 ms before stimulus onset. Their results suggest that prestimulus activity in the right inferior parietal cortex is solely linked to perceptual reversals seeing as no activity in this area was observed preceding stable trials. Pre-motor and post-stimulus activity in this area has been previously identified in fMRI studies on bistable perception (Kleinschmidt et al., 1998; Inui et al., 2000; Slotnick & Yantis, 2005) and has been linked to the appraisal of a perceptual reversal. However, due to the low temporal resolution of BOLD signals, temporal conclusions remain a challenge.

Britz et al. (2009)'s pre-stimulus findings, the momentary activity in this region seems to predict a perceptual switch of an unchanging ambiguous stimulus. Moreover, they found that this area is differentially activated only preceding reversal trials and not after stimulus onset. In EEG studies, this area of the brain has been previously linked to change detection and change blindness (Beck et al. 2001; Pessoa and Ungerleider 2004; Kim and Blake 2005; Beck et al. 2006). Ehm et al. (2011) found similar results in their study using EEG and the Necker Lattice. Their results showed an increase in lower gamma-band activity (26–40 Hz) at the right-hemispheric central and parietal electrodes and an occipital decrease of higher gamma-band activity (40–65 Hz) only on reversal trials, 200 ms before ambiguous stimulus onset. These modulations were absent in exogenous reversals of unambiguous lattice variants (Ehm et al., 2011). Britz et al. (2009) and Ehm et al. (2011) used similar experimental designs, whereby the stimulus was presented intermittently with similar presentation times and inter-trial intervals across the experiments. The main thing that differed between the two is the stimulus used. These pre-stimulus results are in line with a previous EEG study by Müller et al.

(2005) in which they used an alternating dot pattern that induced illusory motion with ambiguous direction. They found activity that dissociates between reversal and stable trials appearing in the 300 ms preceding the onset of the multistable stimulus.

In a recent study, Rassi, Wutz, Muller-Voggel and Weisz (2019) used MEG to investigate the link between pre-stimulus spontaneous fluctuations and the perceptual outcome when viewing Rubin's Face-Vase. They used the same experimental paradigm as Hesselmann et al. (2008). Their results showed no differences in oscillatory power between face vs. vase reports in V1 or in FFA, indicating similar levels of neural excitability. This goes against previous fMRI findings (e.g. Hesselmann et al., 2008) albeit MEG may not have the spatial resolution to effectively isolate activity from these regions. However, they did find stronger connectivity of low frequency oscillations between V1 and FFA on face trials than on trials, which were reported as vases. They found that the strength of the prestimulus feedback connectivity from FFA to V1 predicted both the upcoming percept (face or vase) and the strength of post-stimulus neural activity associated with the reported percept. They found that before the onset of their Face-Vase stimulus, the FFA was more strongly connected to V1 on face reported trials, specifically in the feedback direction of FFA to V1. Connectivity between these two regions was found to take place in the alpha and beta frequency bands. They found that the time-frequency window during which the FFA was found to be mostly predictive of the perceptual outcome was correlated with the strength pre-stimulus feedback connectivity. These findings suggest that fluctuations in neural activity before the onset of the stimulus can bias subsequent perceptual outcome. In a study by Piantoni et al. (2017) the results showed that occipital alpha oscillations during inter-trial intervals (and therefore in the pre-stimulus period) are predictive of the duration of the sustained perceptual interpretation (stability) of the ambiguous stimulus. More specifically, they found that high alpha power in the high-level visual cortex promotes perceptual stability.

1.3.2. Post-Stimulus

Some of the previous findings on the activity occurring in the period before the onset of the ambiguous stimulus have suggested that this activity can also influence the activity observed in the post-stimulus period (e.g. Rassi et al., 2019). Most of the research to date on the underlying mechanisms and physiological bases of ambiguous figure perception concerns neural activity in the post-stimulus time period. These correlates have been associated with several factors (e.g. low-level stimulus processing, destabilization process, etc.).

1.3.2.1. fMRI findings.

Brain imaging research on bistable perception up to date has significantly contributed to locating the brain regions that underlie this phenomenon (Britz, Landis & Michel, 2008; Leopold & Logothetis, 1999; Rock & Mitchener, 1992). Brain-imaging studies indicated that both low-level (primary visual cortex) and high-level regions (higher frontal areas) influence the perceptual alternations in bistable perception (Qiu et al., 2009; Sterzer & Kleinschmidt, 2007; Weilnhammer, Ludwig, Hesselmann & Sterzer, 2013). On the one hand, some studies found that activity in the primary sensory cortex (e.g. primary visual areas) contributed to multistable perception, which was suggested to be the underlying cause of the spontaneous alternations in perception (Andrews, Schluppeck, Homfray, Matthews & Blakemore, 2002). For instance, neuroimaging studies using Rubin's Face-Vase found increased activations in the fusiform face area (FFA) during periods when subjects perceived the faces as the foreground figure versus the vase (Andrews, Schluppeck, Homfray, Matthews, & Blakemore, 2002; Hasson, Hendler, Ben Bashat, & Malach, 2001). Other studies revealed that top-down modulation from high-level regions such as the frontal/parietal cortices determined those alternations (Brascamp, Blake & Knapen, 2015; de Graaf, de Jong, Goebel, van Ee & Sack, 2011). For instance, Lumer et al. (1998) presented results that suggest that frontoparietal regions are activated during binocular rivalry stimuli. Moreover, in a study using Rubin's Face-Vase and Boring's Old/Young Woman, Kleinschmidt et al. (1998) found responses in the extrastriate visual cortical areas, most prominently in bilateral ventral occipital cortex (middle fusiform gyrus) and posterior intraparietal as well as in other occipital and some frontal areas during perceptual reversals.

Kornmeier and Bach (2012) have linked several findings in the fMRI and multistable perception literature to the destabilization process. One of those findings is Lumer et al. (1998)'s study in which they found selective right-hemispheric BOLD (fMRI) activation during perceptual reversals of the ambiguous variants of binocular rivalry stimuli, but not for their unambiguous counterparts, whereby two different unambiguous stimuli are presented successively (e.g. presenting a left-facing Necker Cube followed by a right-facing one; see Figure 5 in Chapter 2).

In line with this, Sterzer and Kleinschmidt (2007) found increased fMRI response in the right inferior frontal cortex (IFC) with endogenous motion reversals of the Stroboscopic Alternative Motion (SAM; von Schiller, 1933) stimulus but not with exogenous reversals. They found an earlier onset of the BOLD response in the right IFC associated with endogenous perceptual reversals, compared to the exogenous ones. Their results showed no onset difference in the occipital and parietal regions. This suggests that the right IFC plays a role in perceptual reorganizations (Leopold & Logothetis, 1999; i.e. destabilization, Kornmeier & Bach, 2012).

Similarly, Ilg et al. (2008), using the spinning wheel illusion (Wertheimer, 1912) found posterior right-hemispheric fMRI activity only with endogenous reversals. Zaretskaya et al. (2010) found during perceptual reversals of a rivalrous face/house stimulus a stronger BOLD response in the right intraparietal sulcus for some participants and in the left intraparietal sulcus for others. The top-down role of the IFC on visual processing during perceptual reversals has been widely studied using a multitude of ambiguous stimuli. For instance, using the Lissajous figure, a type of Structure from Motion ambiguous figure (Weber, 1930), Weilnhammer et al. (2013) found greater activation in a right-lateralized frontoparietal network during reversals. To further these findings and our understanding of the functional role of the frontoparietal network, Brascamp et al. (2015) used a binocular rivalry procedure to investigate the activity in this network for unreportable switches in bistable perception. They developed this type of stimulus by presenting different inputs (different sequence of quasi-randomly moving dots – they differed in in position and motion direction but had the same dot density and overall motion content) to each eye of the participant simultaneously. The subjective switching between these two percepts is so inconspicuous as to become unreportable. They found that reversal related activity in this region was minimized by this procedure, suggesting that the frontoparietal regions are involved in reversals that have been consciously registered.

Wang et al. (2013) conducted an experiment using Multivariate Pattern Analysis on fMRI data. Wang et al. (2013) used this type of analysis in order to decode patterns of activity associated with perceptual reversals in two ambiguous stimuli (Necker Cube and Face-Vase) with their unambiguous variants (see Figures 4&5 in Chapter 2). They found that activation patterns right before button press in medial and orbitofrontal cortices, precentral/central sulci, and ventral temporal and insular regions were able to decode upcoming perceptual reversals. This means that the pattern of activity linked to perceptual reversal trials in those regions is significantly distinguishable from the activation pattern linked to perceptual stability trials.

The results of this study showed that as time progressed following the button presses, activity related to the percept moved from frontal and anterior temporal regions to posterior visual cortices (Wang et al., 2013). Moreover, Wang et al. (2013) found that areas in frontoparietal, anterior, and ventral temporal cortices showed similar results for the unambiguous and ambiguous conditions. This suggests that there are similar patterns of activity between unambiguous stimuli and the corresponding perceptions of ambiguous stimuli in these regions. However, this was not the case for the activity pattern observed in V1. This is because low-level features of the stimuli were different between ambiguous and unambiguous conditions. These findings were consistent across both types of stimuli.

Functional neuroimaging studies have outlined a plausible anatomy of perceptual multistability but the specific results vary as a function of the type of multistable stimulus and probably also with the mechanisms underlying changes in perceptual interpretation. Functional neuroimaging studies show that transient event-related signal changes time-locked to changes in percept choice occur in those functionally specialized areas that are sensitive to the perceptual content (e.g. increased FFA when perceiving faces in Rubin's Face-Vase) that is perceived to change (Lumer et al., 1998; Kleinschmidt et al., 1998; Lumer & Rees, 1999; Sterzer et al., 2002). However, fMRI suffers from a temporal resolution problem, making the specific time-locking of events difficult.

1.3.2.2. EEG findings.

In order to resolve the temporal resolution problem in the underlying mechanisms behind ambiguous figure perception, the literature using EEG to investigate these mechanisms is growing (Kornmeier & Bach, 2014, p.950; Orbach, Ehrlich, & Heath, 1963; Orbach, Zucker, & Olson, 1966). For instance, in their first experiment, Kornmeier and Bach (2004) used a Necker Lattice and found that the processes of disambiguation started 130ms and ended 260ms after stimulus onset. The distribution was found in the occipital and parietal electrode positions. In a later experiment, they used Boring's Old-Young woman illusion (2014) and found an early occipito-temporal N170 (that is usually reported as a response to face perception (Itier & Taylor, 2004; Rossion et al., 2003)) ERP correlate of reversals between the perception of the old woman and the perception of the young woman. This disambiguation and gestalt construction was finished at 170ms. The electrophysiological counterpart of FFA activation is the N170/vertex positive potential (VPP) component, which is elicited selectively by stimuli that include faces or facial features (Itier & Taylor, 2004; Rossion, Joyce, Cottrell & Tarr, 2003; Allison, Puce, Spencer, &McCarthy, 1999; Jemel, George, Olivares, Fiori & Renault, 1999).

Pitts et al. (2011) found that, similar to what happens to the FFA region in fMRI studies, the N170 was larger when participants perceived the Rubin ambiguous figure as faces compared to when the same visual input was perceived as a vase. This is in line with previous studies that found larger N170 amplitudes associated with the perception of faces vs. non face objects (e.g. Holmes et al., 2005; Itier & Taylor, 2004). They also identified two components preceding it. In their experiment, using Rubin's Face-Vase, each button press triggered a probe flash, either to the face region, the vase region or to the border between the two. These two components were suggested to be associated with early stages of figure-ground perception. The first component, the Border difference (Bd) is an early difference at around 110ms that is elicited by border probes when subjects perceived the faces versus the vase as figure. Pitts et al. (2011) suggest that this component reflects the early 'border ownership' stage of figure-ground processing. It is followed by a positive component, the Figure-Ground difference (FGd) at around 150-200ms when the region perceived as figure (vs. ground) was probed. This is the case for both the face and vase regions. This component seems to reflect the subsequent 'figure-ground segregation' stage of processing. Both the Bd and the FGd were localised to the ventral area of the Lateral Occipital Complex using source localization estimation. This area is important for shape and object processing (Eger, Ashburner, Haynes, Dolan, & Rees, 2008; Martinez, Ramanathan, Foxe, Javitt, & Hillyard, 2007; Hasson, Harel, Levy, & Malach, 2003; Kourtzi & Kanwisher, 2000). Moreover, similar to previous findings, Pitts et al. (2011) found N170 modulation in the right fusiform gyrus (Itier & Taylor, 2004; Rossion et al., 2003; Allison et al., 1999; Jemel et al., 1999; Puce et al., 1999) using source estimation.

A difference ERP (dERP) is obtained by substracting one ERP waveform from another in order to isolate brain activity that is related to the difference between two conditions. There are two dERP components that have received significant attention over the past 10-15 years. Both have been linked to perceptual reversals: the Reversal Negativity (RN – see Figure 3B) and Reversal Positivity (RP – see Figure 3A). dERPs are difference traces whereby the ERP waveform from one perceptual state (here Stability, i.e. no change in interpretation of the presented ambiguous stimulus) is subtracted from the ERP waveform of the other perceptual state (here Reversal). This is done in order to study the relationship between the two raw ERP traces of the Reversal trials and the Stability trials. Therefore, the interesting aspect of the RN and RP components is that they isolate the reversal-related activity by comparing the reversal and stability trials whereas some of the components mentioned previously focus on aspects of the identity of the stimulus (e.g. larger N170 for face reports in experiments using Rubin's Face-Vase stimulus; Pitts et al., 2011).

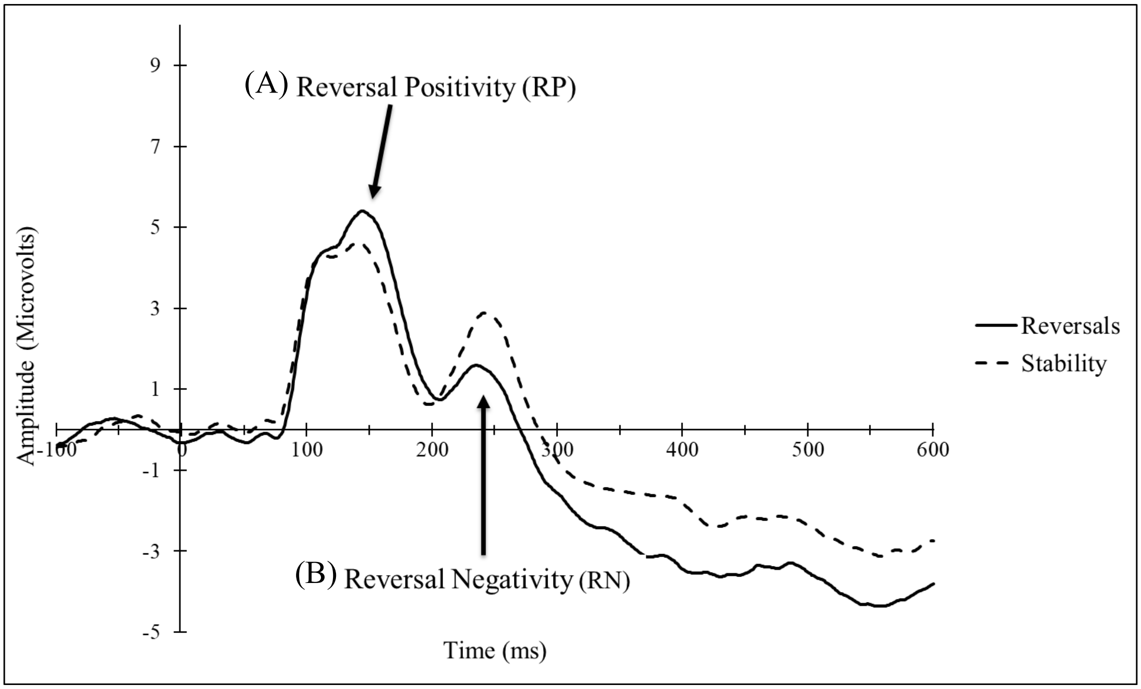


Figure 3. Example of the different ERP components that are suggested to be reversal related: (A) The Reversal Positivity and (B) The Reversal Negativity. The data illustrated in this figure corresponds to the response trials of the identity task from Experiment 1 (Necker Lattice) (see Figure 3.3C).

Kornmeier and Bach (2004, 2005) have produced these two dERPs. The RP (Figure 3A; Kornmeier & Bach, 2005; 2006; Kornmeier, et al., 2007; Britz, et al., 2009) appears approximately 130 ms after stimulus onset as a more positive amplitude on reversal trials than on stable trials at, primarily, occipital electrode positions. The RP has been found for a range of multi-stable stimuli including the Necker Lattice (e.g., Kornmeier & Bach, 2005, 2006), the Necker cube (e.g., Kornmeier, Pfäffle, & Bach, 2011), Boring's Old/Young Woman (Kornmeier & Bach, 2014), and during binocular rivalry (e.g., Britz and Pitts, 2011). The RP is present only for endogenous reversals and not for exogenous reversals. This suggests that the RP may be specifically linked to processes of internally-generated perceptual reversals rather than changes in sensory input. Furthermore, the RP appears to be insensitive to low-level stimulus differences such as size (e.g., Kornmeier et al., 2011). However, perhaps because of its small amplitude, the RP has not been observed universally across studies (e.g., Pitts, et al., 2007; Intaitė, et al., 2010). Kornmeier and Bach (2012) have suggested that the RP is a marker of perceptual ambiguity detection or perceptual decision conflict that occurs only on reversal trials when perception is changing from one interpretation to another (Pomerantz and Kubovy, 1981; Kornmeier et al., 2011). According to them, the RP is a marker of the disambiguation process described previously.

The second component, the RN (Figure 3B), appears approximately 260 ms post-stimulus and has been observed with a range of ambiguous stimuli (e.g., Kornmeier & Bach, 2004; 2005; Pitts, et al., 2007, 2008; Britz, et al., 2009; Intaite, et al., 2010). The RN is opposite in polarity to the RP with reversal trials having more negative amplitudes than stable trials in mostly occipital/parietal locations. There has been substantial debate about whether it reflects higher-level, top-down influences over perceptual reversals (e.g., Pitts et al., 2008). As was mentioned previously, researchers have investigated the effect of both bottom-up (e.g. presentation mode and ISI; Kornmeier et al., 2007) and top-down processes (e.g. voluntary control; Pitts et al., 2008) on the RN. For instance, in an experiment conducted by Pitts et al. (2008), the results showed that the amplitude of the RN increased when participants voluntarily controlled for reversals compared to passive reversals. Furthermore, the RN cannot be linked uniquely to endogenous perceptual reversals because it also appears for exogenous (i.e., stimulus-induced) reversals (e.g., Kornmeier & Bach, 2006).

The RP and RN have been previously studied in experiments using the 'Reversal Task' (e.g. Kornmeier & Bach, 2004a, 2005; explained and discussed in more detail in section 2.2.2 in Chapter 2 and 3.1.4 in Chapter 3). In this type of task, participants are presented with an ambiguous stimulus intermittently and have to report on each trial whether they experienced a perceptual reversal or not. This type of task involves monitoring for reversals and is similar to a change detection task (i.e. reversal trials contain a change to detect and stable trials do not; Rensink, 2002; Cohen et al., 2005). Previous ERP studies have found, in a change detection task, a posterior negative amplitude enhancement, similar to the RN, on trials with detected changes (Pazo-Álvarez, et al., 2017). Thus, it is possible that RN effects, when assessed using the reversal task, could be related to other processes (e.g. visual oddball detection) rather than perceptual reversal processes as is generally assumed.

The functional role of the RN remains unclear and the implications of the reversal task used to study it (and the RP) are discussed in more detail in Chapters 2&3. In order to control for the response factor and to avoid any contaminations of their ERP components by a motor component, Kornmeier and Bach (2004a) changed the button-press task in half of the trials (respond to reversals vs. respond to stability) and counterbalanced the reversal and stability blocks. Following this, they classified participants' responses into four EEG waveforms: reversal indicated via response, reversal indicated via non-response in the blocks where participants were asked to respond only when they experienced perceptual stability, stability indicated via response and stability indicated via non-response. In order to study the RN, Kornmeier and Bach (2004a) collapsed over response and ended up with two waveforms, one for reversal and one for stability. In another experiment, Kornmeier and Bach (2004b) only used the response trials and found the RP component. Pitts et al. (2007), as was mentioned previously, however, did not detect the RP component in their experiment for all different types of ambiguous stimuli. In their experiment, they only had one type of block where participants had to press a button whenever they experienced a perceptual reversal and wait for the next stimulus to appear whenever they experienced a perceptual stability. In their analyses, they computed the difference waves by subtracting the reversal (indicated via button press) and stability waveforms (defined by no button press). These results suggest that, although Kornmeier and Bach (2004a) did not find a significant main effect of response in their analyses, response could influence the RP component.

In addition to these findings, several experiments have also shown that the RP and RN are sensitive to certain factors. This sensitivity, in some cases, leads to the absence of, differences in the spatial distribution of, and/or amplitude of these components. For instance, the RP was not found in Pitts et al. (2007)'s experiment using Rubin's Face Vase, Schroder's Staircase and Lemmo's Cheetah. Kornmeier and Bach (2012) suggested that the absence of that effect is due to the very small amplitude of the RP and the small number of trials per condition in Pitts et al. (2007)'s experiment. Moreover, in a study conducted in order to understand the functional role of the RP where the experimenters varied the dimensions of the stimulus, Kornmeier, Pfaffle and Bach (2011) found that it is largely unaffected by cube size and is dependent on the percept (monitoring for reversal vs. stability). Kornmeier, Pfaffle and Bach (2011) suggest that this indicates that the RP is related to a processing conflict related to perceptual reversals (i.e. disambiguation).

As for the RN, Kornmeier and Bach (2014) found that it was not present in a study using Boring's Old-Young woman stimulus and found a shift in its location from a predominantly parietal-occipital distribution to a temporal one, in a previous study using that same stimulus (2004a). This location shift of the RN is also present for Rubin's Face-Vase (Pitts et al., 2007) with a spatial lateralization of this component to the left. However, the RN has a bilateral distribution in experiments using Schroder's Staircase (Pitts et al., 2007) and the Necker Lattice (2004). Pitts, Gavin & Nerger (2008) also found in their experiment on volitional control, an earlier onset of the RN and an increase in its amplitude. Moreover, these components are obliterated in experiments using the Manual Response Paradigm. This could be due to the variance in reaction times (discussed in more detail in section 2.2.1 in Chapter 2; Kornmeier & Bach, 2012). This shows that there are several factors that come into play with regards to the RP and the RN. Therefore, in order to further understand the underlying mechanisms of perceptual reversals, we must understand the processes underlying these two components.

In addition to these components, a left-hemispheric continuous alpha decrease on reversal trials (8–15 Hz) starting at around 130ms, ranging from the occipital to frontopolar electrode has been identified with endogenous reversals (and not exogenous ones; Isoglu-Alkac et al., 2000, Isoglu-Alkac and Strüber, 2006, Strüber and Herrmann, 2002). Isoglu-Alkac and Strüber (2006) suggest that the decrease in alpha amplitude reflects an automatic arousal reaction, which triggers attentional processing during perceptual reversals in a stimulus processing related manner. Desynchronisation of higher alpha activity might be more closely related to excitation/activation, attention and top-down modulation of perceptual processing, execution of cognitive tasks or temporal segmentation of perception and consciousness (Klimesch, 1999; for a review, see Palva and Palva, 2007). The alpha power reduction has been found to last about 60ms for the Necker Lattice. Kornmeier and Bach (2012) interpret this power reduction as disambiguation time. More recently, in a study exploring alpha activity during perceptual reversals in a Necker Cube in two different sleep conditions (normal sleep vs. sleep deprivation), Piantoni et al. (2017) found that an increase in alpha after sleep deprivation increases dwell/stability times (i.e. increases the perceived duration of an interpretation). They found that local alpha power around the parieto-occipital sulcus within the first second after percept choice predicted the length of this representation. This is in line with previous studies and suggests that high alpha power promotes stability and suppresses reversals. This also furthers the idea that alpha activity/desynchronisation is closely related to top-down processes.

Following the RP and the RN, is the Frontopolar Positivity (Kornmeier & Bach, 2004b) occurring at around 300ms on exogenously induced reversal trials and 340ms on endogenous reversal trials. It is mostly found at the frontopolar electrodes. In an experiment conducted by Kornmeier and Bach (2006) using the Onset Paradigm in a go-nogo task (go – percepts indicated via button press; nogo – percepts indicated via non-button press) to study perceptual reversals in the Necker Lattice, they found an interesting effect on the Frontopolar Positivity that suggests that a role of working memory underlies this component. They found that the Frontopolar Positivity is absent on trials in which participants did not respond (no-go trials) and that on go trials, there was an increase of the positivity at 300ms and a decrease in that positivity at 400ms from parietal to frontopolar electrodes for exogenous reversals (i.e. unambiguous trials). They observed the same effect for the ambiguous trials. According to Kornmeier and Bach (2006, 2012)'s interpretation of these results, this suggests a working memory role related to the delayed response in the subsequent ISIs of the go trials. There was no delayed response in the no go trials and thus no related memory is necessary. This suggests that some response-related brain instance must already know about the perceptual outcome at 340ms and that perhaps this component is not solely related to perceptual reversal processing, but to response factors as well.

Following this component is the Parietal Positivity which is also referred to as the Late Positive Component (LPC) at around 400ms for exogenous reversals and 470ms for endogenous ones (O'Donnell et al., 1988; Britz et al., 2009; Britz & Pitts, 2011; Kornmeier and Bach, 2006; Pitts et al., 2008). More specifically, the Parietal Positivity occurs between 400 and 500ms in studies using the Onset Paradigm and between 250 and 125ms before button press/manual indication in studies using the Manual Response Paradigm (i.e. paradigms where events are time locked to manual response; Isoglu-Alkac et al., 1998). In a study using source localization, the Parietal Positivity was localized in the bilateral superior and middle temporal as well as left inferior frontal areas. Several authors identified the Parietal Positivity with the P3b component (Britz & Pitts, 2011). The latter occurs in oddball paradigms (Picton, 1992). Verleger et al. (2005) demonstrated the persistence of the P3b component in both experiments using the onset paradigm and manual response paradigm. The P3b occurs if perceptual processing of a stimulus reaches consciousness, whereas this component is absent, when the stimulus is subliminal (Dehaene and Changeux, 2011). This means that it is involved in voluntary target detection (e.g. indicating the color of the percept in the binocular rivalry experiment by Britz & Pitts, 2011).

There are several interpretations of the Parietal Positivity that are focused on or surround the idea of conscious perception of the stimulus. Previously, researchers interpreted this component as an indication of attentional and cognitive processes during a perceptual reversal (e.g. O'Donnell et al., 1988) or following it (İşoğlu-Alkac et al., 2000). More recently, researchers have attributed this component to the indication of the ending of a reversal process (Strüber et al., 2001), or its cognitive/conscious recognition (Strüber and Herrmann, 2002; Kornmeier and Bach, 2006; Britz and Pitts, 2011). The findings from more recent studies (e.g. Kornmeier & Bach, 2006; Britz & Pitts, 2011) suggest that this component does not reflect the reversal event itself but its cognitive analysis seeing as it occurs ~300ms after the RP in the early visual areas (the RP is considered to be a marker of the destabilization process and therefore reflect perceptual change; Britz & Pitts, 2011; Kornmeier & Bach, 2012) and after the 'resolution' of the reversal event itself. Kornmeier and Bach argued that the 'decision' about the perceptual outcome takes place ~260ms after stimulus onset at the latest (same latency as the RN; Britz et al., 2009; Kornmeier & Bach, 2004, 2005, 2006; Pitts et al., 2007). In addition to that, the interpretation related to this component is also because of its similarities with the P3b component.

Other signatures that occur for both exogenous and endogenous reversals that take place after the reversal event have been identified. For instance, the beta and gamma modulations that occur during perceptual reversals. In studies using the Onset Paradigm, there is a left-central increase in gamma activity (40–65 Hz) at about 150 ms for exogenous reversals and 250ms for endogenous ones (Ehm et al., 2011). This is followed by a bilateral central increase at around 260 ms for exogenous reversals and a right-central increase at 320ms for endogenous in beta activity (14–26 Hz) (Ehm et al., 2011). Moreover, several studies using the Manual Response Paradigm found an increase in frontal gamma activity in 1000 ms window before the manual indication of a reversal (e.g., Basar-Eroglu et al., 1996; Strüber et al., 2000). The functional role of these post-stimulus beta and gamma modulations remains unclear (Ehm et al., 2011). Ehm et al. (2011) attempted to investigate the role of the gamma modulations and investigate whether they could attribute them to binding processes (i.e. during disambiguation, the perceptual system tries to match the visual information to one of the perceptual interpretations existing in memory). Due to its temporal delay, Ehm et al. (2011) argue that the observed increased gamma activity casts doubt on whether it can be attributed to the binding process seeing as it was transient and did not continue into the stable periods. It was hypothesized that these transient modulations could potentially signify the buildup of a coherent percept rather than its maintenance. However, this has yet to be tested.

1.4. Aims and Hypotheses of Current Thesis

All of the above findings indicate that there are likely several processes that contribute as underlying mechanisms of ambiguous figure reversals. These findings come from two primary experimental paradigms (onset paradigm, manual response paradigm) with different presentation times (long, short, continuous) and inter-stimulus intervals (short, long). There are several theories that have attempted to explain the underlying processes that take place during a perceptual reversal. In summary, behavioral studies indicate that reversal rates are sensitive to a multitude of factors: experimental paradigm, presentation time and inter-stimulus interval. There are several suggestions used to explain this sensitivity. In order to try to explain this variability and the occurrence of reversals in the first place, experimenters have also used neuropsychological tools (e.g. EEG, MEG, fMRI, etc...) exploring pre-stimulus and post-stimulus activity. We find that this type of research also uses the same multitude of experimental paradigms with differing presentation times and inter-stimulus intervals in order to investigate the mechanisms that have been linked to ambiguous figure perception (e.g. neural fatigue, adaptation, attention, etc…).

Some studies, providing relatively precise temporal information, indicate that there is activity that precedes perceptual reversals that has a predictive character. For instance, as was mentioned previously, researchers have found right-hemispheric central gamma modulation pre-onset on reversal trials. This activity has been linked to the destabilization process suggested by Kornmeier and Bach (2012). However, this activity results from averaging across several trials. This necessarily involves a loss of information due to averaging (e.g. in ERP analyses, the pre-stimulus activity is usually averaged out and baseline corrected). Furthermore, most of the previous work exploring pre-stimulus effects is done in a univariate fashion, which focuses on only a narrow range of frequencies, time ranges, and sets of electrodes. This is often done in order to reduce statistical corrections associated with searching across these dimensions of brain activity. However, if perceptual reversals involve the convergence of multiple mechanisms then multivariate methods such as Multi-Variate Pattern Analysis (MVPA; described in detail in section 2.3.2 in Chapter 2) may be more appropriate. MVPA refers to a set of methods that analyze neural responses as patterns of activity, thus affording investigation of the widespread brain states that incorporate all of the involved mechanisms. Much work in fMRI, and increasingly in EEG, has now embraced multivariate analysis methods to identify patterns of brain activity associated with particular cognitive processes.

With EEG, it is possible to assess the emergence of representations across time with high temporal resolution. This means that when using MVPA at each time point, the pattern of activity associated with one cognitive/perceptual state (e.g. perceptual reversal) is compared against and distinguished from the pattern of activity associated with another cognitive/perceptual state (e.g. perceptual stability). Multivariate pattern analysis of EEG has potential to reveal unique spatiotemporal patterns of neural activity distinguishing between behavioural states. Using this type of analysis would allow us to identify the period during which these two patterns of activity are significantly different from one another. This, in turn would indicate whether this time period is predictive of a perceptual reversal and allows us to explore the patterns of activity across the whole scalp in the pre-stimulus period.

Another aspect of this type of analysis is that it operates in the time-frequency domain as well as the time domain. Previous findings in the literature have shown that there is oscillatory activity in the pre-stimulus period that is linked to perceptual reversals (see section 1.3.1 above). These findings suggest that this observed activity is linked to several processes such as ongoing spontaneous fluctuations in the pre-stimulus period (e.g. Britz et al., 2009; Hesselmann et al., 2008). Similar to univariate analyses, MVPA would allow the identification of frequency modulations that occur across the pre-stimulus period that are linked to perceptual reversals and subsequent percept choice. However, unlike univariate analyses, MVPA looks at multivariate patterns from across the scalp. This is more likely to give a sense of time and frequency ranges involving multiple mechanisms across the brain. MVPA in the time-frequency domain compares the pattern of activity associated with the different perceptual states for each time point at each frequency level and would allow us to identify the time-frequency window during which these patterns of activity are predictive of the upcoming perceptual state. Experiments 3 and 4 in Chapter 5 will explore the patterns of pre-stimulus neural activity that are associated with each perceptual outcome (e.g., face and vase for face/vase stimulus) of the ambiguous Necker Lattice (Experiment 4) and Rubin's Face-Vase (Experiment 3) and the patterns of pre-stimulus activity that are associated with reversal in the subsequent stimulus presentation. The design of these experiments is catered to allow for the investigation of the pre-stimulus period across a large time window (described and discussed in section 2.2.2 in Chapter 2).

Other studies, exploring post-stimulus activity and investigating the re-stabilization/disambiguation process that takes place during ambiguous figure perception have linked two ERP components to perceptual reversals, the RN and the RP. The nature of these two components and their underlying mechanisms has yet to be fully understood. As was mentioned previously, the two ERP components associated with perceptual reversals (the RN and the RP) have been studied in experiments only using a reversal task where participants have to monitor for reversals and indicate on each trial whether or not their interpretation has reversed from their previous one. This raises the question about whether these two components are dependent on monitoring for reversals and are therefore linked to task demand processing or if they are linked to reversal processing. In terms of the task previously used, reversal trials could be seen as relatively rare, task-relevant targets in a stream of more prevalent non-target stable trials. This also raises the question about whether these components are dependent on target status. If these two components are dependent on task demands and target status, then we suspect that they would be absent in a task where participants would not monitor for perceptual reversals. However, if they were not dependent on task demands and are related to perceptual processing, then there should not be any differences in the effects observed between differing tasks. Therefore, in order to address the question about whether these ERP measures of reversal-related activity are dependent on task-relevance, we introduce the ‘identity task’ in addition to the ‘reversal task’ in Experiments 1 (Necker Lattice) and 2 (Face-Vase) (details of this experiment are described in more in section 3.1.5 in Chapter 3). In this task participants have to report the perceived identity on each trial of the ambiguous figure (e.g. perceived orientation – left-facing vs. right-facing – for the Necker Lattice in Experiment 1 and face vs. vase for the Face-Vase in Experiment 2). The presence of both components (RN and RP) in the identity task would eliminate the assumption that these components are dependent on monitoring for reversals vs. stability. Reversals or stability trials could be treated like target/non-target trials and this may mean that any ERPs related to them differ in executive or attention processes rather than just perceptual processes. The identity task is meant to eliminate this by making the reversal vs. non-reversal distinction task irrelevant.

In addition to the effect of task, we wanted to determine whether these two components are targets for response. The nature of the task used in Kornmeier and Bach (2004a, 2005) inevitably introduces a motor component. However, their findings have suggested that there is no significant effect of response (Kornmeier & Bach, 2004a). Moreover, studies focused on differentiating perceptual from motor processes have found that the brain response to perceptual reversals differs from motor-related processes elicited by the button press indicating the perceptual reversal (Mathes, Pomper, Walla, Basar-Eroglu, 2010). Also, the ERP components found to be related to response (Bereitschaftspotential) have a later latency than those of the ERPs of interest. However, these previous studies on the RN and the RP have not compared the effect of the different response conditions on these two components. As was mentioned previously, these components have either been a result of a collapse between the response and non-response condition (e.g. the RN in Kornmeier & Bach, 2004a), or a result of only looking at response trials (e.g. the RP in Kornmeier & Bach, 2004b) or subtracting reversal indicated via button press from stability indicated via non-button press (Pitts et al., 2007). These experiments have not explored the differences in the dERP waveforms for trials on which participants responded (reversal and stability indicated via button press) versus the waveforms for trials on which participants did not respond (reversal and stability indicated via non button press). Therefore, in order to determine if the RN and RP are dependent on response demands, we added response as a factor in Experiments 1 and 2. Any dependence on response by these two components signifies that they’re not solely linked to perceptual reversals but to response factors as well. We investigated whether these two components are targets for response by varying the response style across blocks (this is described in more detail in Chapter 3).

In section 1.3 of this chapter, I described the electrophysiological bases of ambiguous figure perception in both the pre-stimulus and post-stimulus period. Most of these findings are of ERP correlates or of oscillatory activity that are linked to perceptual reversals or one of the perceptual interpretations of the ambiguous figures. We have seen that there is a lot of information provided with regards to the post-stimulus onset activity linked to perceptual reversals. This activity is ongoing starting at stimulus onset and lasting for about 600-700ms. This activity can be observed at several frequency levels and at different electrode and channel locations. All of the post-stimulus findings have been linked to different processing stages of perceptual reversals (e.g. stimulus detection, destabilization process, etc.). As was mentioned previously, the types of analyses used in order to investigate these components involve loss of information due to averaging and the focus is on only a narrow range of frequencies, time ranges, and sets of electrodes. However, the questions that we are interested in answering are related to the varying brain states in cortical region and whether or not these brain states could be decoded and classified into different groups of interest based on the different types of information provided. These questions involve taking into account the entire pattern of activity in the brain across time and frequency. Therefore, in addition to using MVPA on the pre-stimulus period in the experiments designed to allow for the exploration of this period (Experiments 3 and 4), I will also use MVPA on the data from Experiments 1 and 2. I will do this in order to identify the time-frequency windows during which perceptual reversals can be significantly predicted from the patterns of activity during those windows in the post-stimulus period (Chapter 4). This would also allow me to further investigate whether the pattern of activity during the time windows of the reversal-related dERP components (i.e. the RN and the RP) is predictive of perceptual reversals and whether or not these differ across response conditions.

The last question I want to explore in this thesis is whether the mechanisms underlying perceptual reversals differ between ambiguous stimulus types. In my experiments, I will use the Necker Lattice (Experiments 1 & 3; Necker, 1832) and Rubin's Face-Vase (Experiments 2 & 4; Rubin, 1915). The choice of these stimuli is justified in the next chapter (section 2.1.1 in Chapter 2). The literature shows that the latency, spatial distribution, amplitude and presence of the RN and the RP are found to be affected by several factors (e.g. number of trials, ambiguous stimulus type, inter-trial interval, etc…). These factors have been discussed previously and will also be discussed in more detail in the third chapter. Moreover, the types of reversals are different between the two ambiguous stimuli I chose in my experiments (e.g. figure ground reversals for Rubin's Face-Vase vs. perspective reversals for the Necker Lattice; discussed in detail in section 2.1.1.1 in Chapter 2). Therefore, I suspect that there could potentially be observable differences in our electrophysiological results across stimulus types. To address this issue, I will conduct my experiments with both stimuli.

Therefore, in order to address the issues raised throughout this thesis and especially in this section I have structured my thesis in the following way. In the second theoretical chapter of this thesis (Chapter 2), I will discuss and justify the methods I used in my experiments and empirical chapters. In my first empirical chapter (Chapter 3), I present two experiments (Experiment 1: Necker Lattice and Experiment 2: Face-Vase) that examined whether the RN and RP are dependent on response and/or task demands or if they are purely related to processing involved in perceptual reversals. In this chapter, I will attempt to primarily replicate the previous RN and RP findings in experiments using the Necker Lattice and the Reversal Task (e.g. Kornmeier & Bach, 2004a, 2005), with the aim of furthering these findings and investigating what factors influence these components by adding the Identity Task and varying response styles across blocks. I used ERP analyses of EEG data to investigate these components.

In my second empirical chapter (Chapter 4), I will use the EEG data from my first two experiments (Experiment 1&2) and run MVPA on the post-stimulus period (from stimulus onset until stimulus offset) in order to identify what time and time-frequency windows is most predictive of perceptual reversals and to investigate whether this differs across response conditions. This will also allow me to observe whether there are time periods of the EEG signal, in addition to the RN and RP, during which the multivariate pattern of brain activity is predictive of perceptual reversals.

In my third and final empirical chapter (Chapter 5), I present two other experiments (Experiment 3: Face-Vase and Experiment 4: Necker Lattice) that are designed to allow for the investigation of the pre-stimulus period with minimized carryover effects from the post-stimulus period of the preceding trials. These experiments only involve the Identity Task and have different stimulus presentation and inter-trial interval lengths. In this chapter, I will use MVPA on EEG data in order to identify the time and time-frequency windows in the pre-stimulus period during which the pattern of activity across the scalp is significantly predictive of an upcoming perceptual reversal and of the subsequent perceptual interpretation of the ambiguous images.

Chapter 2: Methods

Several methods and stimuli have been used to understand both the bottom-up and top-down mechanisms underlying ambiguous figure perception and perceptual reversals. These methods have been designed to focus on either one or a few mechanisms. For instance, as was mentioned previously, one way in which attention in ambiguous figure perception and perceptual reversals was studied was by using experiments involving voluntary control. In this chapter, I outline and justify the methods used in the experiments that follow as well as discuss the general issues around the choice of these methods.

2.1. Physical Stimulus Considerations

2.1.1. Stimulus Choice

The stimuli we chose in our experiments differ in their kind of perceptual switching. Previous research shows that the perceptual switches that occur in Face-Vase perception involve figure-ground assignment (Rubin, 1915, 1921; Pitts et al., 2011). As for Necker Cube perception, researchers suggest that the reversals are associated with its transparent 3D structure, which involves depth perception (Necker, 1832; Purves & Andrews, 1997). These findings suggest that there are multiple factors that can influence ambiguous figure perception and that some of those factors differ across and are specific to each different ambiguous image. This brings forth the question of whether or not different types of reversals share the same underlying mechanisms and whether the electrophysiological correlates that appear for one type of ambiguous stimulus will also be present when perceiving a different one. Several experiments have shown that the latency (Pitts, Gavin & Nerger, 2008), scalp distribution (Kornmeier & Bach, 2014; Pitts et al., 2007) and presence (i.e., component present or not; Pitts et al., 2007; Kornmeier

& Bach, 2014) of some ERP components (e.g. Reversal Negativity and Reversal Positivity) are sensitive to the type of ambiguous figure.

To address the issue of generalizability of our findings across stimuli, we chose two different ambiguous stimuli: Rubin's Face-Vase and the Necker Lattice. These two stimuli have been widely used to study the underlying mechanisms of ambiguous figure perception. There are several established electrophysiological correlates, both in the pre-stimulus (e.g., Hesselmann et al., 2008; Ehm et al., 2011) and post-stimulus (e.g., Kornmeier & Bach, 2004a; Pitts et al., 2007) periods, linked to bistable perception of these two figures (see section 1.3 in Chapter 1). Because the literature using these two figures to study bistable/multistable perception is extensive with established markers, we decided to use them in our experiments as well in order to extend prior EEG findings on the underlying mechanisms of ambiguous figure perception.

2.1.1.1. Rubin's Face Vase.

One of the most well-known images to induce perceptual bi-stability, used in some of our experiments (Experiments 2 and 3), is Rubin's Face-Vase illusion (Rubin, 1915; 1921). This image involves figure-ground organization. Figure-ground organization involves the automatic segregation of regions of a visual scene into 'figures' (shapes) bounded by the shared border in front of a 'ground' (shapeless background) that seems to continue behind the figure (Kim & Feldman, 2009). In ambiguous stimuli, different interpretations are typically mutually exclusive. This means that the different percepts cannot be perceived simultaneously. In the case of Rubin's Face-Vase, where a border is shared between the two percepts, research suggests that the shared border is one of the reasons why the two percepts are not perceived simultaneously. According to Driver and Baylis (1995a,b; 1996) shared borders are assigned to a shape on just one of the sides of that dividing edge and the edge is seen as belonging just to the figure (e.g. either Face only or Vase only).

2.1.1.1.1. Brief background on Figure-Ground Organisation.

Following identification of contours and regions in an image, researchers hypothesize that the perceptual system carries out a process called ‘border ownership assignment’. This is also known as figure-ground organization or edge-assignment. In the case of ambiguous stimuli like Rubin’s Face-Vase, this means that each edge is assigned to one of the regions which it bounds (von der Heydt, Zhou, & Friedman, 2003; Albright & Stoner, 2002; Zhou, Friedman, & von der Heydt, 2000; Koffka, 1935; Rubin, 1921). For instance, in Rubin’s Faces-Vase image (see Figure 2.1A), the shared borders are perceived as the occluding edge of either the central region or as occluding edges of the two flanking regions. (see Figure 2.1B for Faces region and Figure 3C for Vase region). If the two edges are assigned to the flanking regions then these figural regions are perceived as in front of and overlapping the central region. Importantly, only the regions to which the edges are assigned appear to have shape at the edges. The central ground region, in this case, appears to be shapeless at the edge and instead extends behind the figural regions (i.e., partial occlusion). The figure is said to own the borderline. When figure–ground reversals occur, the border ownership switches as well (Wagemans et al., 2012b).

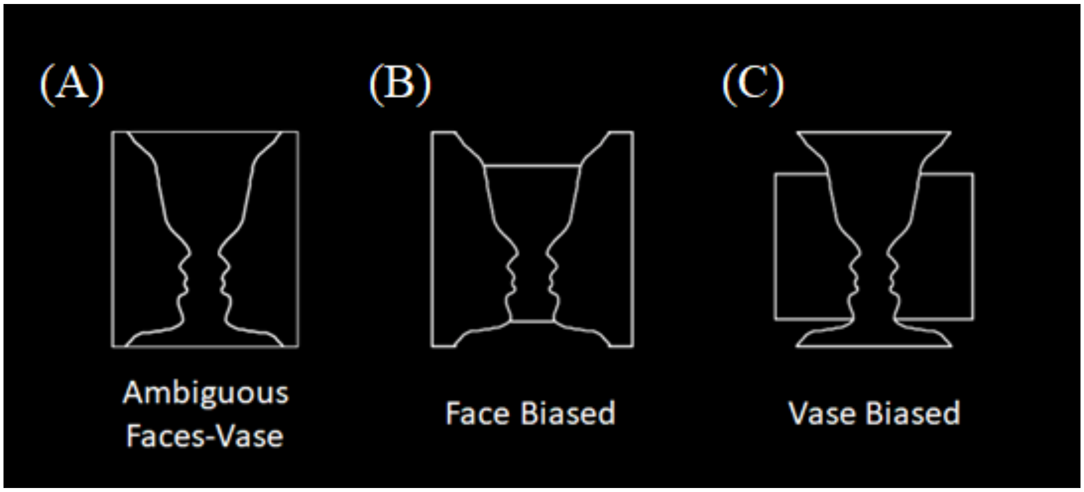


Figure 2.1. Example of the Ambiguous Faces-Vase image (A) with its unambiguous variants (B, C). To create the unambiguous stimuli to show how the edges would belong to one of the figures, we adjusted the ambiguous image to include T-junction partial occlusion cues. These were used as stimuli in our experiments (2 & 3).

There are several theories around what causes the visual input to be organized into figure and ground and in turn what leads to perceptual switches. Early Gestalt psychologists proposed that this organization is based on factors that are stimulus-related (e.g., Rubin, 1915; Kanisza & Gerbino, 1976; Peterson, 2001; Pomerantz & Kubovy, 1986). This means that they suggested that 'configural' properties determined which regions become to figures, without resorting to past experience. These properties included 'convexity, symmetry, small area and enclosure' (e.g., Wagemans et al., 2012a, b; Peterson, 2014). More recent work has found that higher-level properties come into play as well in figure-ground organization such as attention, intention, past experience, competition and feedback (Driver & Baylis, 1996; Hoffman & Richards, 1984; Kienker et al., 1986; Peterson & Gibson, 1994; Peterson et al., 1991). Some have found that the viewer's 'intention' (perceptual set intention) to perceive one side of a border as the ‘figure’ increased the likelihood of that side being reported as a figure (Peterson et al., 1991). Combined with that is the effect of other figure-relevant properties such as fixation. Part of that empirical data also showed that fixated regions are more likely than unfixated regions to be perceived as figures (Peterson & Gibson, 1994). Attention and fixation are often coupled. Research focused on separating and coupling attention and fixation, shows that the attended region is perceived as the figure and that volitionally allocated (fixated) attention can affect figure assignment (Driver & Baylis, 1996; Kienker et al., 1995; Hoffman & Richards, 1984).

2.1.1.2. Necker Lattice.

The other ambiguous stimulus used in our experiments is a variant of the Necker Cube (Necker, 1832), known as the Necker Lattice. As was mentioned previously, the Necker Cube (Necker, 1832) has been widely used in experiments trying to understand the underlying mechanisms involved in visual processing (more specifically perceptual inference). The Necker Cube represents structural perspective reversals (see Figure 2.2A). This 2D figure suggests a 3D object, but the drawing of the Necker Cube also gives contradictory cues for depth perception. The 2D figure is unstable because in the real 3D world, these figures could equally exist in one of two different configurations (see Figures 2.2B&C). This results in perceptual reversals.

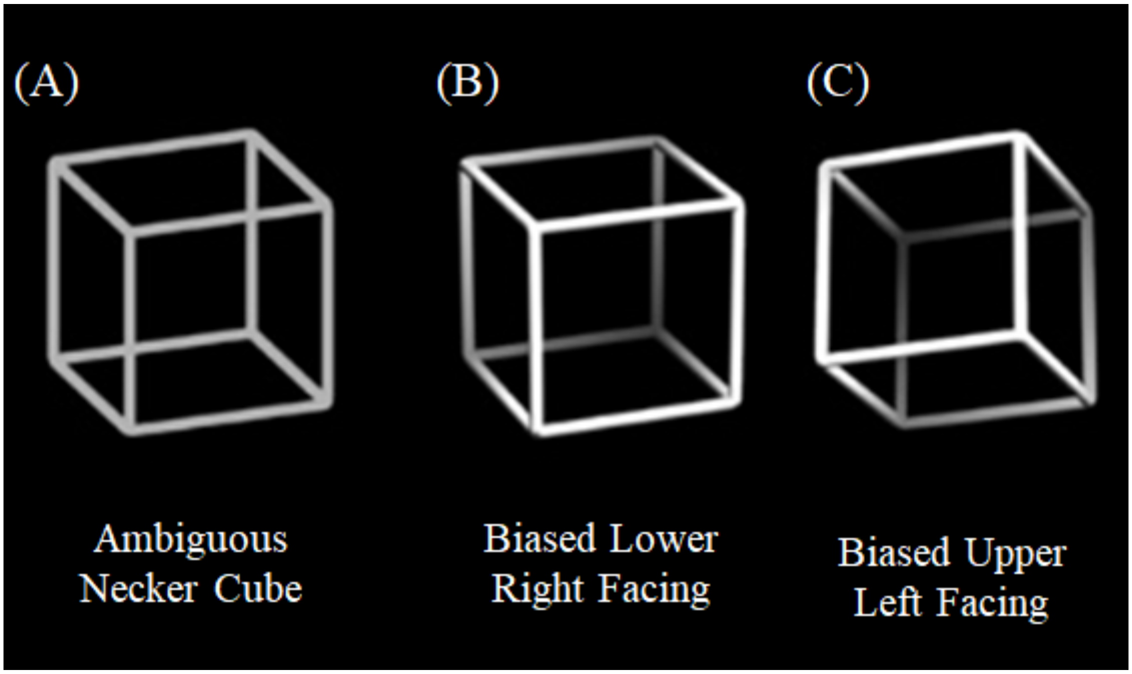


Figure 2.2. Example of the Ambiguous Necker Cube image (A) with its unambiguous variants (B, C).

Our perception of the Necker Cube is sensitive to other sensory information and context. For instance, when depth cues favoring a particular orientation are added to an ambiguous depth figure, like the Necker cube, the perception appropriate to that orientation dominates with a marked decrease in the number of spontaneous reversals (see Figures 2.2B&C). Moreover, as was mentioned previously (see section 1.2.1.1. in Chapter 1), the rate of reversals in Necker Cube perception is influenced by the length of stimulus presentation and the inter-stimulus interval (Orbach et al., 1963; Kornmeier et al., 2002; Kornmeier et al., 2007; Leopold et al., 2002; Maier et al., 2003; Kanai et al., 2005; Noest et al., 2007; Sterzer and Rees, 2008).

In our experiments (Experiment 1 and Experiment 4), we used a variant of the Necker Cube, known as the Necker Lattice. Kornmeier and Bach (2004) used the Necker Lattice in their experiments in order to ‘amplify the Necker-cube effect’. Based on texture segregation experiments (Bach & Meigen, 1992), Kornmeier and Bach (2004, 2012) combined nine Necker Cubes into a ‘Necker Lattice’ (Figure 2.3A) in order to get larger ERP amplitudes. They also created its unambiguous variants (see Figure 2.3B&C). We use these variants in our experiments (Experiments 1&4) in order to replicate some of Kornmeier & Bach’s (2004, 2005) electrophysiological findings and make our results comparable to theirs (Experiments 1&4).

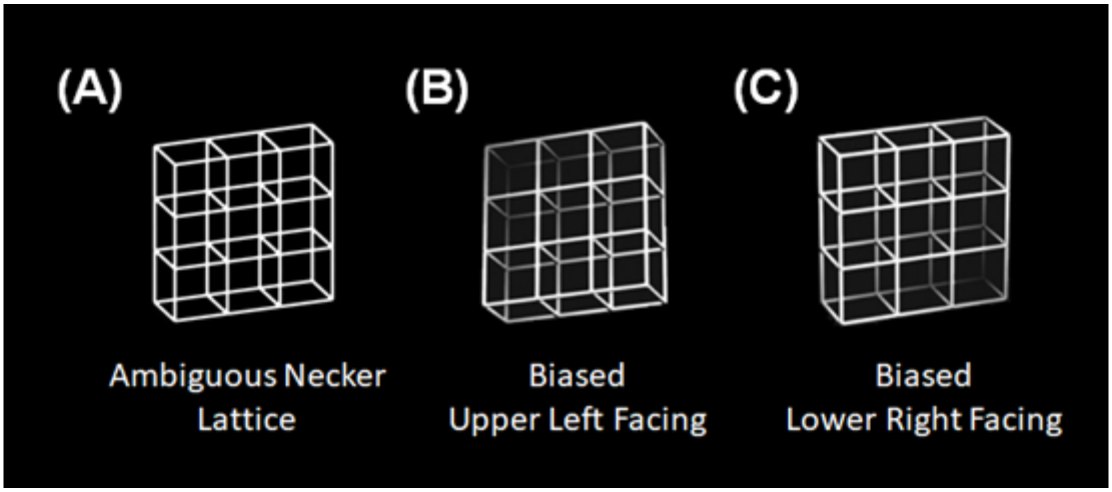


Figure 2.3. Example of the Ambiguous Necker Lattice image (A) with its unambiguous variants (B, C).

Rubin’s Face-Vase and the Necker Cube/Lattice are widely studied figures with a strong literature and clearly established paradigms. Thus, for comparability with previous research and to benefit from established paradigms, we have chosen to use these two stimuli to investigate the underlying mechanisms of ambiguous figure perception. In addition to that, manipulating and maximizing the ambiguity of the stimulus are easy with these two stimuli. For instance, ambiguity of Rubin’s Face-Vase (i.e. obtaining approximately 50% reported face percepts and 50% vase percepts) can be manipulated by varying the distance between the two contours of the faces and by varying the width of the stimulus (this is described in more detail in Chapter 3, section 3.2.1.2.). As was mentioned previously, for the Necker Lattice, size of the stimulus does not have an effect on the rate of reversal or ambiguity of the stimulus (Kornmeier et al., 2011; Toppino, 2003). Therefore we based the size of our stimuli on pre-existing parameters in the literature for compatibility. Moreover, with the help of the existing findings, it is easy to achieve a predictable level of reversals with these two stimuli. As was mentioned previously in Chapter 1, section 1.2.1.1., the rate of reversals of these stimuli can be manipulated by varying the inter-trial interval and stimulus presentation durations (Kornmeier & Bach, 2012; Kornmeier et al., 2007). The inter-trial interval, stimulus presentation durations and experimental paradigm used in our studies will be discussed below in section 2.2.2..

2.2. Manual Response Paradigm vs. Stimulus Onset as Time Reference

Computing an event-related potential (ERP) waveform requires averaging many segments of EEG data associated with the same event of interest. These events can include the presentation of a stimulus, a button press to indicate a response, or any other event that can be linked to a specific moment in time. EEG data around the event is isolated to create a segment for each instance of the event. This typically includes a small pre-event portion of data and the post-event period. These segments are then averaged to create the ERP, which isolates brain activity evoked by the event in the post-stimulus period. Only brain activity that is systematically time-locked to the onset of the event, remains in the average. In contrast, any noise, which is not systematically time-locked to the event, will cancel out in the averaging process.

The event of true interest in most studies of ambiguous perception is the moment of perceptual reversal. However, this is a purely subjective event, which cannot be defined objectively in time. Researchers need an objectively observable event that can be used as a proxy for subjective perceptual reversal. Two major approaches have been developed to resolve the issue about which event should be the focus of time-locking. Some studies have focused on the response button press that participants use to indicate that they have experienced a reversal. This is typically used for studies in which participants are viewing a continuously presented ambiguous stimulus and need to indicate when their perception changes throughout the presentation. Other studies present ambiguous stimuli intermittently (e.g., for 150 ms each) and participants respond after each stimulus. These paradigms often, although not always, time-lock to the onset of the stimulus with the assumption that the reversal occur at or near the moment of stimulus presentation. I will describe paradigms using both approaches and justify why I used time-locking to the stimulus onset in my experiment.

2.2.1. The "Manual Response Paradigm"

In the 'manual response paradigm' an ambiguous stimulus is presented continuously (always appearing on the screen) and participants make a manual response (i.e., button press) when they experience a perceptual reversal. These reversals are then used as a time reference to segment the data. Unlike most ERP analyses which focus on the post-stimulus activity evoked after an event, the data of interest is typically that before the response (i.e., leading up to the reversal).

Studies using this paradigm have found gamma-band power increases and alpha-band power decreases in a time interval approximately 1000 ms before participants' manual response (Isoglu-Alkac, 2000; Struber & Hermann, 2002; Basar-Eroglu et al., 1996; Mathes et al., 2006). These power changes have been interpreted as evidence of a slow bottom-up and top-down cognitive destabilization process underlying perceptual reversals during the active interpretation of the ambiguous stimulus. This means that, in line with the destabilization process of Kornmeier and Bach (2012) defined in Chapter 1, the results from Struber and Hermann (2002)'s study show that the depth of the representation of the perceived motion direction of the SAM stimulus (used in their experiment) slowly becomes shallow to the point of instability of the representation leading to a reversal where the alternative motion direction reaches visual awareness. The observed alpha and gamma activity reflects this visual awareness of the perceived interpretation (Sewards & Sewards, 1999) with the decrease in alpha activity reflecting a passive and automatic process (e.g. neural satiation; Hochberg, 1950) and the increase in gamma activity reflecting top-down processing (e.g. attention; Struber et al., 2000, 2001). In addition to these findings and interpretations, these studies also found that between 500 and 250 ms before manual response, a P300-like parietal positivity ERP occurs. The latter is interpreted as conscious recognition of a perceptual reversal. This implies that there was a change in visual awareness and therefore the reversal event must have taken place earlier (Struber and Herrmann, 2002; Mathes et al., 2006). This was taken as evidence for top-down processes related to the reversal events.

One of the problems with these results is that they incorporate information from a long time window making it difficult to pinpoint the moment at which a perceptual reversal occurs. This paradigm also makes it difficult to identify whether the electrophysiological results observed are linked to the reversal event itself or to response related processes. This means that the information included in that window could be a combination of several factors related to both the stimulus, the reversal event and response. This was shown in a study by Struber et al. (2000) where they analysed the differences in gamma activity between high-reversal rates and low reversal rates. They found that they could not give an exact time course of the gamma activity because of the lack of stimulus onset. They used a non-phase locked approach in order to interpret their results. This is because, using the manual response paradigm makes the interpretation of phase-locked gamma activity in multistable perception difficult. Struber et al. (2000, 2002)'s results showed that the motor response by which the subjects indicated that they experienced a perceptual reversal creates a remarkable jitter due to the variability of the response times both inter and intra-individually. Struber et al. (2002) found that there is a remarkable difference in the morphology of the P300-like component following the exogenous reversal which was dependent on whether the averaging was stimulus-locked or response-locked. This indicated an increased jitter of the perceptual reversal-related activity caused by a 'smearing out' of the cognitive components which is due to the reaction time variability (İşoğlu-Alka et al., 1998). Inter- and intra-individual variability in reaction time decreases the signal quality of perceptual reversal related potentials. This poses a problem for the questions I want to answer in my PhD seeing as I am interested in identifying the time-window both in the pre-stimulus (Experiments 3&4) and post-stimulus (Experiments 1&2) period during which the activity is predictive of perceptual reversals and percept choice (e.g. Face or Vase in Rubin's Face-Vase). Using the manual response paradigm would make it difficult to identify what event the identified components are linked to.

This problem of reaction time variability with the manual response paradigm would make it difficult to address some of the aims of my research. Backward averaging with respect to participant's response obliterates the early visual ERP components whereby the earliest observed component is the P300-like Parietal Positivity. This is due to reaction time variance (Kornmeier & Bach, 2004a, 2012). Kornmeier and Bach (2004a) found a relatively large interquartile range in reaction time which affected the presence of ERP traces when the EEG is backward averaged with respect to participants' response. These traces were sharply defined when the EEG is averaged with respect to stimulus onset. The reversal related components (RP and RN, Kornmeier & Bach, 2004a, 2005) that we are interested in investigating occur before the P300-like Parietal Positivity which, to our knowledge so far, cannot be studied in experiments using the manual response paradigm.

Due to our interest in the time windows during which the patterns of activity are linked to perceptual reversal (Experiments 3 & 4) and our interest in 'early' reversal related components (Experiments 1 & 2), both of which cannot be studied using the manual response paradigm, the Onset Paradigm, with stimulus onset as time reference, is adopted in the experiments we conducted.

2.2.2. Stimulus Onset as Time Reference

Kornmeier, Bach and other collaborators (2004a, 2005, 2006, 2007, 2008, 2010, 2011) in experiments using variants of the Necker Cube (Necker Lattice), have found reversal-related ERP responses earlier than the P300-like parietal positivity found in experiments using the manual response method. In their approach, they used stimulus onset as the event of interest, known as the 'Onset Paradigm'. In this type of paradigm, stimuli are presented intermittently and ERPs are time locked to the stimulus onset. The latter was found to be a more precise time reference of the reversal event than reaction times. The assumption of this method is that stimulus presentation provokes a reversal and thus serves as a good temporal indicator of it.

This paradigm has been found to improve the temporal resolution of the findings on the underlying processes involved in perceptual reversals (e.g. Kornmeier & Bach, 2004a, 2005). Using the Onset Paradigm, Orbach et al. (1963, 1966) suggested that the results from their EEG studies reveal that reversals usually occur near stimulus onset if the presentation time was short enough and if the ISI was long enough.

O’Donnell et al. (1988) were the first researchers to use stimulus onset as time reference to investigate reversal related ERPs. Their experiment had two conditions: endogenous reversals where participants viewed successive intermittent presentations of the ambiguous Necker Cube and exogenous reversals where participants were presented with the unambiguous variants of that stimulus. After each stimulus offset, participants indicated via button press whether or not they experienced a perceptual reversal. O’Donnell et al. (1988) used relatively short presentation times (700ms) and long ISIs (3300ms) and compared reversal trials with non-reversal trials and found a late parietal/frontal positivity for both conditions that is similar to the positivity found with the Manual Response Paradigm (Basar-Eroglu et al., 1996; Struber et al., 2000, 2002).

Using the ‘Onset Paradigm’ has helped researchers identify more ERP signatures and other electrophysiological correlates related to perceptual reversals located in the early visual areas (occipital lobe) and with an earlier latency than the P300 positivity that start in the pre-stimulus period (e.g. Britz et al., 2009; Muller et al., 2005; Ehm et al., 2011; for a detailed review of the electrophysiological correlates identified with perceptual reversals and ambiguous figure perception please refer to the section titled 'Physiological Bases of Ambiguous Stimulus Perception' in Chapter 1)., Among these components are two components that we investigate in two of our experiments (Experiments 1&2): the Reversal Negativity (200-400ms after stimulus onset) and Reversal Positivity (100-200ms after stimulus onset) (Kornmeier & Bach, 2004). These two were not detected in studies using the manual response paradigm for reasons discussed in detail the previous section, whereby the necessary temporal resolution to identify these components is not available (Kornmeier & Bach, 2012).

Although most of the studies using this paradigm or a variant of its original design (e.g. Kornmeier & Bach, 2004a; for the original design see Orbach et al., 1963, 1966 and O'Donnell et al., 1988) suggest that reversals occur near stimulus onset (Kornmeier & Bach, 2004a, 2005; Pitts et al., 2007), other researchers using this paradigm have found frequency modulations in the pre-stimulus period linked to perceptual reversals (Britz et al., 2009; Muller et al., 2005; Ehm et al., 2011). This type of analysis is not possible with the manual response paradigm with its current temporal resolution caused by temporal blurring related to reaction time variability.

As was mentioned previously, I am interested in the spatio-temporal mechanisms underlying perceptual reversals and percept choice in ambiguous figures (Necker Lattice & Face Vase). Therefore, I use an adapted version of the original Onset Paradigm (Orbach et al., 1963, 1966; O'Donnell, 1988) due to its higher temporal resolution compared to the manual response paradigm. This in turn would allow for a more sensitive temporal investigation of the ERP components of interest (Experiments 1&2)

and an investigation of the pre-stimulus period in order to identify a spatio-temporal window during which the pattern of activity is significantly predictive of a perceptual reversal.

2.2.2.1. Intermittent Stimulus Presentation.

The gain in temporal resolution while using this paradigm to study the endogenous reversal process comes at the cost of presenting the stimulus intermittently. This begs the question about whether the findings from studies using this paradigm are applicable to the continuous case. This question is raised because, generally, we do not experience our visual world intermittently but rather in a continuous manner with our brain constantly resolving the instability of the visual information we receive. Moreover, some researchers (e.g. Noest et al., 2007) argue that the existing neural findings of perceptual reversals during continuous viewing of an ambiguous stimulus do not explain why the same percept reappears across trials in a paradigm presenting the ambiguous stimulus intermittently. Noest et al. (2007) recently discussed the neural differences between the reversals occurring during continuous stimulus presentation and during intermittent stimulus presentation. They suggest that the underlying mechanisms differ between the two with the reversals occurring during the intermittent case being a ‘percept choice’ whereas the ones occurring during continuous presentation being a ‘percept switch’ (Guckenheimer & Holmes, 1983). According to Noest et al. (2007), ‘percept choice’ involves complex ambiguity resolution behavior whereby the near-threshold interaction of the competing neural representations is controlled by the timing of stimulus on and off times. This suggests a sort of perceptual decision about the representation of the ambiguous stimulus that is presented intermittently (Kornmeier &

Bach, 2012). ‘Percept switch’, on the other hand, occurs after prolonged stimulus presentation when neural adaptation of the current percept representation has slowly destabilized its own attractor and neural noise will push the system to escape from what is left of the attractor to the other attractor (Noest et al., 2007). This in turn leads to the other percept representation.

Kornmeier and Bach (2012) argue however, that the variation that they applied to the original design of the Onset Paradigm with a shorter ISI and a longer presentation time than the ones used in Orbach et al. (1963, 1966) and O’Donnell et al. (1988)’s experiments may lead to perceptual reversals that involve ‘percept switch’ mechanisms and that the results observed in their studies apply to the continuous case. Orbach et al. (1963, 1966) presented a Necker Cube discontinuously, varied presentation time and ISI and found that reversal rates can be modulated as function of ISI and presentation time. The results of their studies coupled with the results from other studies (e.g. Kornmeier et al., 2007; Kornmeier & Bach, 2012, Leopold et al., 2002; Maier et al., 2003)’s studies suggest that reversal rates are modulated in a non-monotonic manner as a function of ISI, with an increase in reversal rates with ISI up to 400ms after stimulus onset and then a decrease in those rates with further ISI increase. These results show a smooth monotonic decrease in reversal rates similar to the continuous case for shorter ISIs (see Figure 2 in Chapter 1). They also found that continuous stimulus presentation also involves short interruptions due to eye-blinks that lasts about 200ms with a mean frequency of 4s (Caffier et al., 2003).

Previous findings have shown so far that the Onset Paradigm successfully synchronizes endogenous perceptual reversals of ambiguous figures with stimulus onset.

It provides a series of EEG signatures related to endogenous reversals. This paradigm that involves presenting the stimulus intermittently is suitable for the type of analyses conducted in our experiments. These analyses involve exploring the factors that influence the ERP signatures that have been suggested to be reversal related (the RP and the RN – Experiments 1&2) and investigating the pre-stimulus period in order to see if there is a period during which the spatio-temporal profile in that window is predictive of an upcoming perceptual reversal. These involve time-locking events to stimulus onset which in turn means that the paradigm we use in our experiments involves presenting the stimulus intermittently.

Based on the focus and aims of the research, experimenters have used the Onset Paradigm with differing stimulus presentation times and ISIs. For instance, Hesselmann et al. (2008) presented Rubin's Face-Vase stimulus (1915) for a very short period of time (150ms) and had long ISIs (>20s). The reasons for this experimental design are explained in more detail in the next section. This type of experimental design, however, allowed them to explore the pre-stimulus period in more depth and avoided any overlap of effects from the previous stimulus. We use a similar paradigm in two of our experiments (3&4) in order to study the pattern of activity across time (until stimulus onset) in the pre-stimulus time window and see if there is a spatio-temporal profile that is linked to perceptual reversals. As for Kornmeier and Bach (2004a, 2005), their experimental design involved using longer stimulus presentation times (800ms) and shorter ISIs (400 – 1000ms) in order to investigate ERPs that are related to perceptual reversals with the idea that reversals occur at stimulus onset. In order to investigate whether or not these ERPs are dependent on higher level factors (e.g. task or response demands), we used a similar paradigm in our other two experiments (1&2).

2.2.2.1.1. Intermittent Stimulus Presentation: Inter-stimulus interval and presentation times.

I used two different experimental paradigms with different inter-trial intervals and stimulus presentation times in order to investigate both the pre-stimulus and post-stimulus time period. In this subsection, I describe the length of the times chosen for the inter-trial intervals and stimulus presentations in both experiments and the experiments on which they are adopted from.

Post-stimulus analysis focused experiments: Short ISIs and relatively long presentation times (Experiments 1&2).

Experiments 1 and 2 used an adapted version of Kornmeier and Bach (2004)'s experiment with long presentation time (800ms) and relatively short inter-trial interval (400ms when participants don't respond – 1000ms when participants respond). The full experimental design is detailed in Chapter 3.

As was mentioned previously, Kornmeier and Bach (2004a) adopted O'Donnell et al.'s (1988) intermittent stimulus presentation experimental paradigm and modified it. They did this by shortening their ISI in order to be as close to the continuous viewing condition as possible. In an experiment conducted by Kornmeier et al. (2002) where they presented the Necker Cube discontinuously with varying ISIs increasing the ISI from 0ms (continuous observation) to 1200ms, the researchers found that increasing the ISI from 0 to 400ms, more than doubles the reversal rates (Orbach et al., 1963). At longer ISIs these rates decrease to almost 0 (Leopold et al., 2002; Maier et al., 2003).

After any button press however, Kornmeier and Bach (2004a) extended the ISI to 1,000 ms so that stimuli were not compared across intervening manual reactions. The idea behind their design was to make percept and task separable. Moreover, it avoids motor tasks between successive stimuli. In addition to shortening the ISIs, they lengthened the presentation time, long enough to allow the full development of the P300-like positivity and short enough to keep the probability of re-reversals (the occurrence of another reversal during stimulus presentation) low. Using these timings in our experiments (1&2) would yield a sufficient number of both reversal and stable trials for our analyses. This speculation is based on the previous behavioral findings of these experiments where the percentage of reversal trials is high enough to investigate the ERP correlates underlying them (e.g. Kornmeir & Bach, 2004a, 2005; Pitts et al., 2007).

Using this experimental paradigm, Kornmeier and Bach (2004a, 2005) were able to identify two reversal related ERP components, the RN and RP. One of the questions of this thesis is around the nature and underlying mechanisms of these two components and what they can tell us about ambiguous figure perception and perceptual reversals. However, although Kornmeier and Bach (2012) suggested that the RP is a marker of the destabilization process described in Chapter 1, it is unclear what the function role of the RN is and to what extent these two components reveal reversal related processes rather than task or response demand processes. As was mentioned previously, these correlates are sensitive to several factors (stimulus used, length of ISIs and presentation times, number of trials used, etc…). The task typically used to evoke the RN and RP components is what we call the “Reversal Task”. This task involves, on each trial/stimulus, monitoring for whether there was a reversal or not. This has similarities to a change detection task (e.g., Rensink, 2002; Cohen, et al., 2005) in which reversal trials contain a change to detect (relative to the last stimulus) and stable trials do not. Moreover, the RP and RN share a similar timeframe and scalp distribution to other ERP components (e.g. N2b component shows similarities to the RN; Courchesne et al., 1975; Potts, 2004; another component is the Selection Negativity; Anllo-Vento & Hillyard, 1996).

In order to address this, we used an adapted version of Kornmeier and Bach (2004a) and Pitts et al. (2007)'s experimental paradigms and varied response and task requirements. In addition to the reversal task, we introduced a second task called 'Identity Task'. It is a modification of the reversal task paradigm (Kornmeier & Bach, 2004a, 2005; Pitts et al., 2007) where participants were asked to identify which of the two possible interpretations best matched their interpretation of the stimulus (i.e. Experiment 1: Left-Facing or Right-Facing for Necker Lattice; Experiment 2: Faces or Vase for Face-Vase). Moreover, in order to be more time efficient we used a similar paradigm to Pitts et al. (2007) where they presented ambiguous images intermittently and instructed participants to respond after each stimulus presentation about whether or not they experienced a perceptual reversal as opposed to Kornmeier and Bach (2004a) who used a paired-stimulus paradigm in which two ambiguous figures are presented in quick succession and participants indicated after the second stimulus whether they experienced a reversal or stable trial. This allowed us to address the task and response factors using a within-subjects design with a single testing session for each subject. These experiments (1&2) are explained in more detail in Chapter 3. These experiments are designed to answer the ERP related questions of my research and to identify whether or not there is a spatio-temporal profile that is linked to perceptual reversals in the post-stimulus period.

Pre-stimulus analysis focused experiments: Identity Task only, short presentation time and long ISIs (Experiments 3&4).

In order to investigate the pre-stimulus period, we used an experimental paradigm that is adapted from Hesselmann et al. (2008)'s experiment. A brief, sparse, uncued presentation paradigm was employed with unpredictable onsets. Ambiguous stimuli were presented for a short duration of 150ms followed by a 100ms mask of white noise. The long inter-stimulus intervals (ISIs) were drawn from a truncated Poisson distribution with a minimum of 3s and a maximum of 14s. After each stimulus presentation participants were required to report their perception. A detailed description of this experimental paradigm is written in Chapter 5.

Due to the brief presentations, only one percept per trial was possible. Their percept was established through participants' manual responses. Long and sparse ITIs were chosen in order to explore the pre-stimulus period, to maximize the unpredictability of stimulus onset, and therefore minimizing volitional control of perception, obtaining independent responses in successive trials, and minimizing the occurrence of a re-reversal. In previous psychophysical piloting, these settings were found to lead to roughly similar percentages of faces and vase percepts and to prevent perceptual switching within single trials. The purpose of this thesis is to explore the underlying mechanisms of endogenous perceptual reversals. One of the aims is to explore the activity in the pre-stimulus period with regards to endogenous perceptual reversals and ambiguous figure perception. Therefore, we want to minimize the influence of task related activity on the effects measured. This means minimizing the influence of exogenous high-level factors, such as volitional control, on reversal rates is necessary. This is done via the unpredictability of stimulus onset. As was mentioned previously, volitional control has a modulatory effect on perceptual reversals (see section 1.2.2.1. in Chapter 1), rendering these reversals exogenously induced instead of purely endogenous reversals. In addition to that, seeing as we are exploring the activity in the pre-stimulus period with regards to ambiguous figures, we need to avoid any carry-over effects between successive trials. In order to ensure that, independent responses in successive trials are important.

Previously, activity in the pre-stimulus period has been baseline corrected and discarded as unexplained variance when investigating the neural correlates underlying trial-by-trial response variations. However, a growing body of literature has suggested that these variations are linked to spontaneous ongoing fluctuations in the pre-stimulus period (e.g. Coste et al., 2011; Sadaghiani et al., 2010). As was mentioned previously, using a paradigm with long ITIs and short presentation time, Hesselmann et al. (2008) found that prestimulus activity in the FFA was higher when subjects subsequently perceived faces instead of the vase. They suggested that this finding indicates that endogenous variations in activity in the prestimulus time period biased subsequent percept. These findings suggest that ongoing slow activity fluctuations have an impact on how we make up our mind during subsequent perceptual inferences from sensory input.

Ronconi et al. (2017) conducted an experiment using EEG and a different type of analysis (e.g. pattern classification defined in the next section) with a similar paradigm (short presentation times and long ISIs) to study the pre-stimulus activity linked to bistable/multistable perception. They suggest that their findings confirm the notion of the presence of ongoing fluctuations in the pre-stimulus period that biases subsequent perception. They found that there are frequency modulations in the pre-stimulus period that bias subsequent interpretation of the ambiguous stimulus. These modulations occur early on in the pre-stimulus window (~500ms before stimulus onset). They found two significant time windows that are predictive of the upcoming percept in the pre-stimulus period that differed between the two types of ambiguous stimuli they used. Other studies have found frequency modulations that occur at different time windows during the pre-stimulus period as well. For instance, Ehm et al. (2011) found gamma modulations on reversal trials 200ms before stimulus onset. Muller et al. (2005) found changes in EEG activity on reversal trials 300ms before onset. These variations could be due to the different ambiguous stimuli used. However, the common theme in these findings is that they seem to suggest a presence of an unknown intermediate mechanism at later and perhaps even earlier times which are not identified through the analyses conducted and parameters included in these analyses.

Based on these findings, the experimental paradigm used in Experiments 3 (Necker Lattice) and 4 (Face-Vase) is designed in order to investigate a large pre-stimulus window and not the activity occurring during stimulus onset or after it. This would allow to further explore a wider time window than has been investigated in previous studies. It may be that activity is predictive for a long period before reversals rather than just at the moment of presentation.

2.3. Electrophysiological Data Acquisition and Analysis

In order to investigate the underlying neural mechanisms behind participants' behavioral responses, I used EEG in my experiments. EEG provides the necessary temporal precision with a millisecond resolution of the neural processes underlying perceptual reversals. The aims of this research is to explore what factors influence components that are reversal related (Chapter 3) and to identify the spatio-temporal profile of brain activity that is most predictive of perceptual reversals and percept choice in ambiguous figures (Chapters 4 and 5). My studies require a data acquisition system with high temporal resolution in order for me to identify the moment-to-moment variations that are related to perceptual reversals in both the pre and post stimulus periods. Furthermore, some of my questions are related to established ERP markers (e.g., RN and RP; Kornmeier & Bach, 2004a, 2005). Therefore, in order for me identify what factors (if any) influence these ERP correlates (RP and RN), a similar data acquisition system is required to ensure that any potential differences in results observed are due the changes in our experimental paradigms and not because of a change in the temporal resolution (Chapter 3).

2.3.1. Event-Related Potentials (ERPs) Analysis

As was mentioned previously, another aim of this thesis is to explore the factors underlying the RP and the RN (Experiment 1 and Experiment 2 in Chapter 3). These two components have been suggested to be markers of different processing stages of perceptual reversals. However, several factors have been identified that bring into question the nature of these two ERP components. These factors have been shown to influence the latency, amplitude and occurrence of these components. Therefore, in order to investigate the underlying mechanisms of perceptual reversals, we chose to investigate whether these two ERP components are related to perceptual reversal processing or to other factors.

Event related potentials (ERPs) as brain responses to certain cognitive, sensory and motor events, can serve as neural correlates of perceptual processing. ERPs are calculated by trial-averaging stimulus-evoked EEG signals. The ERP technique, according to Luck (2014), is more appropriate for answering some questions than others. Due to their high temporal resolution, ERPs provide a moment-by-moment measure of activity from before the stimulus and extending past the response. Thus, ERPs could help shed light on perceptual dynamics before and after stimulus presentation. Moreover, ERPs help determine which process is influenced by experimental manipulation (Luck, 2014). This means that ERPs can be useful in determining what stage(s) of processing are influenced (or not) by a certain experimental manipulation. The change in latency, amplitude and lateralization of an ERP could be indicative of what brain processes are involved in the experimental paradigm. Moreover, according to Luck (2014), ERP recordings provide a much richer data set, often making it clear that a given experimental manipulation could influence more than one ERP component and that a given pattern of behavior might be caused by different mechanisms in different experiments (e.g. different manipulations of attention influence different ERP components; Luck & Hillyard, 2000; Luck & Vecera, 2002).

For instance, Pitts et al. (2008) compared ERPs associated with voluntary perceptual reversals (i.e. inducing a perceptual reversal while perceiving an ambiguous Necker Lattice) to those associated with involuntary reversals (passively observing the

Necker Lattice) and found differences in the latencies, topographies and amplitudes of these components. Here, the ERP results reveal that although the behavior is the same (experience of perceptual reversals), the underlying mechanisms differ based on the experimental manipulation associated with that behavior (voluntary vs. involuntary reversals). This is not unique to ERP analyses. For instance, an fMRI study by Sterzer & Kleinschmidt (2007) showed an increased activation with endogenous motion reversals in the right inferior frontal cortex but not with the exogenous ones although the behavior observed and reported is the same (i.e. reversals).

The features and characteristics of ERP analyses (although not all unique to ERP analyses) taken together will help us identify what factors influence the changes we might observe in the RP and the RN in our experiments (Experiments 1 & 2). However, we cannot use this type of analysis in order to identify what spatio-temporal profile is most predictive of perceptual reversals and percept choice in ambiguous figure perception.

2.3.1.1. 'What are ERPs bad for?' (Luck, 2014).

As was mentioned previously, the ERP technique is well suited for answering questions of time when the components are time-locked to an event (i.e. stimulus onset). However, it is also bad for answering others (Luck, 2014). The waveforms recorded on the scalp represent the sum of several underlying components making it difficult to decompose this mixture into individual underlying sources (i.e., the superposition problem where multiple components are superimposed onto the same waveform) arising from specific brain areas.

Another limitation of this type of analysis is that some cognitive processes may not have distinct ERP components. This is because ERPs are measurable only when a certain set of criteria are met. For instance, a large number of neurons must be activated at the same time or the individual neurons must have similar orientations (Buzsaki et al., 2012; Luck, 2014). Moreover, to use the ERP technique, it is also necessary to have measurable events that can be used as time-locking points. This is a problem for experimental paradigms where the stimulus is presented in a continuous manner whereby the events are time-locked to response. As was discussed previously, with the current temporal resolution of the manual response paradigm, this type of backward averaging obliterates the presence of ERPs that are identified in experiments using the Onset Paradigm. In addition to that, non-time-locked activity is averaged out and effects that are observed using different methods of analyses (e.g. time-frequency analysis) are not observed in the ERP analyses.

Another limitation of ERPs, which would make it difficult to explore the pre- (Experiments 3 & 4) and post-stimulus (Experiments 1 & 2) activity and answer the questions posed in this thesis is that ERPs involve averaging across trials. This leads to the averaging out of activity that is not strictly time-locked, therefore reducing the ability of the analysis to take advantage of activity in single trials. This means that ERP analyses have reduced information, which may be relevant for explaining the trial-to-trial variations in perception in perceptual reversal paradigms. Moreover, the univariate nature of typical ERP analyses means that activity is typically only considered at a few localized positions on the scalp. For instance, the RN is typically quantified by measuring activity at just a few electrodes on the posterior scalp. Yet, theories of perceptual reversals suggest that mechanisms from across the brain may be involved. If this is the case, then the activity that distinguishes between reversal and stable trials may be better indicated by the pattern of activity across the entire scalp. Alternative analyses are required to investigate this quantitatively. Therefore, in order to address this issue, I apply a different type of analysis known as Multi-Variate Pattern Analysis (MVPA). The latter gives us a way to pick up on broad patterns of activity in raw EEG data and incorporates information about the spatial pattern of activity at each time point during each trial. This preserves activity, which may be lost in ERP analyses.

2.3.2. Multi-Variate Pattern Analysis (MVPA)

Over the last decade, researchers have used multivariate pattern-classification analyses (MVPA) of fMRI BOLD to decode various behavioral and cognitive states (e.g. perceiving, attending to, and imagining features, objects, and scenes) from neural activity (for reviews, see Haynes & Rees, 2006, Haynes, 2015, Naselaris et al., 2011, Norman et al., 2006, Pereira et al., 2009 and Tong & Pratte, 2012). In contrast to univariate approaches that analyse the time course of each voxel independently, MVPA is able to reveal patterns of activity across the entire brain (or smaller ROIs), taking into consideration the activation and deactivation of each voxel. MVPA is comprised of a multitude of methods for analyzing neuroimaging data. The common element that unites these different methods is that they take into consideration the relationship between multiple variables (e.g., voxels in fMRI or channels in MEG/EEG), instead of treating them as independent of one another and measuring relative activation strengths. Previous neuroimaging studies using univariate analyses, have suggested that there are different brain areas that are specialized for different perceptual processes (e.g. Gauthier et al., 1999) and for specific categories of stimuli (e.g. Kanwisher et al., 1997; Hesselmann et al., 2008). For example, a well-documented effect is the higher activation of the FFA in both detection and identification of faces vs. non-face objects (e.g. activation in other regions of the ventral occipitotemporal cortex when perceiving cars; Grill-Spector et al., 2004; Kleinschmidt & Cohen, 2006). However, in a study conducted by Haxby et al. (2001) using a form of multivariate pattern analysis, the results suggest that the representation of faces and different categories of objects are widely distributed and overlapping. In particular, they found that one could decode whether the participant was seeing a face or another category of stimulus even from the pattern of brain activity outside of well-known 'face-specific' regions. Patterns of activity that discriminated among all categories (faces and objects) were found even within cortical regions that have been previously reported as being category specific. Their results suggest that regions such as the PPA (Parahippocampal Place Area) or the FFA are not specific to only spatial arrangements or human faces but, rather, are part of a more extended activation pattern for all categories. The results from Haxby et al. (2001)'s study contrast with the typical univariate analysis, which would not pick up differences based on the activation pattern across voxels but rather the comparisons in the activation levels of individual voxels. The type of analysis conducted by Haxby et al. (2001) is known as decoding. It is the most popular application of MVPA, and the approach that we use in our studies.

The term "decoding" refers to the prediction of an outcome (e.g., stimulus category being viewed; reversal trial or not) based on the pattern of brain activity. Consider a simple experimental design in which the participant viewed images of upright faces and inverted faces while their brain activity was recorded (Figure 2.4A). The goal of the decoding analysis is to test whether we can predict, with above chance (50%) accuracy, whether the participant was viewing an upright face or an inverted one based on the pattern of activity across the brain (in response to the different stimuli/experimental conditions recorded using neuroimaging techniques such as EEG, MEG, fMRI, etc). If the experimental stimuli can be successfully "decoded" from the participant's patterns of brain activation, a conclusion can be made that some information relevant to the experimental manipulation exists in the neuroimaging data (Grootswaggers et al., 2017). For instance, if one can accurately decode whether trials are reversals or not, this suggests that the widespread pattern of brain activity holds information about this process. See Figure 2.4 for an illustration of the decoding approach adapted from Grootswaggers et al. (2017)'s figure (Figure 1, p.679).

Decoding in EEG is typically conducted based on the pattern of activity across the scalp. Importantly, to take advantage of the temporal resolution of EEG, the scalp activity pattern can be decoded at each time point across the trial (Figure 2.4E) to obtain a time-course of prediction accuracy values. Timeframes with above chance decoding accuracy hold information about the condition or stimulus category whereas those time frames with chance accuracy do not. This type of analysis is compatible for answering my research questions on identifying the temporal profile of reversal-related brain activity in the pre-stimulus and post-stimulus periods (Chapters 4&5). Seeing as it incorporates information across all electrodes, I expect that it will reveal reversal-related mechanisms beyond those that have been detected using averaged data with univariate methods. This idea is in line with previous findings by Ronconi et al. (2017). In the study mentioned previously (in Chapter 1), conducted by Ronconi et al. (2017), results showed that the perceptual outcome from bistable stimulus perception could be reliably decoded from the phase of prestimulus oscillations in right parieto-occiptal channels. This type of activity cannot be detected with univariate approaches because the pre-stimulus period is usually flattened due to averaging. Decoding analyses can result in earlier detection of differences in activation patterns (Cauchoix et al., 2012; Cauchoix et al., 2014).

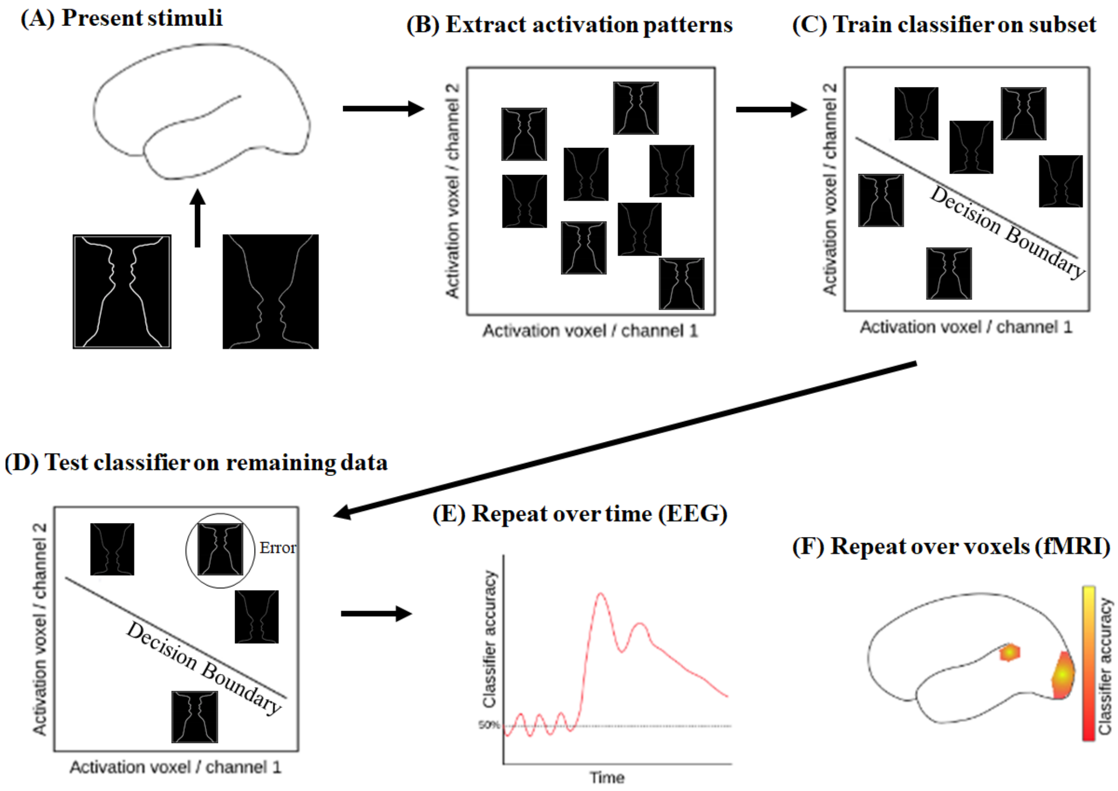


Figure 2.4. An illustration of the decoding approach. (A) Brain responses to participants viewing inverted and upright faces. (B) Patterns of activity evoked by the two stimuli represented in multiple dimension. (C) A classifier is trained on a subset of the data with the aim of discriminating accurately the patterns of activity associated with the different stimuli. (D) Testing the predictions of the trained classifier on the data not used in training to obtain decoding accuracy. This process is repeated (E) across time for EEG data and (F) over regions for fMRI data. This figure was adapted from Grootswager et al. (2017).

Recently, researchers have started applying pattern-classification analyses to electroencephalography (EEG) data (e.g. List et al., 2017; Ronconi et al., 2017). This application to EEG has furthered the findings from the standard ERP analyses. For example, List et al. (2017), using pattern classification, have found that stimulus location and object category can be reliably decoded in the time window between 125-

250ms with a spatio-temporal pattern that mirrored and extended previous ERP findings linked to these to these two types of stimuli. For instance, in one of their results, their topographic maps on faces versus gabors discrimination revealed that this discrimination emerges primarily from the left posterior electrode sites (for most of their participants) with a time frame that is consistent with the N170 component. Moreover, in a second experiment, List et al. (2017) revealed that this type of analysis (MVPA) can decode the scope of attention from EEG data. Their pattern classification analyses identified linear topographies of EEG signals that successfully distinguish, on a trial-by-trial basis, locally-focused vs. globally-focused attention.

Although ERP analyses offer a great deal of information on the underlying mechanisms of perceptual reversals, as indexed by findings in the literature, and would help us identify what factors influence the changes we might observe in the RP and the RN in our experiments (Experiments 1 & 2), there could potentially be effects that are not detected due to the univariate nature of these analyses. This poses a problem for some of the aims of my thesis, seeing as I am setting to explore whether there is any pre-stimulus and post-stimulus activity that has not been identified previously. Experiments 1, 2 (Chapter 4), 3 and 4 (Chapter 5) use MVPA in order to identify the temporal windows in the pre-stimulus (Chapter 5) and post-stimulus (Chapter 4) periods during which the activity and frequency modulations (explained in more detail in Chapter 4 and Chapter 5) are linked to perceptual reversals and to percept choice in ambiguous figure perception. This analysis will help further our (Chapter 3) and previous ERP findings that might not have been able to detect this activity due to the univariate nature of these analyses (Chapter 4). Moreover, they will help us understand the nature of the pre-stimulus activity that has been linked to ambiguous figure perception (Chapters 5).

Chapter 3: Response Dependence of Reversal Related ERP Components in Perception of Ambiguous Figures

The studies in this chapter have been published in Psychophysiology: Abdallah, D., Brooks, J.L. Response dependence of reversal related ERP components in perception of ambiguous figures. *Psychophysiology*. https://doi.org/10.1111/psyp.13685.

3.1. Introduction

The perception of multi-stable or bi-stable visual stimuli (a.k.a., ambiguous or reversible figures) is only temporarily stable and spontaneously fluctuates, or “reverses”, despite no corresponding change in the stimulus information (e.g., Leopold and Logothetis, 1999; Blake and Logothetis, 2002; Schwartz et al., 2012; Cao et al., 2014). Well-known multi-stable stimuli include the Necker Cube (or Necker Lattice version, Figure 3.1A; Necker, 1832) which reverses between facing either left or right and Rubin’s Faces-Vase (Figure 3.1D; Rubin, 1915) which can be seen as either two profile faces or a vase. Perceptual reversals provide a valuable opportunity to dissociate changes in conscious experience from changes in sensory input. Thus, there has been significant interest in studying neural processes related to perceptual reversals (e.g., Kornmeier and Bach, 2004; Kornmeier & Bach, 2012; Hesselmannm et al., 2008; Brascamp, et al., 2018; Lumer & Rees, 1999; Pitts & Britz, 2011).

Because of its relatively high temporal resolution, the event-related potential (ERP) method has been widely used to study the neural correlates of perceptual reversals. For instance, in studies using the “manual response paradigm”, participants continuously view an ambiguous figure and use a button press to indicate when they experience a perceptual reversal. After time-locking ERPs to the manual response, these studies have shown a late (beginning ~300 ms) parietal positivity (e.g., Schiller, 1933; Basar-Eroglu, et al., 1993; Strüber and Herrmann, 2002; Strüber, et al., 2001; Mathes et al.,2006) as well as changes in alpha and gamma band activity associated with perceptual reversals (e.g., Isoglu-Alkaç, et al., 2000; Isoglu-Alkaç and Strüber, 2006; Strüber and Herrmann, 2002). However, because of the high variability in reaction times, the manual response paradigm does not reliably capture early reversal-related ERP components (e.g., Kornmeier and Bach, 2004; Isoglu-Alkaç et al., 1998).

Other studies have employed an “onset paradigm” which involves presenting identical ambiguous stimuli separated by a brief gap (e.g., O’Donnell, et al., 1988; see Kornmeier & Bach, 2012 for a review). Participants then manually report whether their perception of the image reversed from one to the next (i.e., reversal trial) or remained the same (i.e., stable trial). When ERPs are time-locked to the onset of the second image, two posterior reversal-related ERP components appear as differences between the reversal and stable waveforms. These two components have been described previously in section 1.3.2 in Chapter 1. In the following paragraph, the RP and RN will be described again, briefly.

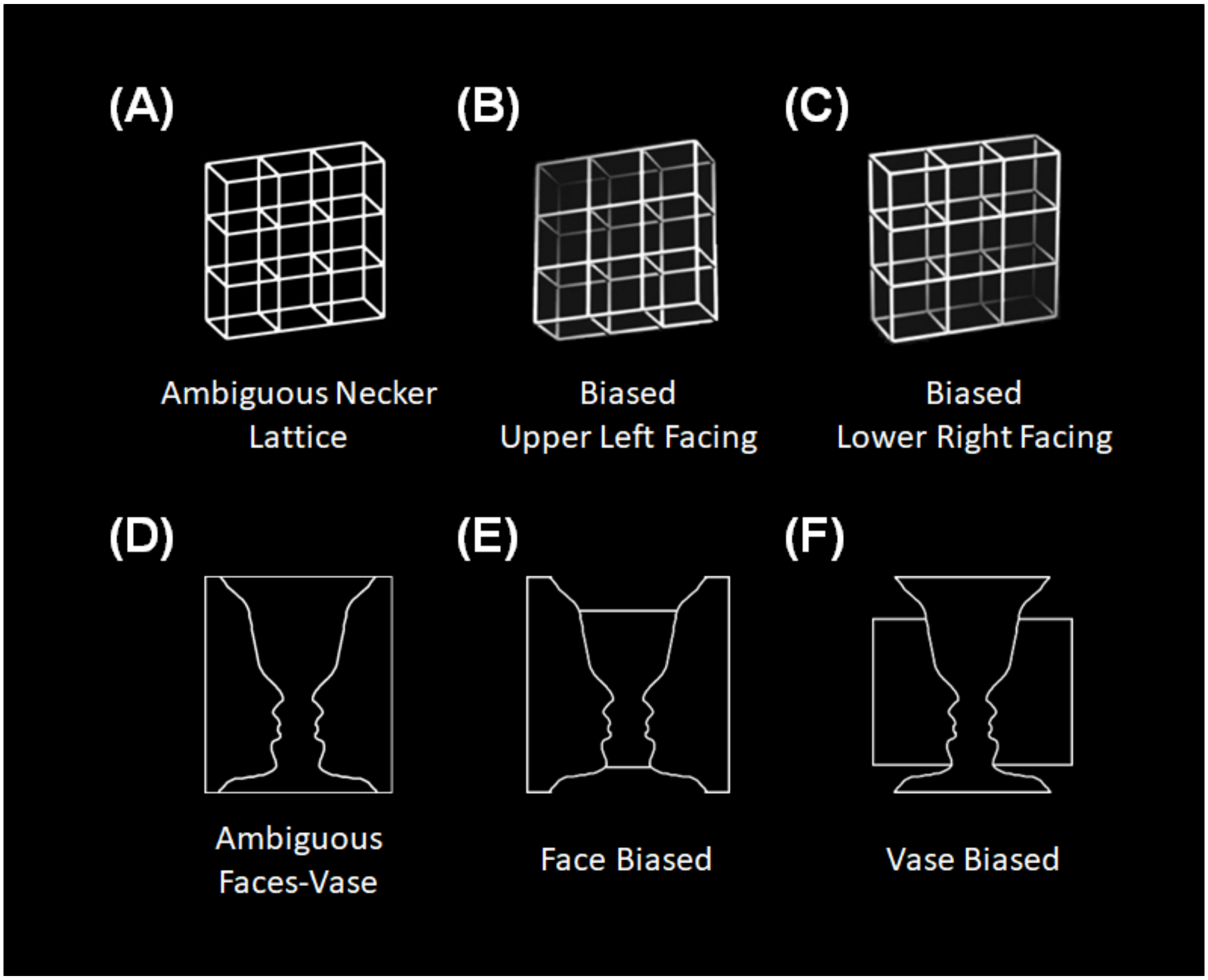


Figure 3.1. Examples of the Necker lattice (A) based on Kornmeier & Bach (2004) and Rubin's Faces-Vase (D) ambiguous figures used in Experiments 1 and 2, respectively. (B) A biased version of the Necker lattice which is typically perceived with its front face towards the upper left. (C) A biased Necker lattice with its front face towards the lower right. (E) A modified faces-vase image biased towards the face interpretation. (F) A faces-vase image biased towards the vase interpretation.

3.1.1. Reversal Positivity (RP)

First, the reversal positivity (RP; Kornmeier & Bach, 2005; 2006; Kornmeier, et al., 2007; Britz, et al., 2009) appears approximately 130 ms after stimulus onset as a more positive amplitude on reversal trials than on stable trials at, primarily, occipital electrode positions. The RP has been found for a range of multi-stable stimuli including the Necker Lattice (e.g., Kornmeier & Bach, 2005, 2006), the Necker cube (e.g., Kornmeier, Pfäffle, & Bach, 2011), Boring's Old/Young Woman (Kornmeier & Bach, 2014), and during binocular rivalry (e.g., Britz and Pitts, 2011). Importantly, the RP is present only for endogenous reversals (i.e., a change in perception without corresponding stimulus change) and not for exogenous reversals (i.e., two different unambiguous stimuli in sequence). This suggests that the RP may be specifically linked to processes of internally-generated perceptual reversals rather than reversals due to changes in sensory input. Furthermore, the RP appears to be insensitive to low-level stimulus differences such as size (e.g., Kornmeier et al., 2011). However, perhaps because of its small amplitude, the RP has not been observed universally across studies (e.g., Pitts, et al., 2007; Intaitė, et al., 2010). Kornmeier and Bach (2012) have suggested that the RP is a marker of perceptual ambiguity detection or perceptual decision conflict that occurs only on reversal trials when perception is changing from one interpretation to another (Kornmeier et al., 2011).

Britz and Pitts (2011) conducted an experiment with the focus of investigating whether the ERP components found in experiments studying ambiguous figure reversals are found in experiments studying binocular rivalry reversals. They also investigated what brain regions may be more or less active during perceptual reversals compared to perceptual stability. They combined spatiotemporal ERP analysis with source imaging and statistical parametric mapping of the source differences between reversals and stability. They found that the RP is the result of modulation in GFP strengths of the P1 component. They found that the RP shows the same topography in the reversal and stable conditions, and that the topography of these two conditions during the latency of the RP is the same as the P1 component. However, Kornmeier et al. (2011) found that the RP and P1 components are different. In an experiment studying the relationship between these two components, they found that the P1 amplitude increases monotonically with an increase in the size of the Necker Cube independently of the participants' reported percepts (reversal vs. stability) whereas the RP is percept-related and unaffected by stimulus size. They suggested that the P1 reflects processing of stimulus-related features, while the RP, as was mentioned previously, is related to a processing conflict that precedes a reversal representing the detection of ambiguity.

3.1.2. Reversal Negativity (RN)

A second reversal-related component, the reversal negativity (RN), appears approximately 260 ms post-stimulus and has been observed with a range of ambiguous stimuli (e.g., Kornmeier & Bach, 2004; 2005; Pitts, et al., 2007, 2008; Britz, et al., 2009; Intaite, et al., 2010). The RN is opposite in polarity to the RP with reversal trials having more negative amplitudes than stable trials in mostly occipital/parietal locations. However, the latency, duration, and spatial distribution of the RN can be sensitive to the length of the response interval (see Kornmeier & Bach, 2012 for review) suggesting that it can be modulated by strategic, non-perceptual factors. The functional role of the RN is still unclear.

Some work has dissociated the RN from attention-related ERP components such as the N2pc. For instance, in an experiment conducted by Intaite et al. (2010) comparing ERPs in response to endogenous and exogenous reversals of two Necker lattices, the results suggested that the RN neither resembled the attention-related N2pc response. They found that the attention-related N2pc component (Eimer, 1996) was only present for exogenous presumably because the visual transients involved in changing stimuli caused shifts of attention. In contrast, endogenous reversals, although reported by the participants, showed no significant N2pc component. Only a significant RN component was observed for endogenous reversals. Moreover, the RN had a different topography than the N2pc and was elicited over a larger area (occipital, temporal, parietal, central and frontal electrodes).

Kornmeier and Bach (2006) found that the RN was present for exogenous reversals (i.e. stimulus-induced reversals) as well as endogenous ones. Therefore, the RN cannot be solely linked to endogenous perceptual reversals. In their experiment, Kornmeier and Bach (2006) presented the unambiguous variants of the Necker Lattice (Figure 3.1B-C) intermittently in one experiment (inducing exogenous reversals) and the ambiguous Necker Lattice (Figure 3.1A) intermittently in another experiment (endogenous reversals). They found that the RN was present in both experiments. Kornmeier and Bach (2006) suggest that due to the presence of this component in both types of reversals, that the component reflects neural processes underlying a ‘Gestalt reconstruction’ in the case of reversals compared to stability, where no reconstruction is necessary. Moreover, there is debate about whether the RN reflects higher-level, top-down influences over perceptual reversals (e.g., Pitts et al., 2008). For instance, an experiment by Pitts et al. (2008) showed that the amplitude of the RN increased when participants voluntarily controlled reversals compared to passive reversals of the Necker Lattice.

3.1.3. Sensitivity of the RP and RN

As was mentioned previously, several experiments have shown that the RP and RN are sensitive to certain factors. This sensitivity, in some cases, leads to the absence of the component or differences in the spatial distribution and/or amplitude of these components. For instance, the RP was not found in Pitts et al. (2007)'s experiment using Rubin's Face Vase, Schroder's Staircase and Lemmo's Cheetah. Kornmeier and Bach (2012) suggested that the absence of that effect is due to the very small amplitude of the RP and the small number of trials per condition in Pitts et al. (2007)'s experiment. Moreover, in a study conducted in order to understand the functional role of the RP where the experimenters varied the dimensions of the stimulus, Kornmeier, Pfaffle and Bach (2011) found that it is largely unaffected by cube size and is only related to perceptual reversals.. According to Kornmeier, Pfaffle and Bach (2011), this finding indicates that higher-level processing (related to the RP) is taking place. This is due to the RP only being present for endogenous reversals and to insensitivity to physical changes in the ambiguous stimulus.

As for the RN, Kornmeier and Bach (2014) found that it was not present in a study using Boring's Old-Young woman stimulus and found a shift in its location from a predominantly parietal-occipital distribution to a temporal one, in a previous study using that same stimulus (2004a). This location shift of the RN is also present for Rubin's Face-Vase (Pitts et al., 2007) with a spatial lateralization of this component to the left. However, the RN has a bilateral distribution in experiments using Schroder's Staircase (Pitts et al., 2007) and the Necker Lattice (2004). Pitts, Gavin & Nerger (2008) also found in their experiment on volitional control, an earlier onset of the RN and an increase in its amplitude. Moreover, these components are obliterated in experiments using the Manual Response Paradigm. This could be due to the variance in reaction times (Kornmeier & Bach, 2012). This shows that there are several factors that come into play with regards to the RP and the RN. Therefore, in order to further understand the underlying mechanisms of perceptual reversals, we must understand the processes underlying these two components.

3.1.4. Reversal Task

The task typically used to evoke the RN and RP components is what we call the "Reversal Task". This task involves, on each trial/stimulus, monitoring for whether there was a reversal or not. This has similarities to a change detection task (e.g., Rensink, 2002; Cohen, et al., 2005) in which reversal trials contain a change to detect and stable trials do not. Furthermore, in many RP and RN studies, behavioural results show that reversal trials are substantially less prevalent than stable stimuli (~ 30 vs 70%, respectively; e.g., Kornmeier & Bach, 2004; Pitts et al., 2007). Thus, in terms of the task, reversal trials could be seen as relatively rare, task-relevant targets in a stream of more prevalent non-target stable trials. ERP studies have shown that rare visual oddball events can elicit more negative amplitudes for rare targets compared to standard stimuli within a timeframe and scalp distribution similar to that of the RN (N2b component; e.g., Potts, 2004; Courchesne, Hillyard, & Galambos, 1975). Furthermore, in a change detection task, visual awareness of a change has been associated with a posterior negative amplitude enhancement, similar to the RN, on trials with detected changes (Pazo-Álvarez, et al., 2017). Thus, it is possible that RN effects, when assessed using the reversal task, could be related to visual oddball target detection processes rather than perceptual reversal processes as is generally assumed.

Some authors (e.g., Pitts, Nerger, & Davis, 2007; Kornmeier & Bach, 2012; Kornmeier and Bach, 2004) have also highlighted similarities and potential equivalence between the RN and the Selection Negativity (SN) ERP component (e.g., Anllo-Vento & Hillyard, 1996). The SN appears as greater negative amplitudes on trials with attended features (e.g., reversals) compared to those with unattended features (e.g., stable trials). If reversal trials attract attention because of their task relevance whereas stable trials do not, then they could evoke an SN. In this account, the RN would be linked to general feature selection mechanisms instead of specifically to processes involved in perceptual reversal.

3.1.5. Identity Task

To investigate whether the RN and RP depend on task demands and target status as described above, we modified the reversal task paradigm used by others (e.g., Kornmeir & Bach, 2004; Pitts, Nerger, & Davis, 2007) to create the “Identity Task”. In our version of this task, participants observed a continuous sequence of 800 ms long intermittently presented ambiguous stimuli (Necker Lattice or Rubin’s Faces-Vase; Figures 3.1 & 3.2). For each stimulus, participants were asked to respond when their perception of the stimulus matched one particular target identity (e.g., respond on face trials only). The target category was varied over blocks. Importantly, although participants did not report when they experienced reversals in this task, each trial can be reclassified by the experimenter as a reversal or stable trial based on the sequence of responses (e.g., face percept preceded by vase percept = reversal trial; see Figure 3.2B below). This means that, although reversal trials are being collected, the distinction between reversal and stability trials was task irrelevant for participants and any task demand differences between reversal and stability trials should be minimised. For instance, reversals will not be explicit response targets in this task and, although reversals may end up being more rare than stability trials, their relative rarity will be less noticeable. Under these conditions, it will be difficult to attribute any brain activity differences between reversal and stability trials (such as the RN and RP components) to task or response differences. This should allow the identity task to more purely isolate perceptual processing differences between reversal and stable trials. To determine whether this change in task demands affected RN and RP amplitude, we had participants do the identity task in half of the blocks of each experiment and the reversal task in the other half.

A version of the identity task has been used in other experiments related to perceptual reversals (e.g. Hesselmann et al., 2008). However, in these studies, the focus has been identifying how activity differs between the different identities rather than on differences between reversal and stability trials. For instance, Hesselmann et al. (2007) focused on identifying differences between trials seen as faces and those seen as vases. This does not isolate activity linked to reversals but rather to the identity of the perceptual outcome of the reversal. Although interesting, this is different from the question that we are asking here about perceptual reversals specifically.

In order to determine if the RN and RP are also affected by whether reversal trials are targets for response, we varied the response style across blocks. In half of the reversal task blocks, participants responded only when they perceived a reversal and withheld response on stable trials whereas in the other half of blocks they adopted the opposite response style (e.g., Kornmeier & Bach, 2004). For the identity task, participants were instructed to respond only to one identity (e.g., faces) in half of the blocks and respond only to the other identity (e.g., vase) in the other half of the blocks. This means that we were able to observe trials with all combinations of trial type (reversal vs. stable) and response action (responded vs. no response) in both reversal and identity tasks. With this design we were able to compute the RN and RP when both types of trials were response targets (i.e., reversal, responded and stable, responded) and when both were not response targets (i.e., reversal, no response and stable, no response). This ensures that the reversal vs. stable trial comparisons, which are used to compute the RN, are not confounded by differences in response demands. Furthermore, we were able to determine whether the task demands also affect RN and RP amplitude. See Figure 3.2B below for an example of how the trials were coded based on a sequence of responses (respond or not) with the participants' subjective perception of the stimulus.

Based on the previous findings in the literature which show the RP and RN occur for various ambiguous figures, we, firstly, expected the results from both experiments (Experiment 1: Necker Lattice and Experiment 2: Face-Vase) to be the same. Furthermore, we expected to measure the RN and RP componentsonly in the reversal task, in which the distinction between reversals and stability was clearly task relevant,and not the identity task in which we argue this distinction is less task relevant.However, we did not expect that response action will have any influence on these two components seeing as previous studies (e.g. Kornmeier & Bach, 2004a; Pitts et al., 2007) suggest that response (response vs. non-response) does not influence the presence of these two components. Nonetheless, we planned to test for this because it has not been systematically explored in some previous studies.

3.2. Experiment 1: Necker Lattice

3.2.1. Methods

3.2.1.1. Participants.

Twenty-five (17 female, 8 male) undergraduate psychology students were recruited from Keele University's Psychology Research Participation Time scheme and received partial course credit for participation. Participants had a mean age of 21.8 years (range: 18 to 48 years). All participants had normal or corrected-to-normal visual acuity (average 0.001 logMAR; Precision Vision Logarithmic ETDRS 2000 chart). Eight (of 25) participants were excluded from the analysis. Six of these were based on a priori exclusion criteria (see data analysis methods below). One exclusion was due to a participant becoming unwell and another was due to experimenter error resulting in data loss. The University Ethics Review Panel at Keele University and the Psychology Ethics Committee at the University of Kent approved this study. All participants gave informed consent ahead of participation.

It is important to note that the number of participants chosen for this experiment was based on the sample sizes of experiments conducted in previous EEG studies investigating the RN and the RP (e.g. Kornmeier & Bach, 2004 used 16 participants; Kornmeier & Bach, 2005 used 21 participants; Pitts et al., 2007 used 21 participants).

3.2.1.2. Stimuli & Apparatus.

We used one ambiguous (Figure 3.1A) and two unambiguous versions of the Necker Lattice (Figure 1B-C; Necker, 1832; Kornmeier & Bach, 2004) as the visual stimuli in this study. All stimuli were presented centrally on a black background using a 24.5 inch BenQ Zowie XL2540 computer monitor at 120 Hz refresh rate and 1920 x 1080 pixels resolution. All stimuli were 5.52° x 5.52° and the maximum luminance of white portions was 373.43 cd/m2 (CIE1931: x = 0.326, y = 0.325). Viewing distance was maintained at 57 cm using a chin rest. The experiment was controlled by PsychoPy2 V1.82.01 (Peirce, 2009). A 0.503° white cross at the centre of the screen served as fixation target ahead of and during stimulus presentation. Participant responses were recorded via a computer keyboard using the up arrow key.

3.2.1.3. EEG and Eye-Tracker Recordings.

EEG scalp voltages were recorded at 1024 Hz using a 24 bit DC-coupled Biosemi ActiveTwo System (Biosemi; Amsterdam, Netherlands) with 64 Ag-AgCl active electrodes on the scalp. Low pass filtering was performed in the Analogue-to-Digital Converter's decimation filter which has a 5th order sinc response with a -3 dB point at 1/5th of the sample rate. Participants wore a cloth cap with 64 10-10 system electrode positions. Three other electrodes were used to measure right and left horizontal electro-oculogram (HEOG; just lateral to canthi) and vertical electro-oculogram (VEOG; 2 cm below the left eye). SignaGel (Parker Labs; https://www.parkerlabs.com/) was used as an electrolyte. Face electrode locations were prepared with an isopropyl alcohol wipe. All electrodes were adjusted to have offsets within a range of -10 to 10 mV of the common mode voltage. The Biosemi system does not require electrode impedance checks. Data were recorded relative to the CMS/DRL circuit and re-referenced offline (see data analysis methods below).

Eye fixation position was recorded at 60 Hz (monocular; left eye) using a LiveTrack Fixation Monitor (Cambridge Research Systems Ltd.; Rochester, UK; https://www.crsltd.com/). Calibration was conducted with nine targets arranged in three rows and three columns separated by 14.0025° horizontally and 7.5281° vertically with the central target at the centre of the screen. Eye-tracker data was collected as an additional precautionary step to ensure that participants were fixated at the fixation cross. However, due to time constraints, no analyses on the eye-tracking data were conducted. It is important to note that the experimenters emphasized during the instructions that participants were required to keep their eyes fixated on the fixation cross at the centre of the screen. Furthermore, in order to ensure that participants were following these instructions, the experimenter was observing the participant's eyes with a camera focused on them throughout the experiment.

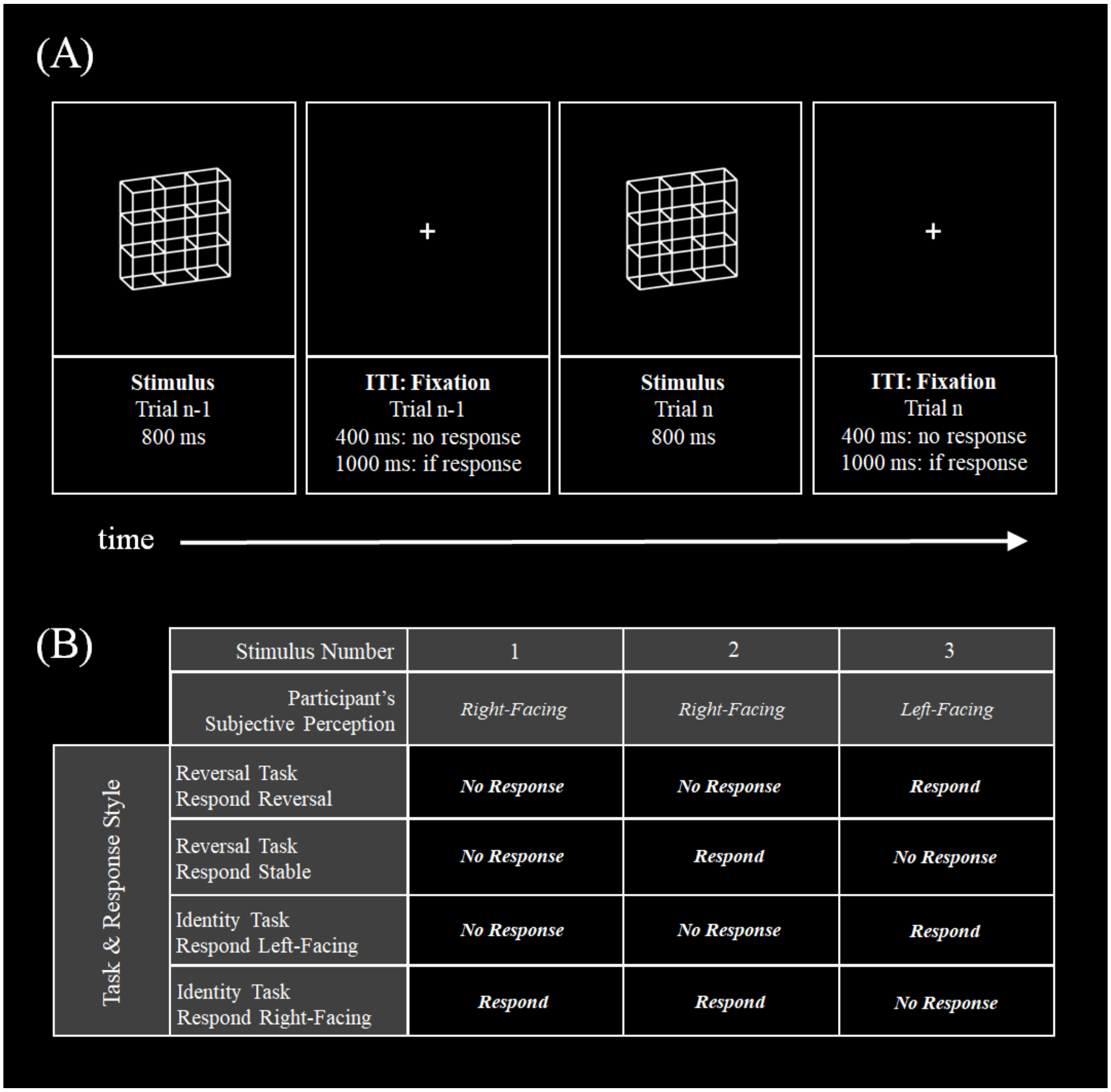
3.2.1.4. Procedure.

During the instructions, the experimenter ensured that each participant was able to distinguish the two interpretations of the Necker Lattice and explained that although the same picture would be presented repeatedly, they may perceive it differently on different trials. While the experimenters prepared the EEG cap, participants completed a practice test comprising eight blocks with 28 trials per block (8 unambiguous). The practice session included both the reversal and identity tasks (described below). After the practice trials, the experimenter calibrated the eyetracker and then the main experiment began.

Each stimulus was presented binocularly for 800 ms followed by an ITI of 400 ms. This ITI was extended to 1000 ms if participants responded at any point during the 1200 ms (stimulus plus ITI) trial period (Figure 3.2). Within each block, approximately 90% of the trials contained the ambiguous Necker Lattice (Figure 3.1A) and the remaining ~10% contained unambiguous stimuli (Figure 3.1B-C; half right-facing). Unambiguous stimuli were presented in either "stable" pairs (i.e., right-facing then right facing or left-facing then left-facing) or "reversal" pairs (i.e., right-facing then left-facing or left-facing then right-facing). Stable and reversal pairs occurred equally often. The unambiguous pairs appeared randomly throughout the sequence of ambiguous stimuli.

There were eight blocks of 150 trials each (4-5 minutes). Participants completed one of two different tasks in each block. In the reversal task blocks, participants determined for each stimulus whether their perception matched (stable trial) or did not match (reversal trial) that of the immediately preceding stimulus. In contrast, in the identity task blocks, participants determined their perception of each Necker lattice stimulus (i.e., front facing left or front facing right) without reference to the preceding stimulus. The reversal task was required in half (four) of the blocks and the identity task in the other half. The experimenter explained these tasks during the instructions period and the computer clearly indicated which task to complete before each block began.

Blocks also differed in the response style. For two of the four reversal task blocks, participants adopted a respond-to-reversals response style. This means that they only pressed a button on trials in which they experienced a reversal. They did not respond at all if their perception of the stimulus was the same as that of the previous stimulus (i.e., stable). For the other two reversal task blocks, participants adopted a respond-to-stable response style. This means that they only responded if their perception of the stimulus was the same as that of the preceding stimulus. They did not respond if there was a reversal in their perception. For identity task blocks, participants adopted a respond-to-left-facing response style for two of the four blocks and a respond-to-right-facing response style for the other two blocks. Thus, across the eight blocks of the experiment, there were four types of blocks: reversal task, respond-to-reversal; reversal task, respond-to-stability; identity task, respond-to-left-facing; and identity task, respond-to-right-facing. Each participant had a different random order of these block types. Participants were given clear on-screen instructions about the response style at the beginning of each block and performance on unambiguous trials was monitored to ensure compliance (see next subsection).



	Stimulus Number	1	2	3
	Participant's Subjective Perception	*Right-Facing*	*Right-Facing*	*Left-Facing*
Task & Response Style	Reversal Task Respond Reversal	***No Response***	***No Response***	***Respond***
	Reversal Task Respond Stable	***No Response***	***Respond***	***No Response***
	Identity Task Respond Left-Facing	***No Response***	***No Response***	***Respond***
	Identity Task Respond Right-Facing	***Respond***	***Respond***	***No Response***

Figure 3.2. (A) The order of trial events in Experiment 1. Intermittent Necker Lattices were presented for 800 ms and separated by an ITI fixation cross of either 400 ms, if no response was made to the stimulus within 1200 ms of stimulus onset. The ITI fixation cross lasted 1000 ms if a response was made with 1200 ms of stimulus onset. Only ambiguous stimuli are shown in this example. (B) Each row (black background) of this table shows a sequence of correct responses (respond or not) for three stimuli given the task and response style condition (different rows) and the participant's subjective perception of the ambiguous stimulus (different columns). In reversal task trials, the participant's response depended on their perception of both a given stimulus and the one that precedes it.

3.2.2. Data Analysis Methods

EEG recordings were manually checked for artefacts from eye movements and an ocular correction independent components analysis was performed in order to help identify eye blinks and amplitude excursions exceeding ±100 mV and high-pass filtered offline at 0.1 Hz. On average, 2.86% (range: 0-4.95%) of trials were excluded due to these criteria. Data were referenced to the Cz electrode offline.

Each trial was coded as either a reversal trial or a stable trial by considering whether there was a response on that trial and which block type it was in. For instance, in a reversal task block with respond-to-reversals response style, a trial would be marked as a reversal trial if there was a response during the trial and would be marked as a stable trial if there was no response. In identity task blocks, a trial would be marked as a reversal if there was a response on the trial but not on the trial before it or vice versa. If a trial had a response and the one before it did as well or both trials had no response, then this was marked as a stable trial. Once all trials were labelled then they were segmented into 1200 ms epochs (-100 to 1100 ms) and sorted into eight conditions. These eight conditions were the combinations of three factors: task (reversal task or identity task), trial type (reversal trial or stable trial), and response action (responded or not) on the trial. All epochs were baseline corrected based with the average amplitude from -100 to 0 ms and then averaged within each condition to form ERPs. ERPs were digitally filtered with a 25 Hz low-pass filter and averaged across participants to create grand average waveforms. Epochs for unambiguous trials were discarded because there were too few for analysis and they are not relevant to the questions of this paper.

Based on our a priori behavioural exclusion criteria (less than 70% correct on the unambiguous trials), no participants were excluded. This indicates that they correctly followed the response style and task instructions for each block. In addition, in order for a participant's data to be included in further analyses, at least 25 non-discarded trials per condition were required. Six participants were excluded because of the low number of non-discarded trials per trial type. The low number of trials for these participants was due to a combination of our EEG artefact rejection criteria and the participant's response pattern (i.e., too few reversal trials).

In line with the analysis steps of previous experiments (Kornmeier & Bach, 2004; Pitts, Nerger & Davis, 2007), we quantified the RN ERP component with a region-of-interest (ROI) of 200-400ms in channels O1, O2, Oz, PO7, and PO8. The ROI for the RP component was 100-200 ms in channels O1, O2, and Oz. Average amplitude was calculated separately for each channel within these temporal ROIs for each participant and condition. Results were submitted to two separate (one for RP and one for RN) repeated measures ANOVAs (5x2x2x2 for RN; 3x2x2x2 for RP) with Channel, Task (Reversal vs. Identity), Trial Type (Reversal vs. Stability) and Response Action (Response vs Non-Response) as factors.

3.2.3. Results

3.2.3.1. Response time.

For ambiguous stimulus trials, participants responded, on average, 676 ms (range = 570-760 ms) after stimulus onset. A 2x2 Repeated Measures ANOVA found no significant effect of Task or Trial Type for response times (RTs), *p* >. 208. However, there was a significant interaction between Task and Trial Type, *F*(1,16) = 15.40, *p* =

.001, $\eta_p^2 = .490$. This crossover interaction was examined by testing the simple effects of trial type in each task. In the reversal task, RTs for stable trials, *M* = 670 ms (*SE* = 13), were significantly faster than those for reversal trials, *M* = 700 ms (*SE* = 15), *t*(16)= 2.89, *p* = .011. In contrast, for the identity task, RTs for reversal trials, *M* = 642 ms (*SE* = 23), were faster than those for stable trials, *M* = 692 ms (*SE* = 13.5), *t*(16)= -2.49, *p* = .024. We also assessed the interaction by testing the simple effects of task in each trial type. There was a significant difference in mean RT between the Reversal and Identity Tasks on reversal trials, *t*(16) = 2.92, *p* = 0.01 whereby participants indicated a faster reversal response in the Identity Task than in the Reversal Task (same means as above). There was however no difference in mean RTs between the Reversal and Identity Tasks on stable trials, *t*(16) = -1.53, *p* = .146. See Table 3.1 for response times (in ms) across task and trial type. Corresponding analyses were not conducted for the unambiguous stimuli because there were too few trials. Mean RTs did not differ between left-facing (M = 682 ms, SE = 20) and right-facing (M = 670 ms, SE = 15) response trials in the identity task blocks, *t*(16) = .727, *p* = .478. See Table 3.2 for mean response times for the two different identities in the identity task.

Table 3.1.

Necker Lattice: Response Times (in milliseconds) across Task and Trial Type

		Mean (ms)	SE
Task	Reversal	691	15
	Identity	673	15
Trial Type	Reversal	676	16
	Stability	688	11
Task x Trial Type	Reversal x Reversal	706	13
	Reversal x Stability	675	15
	Identity x Reversal	647	24
	Identity x Stability	700	11

Table 3.2.

Necker Lattice: Mean Response Time (in ms) of the two Trial Types in the Identity Task

	Mean Response Time (ms)	SE
Left-Facing Response Trials in Identity Task	688	20
Right-Facing Response Trials in Identity Task	677	15

3.2.3.2. Unambiguous Lattices.

Across both the identity and reversal tasks, participants correctly responded to 85.95% (SE = 1.74) of the unambiguous lattice pairs. This is significantly greater than chance performance, *t*(16) = 20.64, *p* <.001. In the identity task, participants had above chance orientation discrimination accuracy, 90.72% (SE= 1.70), *t*(16) = 23.99, *p* <.001. In this task, there was a correct answer for every trial. This means that the responses to both stimuli that appeared sequentially were included in our calculations. In the Reversal Task, participants had above chance reversal detection accuracy, 76.72% (SE = 3.32), *t*(16) = 8.05, *p* <.001. As participants compared the second image to the preceding one in this task, there was only one correct answer per unambiguous pair.

3.2.3.3. Ambiguous Lattices.

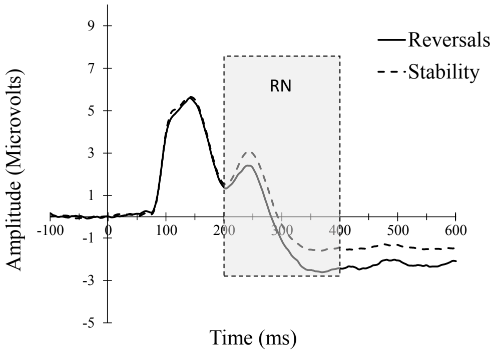
In the Reversal Task, 33.66% of trials, on average, were classified as reversal trials (66.34% stable). In the Identity Task, on average, 32.03% of trials were reversals (67.97% stable). There was not a significant difference between the percentage of reversals in the Reversal and Identity Tasks, *t*(16) = .679, *p* = .507. In the Identity Task only, 57.03% (SD = 8.22%) of trials were reported as right-facing lattices (42.97% left-facing). A one sample t-test revealed that the percentage of right-facing trials reported is significantly greater than 50%, *t*(16) = 3.526, *p* = .003. Our results are consistent with previous studies which have found that participants have a bias for right-facing perception (Sundareswara & Schrater, 2008; Kornmeier et al., 2009; Troje & McAdam, 2010).

3.2.3.4. Electrophysiological results.

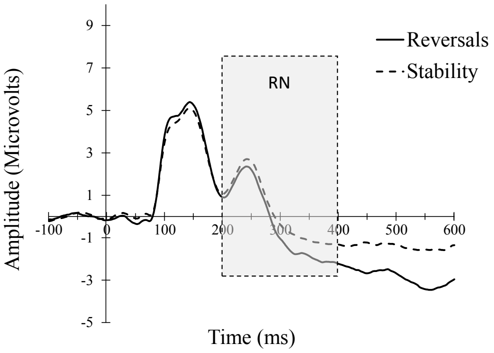
Figure 3.3A-D shows the grand average ERP waveforms for reversal trials and stability trials (ambiguous only) for the four conditions resulting from the combination of the task (identity task vs. reversal task) and response action (responded vs. non response) factors. The RN and RP ROIs are indicated with shading. For all analyses, the Greenhouse-Geisser correction was applied when Mauchly’s test of sphericity was significant at the $p = .05$ level.

RN ROI (O1, Oz, O2, PO7, PO8)

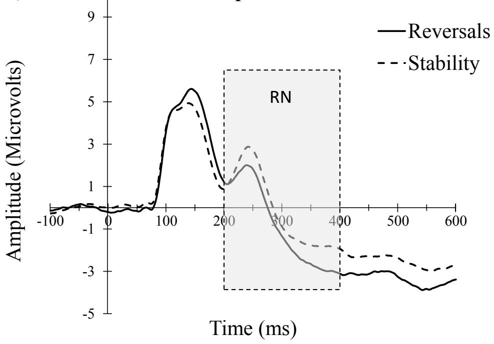
(A) **Reversal Task**



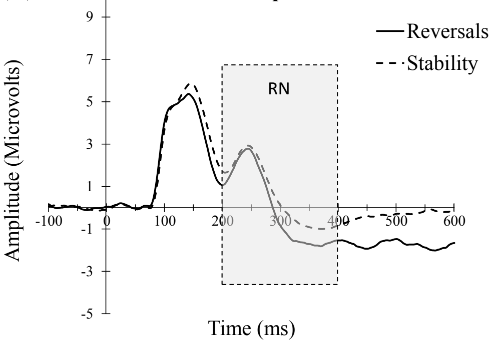
(B) **Identity Task**



(C) **Response Trials**

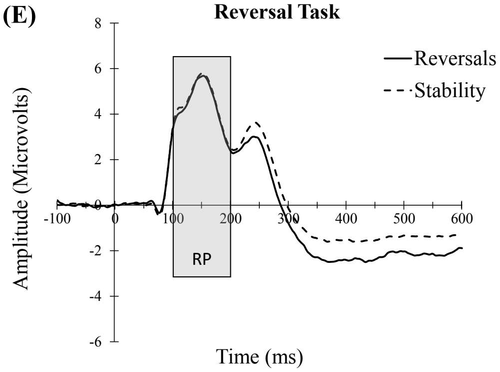


(D) **Non Response Trials**

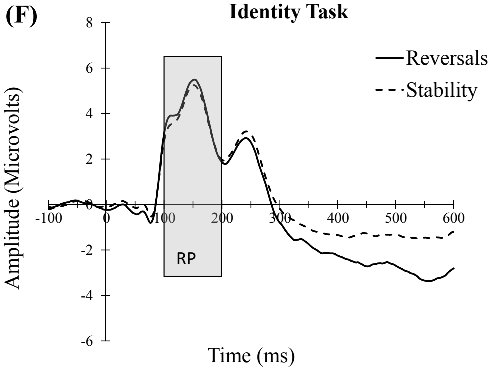


RP ROI (O1, Oz, O2)

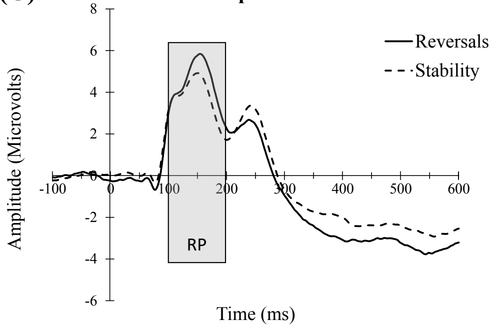
(E) **Reversal Task**



(F) **Identity Task**



(G) **Response Trials**



(H) **Non Response Trials**

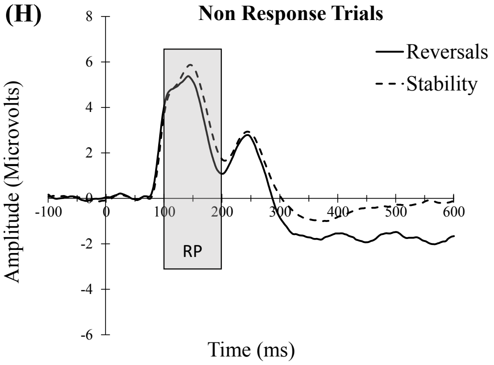


Figure 3.3. Each panel plots the grand mean ERP waveforms for reversal (solid line) and stability trials (dashed line) in Experiment 1 (Necker lattice) under different response and task conditions. Panels A-D are averaged over the RN ROI (O1, Oz, O2, PO7, PO8) and panels E-H are averaged over the RP ROI (O1, Oz, O2). (A & E) ERP waveforms in the reversal task (collapsed over response); (B & F) ERP waveforms in the identity task (collapsed over response); (C & G) ERP waveforms for the response trials (collapsed over task); (D & H) ERP waveforms for the non-response trials (collapsed over task). The boxes indicate the ROI time-windows used to quantify the RN (dashed outline, light grey fill) and RP (solid outline, dark grey fill) ERP component mean amplitudes (see 3.2.2. Data Analysis Methods section). Figure 3.4 shows ROI mean amplitudes.

3.2.3.5. Reversal Negativity.

Mean amplitude across the RN ROI was calculated in each condition for each participant (see Data Analysis Methods section). Figure 3.4A shows the average (across participants) mean RN ROI amplitude for reversal (black bars) and stability (grey bars) trials as a function of task type (reversal vs. identity) and response action (response vs. non-response). We conducted a 5x2x2x2 repeated measures ANOVA with the factors Channels, Task (Identity Task vs. Reversal Task), Trial Type (Reversal vs Stability), and Response Action (Response vs. Non Response). There were significant main effects of Channels, $F(2.33,16) = 4.209$, $p = .018$, $\eta_p^2 = .208$, Trial Type, $F(1,16) = 18.272$, $p = .001$, $\eta_p^2 = .533$ (i.e., a significant RN), and Response Action, $F(1,16) = 16.496$, $p = .001$, $\eta_p^2 = .508$. There was also a significant interaction between Channel and Trial Type, $F(4,16) = 4.346$, $p = .015$, $\eta_p^2 = .214$. To explore this interaction, we tested whether there was an effect of trial type at each electrode and found that there was (all *p*

< .003). None of the other factors or interactions were significant, all $p > .150$ (see Table 3.3 below for full ANOVA results). We verified that there was a significant Reversal Negativity (i.e., difference between reversal and stability trials) in both the reversal task, $F(1,16) = 12.527$, $p = .003$, $\eta_p^2 = .439$ and in the identity task, $F(1,16) = 5.336$, $p = .035$, $\eta_p^2 = .250$.

To check whether the significant effect of Trial Type identified in our results was statistically powerful, we conducted post hoc power analyses using GPower (Faul & Erdfelder, 1992) with $\alpha = .05$, two-tailed. This showed us that the power ($1 - \beta$) of our significant effect is 1.

Table 3.3.

Necker Lattice - Reversal Negativity: Full ANOVA Results Table

	df1	*df2*	*F*	η_p^2	*p*
Channels	2.329	37.258	4.209	0.208	**0.018**
Task	1	16	0.042	0.003	0.84
Trial Type	1	16	18.272	0.533	**0.001**
Response	1	16	16.496	0.508	**0.001**
Channels x Task	2.692	43.074	1.005	0.059	0.393

Channels x Trial Type	2.427	38.829	4.346	0.214	**0.015**
Task x Trial Type	1	16	0.248	0.015	0.625
Channels x Task x Trial Type	1.951	31.215	0.201	0.012	0.814
Channels x Response	2.268	36.289	0.847	0.05	0.45
Task x Response	1	16	1.435	0.082	0.248
Channels x Task x Response	2.881	46.103	0.729	0.044	0.535
Trial Type x Response	1	16	0.068	0.004	0.798
Channels x Trial Type x Response	1.807	28.905	2.057	0.114	0.15
Task x Trial Type x Response	1	16	1.528	0.087	0.234
Channels x Task x Trial Type x Response	2.033	32.525	1.872	0.105	0.169

Note. Full ANOVA RN results table for Experiment 1 (Necker Lattice) with Greenhouse–Geisser correction.

3.2.3.6. Reversal Positivity.

Mean amplitude across the RP ROI was calculated in each condition for each participant (see Data Analysis Methods section). Figure 3.4B shows the average (across participants) mean RP ROI amplitude for reversal (black bars) and stability (grey bars) trials as a function of task type (reversal vs. identity) and response action (response vs. non-response). A 3x2x2x2 repeated measures ANOVA with the factors Channels, Task, Trial Type (Reversal vs. Stability), and Response Action revealed a significant interaction between Trial Type and Response Action, $F(1,16) = 4.895$, $p = .042$, $\eta_p^2 = .234$. This analysis also revealed a marginally significant main effect of Task, $F(1,16) = 3.753$, $p = .071$, $\eta_p^2 = .190$. This main effect has no bearing on hypotheses related to the RN because it does not interact with the Trial Type effect which defines the RN. Thus, it will not be discussed further. None of the other factors or interactions were significant, all $p > .118$ (see Table 4 below for full ANOVA results).

To explore the Trial Type x Response Action interaction, we examined the effect of Trial Type separately for Response and Non Response trials. This revealed a significant Trial Type effect (i.e., a significant RP) in the Response trials, $F(1,16) = 4.803$, $p = .044$, $\eta_p^2 = .231$. In contrast, there was no significant effect of Trial Type in the Non-Response trials, $F(1,16) = 2.892$, $p = .108$, $\eta_p^2 = .153$ (i.e., no RP).

To check whether the significant interaction of Trial Type x Response Action identified in our results was statistically powerful, we conducted post hoc power analyses using GPower (Faul & Erdfelder, 1992) with $\alpha = .05$, two-tailed. This showed us that the power $(1 - \beta)$ of our significant interaction is 0.9998541. Furthermore in order to check whether the non-significant main effect of Trial Type was due to a lack of statistical power, we conducted a second post hoc power analysis using GPower (Faul & Erdefelder, 1992) with power (1 - β) set at 0.80 and α = .05, two-tailed. This showed us that sample size would have to be N = 17 in order to reach statistical significance at the .05 level. Therefore, it is unlikely that our negative findings can be attributed to a limited sample size.

Table 3.4.

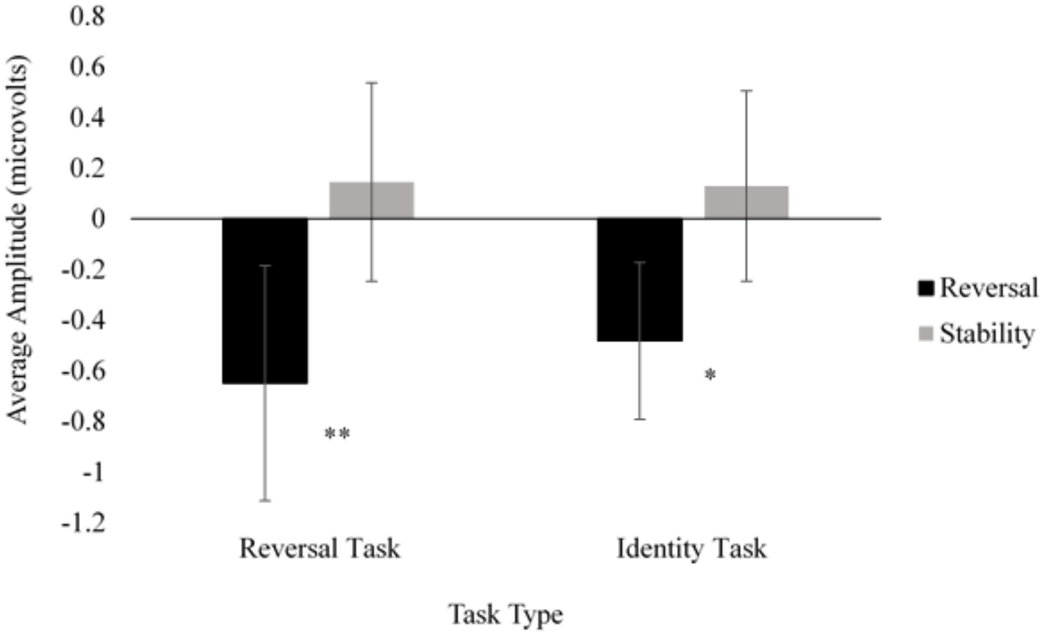
Necker Lattice - Reversal Positivity: Full ANOVA Results Table

	df1	*df2*	*F*	η_p^2	*p*
Channels	1.375	22.005	2.386	0.13	0.129
Task	1	16	3.753	0.19	0.071
Trial Type	1	16	0.036	0.002	0.852
Response	1	16	2.724	0.145	0.118
Channels x Task	2	26.474	0.13	0.008	0.879
Channels x Trial Type	1.473	23.566	0.372	0.023	0.630
Task x Trial Type	1	16	0.421	0.026	0.525
Channels x Task x Trial Type	2	29.615	0.873	0.052	0.427

Channels x Response	1.579	25.268	0.003	0.000	0.991
Task x Response	1	16	1.563	0.089	0.229
Channels x Task x Response	1.253	20.054	0.971	0.057	0.357
Trial Type x Response	1	16	4.895	0.234	**0.042**
Channels x Trial Type x Response	2	27.070	2.126	0.117	0.136
Task x Trial Type x Response	1	16	0.609	0.037	0.447
Channels x Task x Trial Type x Response	2	27.267	0.566	0.034	0.573

Note. Full ANOVA RP results table for Experiment 1 (Necker Lattice) with Greenhouse–Geisser correction.

(A) Reversal Negativity (RN) – Collapsed Across Response



(B) Reversal Positivity (RP) – Collapsed Across Task

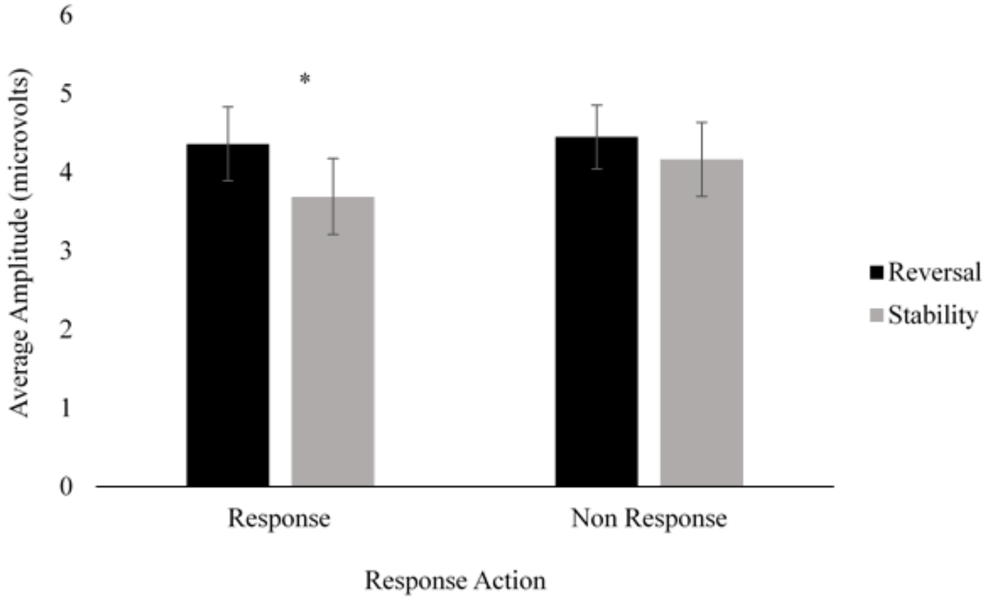


Figure 3.4. ERP results for the RN and RP components for Experiment 1 (Necker Lattice). Mean amplitudes (with SEMs) in the RN ROI (A) and RP ROI (B) for Reversal Trials (in black) and Stability Trials (in grey) as a function of Task Type (Reversal vs. Identity) and Response Action (Response vs. Non Response). A significant RN or RP in each condition (i.e., difference between black and grey bars) is indicated with ** (p<.01) or * (p<.05) above the bars. Error bars represent the standard error of the mean.

3.2.4. Interim Discussion

We aimed to determine whether the reversal-related ERP components, RN and RP, are sensitive to task and response factors. We found that the RN was present in all conditions and was not modulated by task or response action factors. This means that the RN, as has been consistently observed in the reversal task across many studies, cannot be accounted for by task and response related differences between reversal and stable trials. In contrast, although the RP was not affected by whether the participants were doing the reversal or the identity task, it was only present on trials in which participants made a manual response (i.e., response trials). When the response style required participants to withhold response on a trial, there was no evidence of a significant RP component associated with these trials. Although the RP is uniquely present for endogenous reversals, our results suggest that it is not a pure measure of perceptual processing related to endogenous perceptual reversals. Instead, our results support the idea that the RP reflects response-related processes as has been suggested by others (e.g., Kornmeier & Bach, 2012).

Before making firm conclusions, we set out to replicate these results in an additional experiment using a different visual stimulus. Because it has been used in RP and RN studies and because it exhibits a different type of reversal (i.e. figure-ground reversals instead of perspective reversals; defined and explained in Chapter 2), we chose Rubin's faces-vase (Figure 3.1D) as the ambiguous stimulus for Experiment 2. Otherwise, the design of Experiment 2 was the same as that in Experiment 1. However, in order to make face and vase interpretations of the stimulus equally probable, the exact distance between the two edges (i.e., inter-edge distance, IED; see Figure 3.5) in the stimulus varied across participants. We used a pre-test procedure to select the IED for each participant that best approximated 50/50 faces/vase reports.

3.3. Experiment 2: Rubin's Face-Vase

3.3.1. Methods

3.3.1.1. Participants.

Twenty-five (14 female, 11 male; different from Experiment 1) undergraduate psychology students were recruited from Keele University's Psychology Research Participation Time scheme and received partial course credit for participation. Participants had a mean age of 21.76 years (range: 18-54 years). All participants had normal or corrected-to-normal visual acuity, average = 0.01 logMAR. Using the same exclusion criteria as Experiment 1, data from six participants were excluded. In addition to that, we excluded two participants from the analyses due technical issues relating to the recording of these participants' EEG data. Ethics and consent arrangements were identical to Experiment 1.

Similar to Experiment 1, the number of participants chosen for this experiment was based on the sample sizes of experiments conducted in previous EEG studies investigating the RN and the RP (e.g. Kornmeier & Bach, 2004; Kornmeier & Bach, 2005; Pitts et al., 2007).

3.3.1.2. Stimuli & Apparatus.

The apparatus and software were the same as in Experiment 1. The stimulus on each trial was either a white outline version of Rubin's ambiguous Faces-Vase (see Figure 3.1D above) or one of two unambiguous versions of the Faces-Vase (see Figure 3.1E-F above). To create the unambiguous stimuli, we adjusted the ambiguous image to include T-junction partial occlusion cues. Each stimulus was presented centrally on a black background. All stimuli were 4.62° vertically. The horizontal frame width (FW; Figure 3.5) and inter-edge distance (IED; distance between the nose tips, Figure 3.5) for each participant's main experiment ambiguous stimulus were determined by a pre-test to maximise ambiguity of the stimulus (see details in procedure below). The horizontal FW for each participant's main experiment unambiguous stimulus was the same as the ambiguous stimulus FW determined by the pre-test. The IED for the unambiguous stimuli was maintained at 2.97°. The average FW in the main experiment for ambiguous stimuli was 9.86° (range: 7.96-13.23°). The average IED in the main experiment was 2.96° (range: 2.55-3.61°). A 0.503° grey cross at the centre of the screen served as fixation target before and during stimulus presentation. Participants made key responses on a computer keyboard. EEG methods for acquisition and analysis were the same as in Experiment 1.

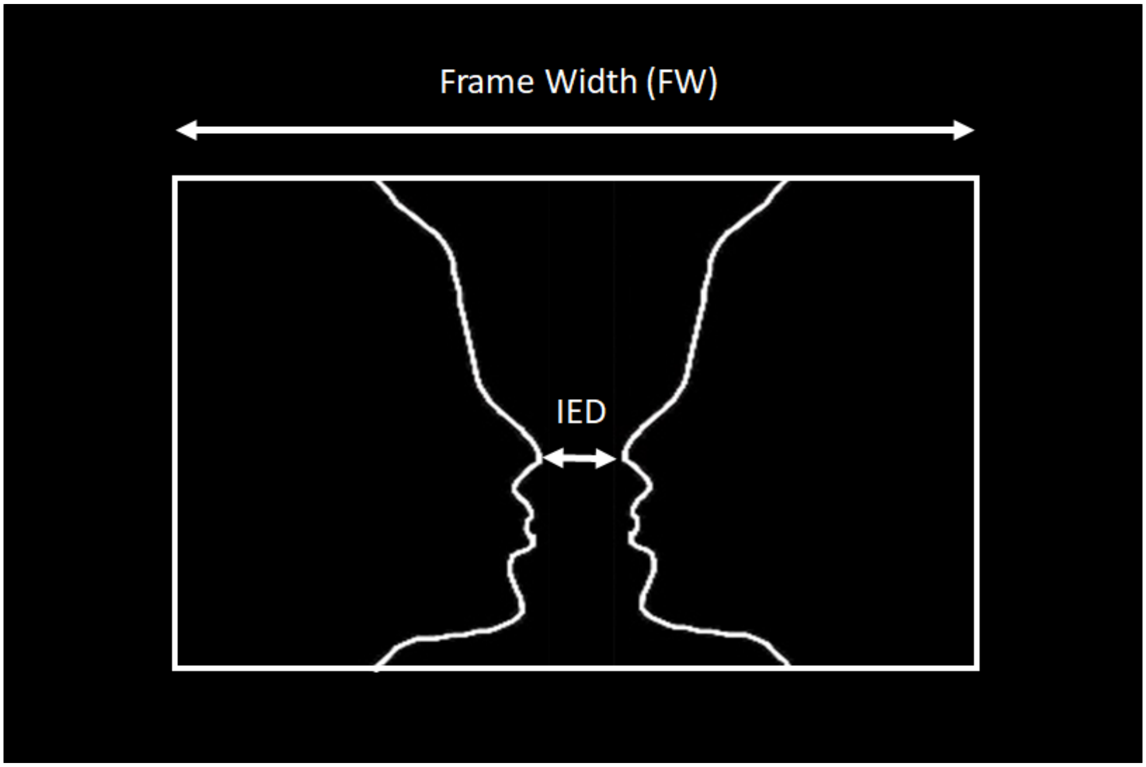


Figure 3.5. The ambiguous faces-vase stimulus used in Experiment 2. The frame width (FW) and inter-edge distance (IED) were adjusted for each participant in a pre-test to determine the maximally ambiguous stimulus for use in the main experiment (see details in procedure section).

3.3.1.3. Procedure.

While the experimenters setup the EEG cap, each participant undertook a 15 minute pre-test to determine the maximally ambiguous configuration of the face-vase stimulus (i.e., closest to 50% faces) using the configural cue of small area (e.g., Rubin, 1958/1915; Castro, Lazareva, Vecera, & Wasserman, 2010; Harrower, 1936). Stimuli representing all combinations of three frame widths (7.96°, 10.60°, and 13.23°) and 8 IEDs (2.13°, 2.34°, 2.55°, 2.76°, 2.97°, 3.19°, 3.40° and 3.61°) were presented to participants for 800 ms each using the method of constant stimuli. There were four blocks of 96 trials each with 16 repetitions of each IED and FW combination. In the pre-test, participants had to report via button press whether they perceived faces (left arrow key) or a vase (right arrow key) on each trial (i.e., identity task). The values of IED and FW which resulted in percentage of vase reports closest to 50% for each participant were used in the main experiment (see average values in Stimuli & Apparatus section above). If the participant's percentage of vase percepts was below 30% or above 70%, then the pre-test was repeated. Three of the 25 participants repeated the pre-test and suitable values obtained on the second run.

The main experiment procedure was similar to that of Experiment 1 except that the Necker lattice stimuli were replaced with faces-vase stimuli. Response options in the identity task for Experiment 2 were "faces" or "vase". Two of the identity task blocks were respond-to-face blocks whereas the other two were respond-to-vase blocks. The ambiguous faces-vase stimulus appeared on 90% of the trials. The remaining trials were either face-biased (5%) or vase-biased (5%) stimuli. Unambiguous stimuli were presented in either stable pairs (face-biased then face-biased; vase-biased then vase-biased) or reversal pairs (face-biased then vase-biased; vase-biased then face-biased). Stable and reversal pairs occurred equally often. Unambiguous pairs were distributed randomly throughout the sequence of ambiguous stimuli. There were four types of blocks with each presented twice: reversal task, respond-to-reversal; reversal task, respond-to-stability; identity task, respond-to-faces; and identity task, respond-to-vase. Each participant has a different random order of the blocks.

3.3.2. Data analysis methods

The steps taken to pre-process, exclude and analyse the data are the same as in Experiment 1. On average, 9.15% (range: 4.42-17.28%) of the trials were excluded due to our exclusion criteria (see Experiment 1). Six out of 25 participants were excluded from Experiment 2 due to insufficient trials in at least one condition (e.g. low number of stability trials in one of the conditions). ROIs and the factorial design were the same as in Experiment 1.

3.3.3. Results

3.3.3.1. Response time.

On average, participants responded 700ms (range = 620-757ms) after stimulus onset. A 2x2 Repeated Measures ANOVA revealed that there was no significant effect of Task or the Trial Type for response times, p>.107. However, there was a significant interaction between Task and Trial Type, $F(1,16) = 22.822$, $p < .001$, $\eta_p^2 = .588$. This crossover interaction was examined by testing the simple effects of trial type in each task. RT for reversal trials (M = 663 ms, SE = 16) was significantly faster than for stability trials (M = 718, SE = 9) in the identity task, $t(16)= -3.406$, $p = .004$. However, there was not a significant difference between reversal (M = 697, SE = 21) and stability (M = 695, SE = 8) trial RTs in the reversal task, $t(16)= .08$, $p = .937$. See Table 3.5 for response times (in ms) across task and trial type. Corresponding analyses were not conducted for the unambiguous stimuli because there were too few trials. In identity task blocks, there was no significant difference between face response trials (M = 702 ms, SE = 36) and vase response trials (M = 705 ms, SE = 29), $t(16) = .08$, $p = .937$. See Table 3.6 for response times (in ms) in the identity task.

Table 3.5.

Rubin's Faces-Vase: Response Times (in ms) across Task and Trial Type

		Mean (ms)	SE
Task	Reversal	696	13
	Identity	691	10
Trial Type	Reversal	680	17
	Stability	707	8
Task x Trial Type	Reversal x Reversal	697	21
	Reversal x Stability	695	8
	Identity x Reversal	663	16
	Identity x Stability	718	9

Table 3.6.

Rubin's Faces-Vase: Mean Response Time (in ms) of the two Trial Types in the Identity Task

	Mean Response Time (ms)	SE
Faces Response Trials in Identity Task	702	36
Vase Response Trials in Identity Task	705	29

3.3.3.2. Unambiguous Faces-Vase.

Overall, participants correctly responded to 83.17% (SD = 7.39%) of the unambiguous Face-Vase pairs. In the identity task, participants correctly discriminated the stimulus on 87.99% (SD = 12.9%) of trials. This was significantly greater than 50%, *t*(16) = 17.01, *p* < .001. Participants scored 73.7% (SD = 17.64) on reversals vs stability discrimination in the reversal task and this was significantly greater than 50%, *t*(16) = 8.99, *p* <.001.

3.3.3.3. Ambiguous Faces-Vase.

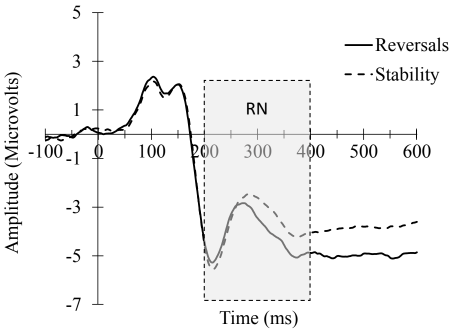
In the Reversal Task, 32.24% of trials were classified as reversal trials (67.76% stable). In the Identity Task, on average, 35.61% of trials were reversals (64.39% stable). There was no significant difference between the percentage of reversals in the reversal and identity tasks, *t*(16) = -.797, *p* = .507. In the identity task, 50.52% (SD = 10.18%) of trials, on average, were reported as faces (49.48% vase) and this was not significantly different from 50%, *t*(16) = .209, *p* = .837. These results demonstrate that the pre-test was effective at making the stimulus maximally ambiguous.

3.3.3.4. Electrophysiological results.

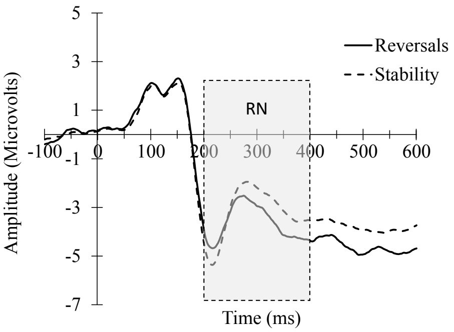
Figure 3.6A-D shows the grand average ERP waveforms for reversal trials and stability trials (ambiguous only) for the four conditions resulting from the combination of task and response action factors. Shaded regions indicate the RN and RP ROIs and these were the same as in Experiment 1.

RN ROI (O1, Oz, O2, PO7, PO8)

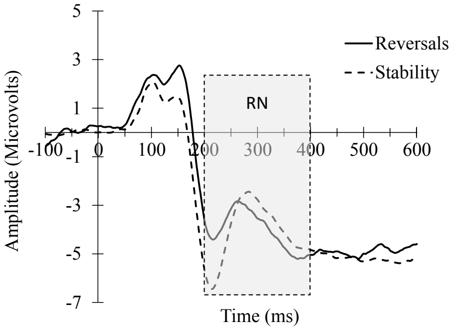
(A) **Reversal Task**



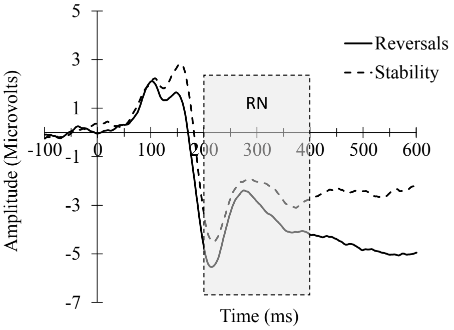
(B) **Identity Task**



(C) **Response Trials**

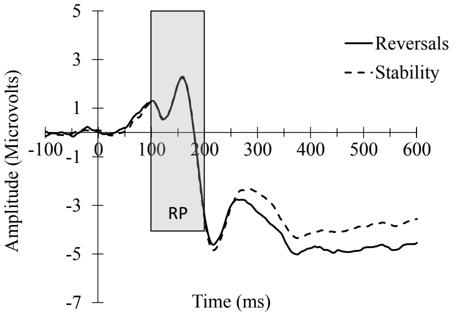


(D) **Non Response Trials**

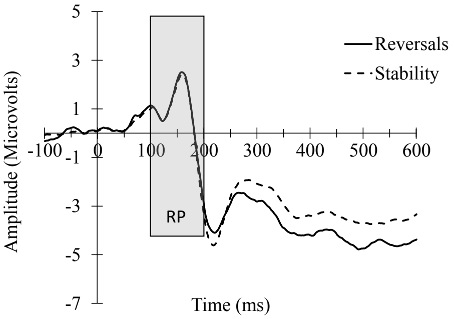


RP ROI (O1, Oz, O2)

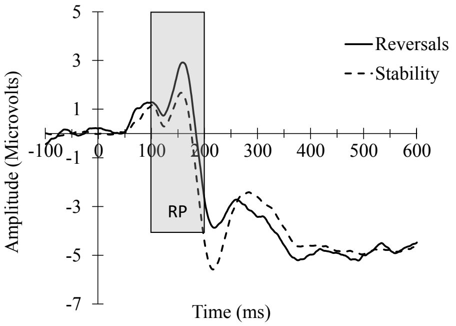
(E) **Reversal Task**



(F) **Identity Task**



(G) **Response Trials**



(H) **Non Response Trials**

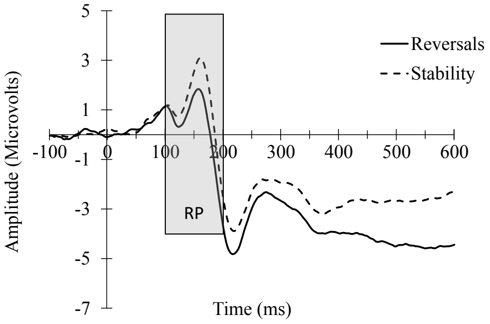


Figure 3.6. Each panel plots the grand mean ERP waveforms for reversal (solid line) and stability trials (dashed line) in Experiment 2 (faces-vase) under different response and task conditions. Panels A-D are averaged over the RN ROI (O1, Oz, O2, PO7, PO8) and panels E-H are averaged over the RP ROI (O1, Oz, O2). (A & E) ERP waveforms in the reversal task (collapsed over response); (B & F) ERP waveforms in the identity task (collapsed over response); (C & G) ERP waveforms for the response trials (collapsed over task); (D & H) ERP waveforms for the non-response trials (collapsed over task). The boxes indicate the ROI time-windows used to quantify the RN (dashed outline, light grey fill) and RP (solid outline, dark grey fill) ERP component mean amplitudes. Figure 3.7 shows ROI mean amplitudes.

3.3.3.5. Reversal Negativity.

Mean amplitude across the RN ROI was calculated as in Experiment 1. Figure 7A shows the mean RN amplitude for reversal (black bars) and stability (grey bars) trials as a function of task type (reversal vs. identity) and response action (response vs. non-response). A 5x2x2x2 repeated measures ANOVA with the factors Channels, Task, Trial Type, and Response Action revealed significant main effects of Trial Type, $F(1,16) = 15.461$, $p = .001$, $\eta_p^2 = .491$, and Response Action, $F(1,16) = 16.495$, $p = .001$, $\eta_p^2 = .507$. There was also a significant interaction between Channels and Task, $F(1.369, 16) = 12.395$, $p < .001$, $\eta_p^2 = .437$. This interaction and the main effect of Response Action were not explored further because they do not involve the trial type factor and thus have no bearing on the hypotheses regarding the RN. No other factors or interactions were significant, $p > .161$ (see Table 3.7 for full ANOVA results below).

Although the Trial Type factor did not significantly interact with Task, in order to address our a priori hypotheses regarding task differences, we tested the effect of trial type separately in the two tasks. The effect of trial type was only marginally significant in the Reversal Task, $F(1,16) = 4.230$, $p = 0.056$, $\eta_p^2 = .209$ but significant in the Identity Task, $F(1,16) = 14.499$, $p = .002$, $\eta_p^2 = .475$.

Following the request of the respected examiners of this thesis, to check whether the significant effect of Trial Type identified in our results was statistically powerful, we conducted post hoc power analyses using GPower (Faul & Erdfelder, 1992) with $\alpha = .05$, two-tailed. This showed us that the power ($1 - \beta$) of our significant effect is 1.

Table 3.5.

Rubin's Face-Vase - Reversal Negativity: Full ANOVA Results Table

	df1	*df2*	*F*	η_p^2	*p*
Channels	2.546	37.770	1.488	0.085	0.216
Task	1	16	0.469	0.028	0.503
Trial Type	1	16	15.461	0.491	**0.001**
Response	1	16	16.465	0.507	**0.001**
Channels x Task	1.369	41.413	12.395	0.437	**0.000**

Channels x Trial Type	2.020	45.542	0.318	0.019	0.865
Task x Trial Type	1	16	0.914	0.054	0.353
Channels x Task x Trial Type	2.25	36.977	1.470	0.084	0.243
Channels x Response	1.454	31.744	2.044	0.113	0.161
Task x Response	1	16	2.093	0.116	0.167
Channels x Task x Response	1.257	37.118	1.649	0.093	0.217
Trial Type x Response	1	16	0.634	0.038	0.437
Channels x Trial Type x Response	1.845	38.163	0.403	0.025	0.656
Task x Trial Type x Response	1	16	0.472	0.029	0.502
Channels x Task x Trial Type x Response	1.858	39.736	0.675	0.040	0.506

Note. Full ANOVA RN results table for Experiment 2 (Rubin’s Face-Vase) with Greenhouse–Geisser correction.

3.3.3.6. Reversal Positivity.

Mean amplitude across the RP ROI was calculated as in Experiment 1. Figure 3.7B shows the mean RP ROI amplitude for reversal (black bars) and stability (grey bars) trials as a function of task type and response action. A 3x2x2x2 repeated-measures ANOVA with the factors Channels, Task, Trial Type and Response Action revealed a significant main effect of Channels, $F(1.529,16) = 7.477$, $p = .005$, $\eta_p^2 = .318$. All other main effects were not significant, all $p > .081$ (see Table 3.8 for full ANOVA results below). There was a significant interaction between Trial Type and Response Action, $F(1,16) = 9.485$, $p = .007$, $\eta_p^2 = .372$.

To further analyse this interaction, we examined the effect of trial type separately for Response and Non Response trials. For Response Trials, there was a significant Trial Type effect in the typical direction of the Reversal Positivity (i.e., reversal trials > stable trials), $F(1,16) = 5.266$, $p = .036$, $\eta_p^2 = .248$. There was also a significant Trial Type effect in the Non Response trials, $F(1,16) = 12.350$, $p = .003$, $\eta_p^2 = .436$. However, this effect was opposite in polarity to the typical RP polarity. There was also a marginally significant interaction between Channels and Response Action, $F(1.258,16) = 3.686$, $\mathrm{p} = .061$, $\mathrm{\eta_p}^2 = .187$. However, this interaction was not explored further because it did not involve the trial type factor and thus has no bearing on the hypotheses for the RP component. No other interactions were significant, $p > .143$.

To check whether the significant interaction of Trial Type x Response Action identified in our results was statistically powerful, we conducted post hoc power analyses using GPower (Faul & Erdfelder, 1992) with $\alpha = .05$, two-tailed. This showed us that the power ($1 - \beta$) of our significant interaction is 0.9999646. Furthermore in order to check whether the non-significant main effect of Trial Type was due to a lack of statistical power, we conducted a second post hoc power analysis using GPower (Faul & Erdefelder, 1992) with power (1 - β) set at 0.80 and , α = .05, two-tailed. This showed us that sample sizes would have to be N = 17 in order to reach statistical significance at the .05 level. Therefore, it is unlikely that our negative findings can be attributed to a limited sample size.

Table 3.6.

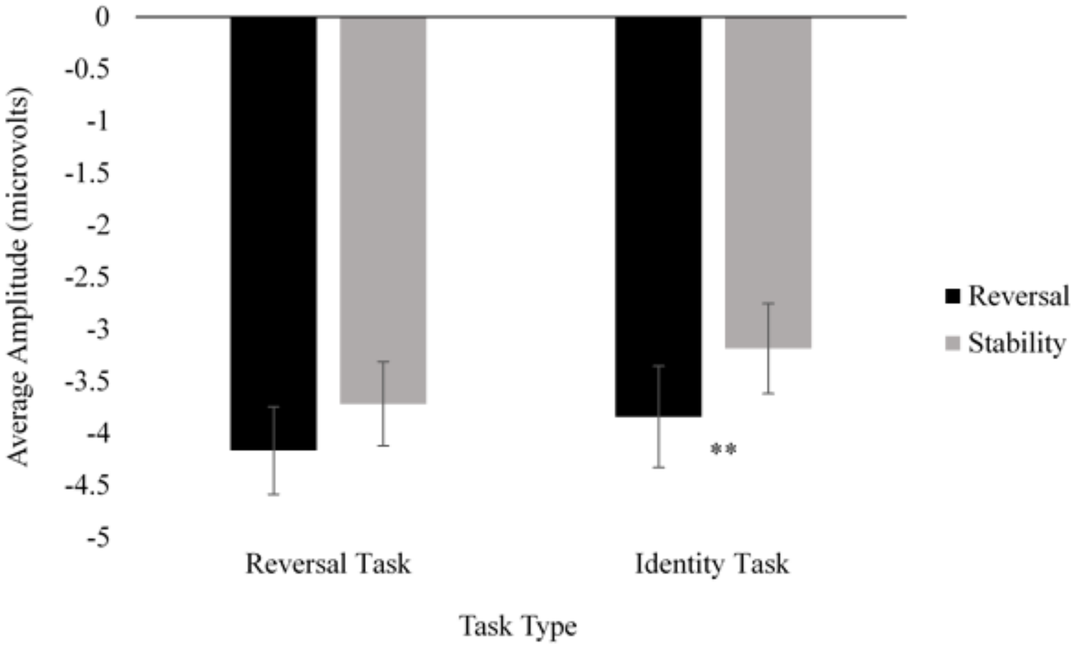
Rubin's Face-Vase - Reversal Positivity: Full ANOVA Results Table

	df1	*df2*	*F*	η_p^2	*p*
Channels	1.529	24.470	7.477	0.318	**0.005**
Task	1	16	0.113	0.007	0.741
Trial Type	1	16	0.007	0.000	0.935
Response	1	16	3.464	0.178	0.081
Channels x Task	1.285	20.561	0.057	0.004	0.871
Channels x Trial Type	2	29.367	0.853	0.051	0.435

Task x Trial Type	1	16	0.074	0.005	0.788
Channels x Task x Trial Type	1.383	22.132	0.599	0.036	0.499
Channels x Response	1.258	20.125	3.686	0.187	0.061
Task x Response	1	16	0.148	0.009	0.705
Channels x Task x Response	1.5	24.006	0.997	0.059	0.362
Trial Type x Response	1	16	9.485	0.372	**0.007**
Channels x Trial Type x Response	1.595	25.513	2.165	0.119	0.143
Task x Trial Type x Response	1	16	0.073	0.005	0.791
Channels x Task x Trial Type x Response	1.874	29.981	0.819	0.049	0.444

Note. Full ANOVA RP results table for Experiment 2 (Rubin’s Face-Vase) with Greenhouse–Geisser correction.

(A) Reversal Negativity (RN) – Collapsed Across Response



(C) Reversal Positivity (RP) – Collapsed Across Task

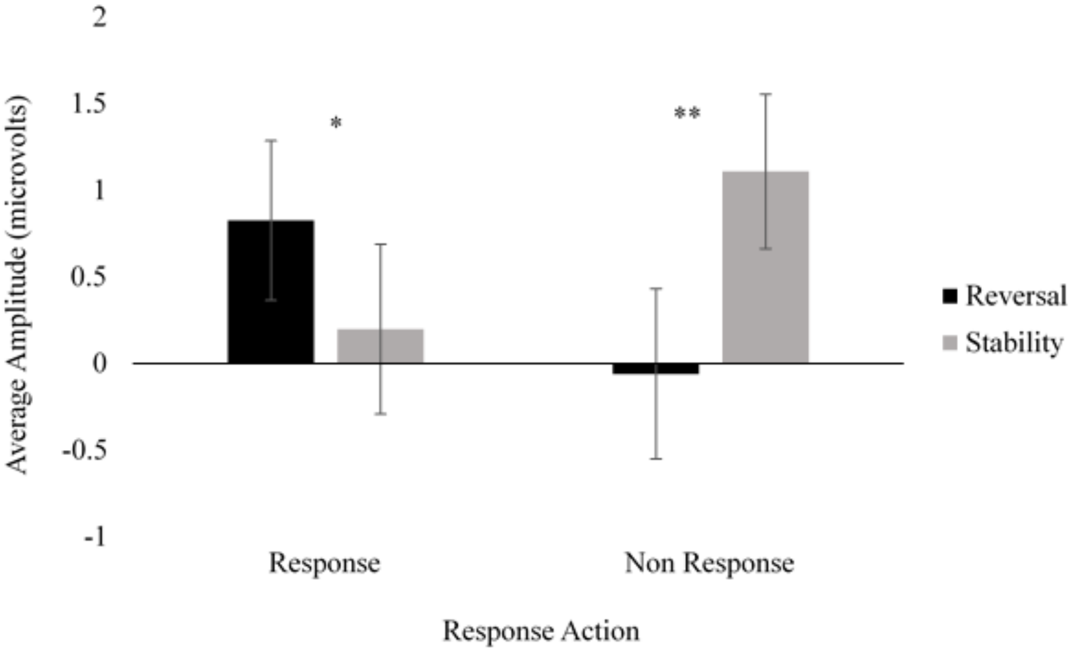


Figure 3.7. ERP results for RN and RP for Experiment 2 (Faces-Vase). (A) Mean amplitudes (with SEMs) in the RN ROI (A) and RP ROI (B) for Reversal Trials (in black) and Stability Trials (in grey) as a function of Task Type (Reversal vs. Identity) and Response Action (Response vs. Non Response). A significant RN or RP in each condition (i.e., difference between black and grey bars) is indicated with ** (p<.01) or * (p<.05) above the bars. Error bars represent the standard error of the mean.

3.4. Comparison of Experiments 1 and 2 ERP Results

To determine whether the RN and RP results were similar across Experiments 1 and 2, we conducted two 2x2x2x2 mixed-factors ANOVAs with Trial Type, Task, Response Action, and Experiment/Illusion (between-subjects; Necker Lattice vs. Faces-Vase) as factors. We collapsed the data over all other factors because none of these interacted with the Trial Type factor in Experiments 1 or 2. Figure 3.8A-D shows the grand average ERP waveforms for reversal trials and stability trials (ambiguous only) collapsed over both experiments for the four conditions resulting from the combination of task and response action factors. Shaded regions indicate the RN and RP ROIs and these were the same across both experiments. Because the RN and RP components are defined by the trial type effect (i.e., the difference between reversal and stability trials), only factors that interact with that factor have any bearing on our hypotheses about these ERP components. Thus, below we present only significant effects and interactions that involve the trial type factor.

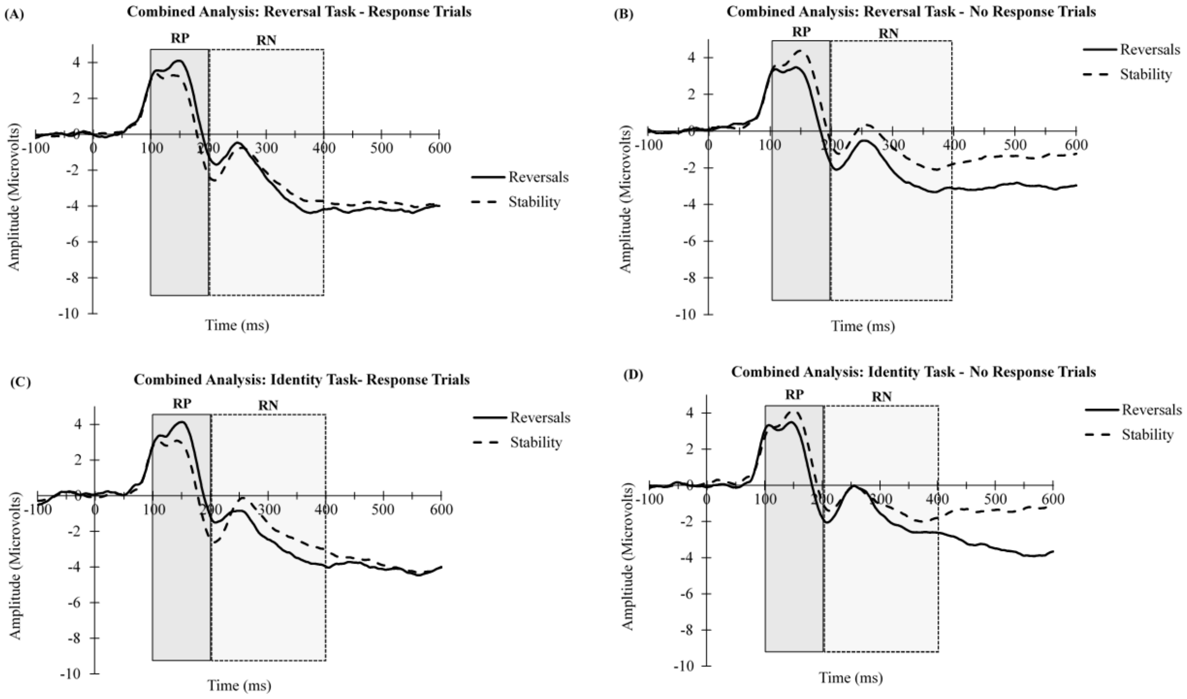


Figure 3.8. Each panel plots the grand mean ERP signals for reversal (solid line) and stability (dashed line) trials collapsed over both experiments (Necker Lattice and Face-Vase). Each panel shows these waveforms for a different combination of the task and response factors as follows: (a) Response trials in the Reversal Task; (b) Non Response trials in the Reversal Task; (c) Response trials in the Identity Task; (d) Non Response trials in the Identity Task. The boxes indicate the ROI time-windows used to quantify the RN (dashed outline, light grey fill) and RP (solid outline, dark grey fill) ERP components.

For the RN analysis, there were significant main effects of Channels, *F*(2.426, 77.629) = 3.496, $p = .027$, $\eta_p^2 = .098$, Trial Type, *F*(1, 32) = 31.579, $p <. 001$, $\eta_p^2 = .497$. The Trial Type effect reflects a significant RN ERP component. The interaction between Trial Type and Experiment was not significant, *F*(1,32) = .449, $p = .507$, which is consistent with there being no difference in the RN between Experiments 1 and 2. For the RP analysis, there was a significant interaction between the Response Action and Trial Type factors, $F(1,32) = 14.025$, $p = .001$, $\eta_p^2 = .305$. These factors did not significantly interact with the Experiment factor, $F(1,32) = .397$, $p = .533$. This is consistent with there being the same general pattern of effects across the two experiments. The full ANOVA results tables are available in Tables 3.9 & 3.10.

To further analyse the Trial Type x Response interaction for the RP, we examined the effect of trial type separately for Response and No Response trials. The Response Trials revealed a significant Trial Type effect (i.e., Reversal Positivity), $F(1,32) = 9.984$, $p = .003$, $\eta_p^2 = .238$ and a significant interaction between Task and Experiment, $F(1, 32) = 4.328$, $p = .046$, $\eta_p^2 = .119$. The analysis conducted on the Non Response Trials also revealed a significant Trial Type effect, $F(1,32) = 11.830$, $p = .002$, $\eta_p^2 = .270$. This difference occurred at the same latency as the Reversal Positivity, however, it was opposite in polarity.

Table 3.9.

Combined Results of Experiments 1 and 2 - Reversal Negativity: Full ANOVA results table

	df	*df2*	*F*	η_p^2	*p*
Channels	2.426	77.628	3.496	0.098	**0.027**

Channels x Experiment	2.426		4.029	0.112	**0.016**
Task	1	32	1.387	0.042	0.248
Task x Experiment	1		0.673	0.021	0.418
Trial Type	1	32	31.579	0.497	**0**
Trial Type x Experiment	1		0.449	0.014	0.507
Response	1	32	36.811	0.535	**0**
Response x Experiment	1		0.191	0.006	0.665
Channels x Task	3.181	101.803	1.352	0.041	0.261
Channels x Task x Experiment	3.181		0.886	0.027	0.456
Channels x Trial Type	2.749	87.96	3.139	0.089	**0.033**
Channels x Trial Type x Experiment	2.749		1.493	0.045	0.225
Task x Trial Type	1	32	0.003	0	0.959
Task x Trial Type x Experiment	1		0.759	0.023	0.39
Channels x Task x Trial Type	2.149	68.777	1.408	0.042	0.251

Channels x Task x Trial Type x Experiment	2.149		0.728	0.022	0.496
Channels x Response	2.322	74.293	4.448	0.122	**0.011**
Channels x Response x Experiment	2.322		0.776	0.024	0.481
Task x Response	1	32	0.07	0.002	0.793
Task x Response x Experiment	1		4.863	0.132	**0.035**
Channels x Task x Response	2.854	91.329	1.23	0.037	0.303
Channels x Task x Response x Experiment	2.854		4.167	0.115	**0.009**
Trial Type x Response	1	32	0.361	0.001	0.552
Trial Type x Response x Experiment	1		0.834	0.025	0.368
Channels x Trial Type x Response	2.337	74.79	0.188	0.006	0.861
Channels x Trial Type x Response x Experiment	2.337		2.64	0.076	0.069
Task x Trial Type x Response	1	32	1.871	0.055	0.181
Task x Trial Type x Response x	1		0.233	0.007	0.633

Experiment					
Channels x Task x Trial Type x Response	2.671	85.481	2.306	0.067	0.089
Channels x Task x Trial Type x Response x Experiment	2.671		0.981	0.03	0.399

Note. Full ANOVA results table of the RN collapsed over both experiments (Experiment 1: Necker Lattice; Experiment 2: Rubin's Faces-Vase) with Greenhouse-Geisser correction.

Table 3.10.

Combined Results of Experiments 1 and 2 - Reversal Negativity: Full ANOVA results table

	df	*df2*	*F*	η_p^2	*p*
Channels	1.627	52.052	1.124	0.034	0.323
Channels x Experiment	1.627		5.874	0.155	**0.008**
Task	1	32	2.002	0.059	0.167
Task x Experiment	1		3.211	0.091	0.083
Trial Type	1	32	0.007	0	0.933
Trial Type x Experiment	1		0.038	0.001	0.846

Response	1	32	6.07	0.159	**0.019**
Response x Experiment	1		0.002	0	0.963
Channels x Task	1.72	55.052	0.058	0.002	0.922
Channels x Task x Experiment	1.72		0.137	0.004	0.841
Channels x Trial Type	1.612	51.596	0.367	0.011	0.649
Channels x Trial Type x Experiment	1.612		0.724	0.022	0.461
Task x Trial Type	1	32	0.219	0.007	0.643
Task x Trial Type x Experiment	1		0.495	0.015	0.487
Channels x Task x Trial Type	1.73	55.373	0.407	0.013	0.667
Channels x Task x Trial Type x Experiment	1.73		1.167	0.035	0.318
Channels x Response	1.603	51.306	0.927	0.028	0.383
Channels x Response x Experiment	1.603		1.087	0.033	0.333
Task x Response	1	32	0.641	0.02	0.429
Task x Response x Experiment	1		1.548	0.046	0.222

Channels x Task x Response	1.389	44.456	0.127	0.004	0.805
Channels x Task x Response x Experiment	1.389		1.834	0.054	0.18
Trial Type x Response	1	32	14.025	0.305	**0.001**
Trial Type x Response x Experiment	1		0.397	0.012	0.533
Channels x Trial Type x Response	1.644	52.622	0.337	0.01	0.673
Channels x Trial Type x Response x Experiment	1.644		3.969	0.11	0.032
Task x Trial Type x Response	1	32	0.606	0.019	0.442
Task x Trial Type x Response x Experiment	1		0.197	0.006	0.66
Channels x Task x Trial Type x Response	1.798	57.538	1.023	0.031	0.365
Channels x Task x Trial Type x Response x Experiment	1.798		0.335	0.01	0.717

Note. Full ANOVA results table of the RN collapsed over both experiments (Experiment 1: Necker Lattice; Experiment 2: Rubin's Faces-Vase) with Greenhouse-Geisser correction.

3.5. General Discussion

The results of Experiment 2 with Rubin's Face-Vase were similar to the results of Experiment 1. We found that both the RN and RP are unaffected by whether participants performed the reversal task or the new identity task that we introduced here. We had hypothesised that the reversal task, which is commonly used to evoke the RN and RP, might create critical task and response-related differences between reversal and stable trials. In particular, reversal trials may stand out as relatively rare targets amongst more common, non-target stable trials. In turn, these differences between reversal and stable trials could be responsible for the reversal vs. stable trial differences in ERP amplitude that comprise the RN and RP. Our results suggest that the RN and RP cannot be explained by our hypothesised task-induced differences between reversal and stability conditions. This is because both components were present with the same amplitude when participants performed the identity task which was designed to control for these differences.

In line with the results of Experiment 1, we found that the RP was sensitive to response action in Experiment 2. Specifically, the RP was present, as normal, on trials in which participants responded due to task instructions. In contrast, non-response trials showed a significant difference between reversal and stable trials in the RP time window but with an opposite polarity to the RP present on response trials (i.e., stable > reversal). This result in the non-response condition of Experiment 2 is different from that observed in Experiment 1 where there was no significant difference in the RP time window for non-response trials. We conducted an overall analysis combining both datasets from the two experiments to test whether this discrepancy would be reflected in a Trial Type x

Response Action x Experiment interaction but it was not. We cannot account for this minor discrepancy between the RP results in Experiments 1 and 2. It could be that this arises from slight processing or time course differences between the faces-vase figure and the Necker lattice. It could also be that the number of trials, as was mentioned previously by Kornmeier and Bach (2012) plays a role in the significance of these components. Nonetheless, it is clear that the RP is sensitive to response action instructions. In contrast to the RP, we found across two studies that the RN is insensitive to response action as has been shown by previous studies (e.g., Kornmeier & Bach, 2004).

Our observed difference in the RP between response and non-response trials cannot be attributed to the extended ITI (from 400 to 1000 ms; see methods) after responses in our procedure. Responses occurred, on average, approximately 700 ms after stimulus onset and the extension of the ITI occurred only after the response occurred. Thus, the extended ITI occurred well after the RP on these trials was already over. This means that the extended ITI and response-related brain activity may have affected the subsequent trial but not retrospectively affected the response trial itself.

It is worth noting that some studies of the RN and/or RP have used a paired-stimulus paradigm in which two ambiguous figures are presented in quick succession and a reversal/stable decision is made only after the second stimulus (e.g., Kornmeier, et al., 2007). This differs from our paradigm in which every single stimulus was judged against the preceding one in a continuous sequence. We see no reason why the effect of response that we observed would not generalise across these two versions of the paradigm. However, this will need to be tested in further work.

We based our response style design (i.e., respond on reversal trials only in some blocks and respond only to stable trials in others) on previous studies which also counterbalanced across blocks whether reversal or stable trials were the target for response (e.g., Kornmeier & Bach, 2004; 2005). For the RN, one can then simply collapse across the response factor and compare reversal and non-reversal trials because response has no significant effect on ERP amplitudes. This design ensures that the reversal vs. stable trial comparison is not confounded with response target status as would be the case if one adopted only one response style across the experiment. However, our results show that averaging over response is not appropriate for studying the RP. Along with other factors such as the RP's relatively short duration, averaging over response and non-response trials may account for why some researchers have found this component difficult to observe.

Previous research has shown, as was mentioned previously, that the RP can be obliterated due to several factors (Basar-Eroglu et al., 1993, Britz et al., 2009; Pitts, Nerger & Davis, 2007; Pitts, Gavin & Nerger, 2008). For instance, in Basar-Eroglu et al. (1993)'s experiment, the RP was not seen in their data at the 100-200ms time window. This could be due to the fact that they averaged backwards from the reaction time. It appears likely that convolution of the reaction-time distribution with the ERP structures has obliterated any sharp early peaks leaving later (and broader) components less affected (Kornmeier & Bach, 2004). Moreover, research shows that the RP is a small component with an amplitude around, and sometimes below, 1 μV (Kornmeier and Bach, 2005; Kornmeier and Bach, 2006; Britz et al., 2009). This makes the signal-to-noise ratio very critical when it comes to its statistical significance. This means that, as pointed out by Kornmeier and Bach (2012), the number of EEG trials per subject that enter the ERP calculation is a critical parameter. In Britz et al. (2009) and Pitts et al’s (2007, 2008) studies, the number of trials per condition and participant on average after the pre-processing of the EEG data might have been too small to get an RP effect in the occipital electrodes (Luck, 2005; Pitts et al., 2007). Another factor that influences the significance of the RP was found to be reaction time variability which occurs in studies using the Manual Response Paradigm.

Moreover, although the RP is considered an early component and, to some, this might suggest that it is driven by bottom up processes, our results suggest that the latency of a component cannot determine the nature of its mechanism. Our results show that this component can depend on higher level processes, such as response monitoring.

Our results challenge any interpretation of the RP as purely related to perceptual processing involved in perceptual reversals. Otherwise, it should occur regardless of response action because the perceptual processes related to reversal must occur regardless of the task and response action required of the participant. Others have suggested that the RP may be related to perceptual ambiguity detection or perceptual decision conflict by the visual system (e.g., Kornmeier & Bach, 2012; Kornmeier, Pfäffle, & Bach, 2011). On stable trials, the ambiguity of the stimulus is relatively low and perceptual decision processes can happen easily. In contrast, on reversal trials, the visual system has detected a state of ambiguity that has arisen. As visual input of the ambiguous stimulus is received, this state of ambiguity is compared against the expectation set up by the preceding stimulus. According to our results, this process must only occur on trials that are response targets. This means that, if the RP truly is a marker for the destabilisation process, then our results suggest that this ambiguity/conflict signal is modulated by whether the trial requires a response or not. It is not clear why this would be the case. It is not possible to tease apart the perceptual and non-perceptual accounts based on our data. Nonetheless, given that the response-dependence of the RP has not previously been demonstrated, our work provides a clear foundation for further investigation of this issue. Furthermore, our results demonstrate that response arrangements must be considered carefully when studying the RP. In particular, collapsing across response and non-response can hide a significant source of variability in the data even in relatively early latency ERP components.

Although ERP-based measures of reversal-related brain activity are useful, ERP analyses do not take full advantage of the multivariate nature of EEG data. In particular, ERPs tend to focus on conducting univariate analyses focused on activity at one small area of the scalp. They do not take into account the entire pattern of activity across the scalp that could be driving perceptual reversals. Given that reversals have been shown to involve a wide range of brain areas, it may be that perceptual reversals are driven by a more complex pattern of activity across the scalp that is not picked up by these univariate analyses. This issue is explored in the next chapter, Chapter 4, where we use Multi-Variate Pattern Analysis in order to investigate the post-stimulus period in full without any a priori set spatio-temporal windows. This will allow us to identify spatio-temporal windows, if any, related to perceptual reversals that have not been previously measured in ERP-based univariate analyses.

Chapter 4: MVPA Analysis of ERP Experiments

4.1. Introduction

A substantial amount of research has been conducted in order to identify the time window during which perceptual reversals of ambiguous figures (e.g. Necker Cube or Rubin's Face-Vase) take place. The literature puts forth many approaches used to answer the question surrounding the temporal framework of perceptual reversals. As was mentioned previously, researchers have used different paradigms, including the Manual Response Paradigm (Basar-Eroglu et al., 1996; Isoglu-Alkac, 2000; Struber & Hermann, 2002; Mathes et al., 2006) and the Onset Paradigm (Orbach et al., 1963; Orbach et al., 1966; O'Donnell et al., 1988; Kornmeier & Bach, 2004a, 2004b, 2005, 2006; Kornmeier et al., 2007, 2009; Ehm et al., 2011), different stimulus presentation modes (e.g. continuous or intermittent), different presentation times and inter-trial intervals in order to time-lock the reversal event. These experiments have presented several electrophysiological correlates linked to perceptual reversals but these have primarily used univariate methods which focus on particular scalp locations and time points one at a time. There has been little attention to the pattern of activity across the scalp to determine whether this holds information about perceptual reversals.

In this Chapter, I use the data collected in Experiments 1 and 2 but go beyond my previous univariate findings in the post-stimulus period by applying multi-variate pattern analysis (MVPA). The goal of this is to identify one or more post-stimulus temporal windows that is predictive of perceptual reversals. MVPA has the potential to exploit spatial information which is not used in typical ROI-based ERP analyses. This approach also does not suffer from the loss of single-trail information due to averaging the occurs in ERP analysis. Thus, we expect the MVPA will be able to reveal new effects across the post-stimulus time course.

The experimental procedure used in those experiments (1&2), as was mentioned previously, follows an intermittent presentation paradigm and treats the moment of stimulus onset as the time-locking event for reversals. In section 2.2.2.1 in Chapter 2, I justify the use of the Onset Paradigm in my studies and this particular experimental paradigm. Briefly, in comparison to the manual response paradigm, using the onset paradigm allows more precise time-locking of reversal related activity. Like the event-related potential approach, MVPA does require some level of time-locking of activity across trials. This is because it is conducted using a moving temporal window. Within each window across time, the MVPA algorithm aims to identify a pattern of activity (i.e., scalp distribution), which is predictive, across most trials, of a reversal. If the predictive scalp distribution is present only on some trials but not others within the temporal window being analysed, then MVPA would not be able to accurately predict reversals from it. In this case, decoding accuracy of MVPA would be low or at chance because there is no reliable predictive information in the signal. Thus, using a method with the best possible time-locking of events in the post-stimulus period is critical. Previous findings have that the Onset Paradigm successfully provides a series of ERP signatures related to endogenous reversals which suggests that stimulus onset has a systematic temporal relationship with the reversal event.

Previous research on identifying correlates related to perceptual reversals has revealed several physiological bases of ambiguous figure perception (see Section 1.3 in Chapter 1 for a short review). Research on ERPs linked to perceptual reversals identified several components like the Reversal Negativity and Reversal Positivity (Kornmeier and Bach, 2004a) studied in the previous chapter (Chapter 3). Previous studies investigating these components have found that several factors affect their spatiotemporal profile (Kornmeier & Bach, 2004b; Pitts et al., 2007; Pitts, Gavin & Nerger, 2008) and in some cases, these factors influence the presence of these components (Pitts et al., 2007; Kornmeier & Bach, 2014). In addition to ambiguous stimulus type, endogenous and exogenous reversals, and other factors identified in the previous literature, the findings from our previous study in Chapter 3 showed that another factor also influences one of these components. Our results showed that although there was no significant interaction between Reversal Negativity and Task (identity and reversal) or Reversal Negativity and Response (response and no response), the Reversal Positivity is dependent on Response. In particular, the RP is only present on trials in which participants responded. Moreover, our results showed that a negative component is present in the same latency of the RP on trials in which participants did not respond. This suggests that the RP could be a result of response processes rather than being linked directly to perceptual processing of reversals.

Alternatively, if we were to couple our results with previous descriptions of the RP, then the RP could be considered a marker of detection of ambiguity modulated by whether the trial requires a response or not. The idea behind detection of ambiguity is that the system reaches a maximum state of ambiguity before stabilizing. According to Kornmeier and Bach (2012), the RP is an indicator of this event. In addition to these components, ERP studies investigating the underlying mechanisms of perceptual reversals have identified other reversal related components such as Frontopolar

Positivity and Parietal Positivity. All of the components mentioned have been described previously in section 1.3 in Chapter 1.

Although powerful and relatively easy to conduct, ERP analyses do not take full advantage of the multivariate nature of EEG data. In particular, many ERP analyses focus on a particular region-of-interest (ROI) on the scalp where a component of interest is known to appear. One reason for this is to avoid inflating Type 1 error rate inflation associated with exploring many locations across the scalp (Groppe et al., 2011). However, a major reason is the traditional statistical tools in the field are univariate. Because of this, ERP analyses on reversal-related components do not take into account the distribution spatial activation pattern that could be driving perceptual reversals. This is especially likely in terms of the integrative theory of perceptual reversals (Kornmeier & Bach, 2012) described in Chapter 1 and the findings from previous studies that support the idea of the interplay of bottom-up and top-down processes driving perceptual reversals (Long & Toppino, 2004; for a review see Toppino & Long, 2005).

In order to investigate whether spatial patterns of activity during post-stimulus period, beyond those hitherto found by univariate analyses, are associated with perceptual reversals, we adopted the multivariate pattern analysis (MVPA) approach (e.g., Cauchoix et al., 2014; Cauchoix, Arslan, Fize, & Serre, 2012; Grootswagers et al., 2017; see section 2.3.2 in Chapter 2 for details). MVPA (sometimes called pattern classification or decoding) first emerged as a method of analysis used on fMRI BOLD signals to decode various behavioural states from the pattern of neural activity across the brain (Haynes & Rees, 2006; Naselaris et al., 2011, Norman et al., 2006; Tong & Pratte, 2012). A key outcome of this work was that it revealed that brain areas which had not previously been identified as involved in a particular function by univariate analysis, nonetheless contained useful information about that function. For instance, in Haxby, et al.'s (2001) classic study, activity from wide areas of extrastriate cortex were used to decode which one of eight stimulus categories was presented to the participant with up to 100% accuracy. This included detecting faces even without including the well known fusiform gyrus face area in the analysis. This is a clear example of how MVPA can reveal information in physiological signals which was not detected by univariate analysis.

Recently, MVPA has also been applied to M/EEG data (Blank et al., 2013; Das et al., 2010; Foster et al., 2016; Garcia et al., 2013; Ratcliff et al., 2009; Philiastides et al., 2006a,b; Thiery et al., 2016; Treder et al., 2014; Zhang et al., 2010; Rassi et al., 2019). As was mentioned in Chapter 2, MVPA pattern classification analyses integrate information across all (or a subset of) electrodes instead of only a select few in an ROI. MVPA is sensitive to patterns of brain activity, which are lost in traditional ERP analyses due to the univariate nature of those analyses. Univariate analyses in ERPs tend to, but not always, assume that relevant brain differences can be detected by analysing one spatial location at a given time. This is especially true for many component-based analyses, which are defined by only looking at an a priori spatio-temporal window (i.e., ROI) for statistical testing. ERP analyses tend to focus on components, which are isolated in time. In contrast, MVPA can show millisecond-by-millisecond changes in representation.

While the use of univariate analyses to investigate the relationship between neural activity and information processing measured by behavioural performance on specific cognitive tasks has provided key findings on the underlying brain mechanisms associated with certain behaviours, this approach does not take full advantage of the multivariate nature of EEG data. MVPA can detect activity that has not been found in ERP measures (Cauchoix et al., 2012). For instance, Das et al. (2010) conducted an EEG study with the aim of comparing pattern classification (using 3 different types of classifiers) to traditional ERP metrics (peak amplitude, mean amplitude and peak latency). They used a face/car paradigm where participants were presented with either a face stimulus or a car stimulus with Gaussian noise added to them. Participants had to rate how confident they were about either perceiving a face or a car. Previous studies have identified EEG waveforms at specific epochs (N1, N170) associated with the presentation of faces when compared to other non-face objects (Gauthier et al., 2003; Taylor et al., 1999). Other studies using univariate approaches have identified other correlates related to face perception that are concentrated in particular temporal epochs (e.g. early trial averaged M100 in MEG associated with the categorization of face; Liu et al., 2002). However, unlike these previous studies, Das et al. (2010) found that the neural activity predicting whether individuals were correctly perceiving and reporting faces vs. cars was distributed through time starting at 120ms. This activity that was identified by pattern classification was sustained for more than 400 ms after stimulus onset. This is different from the previous univariate findings in that an extended time window was identified in the significant classification of patterns of activity associated with face decoding vs. cars decoding.

Previous studies investigating perceptual reversals of ambiguous figures have identified changes in oscillations at different frequencies (see section 1.3 on

Physiological Bases on Ambiguous Figure Perception in Chapter 1 for a detailed explanation of these modulations). There is also debate about the nature of these modulations and how they are linked to the dERP components. For instance, the 60ms power reduction in the alpha band, observed in Necker Lattice perception, takes place during the same latency as the RP and has been suggested to be related to it (Kornmeier & Bach, 2012). It is considered to indicate the recurrent activity between occipital and frontal areas to resolve the perceptual decision conflict indicated by the RP. Kornmeier & Bach (2012) suggest that it reflects disambiguation time. Moreover, beta and gamma modulations occur during the same period as the RN (Kornmeier & Bach, 2006). However, their function in ambiguous figure perception and link to the RN remains unclear. Recently researchers have started to apply MVPA on time-frequency data (e.g. Marti & Dehaene, 2017; Rassi et al., 2019). MVPA of time-frequency data can potentiall exploit more from this very rich representation of the data. Therefore, the second aim of this chapter is conduct MVPA analysis on the time-frequency representation of the data from Experiments 1 (Necker Lattice) and 2 (Face-Vase). This will allow us to identify the time-frequency clusters during which the distinction between reversal and stable trials are significant.

In both experiments (Experiment 1: Necker Lattice; Experiment 2: Face-Vase), in the first instance, we will conduct MVPA to find time window(s) with significant decoding accuracies. This will be done for both time domain data as well as time-frequency data. In addition to this, we will conduct MVPA (reversals vs. stability decoding) on response and non-response trials separately. Findings from Chapter 3 revealed a difference in the RP component between response and non-response trials. As was mentioned in the General Discussion section (section 3.5) in Chapter 3, if the RP truly is a marker for the destabilisation process, then the detection of ambiguity is modulated by response. This in turn would suggest that some mechanisms underlying perceptual reversals might be modulated by response. In order to investigate this further and to identify whether perceptual reversal related activity is modulated by response, MVPA is also applied on the two response conditions (response vs. non-response) separately. This analysis could identify patterns of activity, if there are any, representing the relationship between response and perceptual reversals that cannot be identified with univariate analyses.

The purpose of using MVPA on the data from Experiments 1 (Necker Lattice) and 2 (Face-Vase) was to explore the presence of reversal-related activity across the post-stimulus period moment by moment. We expected to find significant decoding accuracies during the latencies of the RN, RP, and other known reversal-related ERP components spanning the post-stimulus period. Based on the findings in the literature with regards to pre-stimulus activity relating to perceptual reversals, we expected that this analysis would reveal a post-stimulus period of time during which the pattern of activity is predictive of a perceptual reversal even before the timeframe of the known ERP components. We expected that this time window would start at stimulus onset or shortly thereafter.

4.2. Experiment 1: Necker Lattice

4.2.1. Methods

This chapter processes the same data set as was collected in Chapter 3 (Experiments 1 and 2) and full methods details are covered there in sections on

‘Participants’ (section 3.2.1.1), ‘Stimuli & Apparatus’ (section 3.2.1.2), ‘EEG and Eye-Tracker Recordings’ (section 3.2.1.3) and ‘Procedure’ (section 3.2.1.4) in Chapter 3 for a detailed account of the experimental paradigm. The same exclusion criteria were applied as well. Only methods differing from Experiment 1 in Chapter 3 are detailed below.

The number of participants used in this chapter is the same as the number of participants that was used in Chapter 3. The sample size choice here was based on previous studies (e.g., Kornmeier & Bach, 2004, 2005; Pitts et al., 2007). In the literature using MVPA on EEG data, there is no standard way of determining what the required number of participants should be for each experiment. Therefore, we decided to use a sample size that would match or be close to what we’ve read in the ambiguous figure perception EEG literature.

Typically, in order to determine the required sample size or the power of the sample size use, power calculations should be conducted. However, this Chapter and in Chapter 5, no power calculations have been conducted. A power calculation is possible for a number of parametric statistical tests (e.g. T- and F-test). As input for this power calculation, a measure of effect size (e.g. Cohen’s d) is required. A sensible value for Cohen’s d can sometimes be found in published studies (preferably with large sample sizes). As pointed out by Eric Maris (2017) in a thread on FieldTrip with the question of identifying effect size and power in cluster based permutation tests of EEG data, Cohen’s d can easily be obtained from the outcome of a cluster-based permutation test. This is done by calculating “the non-standardised effect sizes by averaging the (sensor, frequency, time)-specific effects within the cluster of interest. Typically, the (sensor, frequency, time)-specific effects are raw differences between the subject averages for the experimental conditions that are being compared. [This is followed by calculating] the standard deviation over the subjects of these non-standardised effect sizes. Cohen's d [is calculated] by dividing the grand average of the non-standardised effect sizes by the standard deviation obtained" ("[FieldTrip] Effect size measure for cluster-based permutation tests", 2020). However, calculating Cohen's d in this manner will be biased, and therefore cannot be used for a power calculation. This type of bias is sometimes known as "double dipping" ("[FieldTrip] Effect size measure for cluster-based permutation tests", 2020). In general, it is extremely challenging to perform power calculations for statistical analyses that involve high-dimensional EEG data. ("[FieldTrip] Effect size measure for cluster-based permutation tests", 2020)

In our experiments, no a-priori power calculations have been conducted. In addition to that, due to the sensitivity of the EEG and to the exclusion criteria, a substantial number of participants' data was excluded from our analyses which led to the lower number of participants included in the analyses.

4.2.2. Data Analysis Methods

4.2.2.1. Pre-processing.

The steps taken to pre-process, exclude and code (but not analyse) the data for the time domain MVPA analysis are the same as in Experiment 1 from Chapter 3. Some of the pre-processing steps differ for the time-frequency MVPA analysis (i.e. no filtering). These differences are described in the following sections.

Furthermore, similar to Chapter 3, the Eye-Tracker data will not be analysed. In this chapter, MVPA was meant to be conducted on the Eye-Tracking data in order to determine whether we can predict a perceptual reversal from participants' eye-movements and how this could influence (if any) the MVPA results of the EEG data. However, due to time constraints, these analyses have not conducted but will hopefully conducted and published in the future.

4.2.2.2. MVPA in the time domain.

The pre-processed data for each participant was exported from BrainVision Analyzer 2.1 and loaded into Fieldtrip under MATLAB r2018a. Using the Fieldtrip Toolbox (version 20190419; http://www.fieldtriptoolbox.org/), the data was segmented into reversal and stability epochs of 1200 ms length (-400 to 800ms). After segmentation, the data were offline referenced to Cz and a bandpass filter of 0.5-30Hz was applied to all epochs in order to align the filtering parameters with those used for the ERP studies. This is important to ensure that the information available to the ERP analyses and this MVPA analysis were equivalent.

At each position in time (increments of 1 ms) from approximately -375 to 775 ms, a separate linear support vector machine classifier was trained to classify trials as reversal or stability using (as features) the single trial voltage amplitudes in a 62 (electrodes) x 50 (samples/ms) spatio-temporal window. For instance, if a participant had 50 reversal trials and 50 stability trials, the process would start at -375 ms and train a classifier to predict reversal vs. stability on the basis of 100 spatio-temporal patterns of EEG amplitudes across 62 electrodes and 50 samples in time from -400 to -350 ms (i.e., 62 x 50 = 3100 voltages per trial). Once this time position was trained and tested to produce a decoding accuracy value, the window would move 1 ms forward and the process would run, independently, on the new (but overlapping) spatio-temporal window to produce a decoding accuracy for that time window. The result of this process for each participant was a time series of decoding accuracy values from -375 to +775 ms. We used the Fieldtrip Toolbox to run the multivariate analysis. This toolbox uses an external toolbox called Donders Machine Learning Toolbox for this type of analysis (https://github.com/distrep/DMLT).

Classifier decoding accuracy was determined using a five-fold cross-validation. This procedure divided the trials into five equally-sized groups. Four of these were designated for training the classifier (i.e., training set) and the remaining one for testing (i.e., testing set). The classifier was trained to discriminate reversal from stability trials. Using this trained classifier, decoding predictions (reversal or stable) were then made about trials in testing set. The predictions were compared against the true trial labels (reversal or stable) and marked as correct or incorrect. This results in a decoding accuracy value. This cross-validation procedure was repeated four more times with a different subset as the training and testing sets. Decoding accuracies were averaged across the 5 training and testing sets to yield the decoding accuracy for that time point. This process was repeated at each time point and for each participant separately. Importantly, the trials are not averaged during this procedure. Where participants had unequal numbers of reversal and stable trials, the number of these two types were equated within each training and testing set by random subsampling from the condition with more trials.

This process created a time-series of decoding accuracies from -375 to +775 ms for each participant. An accuracy of 50% at a particular time point indicates that there was no information predictive of reversal/stability in the spatio-temporal window centred at that time point. Decoding accuracies above 50% indicate the presence of information in the spatio-temporal window. Higher decoding accuracies indicate more information. The decoding accuracy time-series were averaged across participants to create a grand average decoding accuracy waveform.

4.2.2.3. MVPA in the time-frequency domain.

The steps taken and toolboxes used to load and segment the data were the same as the ones conducted for decoding in the time domain described above. The pre-processed data used for this analysis was the same as that used for pattern classification in the time domain except that no low pass filter was applied on the data. This filter was unnecessary because a similar effect could be achieved by simply restricting the spectral analysis to frequencies below 30 Hz (see below).

Following segmentation, the data were transformed into the frequency domain. For each trial, power was computed in the 1 Hz to 30 Hz range (1 Hz frequency resolution) using a wavelet transform (‘mtmconvol’ method in Fieldtrip’s ft_freqanalysis function) with a Hanning window. This analysis was done in from -350 to +750 ms in 10 ms intervals instead of 1 ms in order to reduce computational load. The Hanning window ensures that the temporal spread is fully confined to the specified taper length (time window specified). This analysis produced a time x frequency map (30 frequencies x 100 time points) power map for each trial. These power maps were submitted to the MVPA procedure without averaging. It is important to note that because of the sliding window (10 ms jumps) required to conduct the wavelet analysis, the output from the analysis was truncated by 200ms on each end. This resulted in the trial length for the frequency domain data being shorter.

Classifier training and cross-validation procedures took place using the same linear support vector classifier as in the time-domain analysis. However, in this analysis it was applied to the time x frequency maps at each time point (every 10ms) and each frequency level between 1 and 30Hz (with 1Hz increments). There was no 50 ms time window here because the frequency analysis already involves a windowing procedure across the data. Thus, the classifier training and testing was done on the spatial pattern of power across the scalp at each time-frequency point separately. All other aspects of the MVPA procedure were the same as for the time domain analysis. Grand average decoding accuracy maps were computed by averaging the decoding accuracy maps across participants.

4.2.2.4. Significance testing.

In order to evaluate whether MVPA produced above chance classification accuracy across time (for time domain analysis) and across time x frequency results (for frequency domain results) and to control Type 1 error rate, we conducted cluster based permutation tests using MATLAB r2018a (Mensen & Khatami, 2013; Nichols, 2012; Oosterhof et al., 2016; Smith & Nichols, 2009). This approach is well established in EEG and FMRI contexts and it has been implemented in the Fieldtrip and other toolboxes (Mensen & Khatami, 2013; Nichols, 2012; Oosterhof et al., 2016; Pernet et al., 2015; Salimi et al., 2011; Smith & Nichols, 2009). It typically involves a correction for multiple comparisons and has been shown to control Type I error rates well (e.g., Groppe et al., 2011).

Cluster-based approaches involve an initial cluster identification step in which an uncorrected t-test is performed at every position in time, for time domain analyses, or at each time-frequency position, in frequency domain data. In our analyses, this comprised a one-sample t-test comparing the observed prediction accuracy to 50% (i.e., chance performance). Clusters are then formed by identifying any contiguously connected area of significance. For instance, if all of the time points between -100 to -50 were significant then this would be a single cluster (see Figure 4.1 in the results section below for an example of a significant time domain cluster). For the time-frequency domain, the boundaries of clusters can be irregular across the time x frequency map (see Figure 4.5 in the results section below for an example of a significant time-frequency cluster). For each cluster that was identified, a cluster statistic was formed by summing all of the t-values from the tests of each point in the cluster. This cluster statistic, indicated as tcluster below, served as the inferential statistic for that cluster going forward.

The next step of the cluster-based approach involved determining which of the clusters would be considered to be statistically significant. A permutation approach was used for this (Maris & Oostenveld, 2007). Typically, this involves randomly shuffling the condition labels for each participant and then recomputing the results (i.e., a new t statistic) for each shuffle. This can involve thousands or tens of thousands of different permutations of the results. The resulting set of t-statistics from all of the permutations forms a t distribution, which can be used like a null hypothesis t distribution. The original t-value is compared against this permutation distribution to assess how extreme it is (i.e., how far out in the tail/tails). A p-value can be calculated from this (i.e., only 4% of permuted t-values are more extreme). This p-value then indicates the level of significance for the cluster. For an accessible summary of this approach see Blair & Karnisky (1993) as well as Groppe et al. (2011).

In the present study, predicted accuracy time-series (for time domain analysis) or time-frequency accuracy maps (for time-frequency analyses) were computed for each participant. The cluster-forming test was conducted at each time point or time-frequency point by comparing the distribution of values across participants to 0.5 using a one-sample t-test. Clusters comprised the set of all contiguous significant time (or time-frequency) points in the results of this test. Cluster t-values were computed by summing all of the cluster-forming t-values of points within the clusters.

The permutation distribution was assembled by computing t-tests on 50,000 permutations of the data. For each permutation, a random subset of participants was chosen to have their data permuted. This meant that, for these participants, the direction of the difference between their original accuracy score and 0.5 was reversed (based on Groppe's one-sample t-test function: https://www.mathworks.com/matlabcentral/fileexchange/29782-mult_comp_perm_t1-data-n_perm-tail-alpha_level-mu-reports-seed_state). For instance, if their original accuracy score at a particular time-frequency location was 0.56, the permuted version of that would be 0.44. For the remaining non-permuted participants, the data was left as in the original set. After permutation, a t-test was conducted at each time or time-frequency point using the values from all participants at each point. New cluster statistics were computed for each of the clusters identified in the cluster-forming step describe above.

The permutation distribution was constructed by selecting only the maximum cluster t-value from amongst all of the clusters on each permutation to be added to the permutation distribution. Thus, the permutation distribution comprised the 50,000 maximal cluster t-values. This so-called t max procedure has been shown to control the Type 1 error rate very strongly (Blair & Karnisky, 1993; Groppe, Urbach, & Kutas, 2011). Finally, to determine the p-value for each of the clusters identified in the cluster-forming step, their original t-values were compared against the permutation distribution to assess the proportion of more extreme values in the distribution. This proportion became the p-value for each cluster.

4.2.3. Results

4.2.3.1. Behavioral results.

See Experiment 1 in Chapter 3 for behavioural results.

4.2.3.2. Time domain MVPA results.

Cluster based statistics of the MVPA analysis in the post-stimulus time domain showed that the classifier significantly distinguished reversal trials from stability trials in one post-stimulus time cluster from 42ms to 695ms, $t_{cluster}(16) = 2.665 \times 10^3$, $p < .001$ with a mean accuracy of 0.5290 (min = 0.5102, max = 0.5450). This overlaps with time frames of the RP, RN, Frontopolar Positivity and Parietal Positivity as well as incorporating other time points. See Figure 4.1 for the average (across participants) accuracy across time.

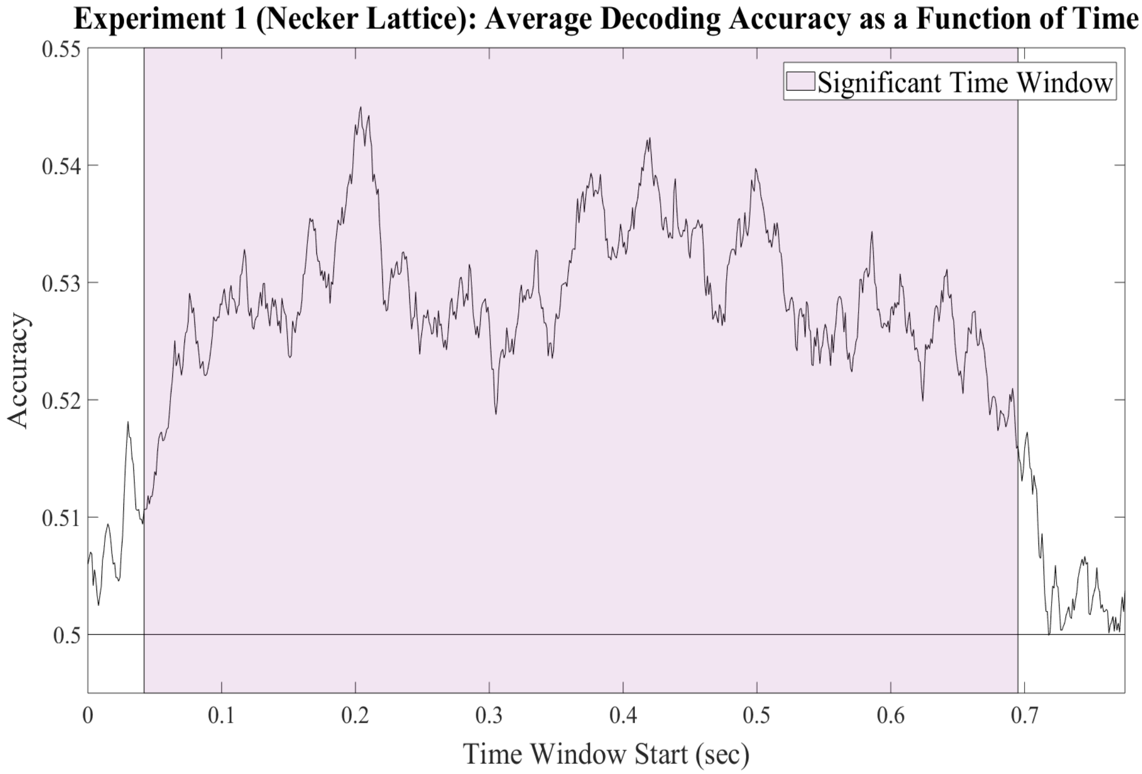


Figure 4.1. Plot of mean reversal vs. stability decoding accuracy across the post-stimulus period in Experiment 1 (Necker Lattice). The area marked in purple represents the significant cluster obtained from cluster-based permutation tests of the accuracy values.

In order to investigate the effect of Response that was observed previously in Chapter 3, we also conducted MVPA separately on Response and No Response trials. Cluster based statistics of the pattern classification analysis in the time domain showed that for Response trials, there was one significant cluster, $t_{cluster}(16) = 3.5047 \times 10^3$, $p < .001$ with mean accuracy of 0.5559 (min = 0.5179, max = 0.6018). This cluster occured from 13 ms until 713 ms after stimulus onset (Figure 4.2). For the non response condition, there was one significant cluster between 15 ms and 567 ms, $t_{cluster}(16) =$

2.2673×10^3, $p < .001$ (Figure 4.3). The mean accuracy value for this cluster was 0.5407 (min = 0.5209, max = 0.5692).

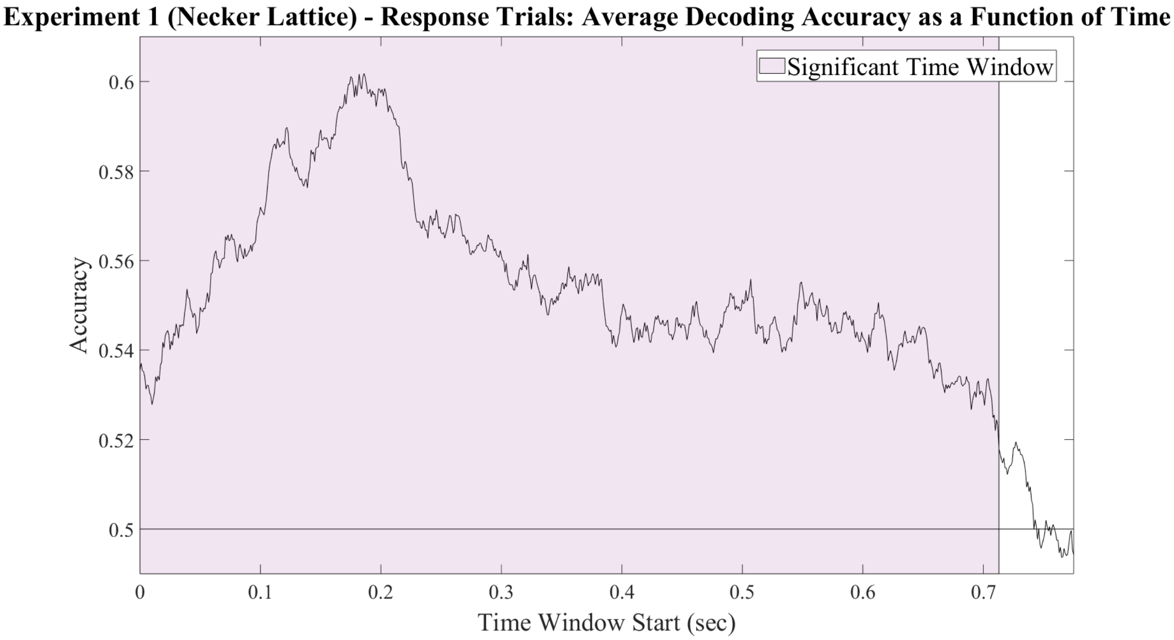


Figure 4.2. Plot of mean reversal vs. stability decoding accuracy across the post-stimulus period in Experiment 1 (Necker Lattice) for the response trials only. The area marked in purple represents the significant cluster obtained from cluster-based permutation tests of the accuracy values.

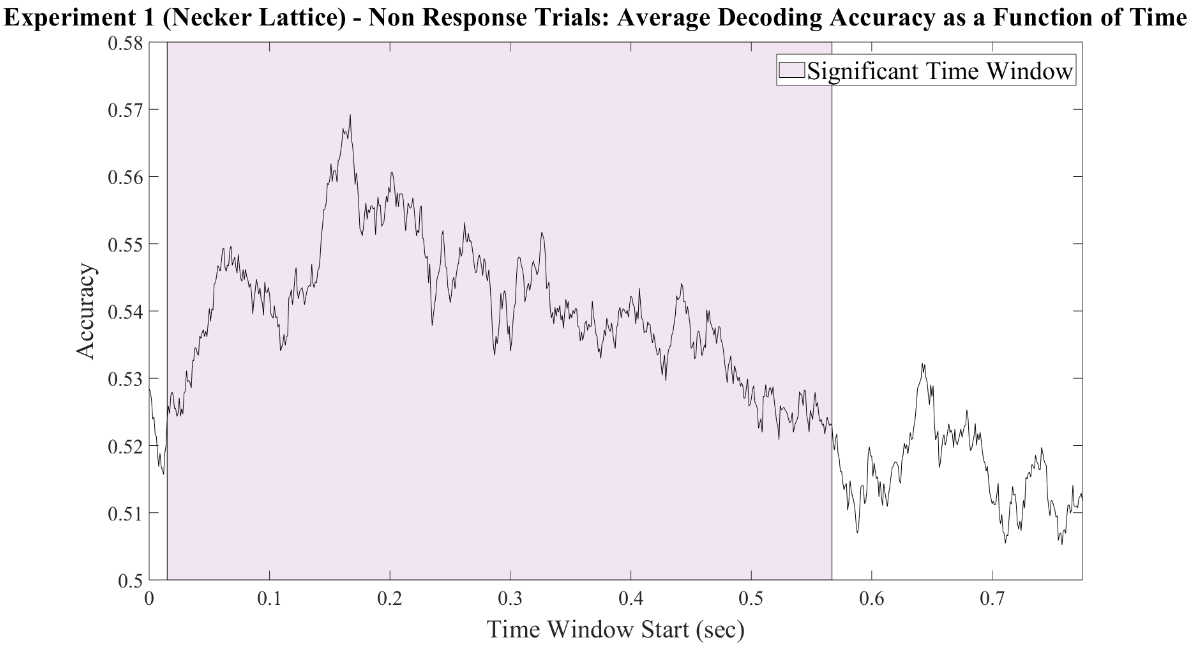


Figure 4.3. Plot of mean reversal vs. stability decoding accuracy across the post-stimulus period in Experiment 1 (Necker Lattice) for the non-response trials only. The area marked in purple represents the significant cluster obtained from cluster-based permutation tests of the accuracy values.

To compare the time-courses of response and non-response decoding accuracies, we used a paired-samples cluster-based approach (Maris & Oostenveld, 2007; van Djik et al., 2008), which is similar to the approach above but using paired-samples t-tests instead of one-sample tests. This revealed three significant clusters during which the mean prediction accuracy of Response and No Response trials differed. The first cluster occurred between 106 and 147 ms, $t_{cluster}(16) = 114.4130$, $p = .0365$ with the mean decoding accuracy value for Response trials in this cluster being 0.5825 (min = 0.5762, max = 0.5898) and for the No Response trials, 0.5431 (min = 0.5341, max = 0.5561). The second cluster occurred between 170 and 216 ms, $t_{cluster}(16) = 137.2378$, $p = .0109$ with mean decoding accuracy value for Response trials in this cluster being 0.5967 (min

= 0.5870, max = 0.6018) and for the No Response trials, 0.5559 (min = 0.5512, max = 0.5620). The third cluster occurred between 576 and 620 ms, $t_{cluster}(16) = 137.6943$, $p = .0108$ with mean decoding accuracy value for Response trials in this cluster being 0.5451 (min = 0.5394, max = 0.5506) and for the No Response trials, 0.5138 (min = 0.5070, max = 0.5198). See Figure 4.4 for an illustration of these significant mean differences in average accuracy across time between response and non-response trials.

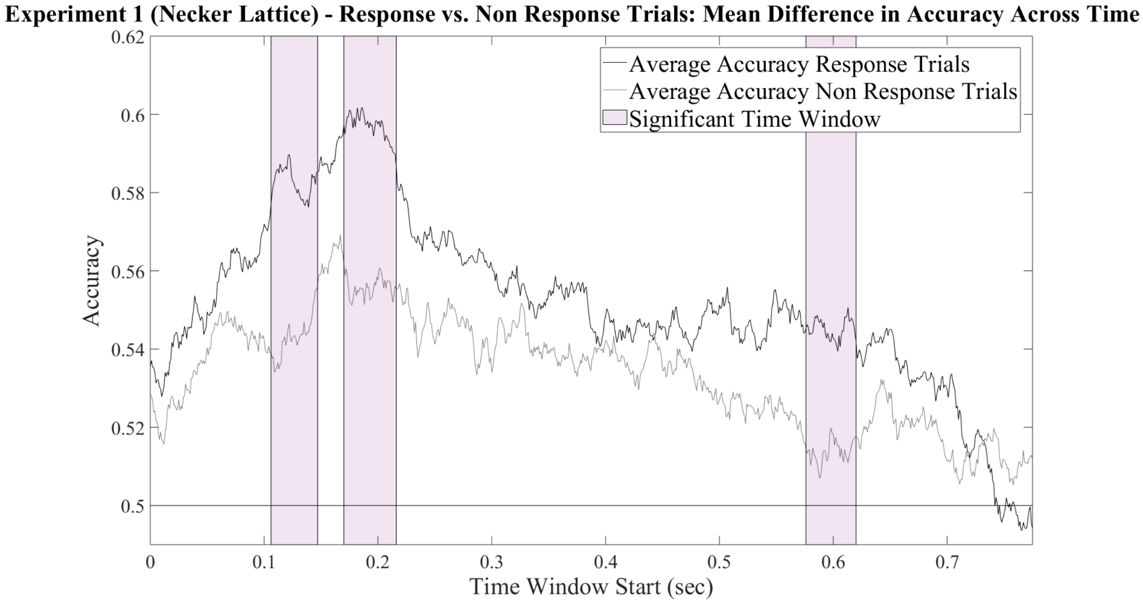


Figure 4.4. Plot of mean reversal vs. stability decoding accuracy across the post-stimulus period in Experiment 1 (Necker Lattice) for the response (black line) and non-response trials (grey line). The areas marked in purple represent the significant clusters obtained from cluster-based permutation tests of the accuracy values. These represent the clusters during which the mean difference in accuracy between response and non-response trials is significant.

4.2.3.3. Frequency domain MVPA results.

Cluster based statistics in the frequency domain showed that the classifier significantly distinguished reversal trials from stability trials in one time frequency cluster, $t_{cluster}(16) = 3.7268 \times 10^3$, $p<0.001$ with a cluster mean decoding accuracy value of 0.5234 (min = 0.5098, max = 0.5547; Figure 4.5). The significant values in the cluster fall in the entirety of the frequency range chosen in our analysis (1-30Hz) between 12 ms before stimulus onset until 535 ms after stimulus onset.

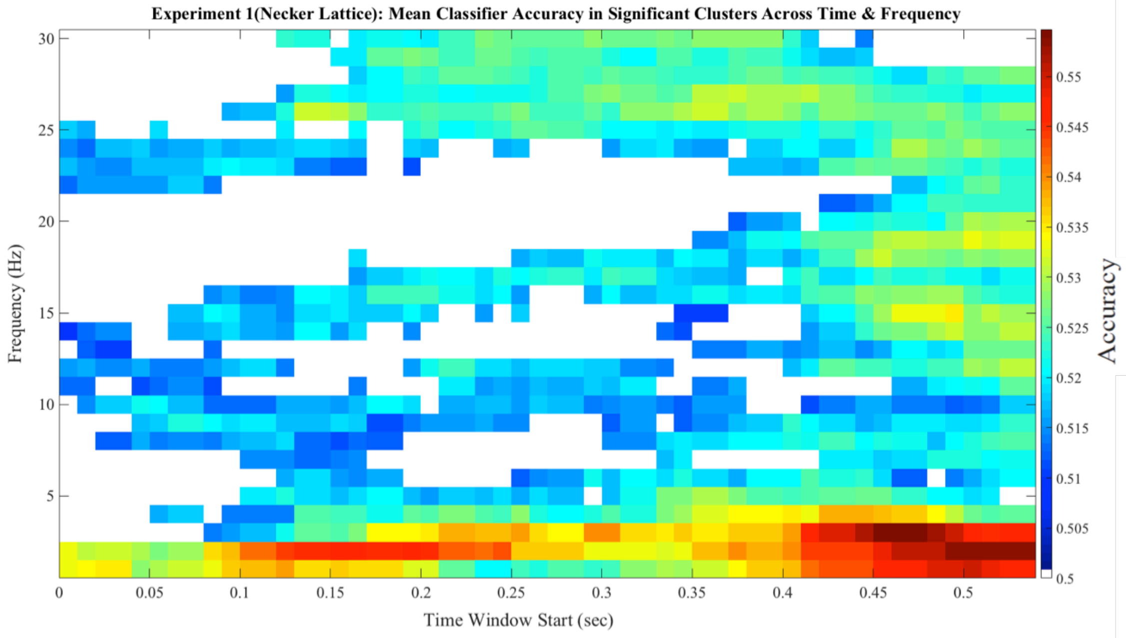


Figure 4.5. Time-frequency map of the significant cluster of reversal vs. stability decoding accuracy values averaged across participants and channels in the post-stimulus period of Experiment 1 (Necker Lattice). This map shows only the significant cluster. Non-significant areas are masked out. The dark red colour reveals the highest period of decoding accuracy (i.e. successful classification). The blue (and darker blue) colour(s) reveals periods of decoding accuracy close to, at or below chance. Due to the sliding window (10 ms jumps) required to conduct the wavelet analysis, the output from the analysis was truncated by 200ms on each end. This resulted in the trial length for the frequency domain data being shorter. Therefore, in the resultant map, the last 200 ms after 540 ms are not represented in the figure.

In order to investigate the effect of Response, we also ran the classifier on Response only trials and on No Response only trials separately. Cluster based statistics showed that for Response trials, there was one significant cluster, $t_{cluster}(16) = 7.1681$ x

10^3, $p < .001$ with a cluster mean decoding accuracy value of 0.5442 (min = 0.5145, max = 0.5822). This analysis showed that significant decoding accuracies occurred at all frequency levels from 10 ms before stimulus onset until 540 ms after stimulus onset. See Figure 4.6 for a map of the decoding accuracies in the significant cluster across time and frequency for the response trials only.

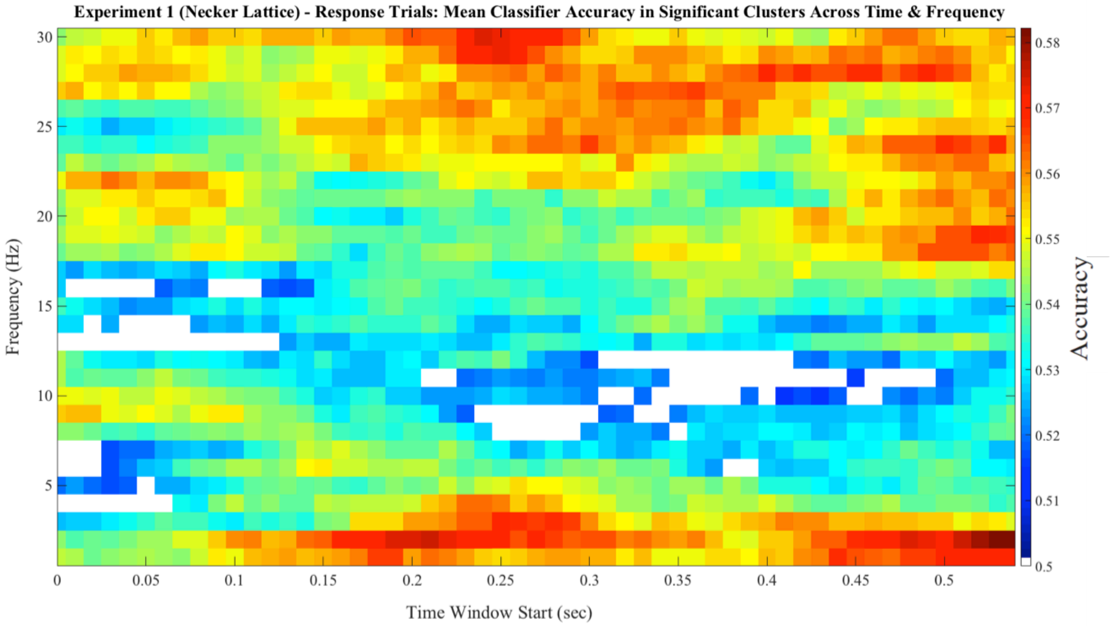


Figure 4.6. Time x Frequency map of the significant cluster of reversal vs. stability decoding accuracy values averaged across participants and channels in the post-stimulus period of the response trials only in Experiment 1 (Necker Lattice). This map shows only the significant cluster. Non-significant areas are masked out. The dark red colour reveals the highest period of decoding accuracy (i.e. successful classification). The blue (and darker blue) colour(s) reveals periods of decoding accuracy close to, at or below chance. Due to the sliding window (10 ms jumps) required to conduct the wavelet analysis, the output from the analysis was truncated by 200ms on each end. This resulted in the trial length for the frequency domain data being shorter. Therefore, in the resultant map, the last 200 ms after 540 ms are not represented in the figure.

Cluster based statistics on the decoding accuracy values in the frequency domain showed that for Non Response trials, there was one significant cluster, $t_{cluster}(16) =$

7.5918×10^3, $p<0.001$ with a cluster mean decoding accuracy value of 0.5486 (min = 0.5148, max = 0.5807). This analysis showed that significant decoding accuracies occurred for all frequencies between 1-30Hz from 10 ms before stimulus onset until 540 ms after stimulus onset. See Figure 4.7 for a map of the decoding accuracies in the significant across time and frequency for the non-response trials only.

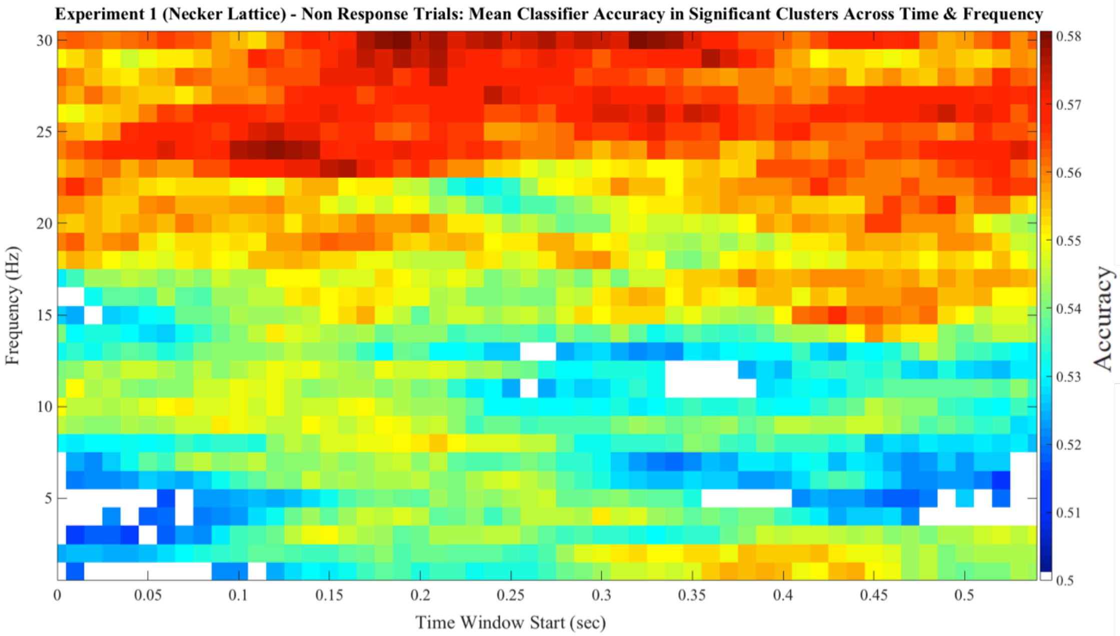


Figure 4.7. Time x Frequency map of the significant cluster of reversal vs. stability decoding accuracy values averaged across participants and channels in the post-stimulus period of the non-response trials only in Experiment 1 (Necker Lattice). This map shows only the significant cluster. Non-significant areas are masked out. The dark red colour reveals the highest period of decoding accuracy (i.e. successful classification). The blue (and darker blue) colour(s) reveals periods of decoding accuracy close to, at or below chance. Due to the sliding window (10 ms jumps) required to conduct the wavelet analysis, the output from the analysis was truncated by 200ms on each end. This resulted in the trial length for the frequency domain data being shorter. Therefore, in the resultant map, the last 200 ms after 540 ms are not represented in the figure.

Paired-samples cluster-based stats revealed that there was one significant cluster during which the mean decoding accuracy of Response and No Response trials differed,

$t_{cluster}(16) = 73.1310$, $p = .0076$ with a mean decoding accuracy value for Response trials in this cluster being 0.5369 (min = 0.5251, max = 0.5470) and for the No Response trials, 0.5698 (min = 0.5578, max = 0.5791). This cluster occurs between 10 and 130 ms at 23-26Hz. See Figure 4.8 for the time-frequency map of the difference in decoding accuracies between response and non-response trials.

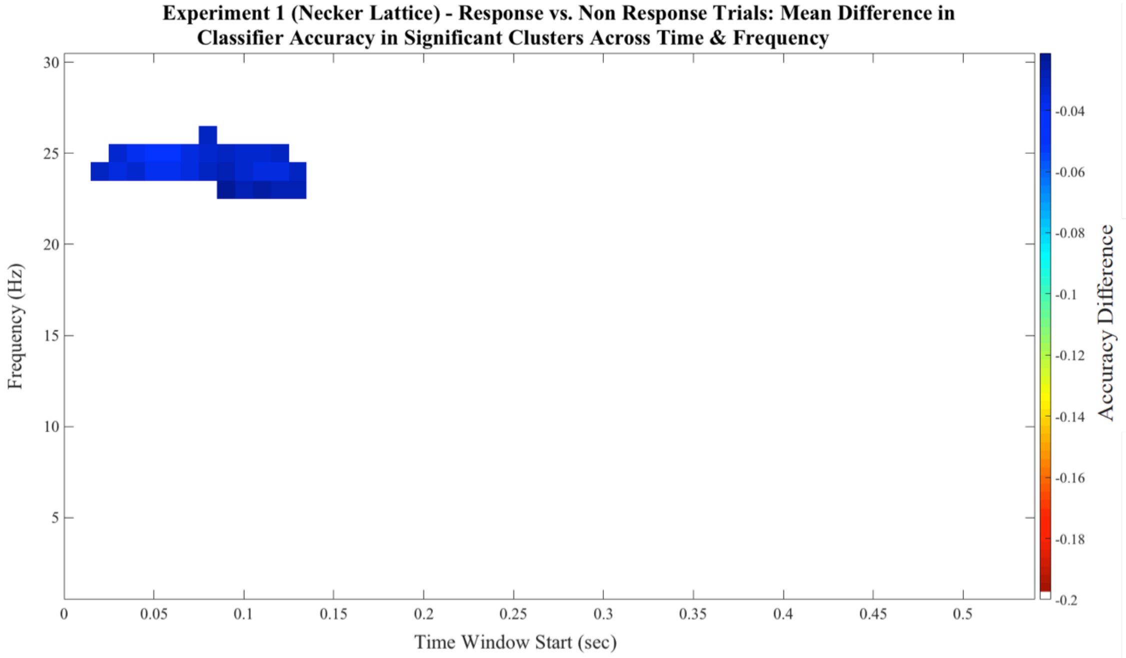


Figure 4.8. Time x Frequency map of the significant cluster of the mean difference of the reversal vs. stability decoding accuracy values in the post-stimulus period between the response and non-response trials in Experiment 1 (Necker Lattice). This map shows only the significant cluster. Non-significant areas are masked out. The accuracy difference corresponds to the subtraction of the accuracy values of the response trials from the decoding accuracy values of the non-response trials. These values are then averaged across participants. The colour bar represents the difference between the accuracy values of the response and non-response trials. Here, all the values are negative indicating that the decoding accuracy values were higher for the response trials than the non-response trials in this significant cluster. Due to the sliding window (10 ms jumps) required to conduct the wavelet analysis, the output from the analysis was truncated by 200ms on each end. This resulted in the trial length for the frequency domain data being shorter. Therefore, in the resultant map, the last 200 ms after 540 ms are not represented in the figure.

4.2.4. Interim Discussion

In Experiment 1, MVPA analyses based on time-domain data could significantly distinguish reversal and stable trials in the post-stimulus period until 720ms. This period overlaps with the latencies of the RP, RN, Frontopolar and Parietal positivities. It is possible that the classifier was picking up on patterns related to these known ERP components. However, as was mentioned previously, MVPA integrates information for the entire scalp. Thus, it is not necessarily the case that the classifier was picking on patterns related to these ERP components. It could be that other patterns of activity drive accurate classification. Figure 4.9 provides an illustration of how the results found from time domain MVPA in Experiment 1 overlap with the time windows of these known reversal-related ERP components highlighted. Figure 4.9 shows that, in addition to these components, the significant cluster includes a time window that precedes the RP. This demonstrates that the pattern of activity associated with the reversal trials can be distinguished from the pattern of activity of stable trials before the RP despite there being no known ERP correlates of this. It is important to note that the time points in the significant cluster also include information from the 25 ms preceding them. This means that the patterns of activity associated with reversal and stability trials can potentially be distinguished from one another as early as 17 ms after stimulus onset.

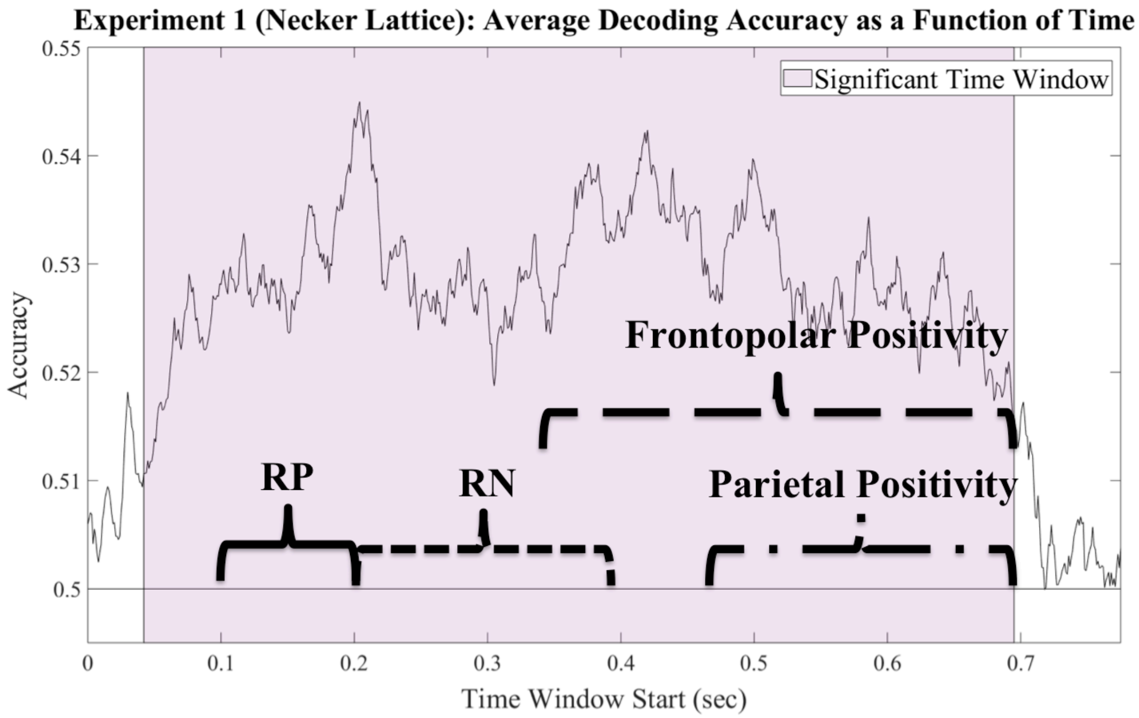


Figure 4.9. Plot of mean reversal vs. stability decoding accuracy across the post-stimulus period in Experiment 1 (Necker Lattice) with braces indicating the latencies of well-known reversal related ERP components. The area marked in purple represents the significant cluster obtained from cluster-based permutation tests of the accuracy values. The solid brace corresponds to the latency of the RP, the dashed brace with narrow spacing corresponds to the latency of RN, the large dashed brace corresponds to the latency of the Frontopolar Positivity and the dashed and dotted brace corresponds to the latency of the Parietal Positivity.

Kornmeier and Bach (2012) have suggested that the RP is the earliest ERP correlate of perceptual reversals during intermittent presentation of an ambiguous figure and that it is a marker of the detection of ambiguity. Moreover, previous findings have suggested that the P100 is the earliest occipital visual evoked response component that peaks at around 100ms after stimulus onset. Our decoding results in Experiment 1 suggest that there are earlier signatures that are predictive of and are linked to perceptual reversals that cannot be detected using univariate approaches. This idea is in line with previous research that suggests that MVPA can detect activity that is hidden in univariate analyses due to focus on only a few electrodes rather than the entire pattern of activity across the scalp (Cauchoix et al., 2012).

The time domain analyses revealed that for the response trials, MVPA significantly distinguished reversal related activity from stability related activity starting at 13ms. As was mentioned previously, because of the 50 ms time windows, decoding at each time point includes information from the activity occurring up to 25ms preceding and following this time point. This means that significant clusters which onset before 25 ms post-stimulus may be basing their decoding partially on data from the pre-stimulus period as well. This is also observed in the time domain analyses of the non-response trials, which showed decoding from 15ms after stimulus onset. Drawing from Kornmeier and Bach (2012)'s integrative theory, this could potentially signify that the brain state at the moment of the onset of the stimulus is unstable and that there is observable patterns of activation that are taking place in order to resolve this instability early on. This activity occurs regardless of response action. However, it is also possible that these early decoding effects rely on patterns of activity that occur in the latter half of the 50 ms window and thus would not involve any pre-stimulus information.

Moreover, our time domain analyses reveal that the periods of significant decoding occur throughout the post-stimulus period (until 695 ms) for the overall trials (Response and No Response combined) and for the Response trials until 713 ms. As for the Non Response trials, decoding in the time domain revealed successful decoding of reversal trials from stable trials from stimulus onset until 567 ms. This suggests that differences between the patterns of activity for reversal and stable trials stops at an earlier time for non-response trials than for response trials. In addition to the results from Chapter 3, which showed response-dependence of the RP component, these new decoding results show a further difference in reversal-related processing that is dependent on response, albeit at a much longer latency. We have not explored that time frame in the ERP study because that analysis was strongly guided by a priori ROIs from previous research in order to maintain Type 1 error rate below 5%.

Our results also show a significant difference in decoding accuracy between Response and Non Response trials around the latency of the RP and the RN (see Figure 4.4 above). Based on our findings from the previous chapter where we found a difference between Response and No Response trials for the RP, these findings are not surprising for the RP time frame. The RP time frame overlaps largely with the MVPA differences between response and no response trials. It is likely that these decoding differences are related to the same mechanisms generating differences in the RP. We saw no differences in the RN due to response in Chapter 3 and similarly, most of the time window for the RN has no decoding differences in our MVPA results.

Some of the significant time domain clusters overlap, in time, with our frequency domain results. Our time frequency results show significant decoding throughout most of the post-stimulus period at all the frequency levels included in our analysis. This differs from the findings in the literature. Previous findings have suggested that specific frequency modulations at specific time periods contribute to perceptual reversals (for a full review of these frequency modulations see Kornmeier & Bach, 2012). For instance, researchers found alpha power left-hemispheric reductions during the latency of the RP (Isoglu-Alkac et al., 2000; Isoglu-Alkac and Strüber, 2006; Strüber and Herrmann, 2002). Kornmeier and Bach (2012) have linked this activity to disambiguation time, which is the time it takes to disambiguate the ambiguous information received from the stimulus. This is because a decrease in alpha activity is suggested to be linked to excitation/activation of perceptual processing. In addition to that, Ehm et al. (2011) reported modulations at the beta and gamma bands with a left-central increase in gamma activity on reversal reported trial at around 250 ms followed by a right-central increase in beta activity starting at around 320 ms. These modulations have been linked to perceptual reversals and take place during the latency of the RN. As was mentioned in Chapter 1, the functional role of these modulations remains unclear. However, they have been suggested to take place after the disambiguation of the stimulus (Kornmeier & Bach, 2012) and have been suggested to indicate the build up of a coherent percept rather than its maintenance (Ehm et al., 2011).

The time-frequency results from MVPA in Experiment 1 reveal, however, that the patterns of activity linked to reversal and stable trials can be distinguished from one another across a wide set of frequencies from 1-30 Hz throughout stimulus presentation (until ~540ms). Interestingly, some of the frequencies in the significant time-frequency cluster are in line with previous findings in the literature. For instance, the results from MVPA show beta effects around 200 ms after stimulus onset spanning throughout the post-stimulus period. This is in line with Ehm et al (2011)'s findings described previously. Although Ehm et al. (2011) refer to the frequency values between 26-30Hz as lower gamma; here we refer to them as beta. The labelling of this frequency range in the literature is variable (e.g. considered as lower gamma in Ehm et al., 2011; considered as beta in Cochin et al., 1998). This however, does not change the interpretation of our results. In addition to that our results show alpha effects that overlap in time with findings described previously from the literature (e.g. Ehm et al., 2011; Isoglu-Alkac et al., 2000, Isoglu-Alkac and Strüber, 2006, Strüber and Herrmann, 2002). However, the effects measured in the significant cluster are not isolated in time and space. Although in our analyses this comes out as one large cluster, it may not represent one homogenous mechanism. It may be made up of several different mechanisms including those previously observed. Alternatively, our findings may represent different mechanisms than the ones than have been found in previous studies.

The periods of non-significant decoding accuracies present in the results of the overall trials (i.e. response and non-response trials included in the analysis) are not fully observed in the separate time-frequency pattern classification analyses of the response and non-response trials. These show that throughout the post-stimulus period, all frequency bands show significant decoding accuracies. However, there are some periods that show non-significant decoding accuracies. These differ between the results of the response and non-response trials. Pattern classification in the time-frequency domain of the response trials reveals that ~210-460 ms (see Figure 4.6), the decoding accuracies at several levels in the alpha band are not significant. This time window falls after the suggested disambiguation time window indexed by alpha modulations in previous studies (Isoglu-Alkac et al., 2000; Isoglu-Alkac & Strüber, 2006; Kornmeier & Bach, 2012; Strüber and Herrmann, 2002). Moreover, the results show significant decoding accuracies measured in the time-frequency cluster in the alpha band before that non-significant window. This could potentially mean that disambiguation has taken place and that a new mechanism driving perceptual reversals is taking place. This needs to be explored further using analyses like temporal generalization that can identify whether the activity observed in the significant cluster is linked to one or several mechanisms (discussed further in the general discussion).

This non-significant period in the alpha frequency band is not observed for non-response trials (see Figure 4.7). Moreover, the highest decoding accuracy values in the significant time-frequency cluster for the non-response trials occur at the higher frequency bands included in the analysis (beta band). This is true throughout the post-stimulus period included in the analysis. If beta band activity were truly indicative of a build up of a coherent percept rather than its maintenance (Ehm et al., 2011), then based on the findings from the time-frequency classification of the non-response trials in Experiment 1, this build up of a coherent percept occurs throughout the post-stimulus period for these trials. This is assuming that the measured activity belongs to one ongoing mechanism throughout the post-stimulus period. Further analyses exploring whether these modulations at the beta, alpha and other frequency bands represent different mechanisms across time are required to investigate this further (discussed in the general discussion). This finding however, further suggests a modulatory role of response on perceptual reversals.

Frequency domain decoding revealed that there is a difference in the mean decoding accuracy between the response and no response trials in the beta band between 10 and 130 ms for the Necker Lattice. This overlaps with part of the RP time window

(Kornmeier & Bach, 2005, 2006) where, based on our previous ERP findings, the RP is only present on response trials. Figure 4.8 reveals that during that cluster decoding accuracies are higher for the response trials than the non-response trials. Beta modulations have been previously found to correlate with endogenous perceptual reversals and with intended or predicted maintenance of the perceptual interpretation of an ambiguous image (Engel and Fries, 2010). In addition to these findings, beta band activity in studies using the manual response paradigm was found to be associated with sensorimotor activity and motion perception (Cochin et al., 1998; Wheaton et al., 2009).

Recent work suggests that beta modulations may be a signature of an active process that promotes the existing motor set whilst compromising neuronal processing of new movements (Engel & Fries, 2010). In a Go/No-Go study by Wheaton et al. (2009), a beta-band power decrease was reported on No-Go trials. Recently, beta band modulations in the motor cortex have been associated with anticipatory processes. They are suggested to reflect a decision about an upcoming action 500ms before button press (Donner et al., 2009). This could potentially overlap with the significant findings of the cluster from the paired samples test comparing the decoding accuracy of response and non-response conditions. This, in turn, would suggest that there are differences in beta modulations that are attributed to response action (e.g. response or no response) for the Necker Lattice. Moreover, the difference in the decoding accuracy values measured between response and non-response conditions further suggests that there are different representations linked to reversal vs. stability decoding between response conditions. The classifier here was better at distinguishing between the two perceptual states for the non-response trials than the response trials, indicated by the negative values of the accuracy difference in Figure 4.8 (the difference time-frequency was calculated by subtracting the time-frequency decoding accuracy value of the non-response trials from the response trials). This suggests that there are different processes that underlie reversal vs. stability decoding that are modulated by response.

In order to test whether our results generalise to a different ambiguous stimulus, we also conducted the same analyses on the data from Experiment 2, which used the Faces-Vase stimulus instead of the Necker cube. Results that overlap between these experiments will suggest general mechanisms for perceptual reversal.

4.3. Experiment 2: Rubin's Face-Vase

4.3.1. Methods

The same data used in Experiment 2 from Chapter 3 is used here. See sections on 'Participants', 'Stimuli & Apparatus', 'EEG Recording' and 'Procedure' in Chapters 3 and 4 for a detailed account of the experimental paradigm. The same exclusion criteria were also applied for completion purposes.

4.3.2. Data Analysis Methods

The steps taken to pre-process, exclude, code and analyse the data are the same as in Experiment 1 above.

4.3.3. Results

4.3.3.1. Behavioural results.

See Experiment 2 in Chapter 3 for behavioural results.

4.3.3.1. Time domain MVPA results.

Cluster-based statistics of MVPA analysis in the time domain across the post-stimulus time window showed significantly above chance decoding in one cluster

(Figure 4.10), $t_{cluster}(16) = 441.2077$, $p<.001$ with a mean decoding accuracy of 0.5196 (min = 0.5122, max = 0.5254). This cluster occurred between 159 ms and 294 ms. This includes part of the latency of both the RP and RN ERP components.

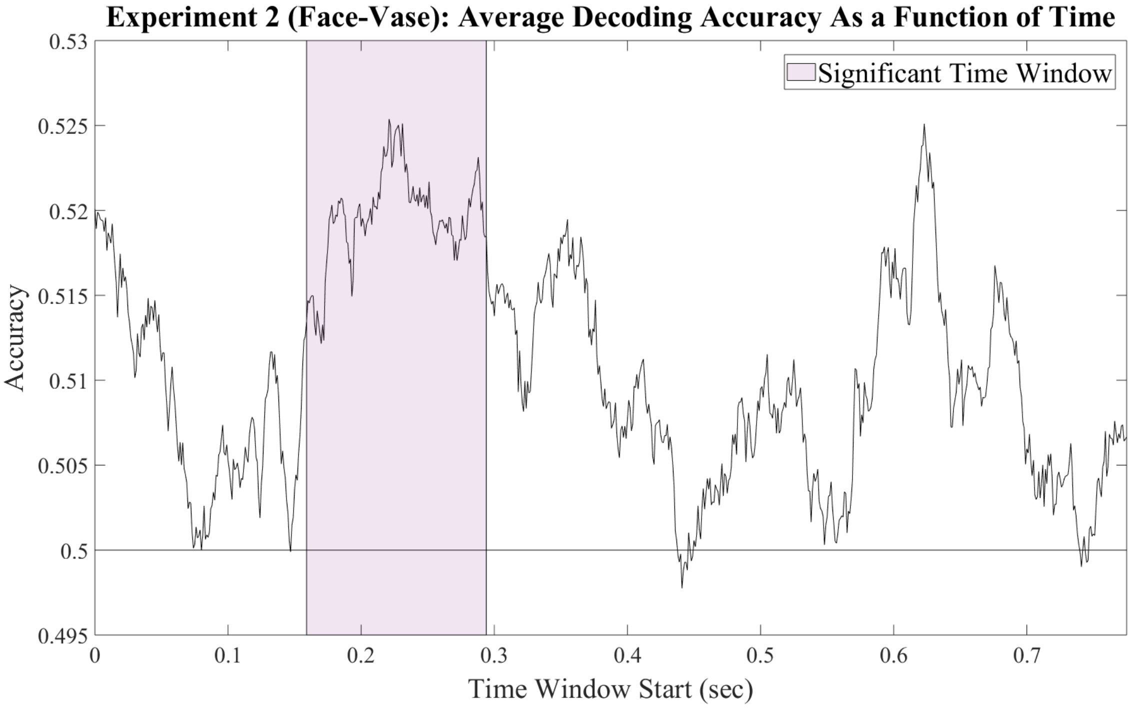


Figure 4.10. Plot of mean reversal vs. stability decoding accuracy across the post-stimulus period in Experiment 2 (Face-Vase). The area marked in purple represents the significant cluster obtained from cluster-based permutation tests of the accuracy values.

In order to investigate the effect of Response on decoding accuracy, we conducted MVPA on Response and No Response only trials separately. The results showed that for Response trials, there was one significant cluster between 113 ms and 303 ms (Figure 4.11), $t_{cluster}(16) = 819.4017$, $p <.001$ with mean decoding accuracy value of 0.5696 (min = 0.5296, max = 0.6127). This corresponds to the latency of the RP and part of the RN. Results for No Response trials showed one significant cluster between 170 ms and 259 ms (Figure 4.12), $t_{cluster}(16) = 387.8413$, $p < .001$ with a mean decoding accuracy value of 0.5421 (min = 0.5254, max = 0.5539). There was also a marginally significant cluster, $t_{cluster}(16) = 162.6658$, $p = .0581$ with mean decoding accuracy of 0.5383 (min = 0.5235, max = 0.5490). This cluster appeared between 51 and 97 ms.

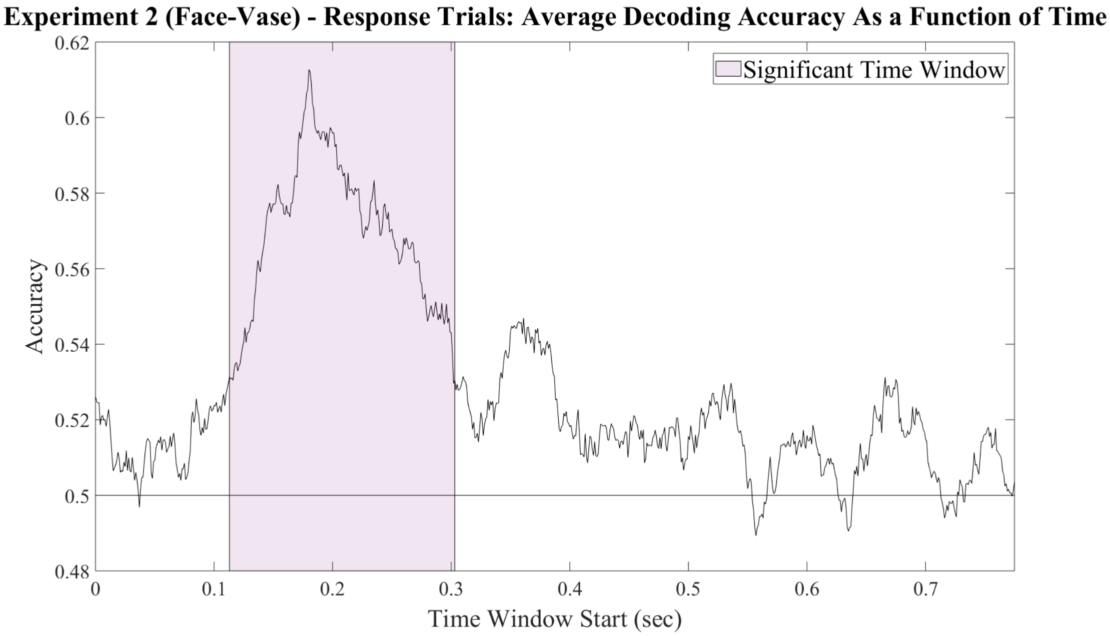


Figure 4.11. Plot of mean reversal vs. stability decoding accuracy across the post-stimulus period in Experiment 2 (Face-Vase) for the response trials only. The area marked in purple represents the significant cluster obtained from cluster-based permutation tests of the accuracy values.

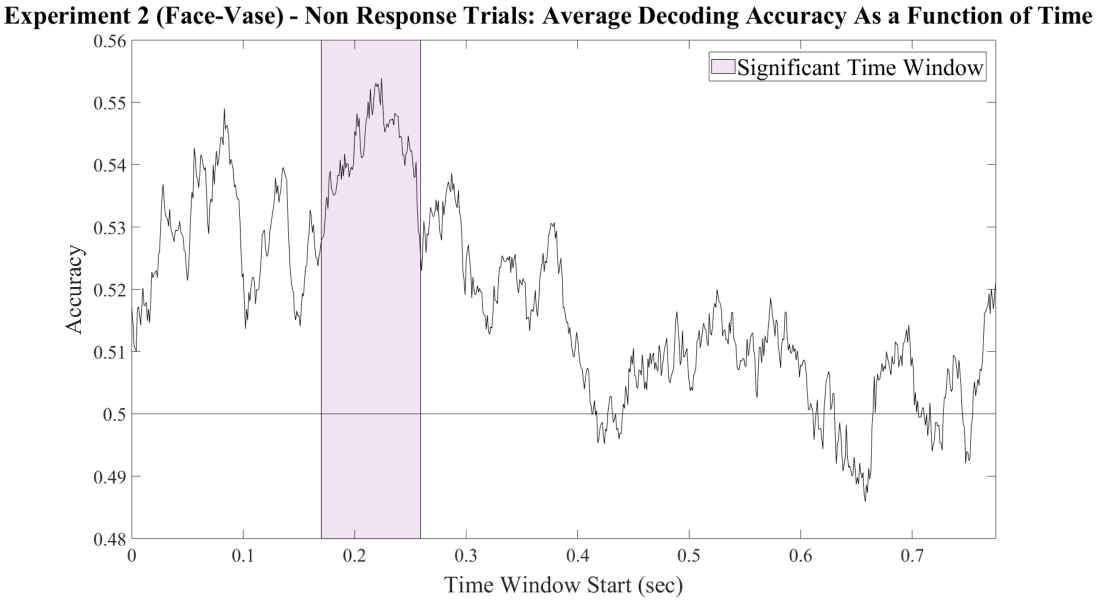


Figure 4.12. Plot of mean reversal vs. stability decoding accuracy across the post-stimulus period in Experiment 2 (Face-Vase) for the non-response trials only. The area marked in purple represents the significant cluster obtained from cluster-based permutation tests of the accuracy values.

Paired-samples cluster based stats revealed that there was one significant cluster during which the mean decoding accuracy of Response and No Response trials differed, $t_{cluster}(16) = 126.56$, $p = .0028$ (Figure 4.13). The mean decoding accuracy value of Response trials in this cluster was 0.5939 (min = 0.5736, max = 0.6127) whereas for the No Response trials it was 0.5349 (min = 0.5237, max = 0.5454). This window occured between 161 ms and 201 ms.

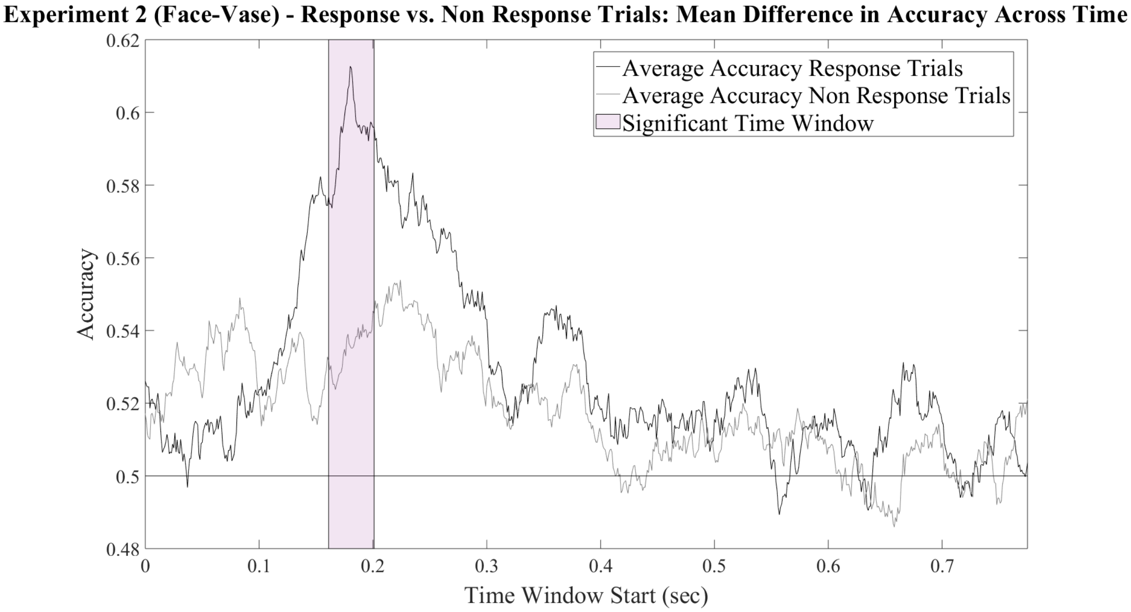


Figure 4.13. Plot of mean reversal vs. stability decoding accuracy across the post-stimulus period in Experiment 2 (Face-Vase) for the response (black line) and non-response trials (grey line). The areas marked in purple represent the significant clusters obtained from cluster-based permutation tests of the accuracy values. These represent the clusters during which the mean difference in accuracy between response and non-response trials is significant.

4.3.3.2. Frequency domain MVPA results.

MVPA analysis in the time frequency domain showed significant decoding in one time-frequency cluster, $t_{cluster}(16) = 4.0314 \times 10^3$, $p<0.001$ with cluster mean decoding accuracy of 0.5149 (min = 0.5076, max = 0.5296). This analysis showed that at each frequency level, there was a significant time window of significant decoding accuracy. The significant time window ranged from 5 ms until 535 ms after stimulus onset at all frequencies 1-30 Hz (Figure 4.14).

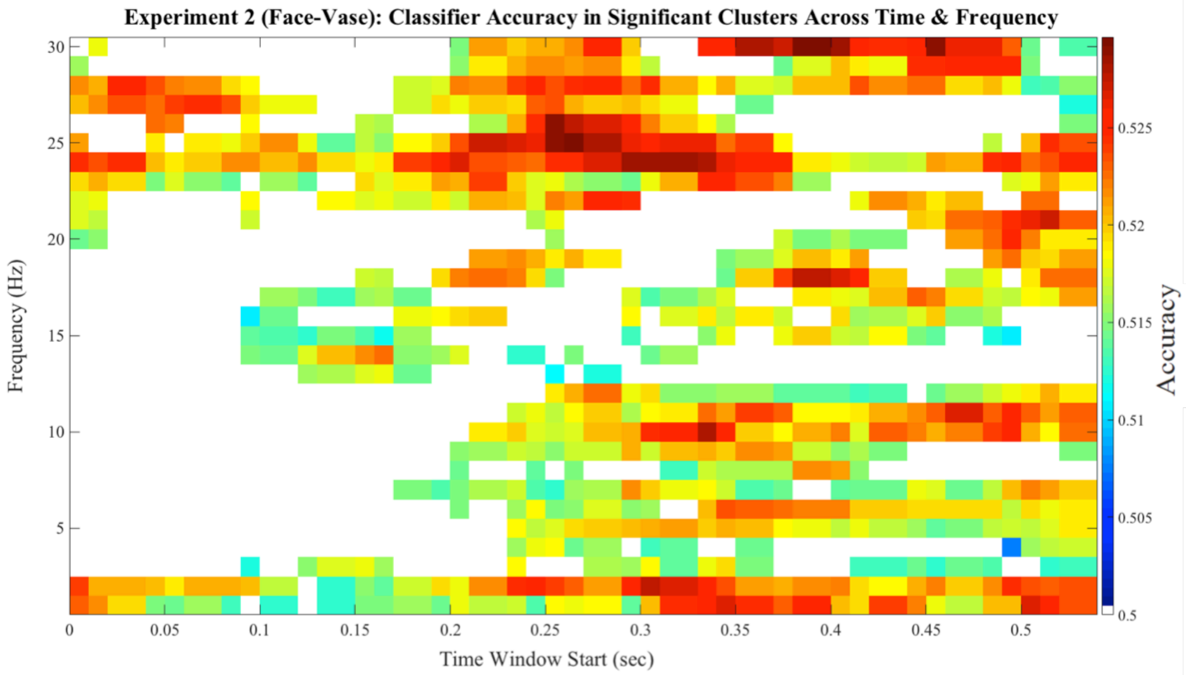


Figure 4.14. Time x Frequency map of the significant cluster of reversal vs. stability decoding accuracy values averaged across participants and channels in the post-stimulus period in Experiment 2 (Face-Vase). This map shows only the significant cluster. Non-significant areas are masked out. The dark red colour reveals the highest period of decoding accuracy (i.e. successful classification). The blue (and darker blue) colour(s) reveals periods of decoding accuracy close to, at or below chance. Due to the sliding window (10 ms jumps) required to conduct the wavelet analysis, the output from the analysis was truncated by 200ms on each end. This resulted in the trial length for the frequency domain data being shorter. Therefore, in the resultant map, the last 200 ms after 540 ms are not represented in the figure.

In order to investigate the effect of Response, we also conducted MVPA on Response and No Response only trials separately. MVPA analysis in the frequency domain showed that for Response trials, there was one significant cluster, $t_{cluster}(16) = 7.8062 \times 10^3$, $p < .001$ with a cluster mean decoding accuracy of 0.5516 (min = 0.5175, max = 0.5801). Significant decoding accuracies occured at all frequency levels from -20ms in the pre-stimulus period until 535ms after stimulus onset (Figure 4.15).

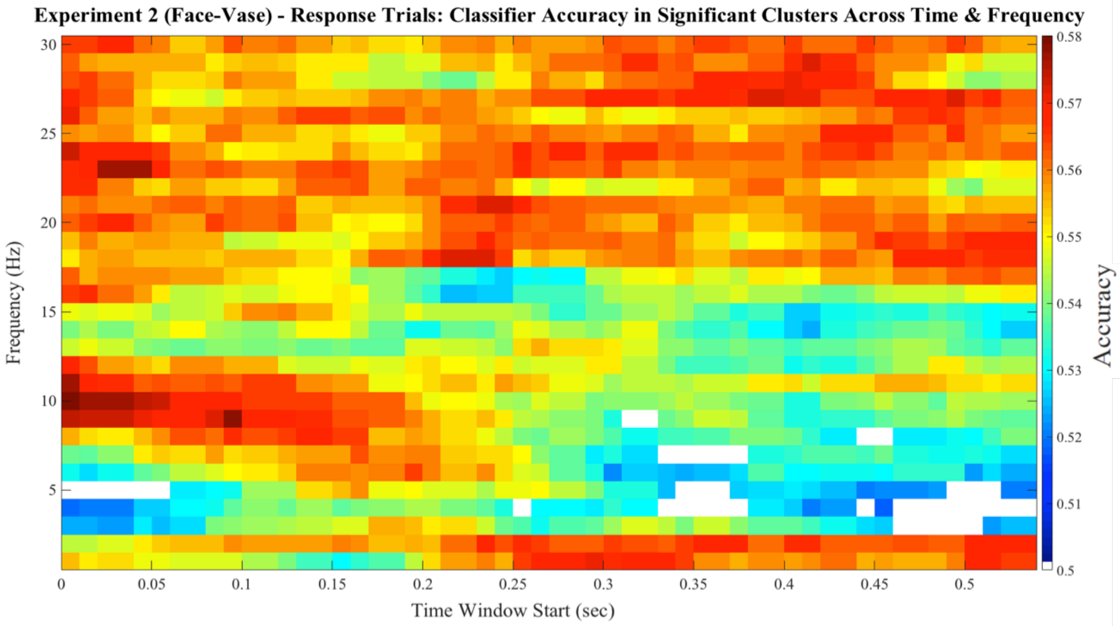


Figure 4.15. Time x Frequency map of the significant cluster of reversal vs. stability decoding accuracy values averaged across participants and channels in the post-stimulus period for response trials only in Experiment 2 (Face-Vase). This map shows only the significant cluster. Non-significant areas are masked out. The dark red colour reveals the highest period of decoding accuracy (i.e. successful classification). The blue (and darker blue) colour(s) reveals periods of decoding accuracy close to, at or below chance. Due to the sliding window (10 ms jumps) required to conduct the wavelet analysis, the output from the analysis was truncated by 200ms on each end. This resulted in the trial length for the frequency domain data being shorter. Therefore, in the resultant map, the last 200 ms after 540 ms are not represented in the figure.

MVPA in the frequency domain showed that for Non Response trials, there was one significant cluster, $t_{cluster}(16) = 6.2984 \times 10^3$, $p < .001$ with cluster mean decoding accuracy of 0.5457 (min = 0.5136, max = 0.5792). The significant decoding accuracies of this cluster occured at all frequency levels from 5 ms before stimulus onset until 535 ms after stimulus onset (Figure 4.16).

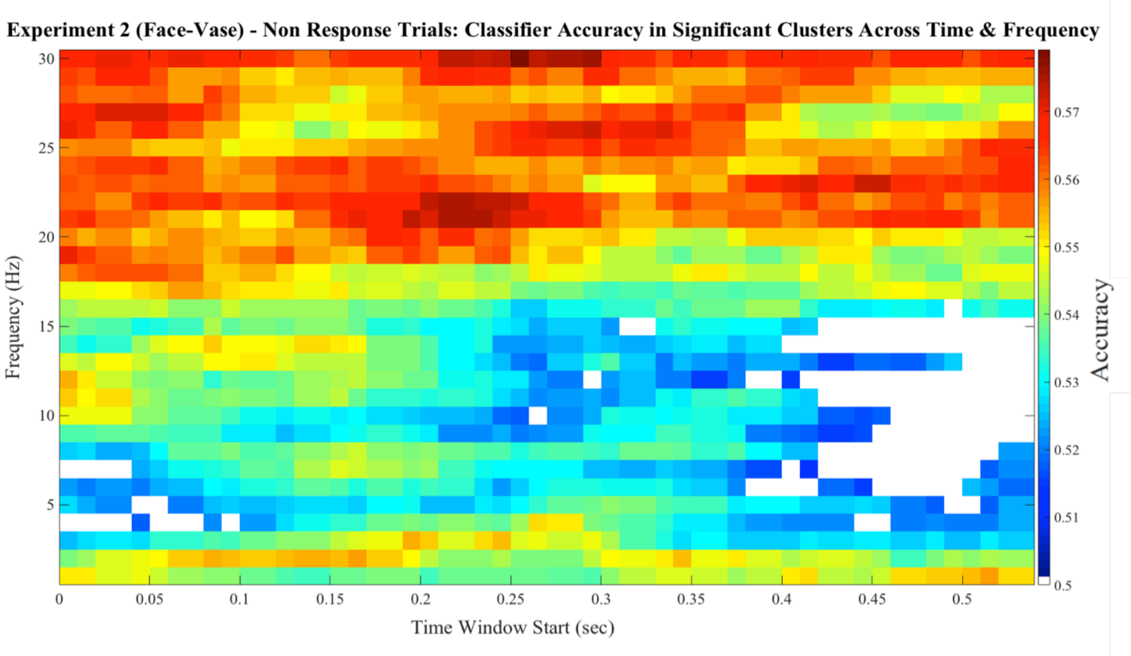


Figure 4.16. Time x Frequency map of the significant cluster of reversal vs. stability decoding accuracy values averaged across participants and channels in the post-stimulus period for non-response trials only in Experiment 2 (Face-Vase). This map shows only the significant cluster. Non-significant areas are masked out. The dark red colour reveals the highest period of decoding accuracy (i.e. successful classification). The blue (and darker blue) colour(s) reveals periods of decoding accuracy close to, at or below chance. Due to the sliding window (10 ms jumps) required to conduct the wavelet analysis, the output from the analysis was truncated by 200ms on each end. This resulted in the trial length for the frequency domain data being shorter. Therefore, in the resultant map, the last 200 ms after 540 ms are not represented in the figure.

MVPA analysis revealed that there was one significant cluster during which the mean decoding accuracy of Response and No Response trials differed, $t_{cluster}(16) = 128.8980$, $p = .0018$. The mean decoding accuracy for Response trials in this cluster was 0.5634 (min = 0.5503, max = 0.5776) and for the No Response trials was 0.5310 (min = 0.5210, max = 0.5413). This cluster occurred between 50 and 235 ms at 8-12Hz (Figure 4.17). There was also a marginally significant cluster that occurred between 425 and 535 ms at 9-13Hz, $t_{cluster}(16) = 79.1582$, $p = .0680$ with a mean decoding accuracy for Response trials being 0.5471 (min = 0.5374, max = 0.5564) and for the No Response trials, 0.5133 (min = 0.5055, max = 0.5190).

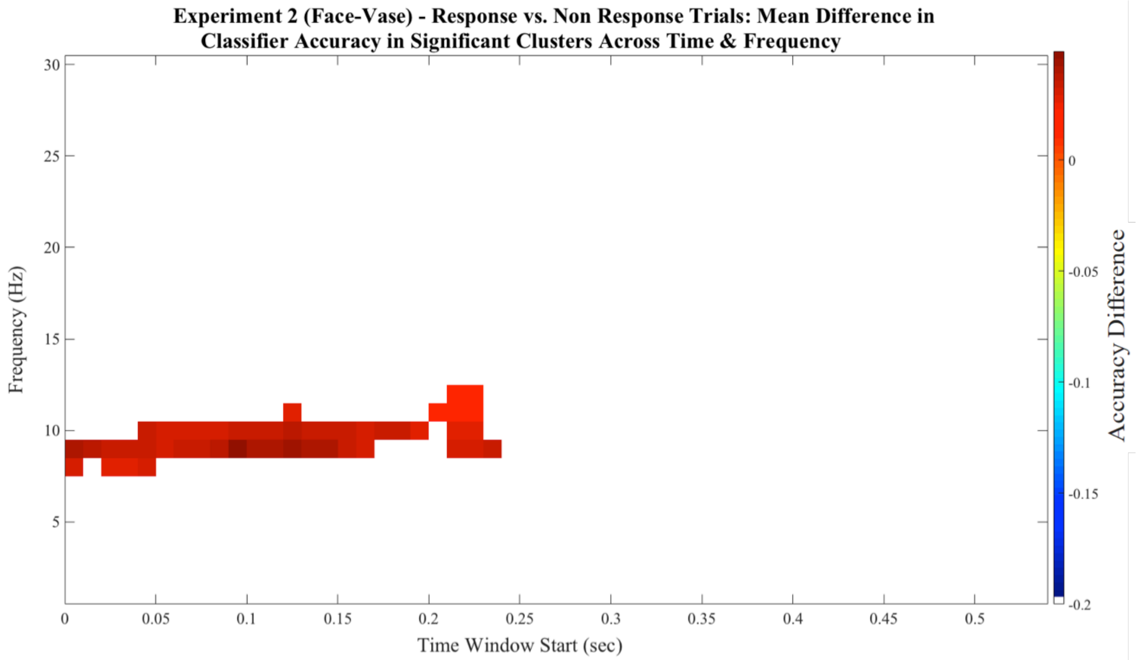


Figure 4.17. Time x Frequency map of the significant cluster of the mean difference of the reversal vs. stability decoding accuracy values in the post-stimulus period between the response and non-response trials in Experiment 2 (Face-Vase). This map shows only the significant cluster. Non-significant areas are masked out. The accuracy difference corresponds to the subtraction of the accuracy values of the response trials from the decoding accuracy values of the non-response trials. These values are then averaged across participants. The colour bar represents the difference between the accuracy values of the response and non-response trials. Here, the values are negative indicating that the decoding accuracy values were higher for the response trials than the non-response trials in this significant cluster. Due to the sliding window (10 ms jumps) required to conduct the wavelet analysis, the output from the analysis was truncated by 200ms on each end. This resulted in the trial length for the frequency domain data being shorter. Therefore, in the resultant map, the last 200 ms after 540 ms are not represented in the figure.

4.3.4. Interim Discussion

In Experiment 2, MVPA analyses based on time-domain data for all trials could significantly distinguish reversal and stable trials in the post-stimulus period until 294 ms. This period overlaps with the latencies of the RP and part of the RN. It is possible that the classifier was picking up on patterns related to these known ERP components. However, as was mentioned previously, pattern classification integrates information for the entire scalp. Thus, it is not necessarily the case that the classifier was picking on patterns associated with these ERP components. It could be that, in addition to these components, other patterns of activity at different electrode sites drive accurate classification. However, unlike the results from Experiment 1 (Necker Lattice), MVPA results in Experiment 2 do not show significant decoding accuracies at later time points, where the Frontopolar and Parietal Positivities are typically measured. See Figure 4.18 for an illustration of the results of the time domain classification of the overall trials with the time windows of these known reversal related ERP components highlighted.

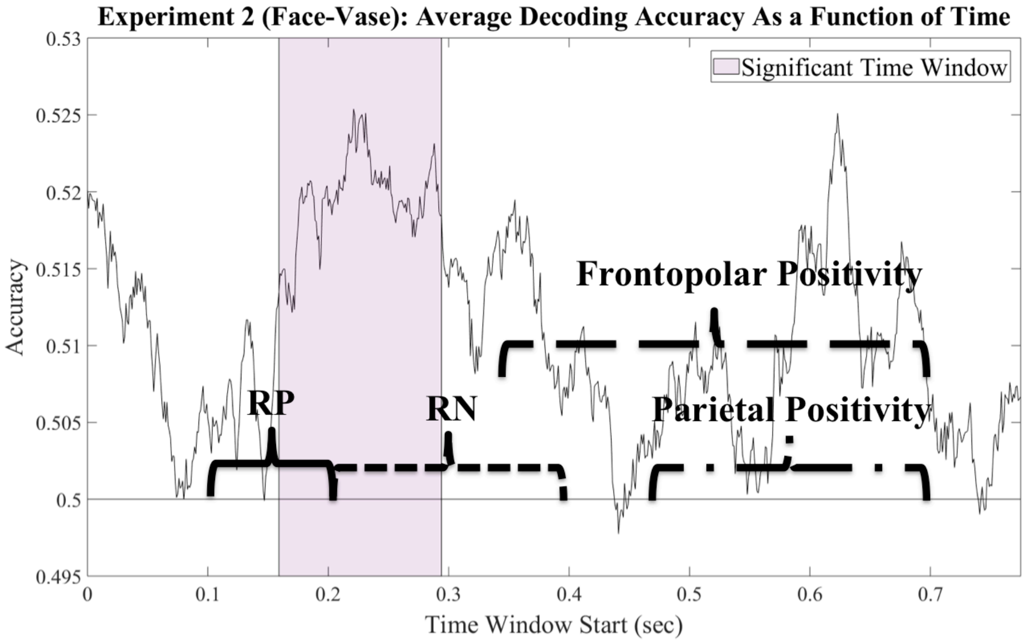


Figure 4.18. Plot of mean reversal vs. stability decoding accuracy across the post-stimulus period in Experiment 2 (Face-Vase) with braces indicating the latencies of well-known reversal related ERP components. The area marked in purple represents the significant cluster obtained from cluster-based permutation tests of the accuracy values. The solid brace corresponds to the latency of the RP, the dashed brace with narrow spacing corresponds to the latency of RN, the large dashed brace corresponds to the latency of the Frontopolar Positivity and the dashed and dotted brace corresponds to the latency of the Parietal Positivity.

Time domain MVPA of the response trials in Experiment 2 successfully classified reversal and stable trials in the response condition in a time window that overlaps with the window of the RP and some of the RN. This significant time cluster identified for the response trials, starts at an earlier time point than the one identified for the overall trials and includes information from the activity occurring 25ms before it (~88ms). This, again, brings into question whether the RP is truly the earliest marker related to perceptual reversals (Kornmeier & Bach, 2012), seeing as MVPA in the time domain for the response trials identified an earlier time window during which the activity representing reversal decoding is significantly distinguishable from the activity representing stability decoding.

Time domain MVPA for the non-response trials, however, revealed that the significant time cluster starts at the peak of the RP until part of the latency of the RN. This does not mean that the classifier identified those correlates but that the patterns of activity associated with the two perceptual states are significantly different from one another during that period of time. However, in line with the findings from Experiment 1 in this Chapter and the findings from Chapter 3, this shows that some of the activity linked to perceptual reversals is potentially modulated by response. Our cluster-based paired samples t-test supports this idea. The results of the cluster based paired samples t-test revealed that the mean difference in the time domain for Response and Non Response trials occurs during parts of the respective significant time clusters identified for the response and non-response conditions. This overlaps with the latency of the RP.

Our frequency domain results in Experiment 2 for the overall trials are similar to the significant results in the frequency domain identified in Experiment 1. Our results in Experiment 2 show that reversal and stable trials can be decoded from one another throughout most of the post-stimulus period (included in the analysis) at all the frequency levels included in our analysis. Although in our analyses this comes out as one large cluster, it may not represent one homogenous mechanism. These findings, similar to Experiment 1, suggest that there are perhaps several consecutive mechanisms taking place during the processing chain of perceptual reversals in this experiment. This is indexed by the change in the modulatory activity detected by our classifier of the frequencies across time. There are observable areas in the time-frequency map (Figure 4.14) during which the decoding accuracies were not significant. Moreover, the significant decoding accuracies, fall in the same time and frequency windows as mechanisms previously identified in the literature (e.g. alpha modulations that have been suggested to be related to disambiguation time). These are the same as in Experiment 1. It may be made up of several different mechanisms including those previously observed. Alternatively, our findings may represent different mechanisms than the ones than have been found in previous studies. These have been discussed extensively in the previous Interim Discussion section (section 4.2.4).

The findings alone from the cluster cannot identify whether or not there are several consecutive mechanisms at play and whether these mechanisms correspond to the ones described in the literature (e.g. destabilization and disambiguation/restabilization or build up of a coherent percept, etc.; Ehm et al., 2011; Kornmeier & Bach, 2012). Further analyses on the classification results from Experiment 2 are required in order to identify how the pattern of activity linked to perceptual reversals changes across time and frequency (discussed in the general discussion).

Similar to the frequency domain results in Experiment 1, the separate results for the response and non response trials in the frequency domain in Experiment 2 identified one significant cluster that spans over the entirety of the frequency range included in our analyses, throughout the post-stimulus period (until ~540 ms). However, unlike Experiment 1, the results from MVPA in the frequency domain for both response conditions in Experiment 2 show that the majority of the post-stimulus period included in the analysis is significant across all frequency levels. However, for the non-response trials, there were no significant decoding accuracies in the alpha and lower beta bands between 400 and 535ms.

Cluster based paired samples statistics comparing the means of the Response and No Response trials revealed that there is a difference in the mean between the two conditions in the alpha band between 50-235ms. This overlaps with the RP time window and the alpha band disambiguation window (Ehm et al., 2011; Kornmeier & Bach, 2005, 2006). These findings suggest that the representation of reversal vs. stability decoding differs between response conditions during that time-frequency cluster. If the modulations observed in these results correspond to the disambiguation of the Face-Vase, then this means that based on our results, the pattern of activity associated with disambiguation differs between response and non-response. Moreover, Figure 4.17 reveals that during that significant cluster, the decoding accuracy values are higher for the response trials than they are for the non-response trials (the difference time-frequency map is a result of subtracting the time-frequency decoding accuracy values of the non-response trials from the response trials). This suggests that the classifier here was better at decoding reversal and stability for the response trials than the non-response trials. This suggests that there are different representations between response conditions for reversal and stability decoding. Further suggesting that there are different processes that are modulated by response that underlie perceptual reversals during the latency of the RP.

The absence of significant decoding accuracies in the time domain that are identified in the time-frequency domain could be due to some effects being hidden in the time domain (discussed below). This could be because the oscillations are not phase aligned across trials (i.e. poorer phase locking across trials due to phase incoherence) and this can't be detected in the time domain but can potentially be picked up in frequency domain analyses. This means that there are potential phase differences between the two perceptual states (reversal and stability) being decoded that are not aligned in time and therefore cannot be picked up in time.

Overall, unlike previous univariate findings in the literature that have isolated time-frequency effects to certain frequency bands in time and space, the results from MVPA in this experiment reveal that there are modulations at several frequency levels that occur at the same time (i.e. significant decoding accuracies in both the beta and alpha bands at the same time). Our findings suggest that the activity in the post-stimulus period underlying perceptual reversals is ongoing. Our results further the previous findings in the literature that have been discussed in the previous Interim Discussion section (section 4.2.4.) in that the processes previously identified to underlie perceptual reversals could be driving significant decoding. This would suggest that these processes involve a wider frequency range than the ones identified to explain them. Alternatively, our findings suggest that several mechanisms take place at the same time that drive significant decoding.

4.4. General Discussion and Conclusion

The purpose of this chapter was to use MVPA in order to identify windows of significant decoding accuracy in the post stimulus period related to perceptual reversals.

To our knowledge, this is the first report of MVPA analyses of perceptual reversals using EEG in the post-stimulus period. It is clear from the results that large clusters of significant decoding exist across the post-stimulus period. These have been summarised in detail above. Importantly, these overlap with the time frames of known ERP components. However, it is difficult to know whether our significant decoding clusters arise from the same signals that give rise to the ERPs or represent new findings. Furthermore, it is unclear whether clusters comprise one single mechanism across their span or contain several mechanisms that are directly adjacent in time or frequency and connect to form one cluster.

In order to identify whether the results obtained from the classifier are markers of several mechanisms taking place representing different processing stages of perceptual reversals, the question of how the underlying neural code evolve in time should be asked. The decoding analysis used in Experiments 1 and 2 cannot answer that question. In the future, further analyses involving temporal generalization on similar data should be conducted in order to answer this question (King & Dahaene, 2014). Temporal generalization asks whether the patterns of activity representing the two perceptual states (reversal and stability) that drive above-chance decoding are constant and the same or are dynamically changing and evolving over time. Temporal generalization analyses how well classification performance for a given time point generalizes to all other time points (King & Dahaene, 2014). In the standard classification analysis used in this chapter, the classifier is applied at each time point and outputs a decoding accuracy for each time point indicating how well the classifier was able to distinguish between the pattern of activity representing reversals from the one representing stability at those time points independently. This means that the decoding accuracy at time t corresponds to the classifier being trained on the activity of a subset of the trials occurring at t and is tested at that time as well on the remaining test trials. With temporal generalization, the classifier is trained at a certain time point t and is tested on its ability to generalize to time t'. If generalization takes place, then that means that the activity observed at time t is the same as the activity occurring at t'. In the case, of the significant pattern clusters identified for Experiments 1 and 2, using temporal generalization would help identify whether there are separate mechanisms occurring at different time points related to perceptual reversals during the significant time-frequency windows and how these mechanisms evolve over time.

The results from separate MVPA of response and non-response trials suggest that perceptual processes related to reversals differ between response conditions. This is apparent in the paired samples statistics results where the means of successful classification of perceptual reversals differ for the two response conditions. The difference between the overall trials and the response and non-response results means that there could be different patterns of activity associated with perceptual reversals between response conditions.

Our cluster based statistics on the time domain clusters in Experiment 1 show that the classification of perceptual reversals persists until 738ms (38ms after the average response time) in the response condition but stops at 592ms in the non response condition. This suggests that the conscious recognition of a perceptual reversal takes longer on trials on which participants responded than on trials on which participants did not respond. This, however, would fall under the assumption that the end of the significant cluster indicates resolution of the reversal event. This would fit well with the latency of the Parietal Positivity and its hypothesized role. The Parietal Positivity has been suggested to indicate cognitive recognition of perceptual reversals (O'Donnell et al., 1988; Isoglu-Alkac et al., 2000; Struber et al., 2001; Struber & Hermann, 2002; Kornmeier & Bach, 2006; Britz & Pitts, 2011) giving some time afterwards for the manual indication of the conscious experience. The Parietal Positivity occurs 470ms after stimulus onset and lasts for more than 300ms (Pitts et al., 2008).

In the significant time-frequency domain cluster results, the mean differences between response conditions takes place during the latency of the RP for both experiments (1: Necker Lattice; 2: Face-Vase) and marginally during the latency of the Parietal Positivity for the second experiment only (Face-Vase). Due to the nature of the analysis (in both the time and time-frequency domains) conducted on the data; the results suggest that the activity during the latency of the RP is predictive of perceptual reversals. Furthermore, the nature of the perceptual reversals seems to differ between response conditions. For the Face-Vase experiment, differences can be observed at the alpha level, whereas for the Necker Lattice, they occur at the beta/lower gamma level. Previous findings have found alpha modulations during the latency of the RP. Kornmeier and Bach (2012) suggest that these modulations and the RP are part of the destabilization process discussed earlier with the alpha modulations representing disambiguation time. Moreover, Ehm et al. (2011) found beta deactivation ~100ms after stimulus onset which they suggest is also related to the disambiguation of bistable visual input taking place after stimulus onset. In both cases, the modulations that occur at those frequency levels during that time window are linked to perceptual reversals.

The results from MVPA in the time frequency domain of the reversal vs. stability trials in Experiment 2 are similar to the results observed for that same analysis in Experiment 1. There are overlapping time-frequency periods between the significant results measured (e.g. significant decoding accuracy values in the gamma band starting at around 200ms, in the alpha band between ~100-200ms). Moreover, they both show that there are observable periods that are non-significant for the overall trials which appear to be significant in the individual response condition analyses where MVPA distinguished reversal related activity across the scalp from stability related activity for response alone and non-response alone trials. These are in line with the findings from Chapter 3 where a modulatory role of response on the Reversal Positivity component was found. The findings suggest that there are different mechanisms that underlie perceptual reversals between response conditions. The findings from both experiments suggest that there are different representations at certain time-frequency windows linked to perceptual reversals across response conditions. This is indexed by the absence of significant decoding accuracy values in the significant time-frequency cluster and the presence of these values in the significant clusters in the response and non-response conditions separately.

However, some differences are identified in the time domain and time frequency classifications of reversal vs. stable trials between the two experiments whereby the classifier suggests that there are shorter windows of significant decoding accuracies in the Face-Vase experiment as opposed to the Necker Lattice where the majority of the post-stimulus onset period is significant. This suggests that there are some different electrophysiological mechanisms that underlie perceptual reversals between the two ambiguous images. Several experiments using the same paradigm to investigate the RN and the RP have shown that the results in relation to these two components differ between different types of ambiguous stimuli (e.g. Pitts et al., 2007; Kornmeier et al., 2014; Pitts et al., 2008). Our findings, coupled with previous findings, therefore suggest that although there is some overlap between different types of ambiguous stimuli in the classification of reversal and stable trials, there are also differences between the two where the mechanisms linked to perceptual reversals in Face-Vase perception cannot be generalized to those in Necker Lattice perception. However, we cannot explore these differences further seeing as these experiments took place at different times and the participants that completed them are different between the two. A future study involving more than one type of ambiguous stimulus in the same experiment is necessary in order to study the paired differences between perceptual reversals experience in Face-Vase perception vs. Necker Lattice perception. This would involve a cross-decoding analysis whereby the classifier used to decode reversal related activity for one ambiguous image is tested on reversal related activity from the other ambiguous image. If the classification is successful across time, then that would mean that the activity underlying reversals in one ambiguous image is the same as the activity underlying reversals in the other ambiguous image. Cross-decoding is when a classifier is trained on data from one cognitive context, and is tested on data from another (Kaplan et al., 2015). These two cognitive contexts have to take place within the same participant in order to be comparable.

The early significant time windows in this analysis coupled with previous findings on pre-stimulus activity linked to perceptual reversals (e.g. Britz, Landis &

Michel, 2009; Muller et al., 2005; Ehm et al., 2008, 2011), suggest that there might be pre-stimulus activity that was not included in the analysis of this chapter. Previous findings have suggested that there is pre-stimulus activity related to perceptual reversals. We explore this in more detail in the next chapter (Chapter 5) with an experiment designed to explore in more depth the pre-stimulus period. However, with the paradigm here, we are unable to do so due to the short window chosen for the pre-stimulus period and the short ITIs for trials on which participants did not respond.

To conclude, MVPA analysis successfully differentiates reversal from stable states in the post-stimulus period across different types of bistable images and response conditions. This type of analysis has been previously used on ambiguous stimuli in order to identify whether activity in the pre-stimulus period is predictive of the upcoming subjective interpretation of the ambiguous stimulus (e.g. face or vase in Rubin's Face-Vase; Rassi et al., 2019). On the other hand, this type of analysis has not been used previously to explore the mechanisms underlying perceptual reversals. The results from this chapter further existing univariate findings in that they reveal that activity linked to perceptual reversals is not indexed by isolated electrophysiological phenomena but is an ongoing process that involves the full scope of frequency bands and spans over the majority of stimulus presentation time. In addition to that, the results from this chapter confirm the results from Chapter 3 in that the mechanisms and patterns of activity linked to perceptual reversals differ across response conditions in certain time and time-frequency clusters, suggesting a modulatory role of response on perceptual reversals.

Chapter 5: Predicting Perceptual Reversals from Patterns of Pre-Stimulus Brain Activity

5.1. Introduction

In the previous chapter (Chapter 4), MVPA in the post-stimulus period furthered previous findings from the univariate literature. Our results showed that activity underlying perceptual reversals is not the result of isolated electrophysiological phenomena but is an ongoing process that involves modulations at several frequency levels across time. Some of the results observed in Chapter 4 start at stimulus onset suggesting that the state of the brain at stimulus onset influences the occurrence of a perceptual reversal. This is in line with previous findings in the literature that have found activity taking place in the pre-stimulus period that is suggested to influence the perceptual interpretation of an ambiguous figure (e.g. Britz et al., 2009; Hesselmann et al., 2008).

Cortical responses to the same ambiguous stimulus can vary from one trial to another. This variation in stimulus-evoked activity has been related to fluctuations in pre-stimulus activity (e.g., Arieli et al., 1996; Fiser et al., 2004; Hesselmann et al., 2008) and demonstrates how ongoing fluctuations in neural activity interact with incoming sensory information. As was mentioned in section 1.2.3 on ‘Spontaneous Fluctuations’ in Chapter 1, these fluctuations may help to explain why repetitions of the same physical stimuli elicit different percepts and responses from trial-to-trial in both animals (e.g. Arieli et al., 1996; Super et al., 2003) and humans (Boly et al., 2007; Rahn & Basar, 1993). The phase of ongoing neural oscillations in the pre-stimulus period in the theta (Busch et al., 2009; Fiebelkon et al., 2013a, 2013b; Hanslmayr et al., 2013) and alpha (Busch et al., 2009; Fiebelkon et al., 2013a; Nunn & Osselton, 1974; Mathewson et al., 2009) bands has been found to be related to trial-by-trial fluctuations in threshold-level perception in the visual domain. Moreover, the phase of oscillations in the time period before the stimulus onset is correlated to large-scale signatures of stimulus processing, such as event-related potentials (ERPs), BOLD response, and connectivity (Hanslmayr et al., 2013; Jansen & Brandt, 1991; Scheeringa et al., 2011; Gruber et al., 2014).

Recently, researchers investigating the pre-stimulus activity in ambiguous figure perception have been attributing the activity observed to ongoing spontaneous fluctuations (e.g. Hesselmann et al., 2008; Ronconi et al., 2017). These images elicit an internal conflict between multiple percepts and our interpretation of them spontaneously fluctuates from one percept to the other. Recent evidence from fMRI studies has shown that the interpretation of an ambiguous image can be associated with activity differences in the pre-stimulus period. For instance, Hesselmann et al. (2008) found a greater BOLD increase in the FFA when participants reported seeing faces rather than vase in the pre-stimulus period for Rubin's Face-Vase illusion. Importantly, they found that ongoing slow activity was related to evoked response shape (see section 1.2.3. for details of this study). The observed pre-stimulus activity was followed by an increased BOLD activity in the FFA in the post-stimulus period for trials on which participants reported seeing faces instead of vase (Hasson et al., 2001). Hesselmann et al. (2008) found that both the pre-stimulus activity and evoked response in the post-stimulus period correlated with perceptual interpretation of Rubin's Face-Vase.

Hesselmann et al. (2008) suggested that the activity measured in the pre-stimulus period can only be attributed to ongoing spontaneous fluctuations because it varied between trials and cannot be found at earlier pre-stimulus time points. These findings cannot be attributed to paradigm related effects either. Hesselmann et al. (2008) used an intermittent stimulus presentation paradigm with long and varying ITIs and short presentation times. This is suggested to maximize the unpredictability of stimulus onset, minimize volitional control and minimize the occurrence of re-reversals (paradigm explained in more detail in Chapter 2, section 2.2.2.1.1.). In addition to the increased activity observed in the FFA on face reported trials in experiments investigating brain activity underlying Rubin's Face-Vase, fMRI and EEG studies have found that the disambiguation process of bistable and multistable figures activates several areas of the brain from the category sensitive inferior temporal lobe regions (Tong et al., 1998) to parietal and frontal cortices (Sterzer & Kleinschmidt, 2007; Vernet et al., 2015).

Although Hesselmann et al. (2008)'s findings suggest that pre-stimulus neural activity in the FFA is related to subsequent perceptual outcomes, the precise time course of this activity is unclear because of the relatively poor temporal resolution of FMRI. Recently, Rassi, Wutz, Muller-Voggel and Weisz (2019) showed this importance in their study using MEG. In order to identify the brain regions that provided informative activity with regards to the activity underlying Rubin's Face-Vase perception, they firstly conducted MVPA analysis on face vs. vase reports over time. They then performed a source reconstruction of the classifier electrode weights (outputted from the MVPA analysis) at different time points. Their results revealed that the regions that were most informative of the reported interpretation (face vs. vase) changed over time. These findings are different from previous univariate findings that have focused on specific ROIs to study the mechanisms underlying ambiguous figure perception. Therefore, in order to identify an informative spatio-temporal window in the pre-stimulus period with regards to ambiguous figure perception, a more temporally sensitive method is necessary.

Rassi et al. (2019) used MVPA on MEG data to investigate the effect of pre-stimulus spontaneous fluctuations on subsequent percept in their experiment using Rubin's Face-Vase. Their classifier revealed that there were no significant pre-stimulus periods during which the pattern of activity underlying face reports was distinguished from the pattern of activity underlying vase reports. This is inconsistent with Hesselmann's (2008) fMRI findings , which showed that pre-stimulus activity differed in FFA between face and vase trials. This difference between the two findings could be due to the timing of the activity measured. Firstly, the effect measured in Hesselmann et al. (2008)'s fMRI study might have occurred significantly earlier (several seconds) than what they reported in their findings. fMRI with BOLD contrast can only detect slow hemodynamic signals that lag the underlying effects by seconds (Logothetis et al., 2001). This means that the effect observed before stimulus onset in Hesselmann et al. (2008)'s findings might have happened several seconds before stimulus onset. The study conducted by Rassi et al. (2019) only included 200ms of pre-stimulus activity on which pattern classification was conducted. Therefore they might have missed effects that could have been measured had they chosen a wider pre-stimulus time window. In addition to that, they performed their pattern classification analysis in the time-domain spanning between 1-33Hz. This means that any effect not identified by their classifier could be because the activity takes place at higher frequencies. On the other hand, another confound could be that the effects are hidden and cannot be picked up in the time domain due to the oscillations not being phase aligned across trials. This activity however, could potentially be picked up in power and detected in the frequency domain.

Moreover, this type of analysis (MVPA) has been used on EEG data in experiments investigating the underlying mechanisms in the pre-stimulus period of ambiguous figure perception. For instance, a recent study by Ronconi et al. (2017) trained a searchlight classifier in the frequency domain on EEG data on two types of bistable stimuli: two flash fusion (stimuli that are repeated in the same location) and apparent motion (stimuli that moved in space). They did this in order to investigate the underlying mechanisms of integration (where two stimuli are integrated into a single percept) and segregation (where two stimuli are separated into two events). Their classifier was successful in distinguishing the patterns of activity representing different percepts of their ambiguous stimuli in the frequency domain. They found that the percept (integration vs segregation) could be successfully decoded in the parieto-occipital channels. However, they found that the highest decoding accuracies varied between the two types of stimuli. They found that for the two flash fusion task, the highest decoding accuracy was in the phase of alpha oscillations at around 400 to 300ms before stimulus onset and that for the apparent motion task, it was in the phase of theta oscillations at around 500 to 400ms before stimulus onset. We are interested in investigating the pattern classification in the time and frequency domains of the identity and reversal trials for both of our stimuli and seeing if they are the same as or different across the two ambiguous stimuli.

The studies above using MVPA on pre-stimulus data were aimed at identifying brain activity which distinguishes between different perceptual outcomes (i.e,. face vs.

vase for Faces-vase or left-facing vs. right-facing for the Necker Cube). When using MVPA analyses, we call this “identity decoding” because it seeks to classify the perceived category identity of the stimulus without regard to the category of the stimulus that came before. However, the same data sets can be examined using a “reversal decoding” approach. That is, the pattern of brain activity can be used to classify each trial as a reversal or stable trial (i.e., whether the perceptual category changed from the last stimulus or not, respectively).

In the present study, we will seek to identify mechanisms that are independent of the direction of the switch (e.g., face to vase or vase to face). This will presumably produce substantially different results than those observed by Rassi et al. (2019), Ronconi et al. (2017) and Hesselmann et al. (2008) because those studies focused primarily on identity specific mechanisms rather than general mechanisms of perceptual reversal. If there are general mechanisms linked to reversal then we should be able to identify these using an MVPA classifier trained together on trials comprising both directions of reversal of a bistable stimulus. We did this, separately, for two types of reversible stimuli: Rubin’s Face-Vase and the Necker Lattice (a variant of the Necker Cube).It is important to note that we are not the first to focus on the reversal event instead of the activity associated with the different percepts of an ambiguous image (see Chapter 3 for studies that developed the Reversal Task and focused on investigating the electrophysiological correlates behind perceptual reversals). Previous studies on studying the pre-stimulus activity underlying perceptual reversals have used univariate analyses (see section 1.3.1.2. for details on the pre-stimulus activity linked to perceptual reversals). For instance, Ehm et al. (2011), using the same intermittent stimulus presentation paradigm as Kornmeier and Bach (2004a) with the Necker Lattice, found an increase in lower gamma-band activity (26-40Hz) at the right-hemispheric central and parietal electrodes and an occipital decrease of higher-gamma band activity (40-65Hz) on reversal trials, 200ms before stimulus onset. The role of these beta and gamma modulations isn't fully understood. However, Ehm et al. (2011) speculate that they are linked to the destabilization process and are indicative of a transient brain state of maximal instability reached before the onset of the stimulus (see section 1.2.4.1.2.).

Although these findings offer a great deal of information on the underlying mechanisms of perceptual reversals, there could potentially be effects that are not detected due to the nature of these analyses that require averaging across trials and time which could lead to loss of information. Furthermore, most of the previous studies involve univariate analyses or only look at MVPA in a very short pre-stimulus time window. The aim of this study is to use MVPA which would allow us to identify a time window and a time frequency window in the pre-stimulus period during which the reversal trials are successfully classified from stable trials. MVPA examines the pattern of activity across the scalp and thus can be sensitive to distributed mechanisms that may not be detectable by univariate mechanisms.

In the present studies using MVPA, we adopted an Identity Task paradigm similar to Hesselmann et al. (2008)'s. Ambiguous stimuli were presented in an intermittent manner separated by long and variable ITIs and short (150 ms) presentation times. Variable ITIs were used in order to ensure that participants could not form expectations about when the next stimulus would appear. Long ITIs reduced effects of the previous stimulus and allowed sufficient time for spontaneous fluctuations in brain activity to develop between stimuli. The long ITIs also allowed us to investigate a longer temporal window in the pre-stimulus period. This is important because, given the poor temporal resolution of fMRI due to the hemodynamic delay, it is likely that the effects observed in Hesselmann occurred seconds before stimulus onset. In the identity task paradigm, participants reported on each trial the perceived identity of the ambiguous stimulus (i.e., Experiment 3: Faces or Vase for Rubin's Face-Vase; Experiment 4: Left-Facing or Right-Facing for Necker Lattice). We used the same experimental paradigm for both the Face Vase (Experiment 3; Figure 5.1A) and Necker Lattice (Experiment 4; Figure 5.8A).

In both experiments (Experiment 3: Face-Vase; Experiment 4: Necker Lattice), we will run the classifier in both the time and frequency domains on Identity Coded trials (Face or Vase for the Face-Face Experiment – Experiment 3; Left-Facing or Right-Facing for the Necker Lattice Experiment – Experiment 4; explained in detail in sections 5.2.2.1. and 5.3.2.). This is done in order to extend the findings from the previous literature on identity related activity in the pre-stimulus period for ambiguous figures (e.g. Hesselmann et al., 2008; Rassi et al., 2019). We will also run the classifier in both the time and frequency domains on Reversal Coded trials (Reversal vs. Stability in Experiments 3 and 4; explained in detail in sections 5.2.2.1. and 5.3.2.). These analyses would allow us to identify whether or not there is a pre-stimulus window during which the pattern of activity representing reversals is significantly different from the pattern of activity representing stability. This finding would suggest that there is pre-stimulus activity that is predictive of an upcoming perceptual reversal.

In this Chapter, we used MVPA to analyse the pre-stimulus period. The experiments used in this chapter were designed in order to explore the pre-stimulus period. Previous studies have found conflicting results with regards to the activity in the pre-stimulus period with regards to identity decoding. We suspect that on one hand this is due to the low temporal resolution of the fMRI in the Hesselmann et al. (2008) study and to the short pre-stimulus window used to analyse the pre-stimulus period in the Rassi et al. (2019) study. Based on Hesselmann et al. (2008), we expect to find significant decoding in the pre-stimulus period but that this may occur at earlier times than were explored during in the Rassi (2019) study (i.e., before -100 ms). Furthermore, based on the previous findings and on the theories in the literature (e.g. Kornmeier & Bach (2012)'s integrative theory), we expected to find significant decoding in the pre-stimulus period leading up to stimulus onset.

5.2. Experiment 3: Rubin's Faces-Vase Experiment

5.2.1. Methods

5.2.1.1. Participants.

Thirty-Seven (24 female, 13 male) undergraduate psychology students were recruited from the Psychology Research Participation Time (RPT) scheme and the 2nd Year Cognitive Neuroscience module at Keele University as well as from the research participation scheme at University College London. Those who were recruited through RPT received partial course credit for participation and the rest were paid £7.50 per hour for approximately two hours. Participants had a mean age of 20.6 years (range: 18 to 40 years). All participants had normal or corrected-to-normal visual acuity as assessed using a Precision Vision Logarithmic ETDRS 2000 series chart. Fifteen (of 37) participants were excluded from the analysis. Four participants were excluded because they did not complete the experiment. Two participants' data were discarded because of missing trigger values. Two participants were excluded because the recording stopped partway. Two participants' data were discarded due to technical difficulties (one participant's data was not recorded and the other participant only received 180 out of 270 of the ambiguous trials due to a fault in the program). One participant was excluded because their eyes were half closed throughout the experiment and reported being sleepy. One participant was excluded because they claimed that their interpretation of the ambiguous image was controlled by their expectation of it. The latter had very fast reaction times. The remaining participants were excluded due to a low number of trials in one of the conditions (see data analysis methods below for a priori exclusion criteria). This study was approved by the University Ethics Review Panel at Keele University, the Psychology Ethics Committee at the University of Kent and the Research Ethics Committee at University College London. All participants gave informed consent prior to participation.

The sample size choice here was based on previous studies (e.g., Ronconi et al., 2017; Rassi et al., 2019). As was discussed in more detail in Chapter 4 (section 4.2.1.), in the literature using MVPA on EEG data, there is no standard way of determining what the required number of participants should be for each experiment. For instance, in the paper described previously by List et al. (2017), the number of participants used was 8 in Experiment 1 and 15 in Experiment 2. On the other hand, in Rassi et al. (2019)'s study, the number of participants was 21. Therefore, we decided to use a sample size that would match or be close to what we've read in the ambiguous figure perception

EEG literature. As far as I have found, there is not a clear way of estimating the sample size using an a priori power analysis for the cluster-based permutation tests, which we use here. We used these tests because they are effective for maintaining Type I error rate in multi-dimensional data sets such as EEG and because simulations show that cluster-based tests are well suited for broad effects. However, they are less sensitive to focally distributed effects. This is a known bias, which must be kept in mind when interpreting the results (e.g., Groppe, et al., 2011).

5.2.1.2. Stimuli & Apparatus.

The apparatus used for stimulus presentation, EEG and Eye-Tracking recordings were the same as Experiments 1 and 2. We used both an adapted upright and inverted version of Rubin's Face-Vase figure (see Figure 5.1A for upright and 5.1B for inverted). Similar to the procedure in Experiment 2 of Chapter 3, the frame width (FW) and Inter-Edge Distance (IED) (see Figure 5.2 for an illustration of IED and FW) of the stimulus varied for each participant which was determined by a pre-test (see sections 3.2.1. in Experiment 2, Chapter 3 for details on the pre-test). The average FW in the main experiment was 5.7855 ° (range = 2.6591° - 13.229°). The average IED in the main experiment was 0.3217° (range = 0.133° - 0.4521°). The maximum luminance of white portions was 373.43 cd/m^2 (CIE1931: x = 0.326, y = 0.325).

All stimuli were presented centrally on a grey background using the 24.5 inch BenQ Zowie XL2540 e-Sports computer monitor set at a resolution of 1920 x 1080 pixels and a refresh rate of 120 Hz. Viewing distance was maintained at 57 cm using a chin rest. The experiment was controlled by Presentation (Neurobehavioral Systems Inc., 2003). A 0.503° white cross at the centre of the screen served as fixation target ahead of and during stimulus presentation. Participant responses were recorded via a computer keyboard using the up and down arrow keys.

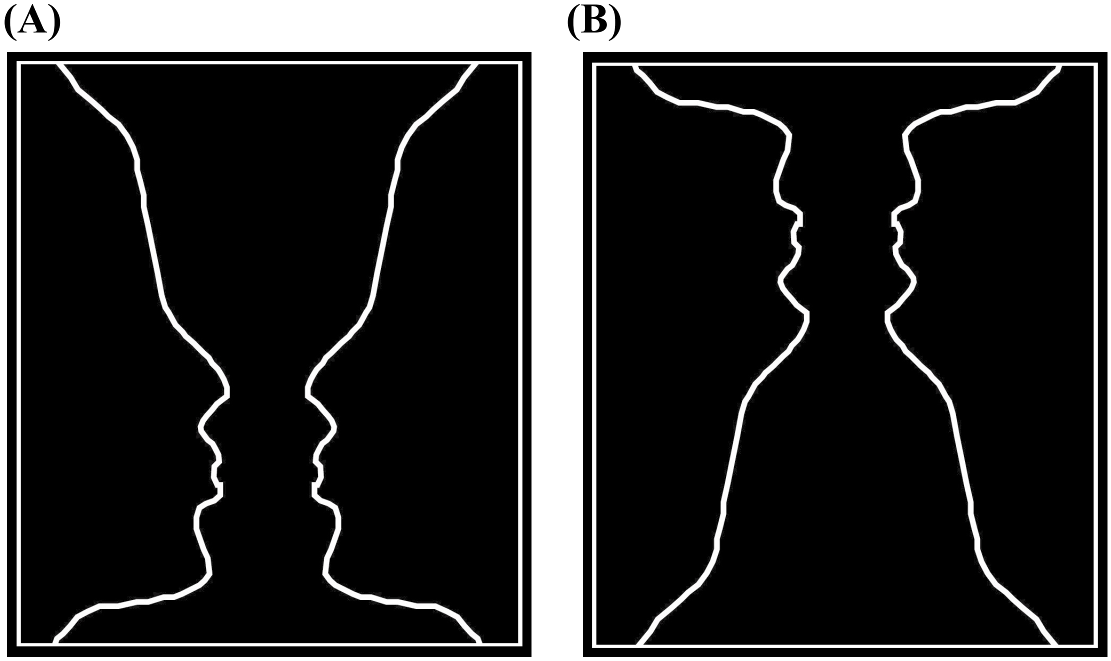


Figure 5.1. (A) Adapted version of Rubin's Face-Vase used in ~90% of the trials in Experiment 3 (B) Inverted Rubin's Face-Vase used in ~10% of the trials in Experiment 3. The Frame Width and Inter-Edge Distance (see Figure 5.2 for illustration) were adjusted for each participant depending on the results of the pre-test.

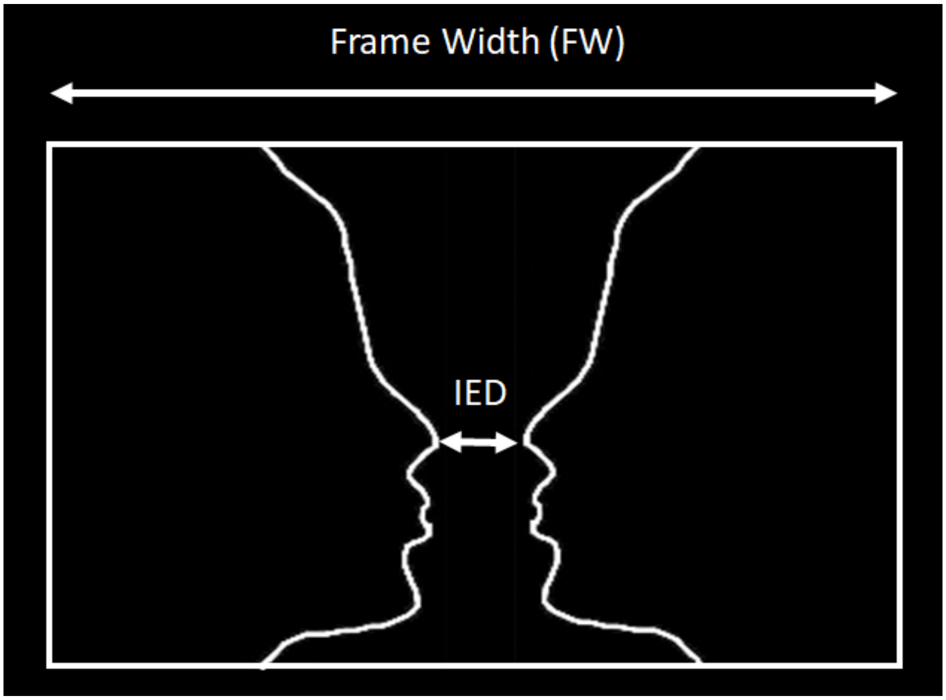


Figure 5.2. The ambiguous faces-vase stimulus used in Experiment 2. The frame width (FW) and inter-edge distance (IED) were adjusted for each participant in a pre-test to determine the maximally ambiguous stimulus for use in the main experiment (see details in procedure section).

5.2.1.3. EEG Recording.

The same Biosemi ActiveTwo EEG system used to record EEG scalp voltages in Experiment 1 was used in this experiment. The same parameters were chosen and the same steps were followed as well in the setup of the EEG cap.

5.2.1.4. Procedure.

Similar to the procedures undertaken in Experiment 2, during the instructions, the experimenter ensured that each participant was able to distinguish the two interpretations of the Face-Vase stimulus. Moreover, while the experimenters prepared the EEG cap, participants completed a pre-test similar to the one used in Experiment 2 in Chapter 3. Upon completion of the pre-test and the EEG cap setup, the participant completed the main experiment.

An intermittent presentation paradigm was employed, with stimuli appearing binocularly for 150ms followed immediately by a 100ms mask of white noise (Figure 5.3). Inter-trial intervals (ITIs) were drawn from a truncated (minimum 3 sec and maximum 14 sec) Poisson distribution with an expected value of 6 seconds. Three hundred trials in total were presented to the participants with a short, self-limited break after every 50 trials. During every second break, participants were asked to confirm the button they were using to report each percept. Within each block, approximately 90% of the trials contained the ambiguous Face-Vase (Figure 5.1A) and the remaining ~10% contained inverted stimuli (Figure 5.1B; half right-facing). The latter were presented randomly throughout the sequence of ambiguous stimuli. These served as attention checks to ensure that participants were actually completing and understood the instructions of the experiment. After each stimulus presentation, participants were required to report their perception by pressing either the up or down button on the keyboard. Both buttons were pressed using the same hand. Button assignment for faces and vase were counterbalanced across participants. Instructions were given to respond with their first impression of the stimulus after onset.

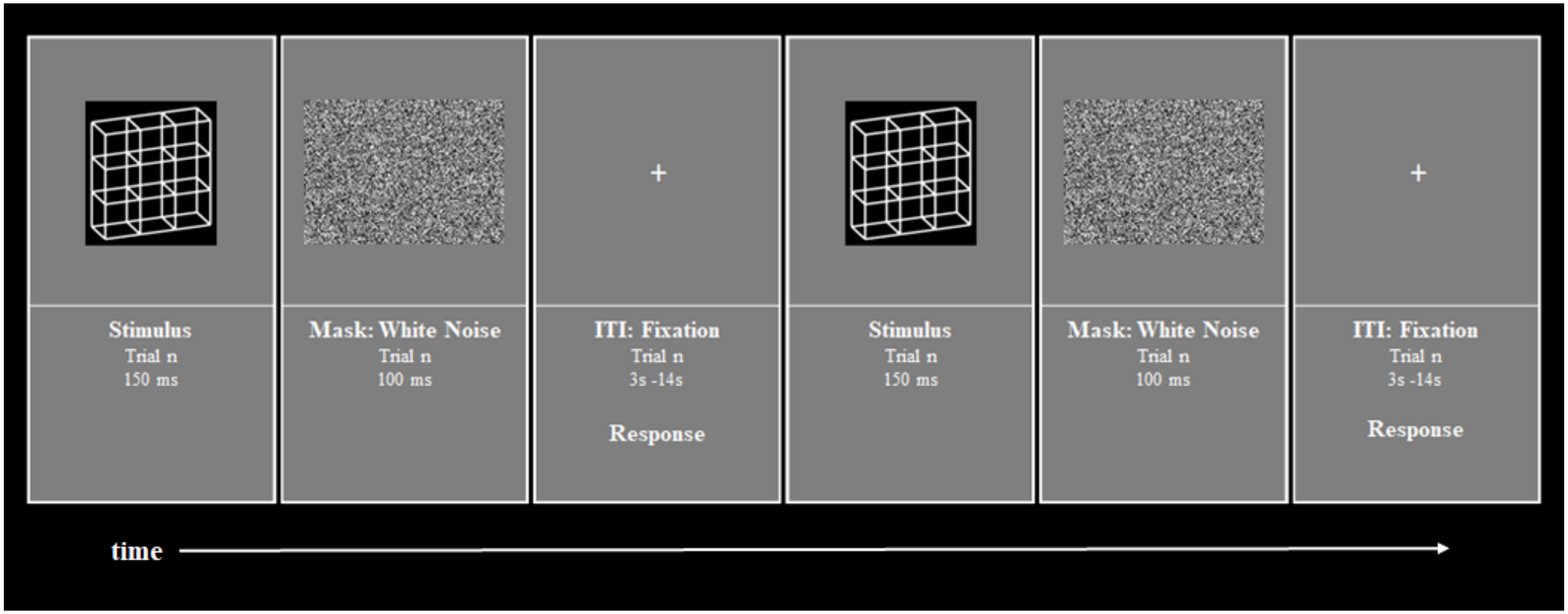


Figure 5.3. The order of trial events in Experiment 3 and 4. Intermittent ambiguous stimuli (Experiment 3: Necker Lattice; Experiment 4: Rubin’s Face Vase) were presented for 150ms, followed by a 100ms mask and separated by an ITI fixation cross from a truncated poisson distribution with a minimum of 3s and a maximum of 14s during which participants responses. Only ambiguous Necker Lattice stimuli are shown in this example.

5.2.2. Data Analysis Methods

5.2.2.1. Pre-processing.

The steps taken to pre-process, exclude and code (but not analyse) the data are the same as in Experiment 1 from Chapter 3. EEG recordings were manually checked for artefacts from eye movements and amplitude excursions exceeding ±100 mV and high-pass filtered offline at 0.1 Hz using BrainVision Analyzer 2.1. On average, 0.35% (range: 0 – 1.85 %) of trials were excluded due to these criteria. For Identity Coding (explained in the next paragraph), each trial was coded either as a Face or Vase trial depending on the participant's response on that trial. For Reversal Coding (explained in the next paragraph), each trial was coded either as a reversal or stability coded trial.

Identity Decoding: Each trial was coded as either a Faces or Vase trial depending on the participant's response on that trial. These trials will be referred to as Identity Coded trials. In order for a participant's data to be included in further analyses, at least 25 non-discarded trials per reported percept were required. Two participants were excluded because of the low number of non-discarded trials per trial type. The low number of trials for these participants was due to a combination of our EEG artefact rejection criteria and the participant's response pattern. The identity coded trials were fed into the classifier in both the time (explained in detail below in section 5.2.2.2.) and frequency domains (see section 5.2.2.3.). This was done in order to investigate what clusters in the pre-stimulus period were predictive of the subsequent reported interpretations of the participants and if these findings furthered the previous findings in the literature (e.g. Hesselmann et al., 2008; Rassi et al., 2019).

Reversal Decoding: In a separate analysis, trials were also coded either as a reversal or stable trial by comparing the reported identity of the trial to the one preceding it. These will be referred to reversal coded trials. For this Face-Vase experiment (Experiment 3), all 22 participants were included in the analysis because the number of trials coded per condition was higher than 25. On average, 88 trials (range: 34-158) were coded as reversal trials (149 average stability trials) with an average of 39 trials coded as Face Reversals (range: 16-79) and 39 coded as Vase Reversals (range: 14-79). The reversal coded trials were then fed into the classifier in both the time (see section 5.2.2.2.) and frequency domains (5.2.2.3.). This was done in order to identify clusters in the pre-stimulus period that differentiates reversal and stability trials.

Furthermore, similar to Chapter 4, the Eye-Tracker data collected in the experiments of this chapter will not be analysed due to time constraints. These were collected for the same reasons stated previously in Chapter 4, section 4.2.2.1..

5.2.2.2. MVPA in the time domain.

In Experiment 3, the data was segmented into Face and Vase epochs of 1600ms each (-1000 to 600ms) for the Identity Decoding, and into Reversals and Stability epochs of 1600ms each (-1000 to 600ms) for the Reversal Decoding. Our pre-stimulus period was significantly longer than in Rassi et al. (-200 to 0 ms; 2019) in order to allow for lower frequency and earlier effects to be captured while still avoiding activity in previous trials.

Following segmentation, the data were offline referenced to Cz. A one pass forward filter of 30Hz was applied to the segmented data. This was done in order to ensure that any observed effect in the pre-stimulus period was not contaminated by activity taking place in the post-stimulus period. The purpose of this study is to determine whether perception can be determined purely by pre-stimulus activity. Standard filters work symmetrically and although they may not shift the centre of activity in the signal, they can blur effects across time in both directions (e.g., Acunzo, et al., 2012). A forward filter ensures that any spreading of signal only goes forward in time (Widmann et al., 2015). This does mean that events in the pre-stimulus period can affect post-stimulus signals. Importantly, some pre-stimulus affects could be spread into or completely moved into the post-stimulus period. However, as we want to ensure that any pre-stimulus effect truly originate before the stimulus we adopted this conservative approach.

Finally, the same cross-validation procedure was applied to training and testing the classifier as in Experiments 1 and 2 in Chapter 4. A linear support vector machine classifier was applied to single trial EEG signals at each time point. At each time point across the trial, the classifier used a spatio-temporal pattern across 62 electrodes (on average) and 50 time points (1 ms each) as features. The window moved along the time dimension in increments of 1 ms. Importantly, to ensure that time labels of the decoding accuracy times series during the pre-stimulus period included only pre-stimulus information in the computation, windows included the 50 ms before the time label rather than 25 ms before and after. For instance, the time labelled -50 ms would include data from -100 to -50 ms when training and testing the classifier. This backward sliding time window was used in order to ensure that any activity in the post-stimulus period did not contaminate time points labelled as pre-stimulus. The outcome was a time-series of identity (face vs. vase) decoding accuracy values. Decoding was done separately for each participant but the decoding accuracy time series were averaged to create a grand average decoding accuracy waveform.

5.2.2.3. MVPA in the frequency domain.

The data segmentation and epochs used here are the same as the ones used for the Time Domain analysis above. However, the data that was fed into the classifier was not filtered here. The methods used for MVPA in the frequency domain for Experiment 3 are the same as the ones used in Experiments 1 and 2 in Chapter 4. Following segmentation, a wavelet analysis was conducted on the data to transform it into the frequency domain. For each trial, the power spectrum was computed in the 1 Hz to 30 Hz range using a Hanning window sliding from - 950 to 550 ms in 10ms intervals. It is important to note that because of the sliding window (10 ms jumps) required to conduct the wavelet analysis, the output from the analysis was truncated by 200ms on each end. This resulted in the trial length for the frequency domain data being shorter.

Following this step, the cross-validation procedure took place using the same linear support vector classifier as in the time-domain analysis. However, in this analysis it was applied to single trial EEG signals at each time point (every 10ms) and each frequency level between 1 and 30Hz (with 1Hz increments). MVPA was conducted only on the spatial pattern of activity here because the wavelet analysis already involved a windowing procedure across the data. The outcome was a decoding accuracy value at each time point and frequency level combination . This was done for each participant separately and then the time-frequency accuracy maps were averaged across participants.

5.2.2.4. Significance testing.

In order to evaluate the statistical significance and reliability of the classifier and its output, we used the same cluster-based permutation tests from the previous chapter (Chapter 4). Significance testing was restricted to the pre-stimulus window seeing as the focus of this study was to investigate pre-stimulus activity.

5.2.3. Identity Decoding Results

5.2.3.1. Response time.

For ambiguous stimulus trials, participants responded, on average, 827 ms (range = 361-1486 ms) after stimulus offset. Average RT for Face trials was 836 ms (range = 368-1583ms) and 824 ms (range = 349-1477ms) for Vase trials. A paired samples t-test revealed no significant difference in the means of the two types of trials, $t(21) = .781$, $p = .443$. This analysis was not conducted for inverted trials because there were too few trials to break them down into the two identities. Mean RT for inverted trials was 945 ms (range = 373-2082ms). A paired samples t-test comparing the means of the ambiguous and inverted trials revealed a significant difference between the two, $t(21) = -3.389$, $p = .003$. This suggests that participants took longer to respond to the inverted trials.

5.2.3.2. Identity trials – Identity responses.

The average vase reports of the inverted trials was 50.78% (SE = 3.8%) of the inverted trials. This is not significantly greater than 50% $t(21) = .205$, $p = .840$. A paired samples t-test comparing the means of the percentage of vase reports in the ambiguous trials (see below) and the ones in the inverted trials revealed no significant difference between the two, $t(21) = .253$, $p = .803$.

5.2.3.3. Ambiguous trials – Identity responses.

For the ambiguous trials, 47.69% of them were reported as being Face percepts (range = 14.23-65.93%) and 52.31% as Vase percepts.

5.2.3.4. Time domain MVPA - Identity Decoding.

Pattern classification in the time domain showed significant above chance identity (face vs. vase) decoding accuracy in one pre-stimulus cluster. The cluster occurred between -910ms and -896ms, $t_{cluster}(21) = 39.5208$, $p = 0.0096$, and had a mean accuracy value of 0.5222 (min = 0.5193, max = 0.5266). See Figure 5.4 for the average (across participants) accuracy value across time.

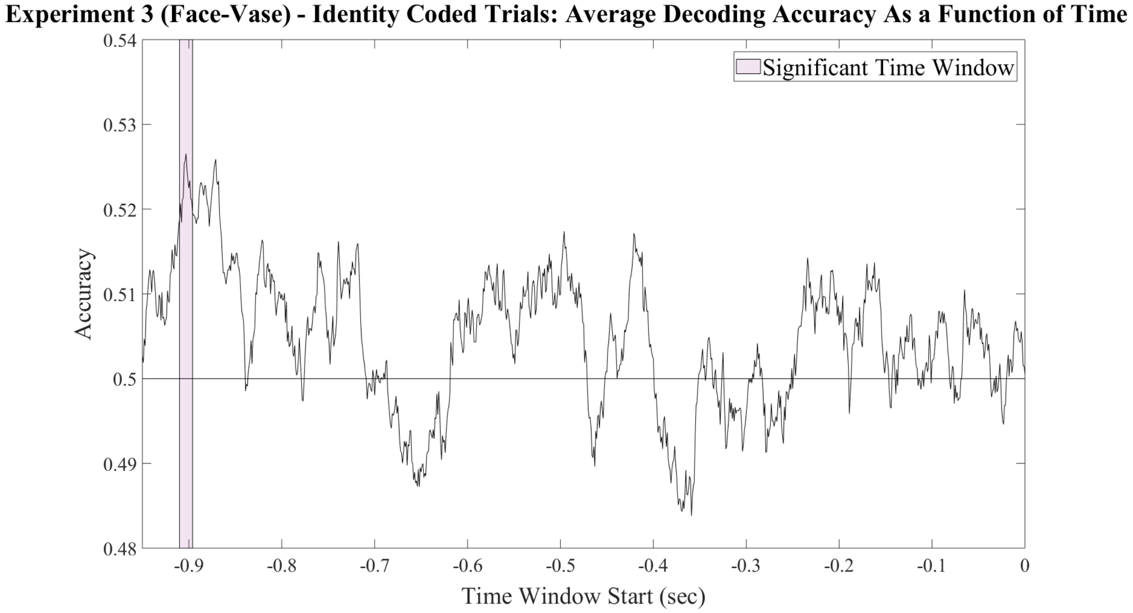


Figure 5.4. Plot of mean identity decoding accuracy across the pre-stimulus period in Experiment 3 (Face-Vase). The time window overlaid with a purple transparent shaded area represents the significant cluster obtained from cluster-based permutation tests of the accuracy values.

5.2.3.5. Frequency domain MVPA – Identity Decoding.

MVPA in the frequency domain showed significantly above chance identity (face vs. vase) decoding accuracy in one cluster during the pre-stimulus period. This cluster spanned between 20 and 30Hz from - 745ms until -95ms before stimulus onset (Figure 5.5), $t_{cluster}$ (21) = 668.8563, p<.001, and had a mean accuracy value for this cluster is 0.5279 (min = 0.5156, max = 0.5525).

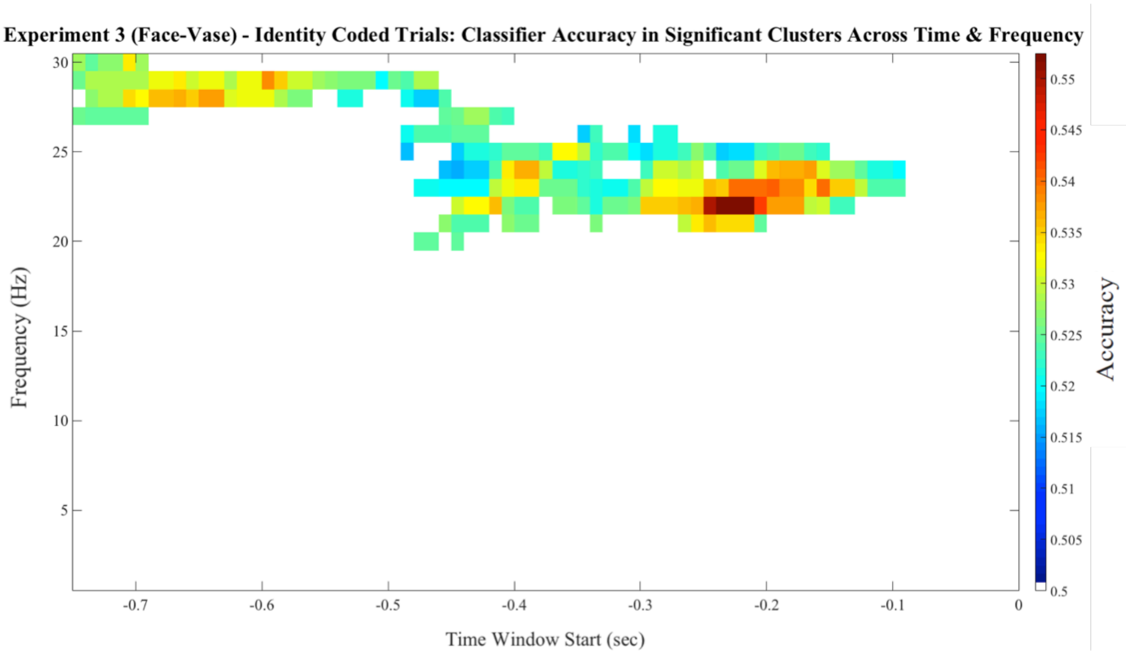


Figure 5.5. Time-Frequency map of the significant cluster of the average identity (face vs. vase) decoding accuracy values averaged across participants and channels in the pre-stimulus period of Experiment 3 (Face-Vase). This map shows only the significant cluster. Non-significant areas are masked out. The dark red colour reveals the highest period of decoding accuracy (i.e. successful classification). The blue (and darker blue) colour(s) reveals periods of decoding accuracy close to, at or below chance. Due to the sliding window (10 ms jumps) required to conduct the wavelet analysis, the output from the analysis was truncated by 200ms on each end. This resulted in the trial length for the frequency domain data being shorter. Therefore, in the resultant map, the first 200 ms before 750 ms are not represented in the figure.

5.2.4. Interim Discussion of Identity Decoding Results

In Experiment 3, MVPA in the time domain of the Identity Coded trials significantly distinguished face from vase trials in the pre-stimulus period. Our time domain analyses revealed that there was one period of significant decoding accuracy at around 950ms. The significant cluster identified also includes the decoding accuracy information from the 50ms preceding it. This is because of the 50 ms backward sliding time window that was used. This means that the period of significant decoding face vs. trials starts at around 1s before stimulus onset according to the results we found. This time window with significant decoding accuracies has not been identified in previous studies exploring the activity underlying Face-Vase perception in the pre-stimulus period. This suggests that, as was mentioned previously, Rassi et al. (2019) might have not detected any activity in their pre-stimulus pattern classification analyses because the pre-stimulus window they included in their analysis was too short (200ms).

Results of Experiment 3 showed no significant decoding of the face and vase trials immediately before stimulus onset. This is different from Hesselmann et al. (2008)'s findings. However, as was mentioned previously, the effect detected in Hesselmann et al. (2008)'s study could have occurred at a much earlier time point but was delayed due to the nature of the BOLD signal. Given the much higher temporal resolution of EEG, we are better able to isolate in any effects in the pre-stimulus period. However, we did not find significant decoding at later times in the pre-stimulus window where others have detected effects (e.g. Britz et al., 2009; Ehm et al., 2011; Muller et al., 2005). Those effects occurred mostly in the frequency domain where we did find evidence of significant effects later in the pre-stimulus period. These frequency domain effects may have been masked in the time domain analysis due to poor phase alignment of oscillations across trials.

MVPA in the frequency domain of the Identity Coded trials successfully distinguished face from vase trials in the pre-stimulus period in one significant cluster spanning over the beta band between -745 and -95 ms. Figure 5.5 reveals that pattern classification was successful in distinguishing face from vase trials in the upper beta band between -745 and -475 ms and in the lower beta band between -475 ms and -95 ms with the highest decoding accuracy value taking place between -300 and -200 ms in the lower beta band. Previous studies have linked beta oscillations in the pre-stimulus period to the endogenous regulation of perceptual states (Engel & Fries, 2010). Beta band oscillations in the pre-stimulus period have been also found to carry category information (Richter et al., 2018).

Taking this into consideration, the findings from MVPA of identity coded trials in the frequency domain could potentially suggest that prior to stimulus presentation, modulations in the beta band already carry information that is predictive of the upcoming percept choice (face or vase). This is in line with the previous findings by Hesselmann et al. (2008). Moreover, the findings from MVPA in the frequency domain further the previous findings by Hesselmann et al. (2008) in that the activity underlying the perceived identity of an ambiguous stimulus (face vs. vase) can, not only be isolated in time (as indexed by the results from MVPA in the time domain) but can also be isolated to certain frequency bands (i.e. beta band). Future analyses using temporal generalization and exploring the topography of the scalp during these significant cluster would help connect with certainty the distinct underlying mechanisms of the effects identified by MVPA in the both the time and time-frequency domain to identify whether these mechanisms differ across time.

The significant decoding accuracy values from pattern classification in the frequency domain stop at 95 ms before stimulus onset, leaving a gap between oscillatory activity measured and perception. This could be due to the limited frequency range that was included in the analysis (only up to 30Hz). There could potentially be activity occurring at higher frequency levels that were not picked up by the classifier (i.e. in the gamma band; Castelhano et al., 2013). The earlier pre-stimulus window detected in time domain MVPA that is not classified as a significant cluster in the frequency domain results could be due to the shorter time-window of the frequency domain due to the wavelet analysis.

5.2.5. Reversal Decoding Results

5.2.5.1. Ambiguous trials.

To conduct reversal decoding, trials were also coded as Reversal and Stability trials based on the sequence of identity responses. Reversal coded trials comprised 37.16% (range = 14.47 – 68.4%) of all trials and 62.83% (range = 31.6 – 85.53%) were coded stable.

5.2.5.2. Time domain MVPA – Reversal Decoding.

Pattern classification in the time domain showed significantly above chance reversal decoding (reversal vs. stability) accuracy in one pre-stimulus cluster, $t_{cluster}(21) = 132.2881$, $p = 0.002$ with mean accuracy value of 0.5256 (min = 0.5163, max = 0.5376). This cluster ranges from -46 ms until stimulus onset. See Figure 5.6 for the average (across participants) accuracy value across time.

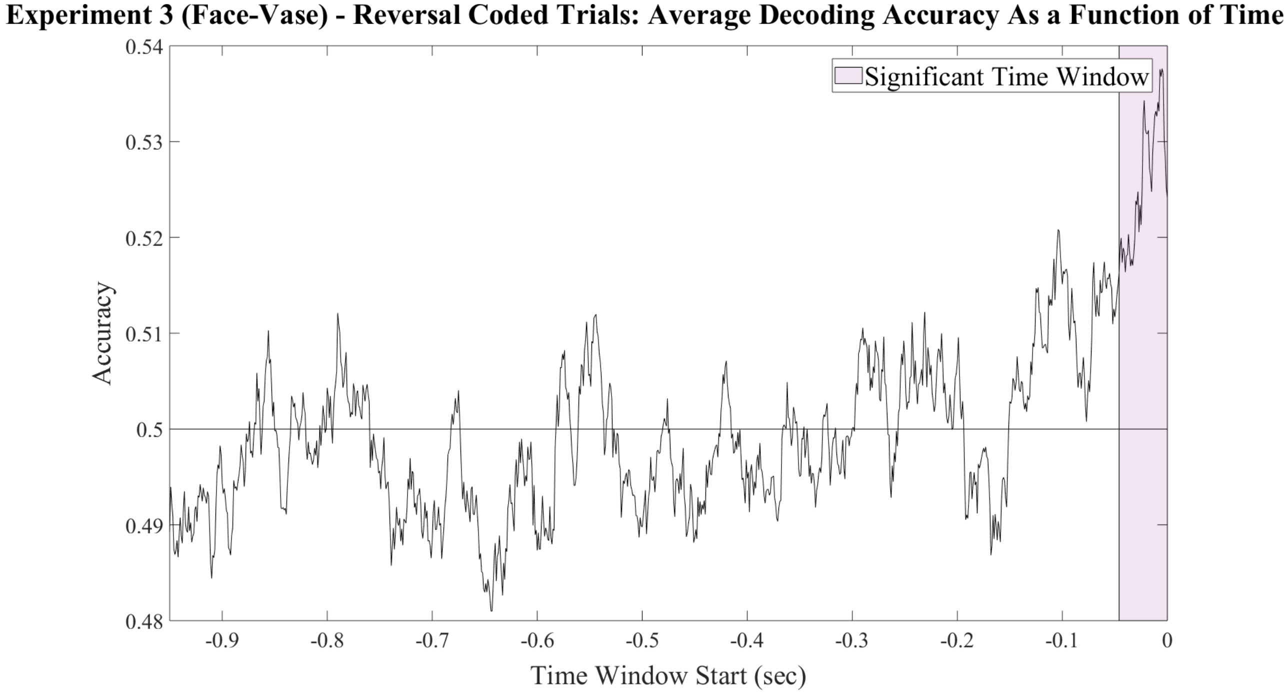


Figure 5.6. Plot of mean reversal decoding accuracy across the pre-stimulus period in Experiment 3 (Face-Vase). The time window overlaid with a purple transparent shaded area represents the significant cluster obtained from cluster-based permutation tests of the accuracy values.

5.2.5.3. Frequency domain MVPA – Reversal Decoding.

Cluster-based statistics on the pre-stimulus reversal decoding accuracy values showed significantly above chance decoding accuracy in one cluster, $t_{cluster}(21) = 115.0380$, $p < .001$. The mean accuracy value of this cluster was 0.5226 (min = 0.5143, max = 0.5326) and it occurred between 485 and 355 ms in the 25-30Hz frequency range. See Figure 5.7 for the map of the average (across participants) accuracies across time and frequency.

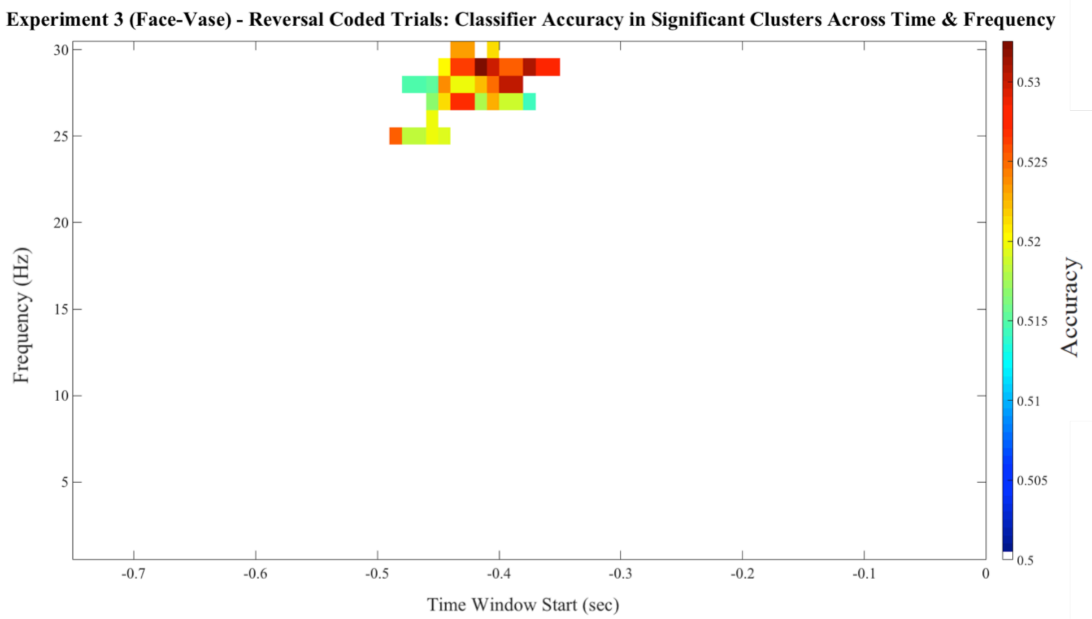


Figure 5.7. Time-Frequency map of the significant cluster of the average reversal (reversals vs. stability) decoding accuracy values averaged across participants and channels in the pre-stimulus period of Experiment 3 (Face-Vase). This map shows only the significant cluster. Non-significant areas are masked out. The dark red colour reveals the highest period of decoding accuracy (i.e. successful classification). The blue (and darker blue) colour(s) reveals periods of decoding accuracy close to, at or below chance. Due to the sliding window (10 ms jumps) required to conduct the wavelet analysis, the output from the analysis was truncated by 200 ms on each end. This resulted in the trial length for the frequency domain data being shorter. Therefore, in the resultant map, the first 200 ms before 750 ms are not represented in the figure.

5.2.6. Interim Discussion of Reversal Decoding Results

Time domain MVPA of the reversal coded trials successfully distinguished the pattern of activity representing reversals from the one representation stability in one cluster occurring right before stimulus onset. This cluster started 46 ms before stimulus onset and included information from the 50 ms preceding it because of the backward sliding time window used in the analysis. In a previous study conducted by Britz et al. (2009) using a similar experimental paradigm as the reversal task from Chapter 3 (see section 3.2.1.4.) and a variant of the ambiguous Necker Cube, activity in the 50 ms before stimulus onset that dissociated the reversal trials from the stability trials was measured. Britz et al. (2009) used EEG and statistical parametric mapping in the inverse space and found that the only significant difference was observed in the right inferior parietal lobe. The latter was found to be significantly more active preceding a perceptual reversal. The findings from the pattern classification in the time domain suggest that the difference between the pattern of activity representing reversal coded trials and the one representing stability coded trials starts at an earlier time window in the pre-stimulus period. Therefore suggesting that the momentary fluctuations of baseline activity that influence perceptual reversals start at an earlier time point than what has been previously identified in the univariate literature. The difference between Britz et al. (2009) and our findings could be due to the type of filter that was chosen. We used a one pass forward filter of 30Hz, whereas, Britz et al. (2009) applied a band-pass filter between 0.1 and 100Hz. Using a bandpass filter has been found to distort and shift the phase of the signal in time (Yael et al., 2018). This suggests that perhaps some of the activity detected in Britz et al. (2009)'s study might have started at an earlier time window than reported. Alternatively, the forward filter and backward time window used in our analyses might have pushed some effects earlier in time.

Frequency domain MVPA of the reversal coded trials successfully distinguished the pattern of activity representing reversals from the one representing stability in one cluster occurring between 485 and 355 ms before stimulus onset in the beta band. This time-frequency cluster has not been previously identified in studies investigating the pre-stimulus reversal related activity. This confirms the idea that pattern classification allows us to isolate in time and frequency the activity that is predictive of the upcoming perceptual state (reversal vs. stability). Previous findings from the univariate literature have identified beta modulations in the pre-stimulus period linked to perceptual reversals. Ehm et al. (2011) speculated that the pre-stimulus beta (they refer to this as lower gamma – addressed in Chapter 4 in section 4.2.4.) and gamma modulations measured in their study are a marker of the destabilization process described in Chapter 1 (see section 1.2.4.1.1.; Ehm et al., 2011) meaning that they are indicative of a transient brain state of maximal instability, ready to switch. The findings from our classifier confirm that beta modulations in the pre-stimulus period carry information about the upcoming perceptual state (i.e. reversal or stability). This is due to the nature of the analysis used to identify the significant time-frequency cluster and due to the experimental design (discussed in more detail in the General Discussion and Conclusion section).

Moreover, beta band oscillations have been suggested to reflect more feedback and endogenous top-down influences (Engel & Fries, 2010). Engel and Fries (2010) suggested that these beta oscillations are expressed more strongly if the maintenance of a percept is intended or predicted, rather than if a change is expected. Hipp et al. (2011) suggest that both power and phase coupling in the beta band in the pre-stimulus period are important in the perception of ambiguous stimuli. These previous findings investigating pre-stimulus activity related to perceptual reversals, have identified modulations at certain frequency levels that are correlated with perceptual reversals or perceptual stability.

These findings have used univariate approaches that are limited to a certain number of electrodes, frequency bands or areas. Moreover, they involve averaging the effects across trials, which could result in some reversal related activity not being detected. The findings from frequency domain decoding approach identified a time-frequency window that has not been previously identified. This window indicates the period during which the pattern of activity linked to a reversal can be significantly distinguished from the pattern of activity linked to stability. Therefore, future analyses exploring the separate topographies of the scalp representing the two perceptual states (i.e. reversal and stability) during the significant time and time-frequency clusters would help us identify the cognitive processes that are taking place. Pattern classification has helped us identify the precise time and time-frequency window where the processes that differentiate between a reversal state and stable state occur. Future analyses exploring the pattern of activity across the scalp during these significant time and time-frequency clusters is necessary in order to identify the topographies across the scalp that constitute a perceptual reversal vs. a perceptual stability.

Similar to the findings from MVPA of the Identity Coded trials, the significant time windows between pattern classification in the time domain and pattern classification in the time-frequency domain do not overlap. The absence of significant time windows in the time domain classification that are classified as significant in the frequency domain could be due to phase incoherence (i.e. oscillations not being phase aligned across trials; discussed in Chapter 4) which leads to oscillations not being detected in the time domain but can picked up in the time-frequency domain. As for the findings where the significant cluster in the time domain included a time window that is not part of the significant cluster in the frequency domain, this could be because of the shorter time window that led to a poorer frequency resolution. Therefore the activity during that time window could not be picked up in the time-frequency domain. Alternatively, this could be due to the forward filter and backward time window applied in the time domain that wasn't applied in the time-frequency domain. This filter and windowing might have shifted everything around between the two.

5.3. Experiment 4: Necker Lattice Experiment

5.3.1. Methods

The methods for Experiment 4 were the same as the ones used in Experiment 3 of this chapter except where noted below.

5.3.1.1. Participants.

Twenty (19 female, 1 male) undergraduate psychology students were recruited both from Keele University's Psychology Research Participation Time (RPT) scheme and from a second year class in Cognitive Neuroscience. Those who were recruited through RPT received partial course credit for participation and the rest were paid £15 for their time. Participants had a mean age of 20.6 years (range: 18 to 40 years). All participants had normal or corrected-to-normal visual acuity as assessed using a Precision Vision Logarithmic ETDRS 2000 series chart (average: 0.004 logMAR). Four (of 20) participants were excluded from the analysis. Two of those participants dropped out because they were not feeling well. The other two participants were excluded due to a low number of trials in one of the conditions (see data analysis methods in Experiment 3 for exclusion criteria). This study was approved by the University Ethics Review Panel at Keele University and the Psychology Ethics Committee at the University of Kent. All participants gave informed consent prior to participation.

The sample size choice here was based on previous studies (e.g., Ronconi et al., 2017; Rassi et al., 2019). As was discussed in more detail in Chapter 4 (section 4.2.1.) and in section 5.2.1.1., in the literature using MVPA on EEG data, there is no standard way of determining what the required number of participants should be for each experiment. Therefore, we decided to use a sample size that would match or be close to what we've read in the ambiguous figure perception EEG literature (e.g. Ronconi et al., 2017; Rassi et al., 2019).

5.3.1.2. Stimuli & Apparatus.

The same apparatus and setup used in Experiment 3 of this chapter (Chapter 5) is used in Experiment 4. The Necker Lattice (Figure 5.8A; Kornmeier & Bach, 2004) used in Experiment 1 was used in this experiment as well. For the unambiguous trials, the same two unambiguous versions of the Necker Lattice used in Experiment 1 (Figure 5.8B-C; Necker, 1832; Kornmeier & Bach, 2004) was used in this experiment. The ambiguous and unambiguous Necker Lattice figures served as the visual stimuli in this study. The size of each stimulus was 5.52° x 5.52°. All stimuli were presented centrally on a grey background. A 0.503° white cross at the centre of the screen served as fixation target ahead of and during stimulus presentation.

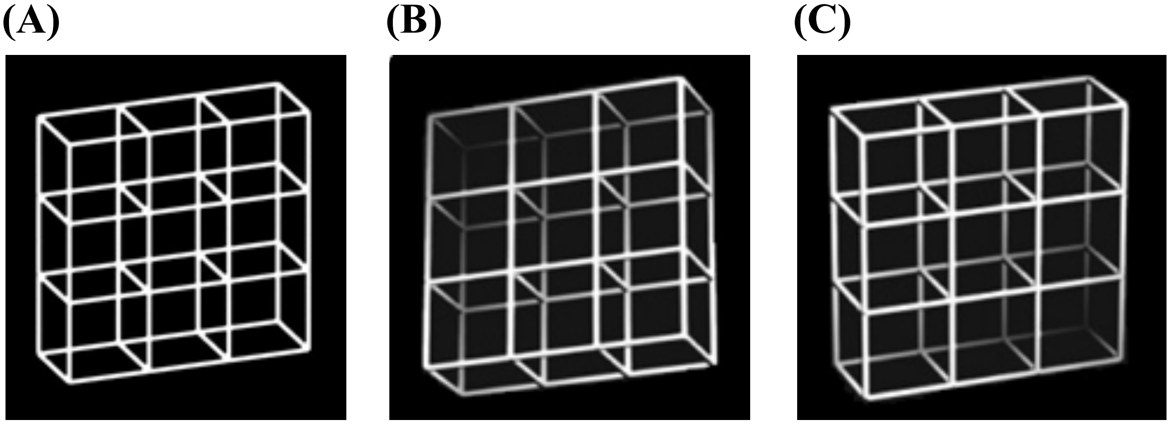


Figure 5.8. Ambiguous Necker lattice (A) appeared on ~90% of the trials and its unambiguous versions with either (B) its front face towards the upper left and (C) its front face towards the lower right appeared ~10% of the trials in Experiment 4.

5.3.1.3. Procedure.

During the setup of the EEG cap in this experiment participants completed a practice test. Each participant selected when to stop the practice test after they were confident with the nature of the task and were familiar with the two percepts (Left-Facing and Right-Facing). The instructions for the practice session were the same as for the main experiment. On each trial, participants had to report the perceived identity of the Necker Lattice (left-facing vs right-facing).

The main experiment procedure was similar to that of Experiment 3 except that the stimuli used here are the Necker Lattice stimuli (see Figure 5.3 for the experimental procedure). Therefore, response options in this experiment were Left-Facing or Right-Facing. The ambiguous Necker Lattice stimuli appeared on ~90% of the trials and ~10% of the trials were unambiguous. The same intermittent stimulus presentation paradigm was employed, with stimuli appearing binocularly for 150ms followed immediately by a 100 ms mask of white noise (Figure 5.3).

5.3.2. Data Analysis Methods

The steps taken to pre-process, exclude and code (but not analyse) the data were the same as in Experiment 1 from Chapter 3. The same data analysis methods (i.e. steps taken to analyse and classify the data) used in Experiment 3 were used in this experiment as well except where detailed below. On average, 2.83% (range: 0 – 33.33 %) of trials were excluded due to the exclusion criteria mentioned previously in Experiment 3 (e.g. amplitude excursions and blinks). For Identity Decoding (explained in the next paragraph), each trial was coded either as a Left-Facing or Right-Facing trial depending on the participant's response on that trial. For Reversal Decoding (explained in the next paragraph), each trial was coded either as a reversal or stability coded trial.

Identity Decoding: Each trial was coded as either a Left-Facing or Right-Facing trial depending on the participant's response on that trial. These trials will be referred to as Identity Coded trials. In order for a participant's data to be included in further analyses, at least 25 non-discarded trials per reported percept were required. Two participants were excluded because of the low number of non-discarded trials per trial type. The low number of trials for these participants was due to a combination of our EEG artefact rejection criteria and the participant's response pattern. The identity coded trials were fed into the classifier in both the time (see section 5.2.2.2.) and frequency domains (see section 5.2.2.3.). This was done in order to investigate what clusters in the pre-stimulus period were predictive of the subsequent reported interpretations of the participants.

Reversal Decoding: In a separate analysis, trials were also coded either as a reversal or stable trial by comparing the reported identity of the trial to the one preceding it. These will be referred to as Reversal Coded trials. For this Necker-Lattice experiment (Experiment 4), only 6 participants would have been included in the analysis because the low number of trials coded per condition. Therefore we cannot make any firm conclusions on the output from our pattern classification analyses (both in the time and time-frequency domains) due to the low number of participants included in this analysis and the low number of reversal trials. The low number of participants is due to our exclusion criteria whereby participants' response trend led to a low number of reversal trials. On average, 32 (range: 3-112) trials were coded as reversal trials (230 stability) with an average of 16 trials coded as Left Facing Reversals (range: 1-55) and 16 coded as Right Facing Reversals (range: 1-57). The analyses conducted on the Reversal Coded trials in this experiment (Experiment 4) will not be included in this thesis.

5.3.3. Identity Decoding Results

5.3.3.1. Response time.

For ambiguous stimulus trials, participants responded, on average, 766 ms (range = 523-1174 ms) after stimulus offset. Moreover, on average, RTs of participants for Left Facing trials was 800 ms (range = 567-1065ms) and 752 ms (range = 435-1225ms) for Right Facing trials. A paired samples t-test revealed no significant difference in the means of the RTs of the two types of trials, $t(15) = 1.780$, $p = .095$. This analysis was not conducted for unambiguous trials because there were too few trials to break them down into the two identities. Mean RT for unambiguous trials was 902 ms (range = 679-

1613ms). A paired samples t-test comparing the means of the ambiguous and unambiguous trials revealed a significant difference between the two, *t*(15) = -3.864, *p* = .002. Participants took longer to respond to unambiguous trials than to report their perceived interpretation of the ambiguous trials.

5.3.3.2. Unambiguous trials – Identity responses.

Participants correctly responded to 84.81% (SE = 3.22%) of the unambiguous trials. This is significantly greater than chance performance, *t*(15) = 10.802, *p*<.001. This means that participants had above chance orientation discrimination accuracy and were completing the task correctly.

5.3.3.3. Ambiguous trials – Identity responses.

Amongst the ambiguous trials, 35.97% were reported as being Left-Facing (range = 17.2-62.19%) and 64.03% were reported as Right-Facing. A one-sample t-test revealed that the percentage of right-facing trials reported was significantly greater than chance *t*(15) = 3.916, *p* =.001. Similar to the results from Chapter 3, our results are consistent with previous studies which have found that participants have a bias for right-facing perception (Sundareswara & Schrater, 2008; Kornmeier et al., 2009; Troje & McAdam, 2010).

5.3.3.4. Time domain MVPA - Identity Decoding.

MVPA in the time domain revealed four significant clusters of above chance identity (left vs. right facing) decoding in the pre-stimulus period. This first (from earliest to latest) cluster had a mean accuracy value of 0.5542 (min = 0.5417, max = 0.5661) and occurred between -950ms and -883ms before stimulus onset, $t_{cluster}(15)$ = 213.6482, *p* = 0.0474. The second cluster with mean accuracy value of 0.5549 (min =

0.5425, max = 0.5715) occurred between -854 and -767 ms. The third cluster with mean accuracy value of 0.5436 (min = 0.5331, max = 0.5525) occurred between -717 and -638 ms, $t_{cluster}$ (15) = 246.1650, p = .0216. The fourth cluster occurred between -484 and -381 ms, $t_{cluster}$ (15) = 335.9063, p = .0013, and had a mean accuracy value of .5385 (min = 0.5253, max = 0.5499). See Figure 5.9 for the average (across participants) accuracy value across time.

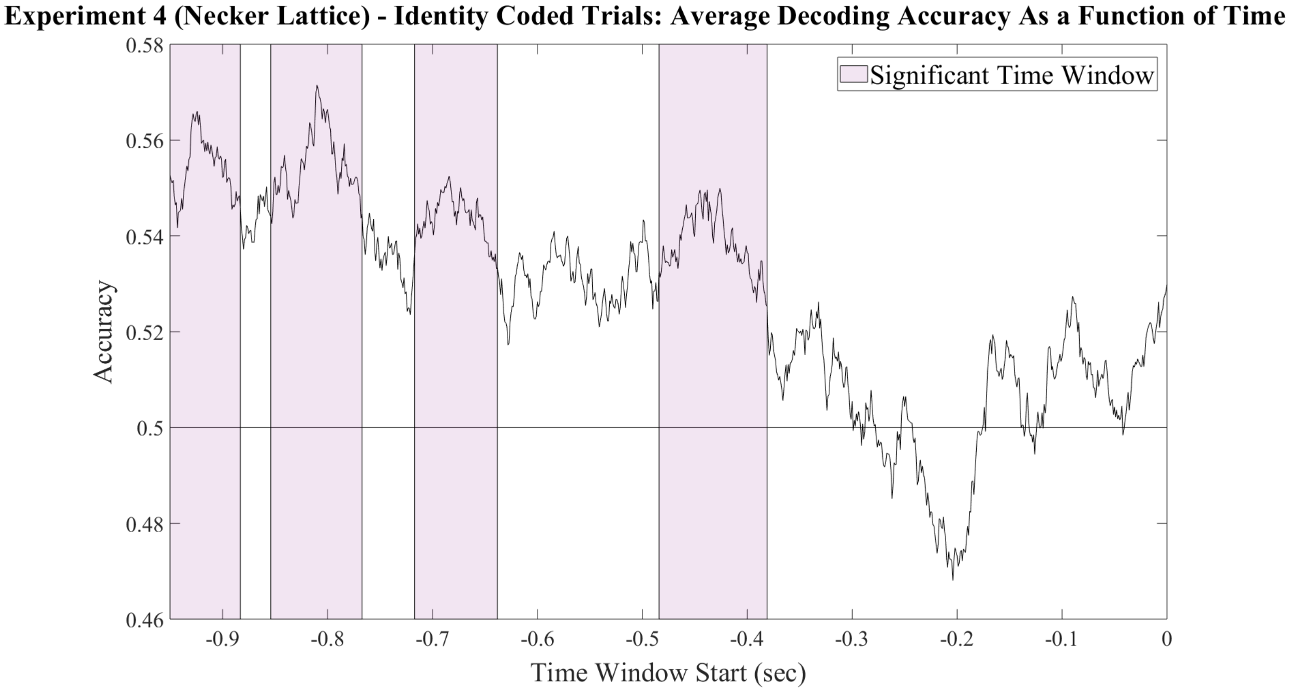


Figure 5.9. Plot of mean identity decoding accuracy across the pre-stimulus period in Experiment 4 (Necker Lattice). The time windows overlaid with purple transparent shaded areas represent the significant clusters obtained from cluster-based permutation tests of the accuracy values.

5.3.3.5. Frequency domain MVPA – Identity Decoding.

MVPA in the frequency domain showed significantly above chance identity decoding in one time x frequency cluster during the pre-stimulus period. This cluster spanned 16 and 30 Hz and -745 ms until stimulus onset, $t_{cluster}(15) = 2.4853 \times 10^3$, $p<.001$, with a mean accuracy of 0.5587 (min = 0.5219, max = 0.5842). See Figure 5.10 for the time-frequency map of the average (across participants) accuracy values of the Left-Facing vs. Right-Facing trials.

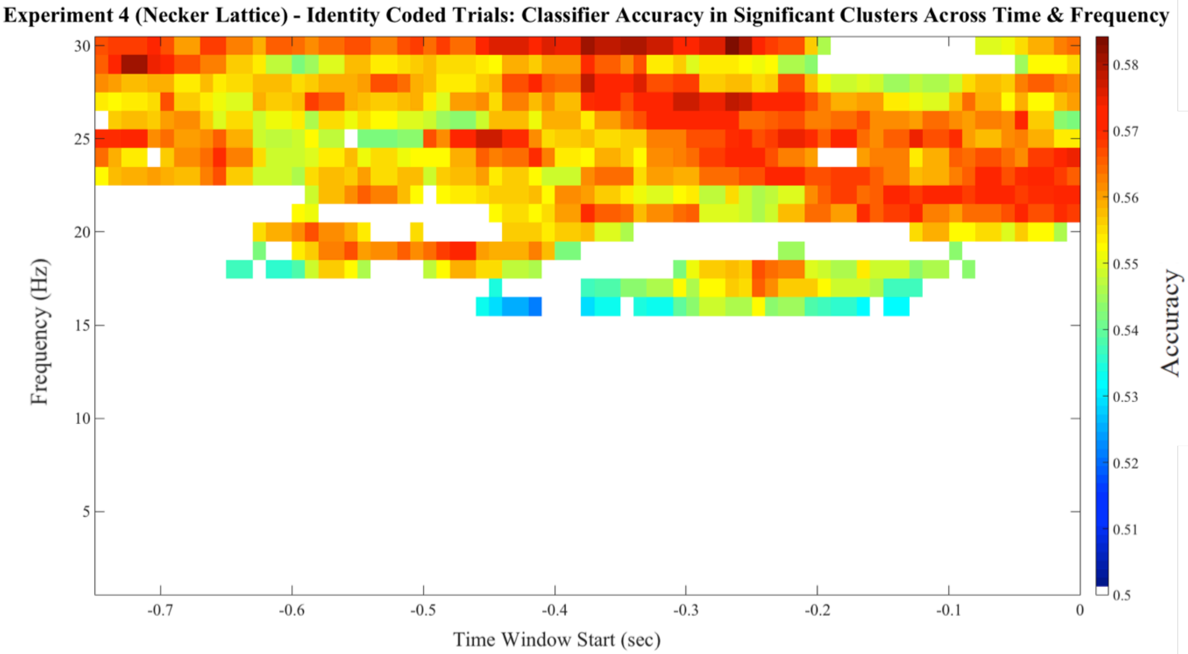


Figure 5.10. Time-Frequency map of the significant cluster of the average identity (left-facing vs. right-facing) decoding accuracy values averaged across participants and channels in the pre-stimulus period of Experiment 4 (Necker Lattice). This map shows only the significant cluster. Non-significant areas are masked out. The dark red colour reveals the highest period of decoding accuracy (i.e. successful classification). The blue (and darker blue) colour(s) reveals periods of decoding accuracy close to, at or below chance. Due to the sliding window (10 ms jumps) required to conduct the wavelet analysis, the output from the analysis was truncated by 200 ms on each end. This resulted in the trial length for the frequency domain data being shorter. Therefore, in the resultant map, the first 200 ms before 750 ms are not represented in the figure.

5.3.4. Interim Discussion of Identity Decoding Results

In Experiment 4, time domain MVPA significantly distinguished left-facing from right-facing trials in the pre-stimulus period with above chance accuracy. Periods of significant identity decoding in the pre-stimulus period occurred early on in this window and were not continuous but intermittent. Pattern classification in the time domain of the Identity Coded trials revealed that there were four periods of significant decoding. The first cluster overlaps with the significant time domain cluster of Identity Decoding in Experiment 3 (Face-Vase). This further suggests that this time window carries category information that is related to subsequent percept choice. The second significant time window starts at 854 ms and ends at 767 ms before stimulus onset. The second cluster however, also includes information from the 50ms window preceding the first significant time point included in the cluster due the backward sliding time window included in the analysis. The third significant time window starts at 717 ms and ends at 638 ms before stimulus onset. The third cluster again, also includes information from the 50ms window preceding the first significant time point included in the cluster due the backward sliding time window included in the analysis.

The fourth cluster occurs between 484 and 381 ms before stimulus onset with activity from the 50ms window preceding it included in the decoding analysis. Previous studies investigating the pre-stimulus activity underlying Necker Cube or Necker Lattice perception have focused on investigating the reversal event. To our knowledge, there are no studies that have explored the pre-stimulus period with regards to the identities of the Necker Lattice (left-facing vs. right-facing). Time domain MVPA has allowed us to identify several time windows in the pre-stimulus period during which the pattern of activity representing left-facing trials is significantly different from right-facing trials. This means that investigating the pattern of activity during those time windows would provide us with enough information to predict what the upcoming percept would be.

The presence of several clusters in the pre-stimulus period suggests that there are ongoing oscillations that influence the perceptual outcome of Necker Lattice perception. In addition to that, these separate clusters suggest that there are perhaps several ongoing mechanisms taking place in the pre-stimulus period. This idea is in line with Iemi et al. (2019)'s findings that suggest that there are different mechanisms in the pre-stimulus period that influence different post-stimulus effects. Further analyses involving temporal generalization are required to explore this idea.

Furthermore, the latest pre-stimulus time of significant decoding accuracy stops at 380 ms before stimulus onset. This suggests that there are intermediate mechanisms at later pre-stimulus times, which have not been picked up by MVPA in the time domain. This is possibly due to phase incoherence seeing as MVPA in the frequency domain identified significant decoding accuracies during the gap between 380ms before stimulus onset and stimulus onset.

Frequency domain MVPA of the Identity Coded trials of Experiment 4 (Necker Lattice) successfully decoded left-facing related activity from right-facing related activity in one significant pre-stimulus cluster. This cluster starts at around -745 ms before stimulus onset until stimulus onset and spans over the beta frequency band. This is similar to the findings from Experiment 3. As was mentioned previously, beta band oscillations have been found to carry category information (Richter et al., 2018). Moreover, researchers have linked beta oscillations in the pre-stimulus period to the endogenous regulation of perceptual states (Engel & Fries, 2010). Our findings are in line with this idea seeing as the observed significant decoding accuracies take place in the beta frequency band throughout the pre-stimulus period. However, in addition to these findings, our results reveal that this process is ongoing, starting at an early time point in the pre-stimulus period until stimulus onset. Alternatively, seeing as the findings from the previous literature have found these beta oscillations in isolated areas of the brain (e.g. visual cortex; Richter et al., 2018) our significant findings might also suggest that there are other mechanisms that are driving this significance. MVPA takes into account the entire pattern of activity across the scalp. Therefore, it could be that activity in other regions carried by beta oscillations are also driving the significant decoding.

The Identity Decoding findings in both the time and time-frequency domains, suggest that the activity underlying the perceptual interpretation of the ambiguous stimulus (left-facing vs. right-facing) can, not only be isolated in time (as indexed by the results from MVPA in the time domain) but can also be isolated to the beta frequency bands. This suggests that the identity of the ambiguous stimulus is influenced by modulations in the beta band in the pre-stimulus period that seem to be carrying information about the subsequent percept (i.e. left facing or right facing).

The earlier pre-stimulus windows detected in time domain MVPA that are not part of the significant cluster in the frequency domain results could be due to the truncation of the results that occurred as a result of the wavelet analysis conducted.

5.4. General Discussion

Experiments 3 and 4 were focused on investigating the relationship between pre-stimulus activity and trial-to-trial variability in the perception of ambiguous figures. Results from our MVPA-based approach support the notion that patterns of pre-stimulus brain activity are related to subsequent perceptual outcome. We approached this in two ways. In identity decoding, we aimed to predict the category of the perceptual outcome (e.g., face or vase for the Rubin faces-vase; left-facing or right-facing for Necker lattice) from the pattern of EEG activity across the scalp at each pre-stimulus time point. For reversal decoding, we used the same trials as in identity decoding but now aimed to predict whether the trial was a reversal or stable trial (i.e., same perceived outcome as preceding trial or not, respectively) based on the pattern of EEG activity at each time point. We conducted decoding based on the pattern of raw EEG voltage (i.e., time-domain) in addition to decoding based on the pattern of power across the scalp at each frequency (i.e.,Frequency domain). The resulting plots of decoding accuracy across time, for time domain or Frequency domain MVPA, show several clusters of pre-stimulus brain activity which are predictive of upcoming stimulus identity and of whether a reversal will occur. These results extend those of Rassi et al (2019), who found no significant pre-stimulus identity decoding, by having a longer pre-stimulus window, and by investigating reversal decoding as well. Our studies also examined two different ambiguous figures with the same experimental paradigm and analyses, allowing us to compare results for similarity.

5.4.1. MVPA for Identity Decoding

We found that when participants were presented with the face-vase stimulus (Experiment 3), the subjective interpretation of this bistable stimulus (face or vase) could be accurately decoded early on in the pre-stimulus time window at around 950 ms before stimulus onset. This early time window has not been previously identified by studies investigating the pre-stimulus period. For instance, Hesselmann et al. (2008) suggest that the increased activity measured in the FFA for face trials occurs right before stimulus onset. However, as was mentioned previously, the low temporal resolution of the BOLD signal might have caused delay in the effect measured. Therefore, the pre-stimulus effect identified by Hesselmann et al. (2008) might have occurred significantly before the onset of the stimulus. Our classifier in the time domain allowed us to localise in time this effect that has not been observed in Rassi et al. (2019)'s experiment. Rassi et al. (2019) did not detect the increased activity of the FFA in the pre-stimulus period for face reported trials. The pre-stimulus time window included in their analyses (both pattern classification and time-frequency) is short. They only investigated the 200 ms time window before stimulus onset. Moreover, the early significant cluster of Identity Decoding in Experiment 3 (Face-Vase) indicates that there are ongoing oscillations in the gap between the significant cluster and stimulus onset that is related to the perceptual outcome (i.e. face or vase).

In addition to the results from the time-domain MVPA, frequency domain MVPA of the Identity Coded trials in Experiment 3 revealed that the reported interpretation of the face-vase could be successfully decoded from the amplitude of the ongoing oscillation within the lower beta band between 475 and 95 ms and within the upper beta band between 745 and 475 ms before stimulus onset (maximum decoding accuracy in the beta band at around 300 to 200ms). These results renewed previous evidence (e.g. Castelhano et al., 2013; Ehm et al., 2011; Engel & Fries, 2010; Richter et al., 2018) of a relationship between the beta oscillations and perceptual outcome (face or vase).

Moreover, our findings for MVPA of the Identity Coded trials in Experiment 3 are in line with the idea the role of beta oscillations in the pre-stimulus period in the endogenous regulation of perceptual states (Engel & Fries, 2010) and that they carry category information (Richter et al., 2018). Our classifier in the time frequency domain furthers these findings because we can now isolate them in time and at certain frequency levels. MEG findings by Rassi et al. (2019) suggest that gamma modulations in the FFA in response to the face-vase stimulus start at stimulus onset with no oscillatory activity in the pre-stimulus period. Other MEG studies on face perception found that it starts at 100ms after stimulus onset (e.g. Perry & Singh, 2014; Uono et al., 2017). These differences in our findings could be due to several factors. Firstly, our analysis takes into consideration the entire pattern of activity of the scalp, whereas their analysis is focused on specific areas (FFA and V1). Rassi et al. (2019) used pattern classification in order to identify favourable regions of interests to investigate the effect of the pre-stimulus connectivity dynamics between early visual regions (V1) and FFA on the upcoming subjective reports. They then used a source reconstruction approach, which localized activity to particular areas and then conducted their time-frequency analyses on those areas. This means that the limited spatial information included in their analyses might have led to the effect not being detected.

These findings in both the time and time-frequency domains are similar to our results from the pattern classification of the subjective interpretation of the Necker Lattice (left-facing or right-facing; Experiment 4). When participants were presented with the Necker Lattice, the identity coded trials could be accurately decoded in the time domain analyses in four significant clusters. These clusters occur early in the pre-stimulus period with the first cluster starting at around 1 s and the last cluster ending at around 381 ms before stimulus onset. The presence of several clusters in the pre-stimulus period suggests that there are ongoing oscillations that influence the perceptual outcome of Necker Lattice perception. Our analyses reveal that the effect that these oscillations have on the perceptual outcome can be isolated in time in the pre-stimulus period. Therefore, an investigation of the representations associated with the two identities of the Necker Lattice (left-facing and right-facing) can be significantly distinguished from one another during those time windows. These time windows have not been previously identified in studies investigating the activity occurring in the period before the onset of the Necker Lattice. Moreover, the studies who have investigated the role of pre-stimulus activity on the perceptual outcome of the Necker Lattice, have focused on the reversal event itself and have used univariate approaches. This means that these studies might have missed effects in the pre-stimulus period that influence the perceptual outcome of Necker Lattice perception as indexed by our pre-stimulus time domain findings.

In addition to the results from our time domain classifier, the identity of the Necker Lattice can be decoded from the phase of the ongoing oscillation within the beta band between 745 ms before stimulus onset until stimulus onset. These are in agreement with previous studies that have found that modulations in the beta band in the pre-stimulus period have been linked to the ambiguous stimulus perception (Basar-Eroglu et al., 1996; Ehm et al., 2011; Engel and Fries, 2010; Richter et al., 2018; VanRullen et al., 2006). However, our findings extend these previous findings in revealing that these modulations start at an earlier time point than what has been previously identified. This means that the ongoing oscillations that determine the perceptual outcome of the Necker Lattice start at an early time point in the pre-stimulus period.

This is similar to the previous findings from pattern classification of the Identity Coded trials in Experiment 3. Identity decoding results in the time-frequency domain suggest that there may be similar mechanisms determining ambiguous stimuli (Necker Lattice and Face-Vase) in the pre-stimulus period. These occurred in the beta frequency band. The same frequency band and time windows that are involved in the Identity Decoding in both Experiments 3 and 4 index this. However, future analyses involving cross-decoding are necessary in order to confirm whether the mechanisms underlying percept choice in the face-vase are the same as or different from the mechanisms underlying percept choice in the Necker Lattice (Kaplan et al., 2015). We cannot explore these similarities further seeing as these experiments took place at different times and the participants that completed them are different between the two. A future study involving more than one type of ambiguous stimulus in the same experiment is necessary in order to study the paired differences between perceptual reversals experience in Face-Vase perception vs. Necker Lattice perception. Briefly, cross-decoding is when a classifier is trained on data from one perceptual state in one ambiguous stimulus, and is tested on data from the same perceptual state in another ambiguous stimulus (Kaplan et al., 2015). These two ambiguous stimuli have to take place within the same participant in order to be comparable.

Cross-decoding would also allow us to explore the differences observed between the two experiments. The results from pattern classification in both the time and frequency domains in both Experiments 3 and 4, illustrated in Figures 5.4, 5.5, 5.9 and 5.10, reveal that there are periods of significant decoding accuracy in Experiment 4 that are not classified as significant in Experiment 3. We found that for Experiment 3 (face-vase), significant decoding accuracies in the upper beta band stop at around 475ms and start in the lower beta band at 475 ms (see Figure 5.5). For Experiment 4 (Necker Lattice), the significant decoding accuracies are found in both the beta band throughout the entirety of the significant time window of the cluster (-745 ms until stimulus onset; see Figure 5.10). In addition to that, pattern classification in the time domain only identified one significant time window of decoding accuracy in Experiment 3 (Face-Vase; see Figure 5.4) versus four time windows in Experiment 4 (Necker Lattice; see Figure 5.9). These differences observed in time and time-frequency results suggest that there are perhaps different ongoing oscillations in the pre-stimulus period that underlie the perceptual outcome of the two stimuli. This idea is in line with Ronconi et al. (2017)'s findings. They found that different ongoing oscillatory activity at different frequency bands determine the perceptual outcome of their ambiguous stimuli at different time windows. Their results revealed that for the two-flash fusion stimulus, the reported interpretation of this bistable stimulus (one flash vs. two flashes perceived) could be accurately decoded from the phase of ongoing oscillations within the alpha band at around 400 to 300 ms before stimulus onset. Whereas, for the apparent motion stimulus, the subjective interpretation of this stimulus (motion vs. alternation) could be accurately decoded from the phase of ongoing oscillations within the theta band between 500 and 400 ms before stimulus onset.

In summary, pattern classification for Identity Decoding can successfully decode the identities of an ambiguous stimulus in both Experiments 3 and 4 in the pre-stimulus period at the beta frequency band. The activity observed suggests ongoing oscillatory activity throughout the pre-stimulus period that biases subsequent percept choice. These findings are new in that they allow us to isolate in time and frequency the exact clusters during which the pattern of activity representing one interpretation is distinguishable from the pattern of activity representing the other interpretation. Interestingly, the clusters during which our decoding accuracies were significant also overlap with clusters from the pattern classification of our reversal coded trials. This is not surprising due to the unstable nature of ambiguous stimuli where there is moment-to-moment variation in our interpretation of them.

5.4.2. MVPA for Reversal Decoding

Following these analyses, we re-coded our trials in order to end up with reversal and stable trials. We did this by comparing the participant’s response on one trial to that given to the previous one. We found that when participants were presented with the Face-Vase stimulus (Experiment 3), successful Reversal Decoding in the time domain occurred right before stimulus onset between 96 ms (46 ms is the first significant time point in the significant cluster but it includes activity from the 50 ms preceding it due to the backward sliding time window used in our analyses) before stimulus onset until stimulus onset. As was mentioned previously, this is temporally close to Britz et al

(2009)'s findings where they found pre-stimulus activity 50ms before stimulus onset in an experiment investigating reversals in a variant of the Necker Cube.

Britz et al. (2009) used a similar experimental paradigm as the reversal task from Chapter 3 (see section 3.2.1.4.) and a variant of the ambiguous (only – no unambiguous trials were used in their experiment) Necker Cube. They used EEG and statistical parametric mapping in the inverse space and found that the only significant difference was observed in the right inferior parietal lobe. Their results revealed activity in the 50ms before stimulus onset that dissociated the reversal trials from the stability trials. The latter was found to be significantly more active preceding a perceptual reversal. Previously, the right inferior parietal lobe has been identified in fMRI studies on bistable perception (Kleinschmidt et al. 1998; Inui et al. 2000; Slotnick and Yantis 2005), and has been suggested to indicate the detection of a perceptual reversal after it has taken place after stimulus onset. However, due to the low temporal resolution of BOLD signals, as was mentioned previously, the temporal allocation of this effect might have been delayed in time. Britz et al. (2009)'s findings confirm this idea, where they found activity preceding the ambiguous stimulus in this area on reversal reported trials. Britz et al. (2009) suggested that momentary activity in this brain area appears to predict an upcoming perceptual reversal despite the absence of any changes in the physical stimulus.

EEG does not allow for the definition of exact underlying neural sources, therefore we cannot confirm that the significant cluster identified by Reversal Decoding in the time domain in Experiment 3 is solely driven by activity in this area. However, our findings do support the evidence that activity occurring right before stimulus onset is predictive of an upcoming reversal and that significant decoding during that time window might have been driven by activity occurring in the right inferior parietal lobe. However, in addition to the findings from Britz et al. (2009)'s study, the findings from the pattern classification in the time domain suggest that the difference between the pattern of activity representing reversal coded trials and the one representing stability coded trials starts at an earlier time window in the pre-stimulus period than the window they identified. Therefore suggesting that the momentary fluctuations of baseline activity that influence perceptual reversals start at an earlier time point than what has been previously identified in the univariate literature.

Reversal decoding in the frequency domain in Experiment 3 showed a significant cluster of above chance accuracy in the same approximate time and frequency window as was seen in identity coding for Experiment 3. This is not surprising given the unstable nature of the stimulus used. The window identified by our classifier and cluster based permutation stats occurs early on in the pre-stimulus period from 535 ms (485 + 50 ms) to 355 ms before stimulus onset and falls in the upper beta band. As was mentioned previously, this frequency band has been previously associated with perceptual reversals in previous findings in the univariate literature (e.g. Basar-Eroglu et al., 1996; VanRullen et al., 2006; Ehm et al., 2011). Specifically, Ehm et al. (2011) found a lower gamma band (26-40Hz; here, we refer to this as beta) increase at the right-hemispheric central and parietal electrodes and an occipital decrease of higher gamma-band activity only on reversal trials, 200 ms before ambiguous stimulus onset. Ehm et al. (2011) identified these beta and gamma oscillations at around 200 ms before stimulus onset and found that they only occur in the pre-stimulus period preceding reversal reported trials. The beta band significant decoding accuracies from our classifier occur at an earlier time window and stop before the activity identified by Ehm et al. (2011). This could be because the frequency range included in our analyses does not include the higher-gamma frequency band. Ehm et al. (2011) found a decrease of higher gamma activity at around 160 ms before stimulus onset.

Future analyses using a wider range of frequencies would be necessary to either support or disprove this idea. The frequency range included in our analyses is similar to the one chosen by Rassi et al. (2019). The reason for this choice was so that our analyses are consistent and similar to the ones conducted in Chapter 4 and across studies using the same experimental paradigm as we did in this chapter. However, the difference in our results can also be attributed to the type of filter used. Ehm et al. (2011) used a band-pass filter of 0.3-70Hz. Using a bandpass filter has been found to distort and shift the phase of the signal in time (Yael et al., 2018). This suggests that perhaps some of the activity detected in Ehm et al. (2011)'s study might have occurred at an earlier time window than reported. Moreover, the time window included in their analyses only included 400 ms of the pre-stimulus window. The window was not wide enough for them to detect earlier oscillatory activity like the ones identified by our classifier. And finally, Ehm et al. (2011) computed short time Fourier Transform time-frequency analyses with a Hanning-Window with four different window widths that range from 160 to 480 ms. This means that some of the effects around the time window of the oscillatory activity that was measured in the pre-stimulus period, might have been averaged out.

Pattern classification in the time and frequency domains of the Reversal Coded trials in Experiment 4 were not included in this chapter. The number participants that were included in this analysis was too small (only 6 participants) due to our a prior exclusion criteria described previously. Future experiments with more subjects and trials for analysis should be conducted in order to investigate MVPA on reversal coded trials when using the Necker Lattice as the ambiguous stimulus. The small sample size used in this analysis is due to the low number of reversal trials that were re-coded in the participants that were excluded from the analysis. We suspect that the low number of reversal trials coded is due to the experimental design. .

The paradigm we used in this experiment is an adaptation of Hesselmann et al. (2008)'s paradigm where we presented ambiguous stimuli very briefly and used long ITIs. As was mentioned previously, we did this in order to study the pre-stimulus period in more depth, to avoid any overlapping information between successive stimuli, to ensure that no re-reversals occur, to maximize the unpredictability of stimulus onset (i.e. minimize volitional control of perception) and obtaining independent responses in successive trials and to get roughly equivalent reports of the different percepts of the ambiguous images used (Hesselmann et al., 2008). We found that the latter was the case for the Face-Vase stimulus where the percentage of faces and vase reported is close to 50% for each of them. Previous findings have shown that IED and FW do affect the percentages of faces vs vase perceived. Therefore, in order to avoid any confound with frequency of percept choice, we also administered the pre-test and based our stimulus' FW and IED on the results of the pre-test for each participant. We also found that this paradigm, coupled with the pre-test, furnished similar behavioural results to the ones found in Experiments 1&2 in Chapter 3 in terms of the percentage of reversal and stable trials that were coded. This allowed us to investigate the pre-stimulus effects of those trials. However, this was not the case for the Necker Lattice reversal coded trials. We expected that, based on previous findings, that the dimensions of the Necker Lattice would not affect percept choice and therefore we did not administer a pre-test similar to the one we did for the Face-Vase experiment. This was not a limitation for our classifier when we ran it on the identity coded trials in the Necker Lattice because of the random subsampling from the condition with more trials feature of the classifier and the relatively high number of trials per percept reported (minimum number of Left Facing trials reported was 52). This gave the classifier enough data to train and test. It was a limitation, however, for the classifier when we administered it to the reversal coded trials. We had to exclude the majority of our participants' data because they had too few trials in one of the conditions (i.e. too few reversal trials) and that would not give the classifier enough trials to train and test. We suspect that this is due to the length of stimulus presentation and ITIs. As was mentioned previously in the section on Presentation Mode and Inter-Stimulus Interval in Chapter 1, Kornmeier et al. (2002), in an attempt to study the effect of varying ISIs on reversal rates, presented the Necker stimulus discontinuously and found that randomly varying ISIs leads to strong modulations of the reversal rates (Orbach et al., 1963). They found that with longer ISIs (>400 ms), reversal rates noticeably drop, down to zero reversals (Leopold et al., 2002, Maier et al., 2003, Sterzer and Rees, 2008) when presentation times are shorter than the individual average stability duration. This was the case in the experimental paradigm used here.

Beta activity in the pre-stimulus period has been previously linked to predictive processing notions that higher areas constantly derive predictions based on incoming evidence and prior experiences and feed those predictions back to lower areas (Bastos et al., 2012). This would suggest that the activity measured in the pre-stimulus period is not spontaneous and might be voluntarily driven to some extent. This possibility cannot be entirely ruled out. However, it is unlikely to be the case because of the design of the experiment (described previously) with short presentation times and difficult-to-predict inter-trial intervals (between 3-14s). Whether the effects in the beta band reflect conscious volitional processes or unconscious physiological activity is not clear, although both types of ongoing activity exist (Vincent et al., 2007; Mason et al., 2007). In order to test this, a further study could be performed in which subjects are asked to volitionally induce one interpretation (e.g. inducing a face percept in a Face-Vase experiment) on certain predefined trials. By comparing the activity in the beta band between conditions where a percept was volitionally induced and where the ambiguous image was passively perceived, it would be possible to discern the nature of the effects in the beta band found in this study.

The significant results from our classifiers in the frequency and time domains do not always overlap in time. We suspect that the absence of overlap in the significant decoding accuracies in the time-windows from our classifier in the time domain and our classifier in the time frequency domain could be due to phase incoherence observed in the time domain. This means that the oscillations are not phase aligned across trials. This can’t be detected in the time domain but can potentially be picked up in power. This means that there are potential phase differences in the oscillations that distinguish between the two perceptual states of Identity Decoding and Reversal Decoding. As for the absence of effect in the frequency domain that we find in the time-domain classifier results could be hidden because of the 200 ms truncation at the beginning and the end of the window included in the wavelet analysis. It is important to note that this truncation process did not affect any effects observed around stimulus onset seeing as it occurred on the first 200 ms and the last 200 ms of the epochs included in the analysis.

5.4.3. Conclusion

The effect we describe is necessarily related to spontaneous fluctuations because it varies between trials and is ongoing (as indexed by the findings from our classifiers). Moreover, It is important to note that sensory input in our experiment was sparse, intermittently presented, included catch trials with inverted versions of the stimulus, and was separated by randomized variable length intervals with long durations. This means that the activity observed in our results cannot be attributed to previous trials. This is explained in detail in Chapter 2, section 2.2.2.1.1.. Due to the brief presentations, only one percept per trial was possible, which was established through participants' responses in order to sort the data post-hoc according to perception. The long and sparse ITIs maximized the unpredictability of stimulus onset, and therefore minimized volitional control of perception, obtaining independent responses in successive trials and minimizing the occurrence of a re-reversal. In previous psychophysical piloting by Hesselmann et al. (2008), these settings were found to lead to roughly similar percentages of faces and vase percepts and to prevent perceptual switching within single trials. Therefore, furthering the idea that these fluctuation vary between trials. Therefore, our findings suggest that ongoing fluctuations have an impact on how we make up our mind during subsequent perceptual inferences from sensory input.

Importantly, we cannot infer causality between the effects measured in this study and the subsequent perceptual outcome. In order to determine the causal role of the measured oscillatory pre-stimulus activity, a study involving Transcranial Magnetic Stimulation (TMS) (e.g. Dugue et al., 2011), in the pre-stimulus time and frequency cluster identified, could be performed. A change in the rate of reversals or percentage of reported face percepts, for example, between stimulation (with TMS) and no stimulation (no TMS) conditions could indicate whether or not the effects found in the pre-stimulus activity has a causal link to the subsequent percept in the post-stimulus period.

The present results are in agreement with and expand upon recent studies providing evidence for a link between pre-stimulus neural oscillations and ambiguous figure perception. MVPA in both the time and frequency domains has helped us more precisely isolate pre-stimulus effects underlying perceptual reversals as well as the particular identity experienced when viewing an ambiguous stimulus. In some cases, these effects can be assigned to oscillatory mechanisms in specific frequency bands. The results from our approach show that a broad range of frequencies are informative. In particular, we found that the most informative frequency bands are the beta band.

Chapter 6: General Discussion

6.1. Overview

In this thesis, I set out to investigate some of the underlying mechanisms of ambiguous figure perception. Specifically, I was interested in investigating the neural activity associated with the perceptual interpretations of ambiguous figures (e.g. Left-Facing and Right-Facing in the Necker Lattice) and their perceptual reversals. In the first chapter of this thesis, I discussed the background literature on multistable perception and the studies up to date that have investigated some of the factors that underlie and influence our perception of an ambiguous image. In summary, behavioural studies indicate that reversal rates are sensitive to a multitude of factors: experimental paradigm, presentation time and inter-stimulus interval. Studies using neurophysiological tools (e.g. fMRI, EEG, MEG, etc…) have found that there is neural activity in both the pre- and post-stimulus periods that influence and are related to our perceptual interpretation of an ambiguous figure and perceptual reversals.

In my thesis, I have tackled two major issues. First in Chapter 3 (Experiments 1 & 2), I investigated well-known reversal-related ERP components in order to identify whether these components are dependent on higher-level mechanisms such as task or response demands or if they are truly markers of the different perceptual processing stages linked to reversals of ambiguous figures. There are long-standing questions over whether reversal-related ERP components reflect top-down or bottom-up mechanisms and the extent to which they are linked to endogenous perception reversals. I was able to address this issue with ERP data using a new study design.

Second, due to the univariate nature of most ERP and EEG analyses, the multivariate nature of EEG data is not fully explored. In particular, the pattern of activity across the scalp is often not considered because ERPs and other EEG measures tend to be quantified with a priori regions of interest (ROIs) for statistical purposes. Given that perceptual reversals have already been shown to involve various cortical areas, it is likely that the pattern of activity across the scalp would hold useful information about perceptual reversal processes. Therefore, in another line of my research, I set out to use multi-variate pattern analysis (MVPA) in the pre-stimulus and post-stimulus periods in order to identify the temporal and time-frequency clusters during which the patterns of activity are predictive of the perceptual reversals (reversal decoding) and the upcoming perceptual outcome (identity decoding).

The following sections of this chapter will summarise the findings from each experiment to address the four main questions that were introduced in Chapter 1: 1) Are ERP measures of reversal-related activity dependent on task demands and/or response demands? 2) What patterns of post-stimulus activity are associated with perceptual reversals of an ambiguous figure? 3) What patterns of pre-stimulus activity are associated with perceptual reversals of an ambiguous figure? 4) What patterns of pre-stimulus activity are associated with each perceptual outcome of an ambiguous figure? Moreover, for each question I will discuss whether the findings remain the same or differ across the two types of ambiguous stimuli used (Rubin's Face-Vase and Necker Lattice). I will then interpret these findings in relation to existing theories on ambiguous figure perception and perceptual reversals, discuss some general limitations of the studies used in this thesis and address how the findings can inform the direction of future research in this area.

6.2. Summary of results and Discussion

6.2.1. Are ERP measures of reversal-related activity dependent on task demands? Response? Are these the same across Necker Lattice and Rubin's Face-Vase perception?

In Chapter 3, we aimed to determine whether the reversal-related ERP components, RN and RP, are sensitive to task and response factors. In order to address this, we used the 'Reversal Task' and the 'Identity Task' and varied response style across blocks in Experiment 1 (Necker Lattice) and Experiment 2 (Face-Vase). With this design we were able to compute the RN and RP when both types of trials were response targets (i.e., reversal, responded and stable, responded) and when both were not response targets (i.e., reversal, no response and stable, no response) for both Reversal and Identity tasks separately. This ensures that the reversal vs. stable trial comparisons that are used to compute the two reversal related components, are not confounded by differences in task or response demands. Therefore, we were able to compare across task and response factors, the differences and similarities observed in the RN and RP amplitude and determine whether these factors affected the two reversal related components. In order to determine whether the effects observed are the same across different types of ambiguous stimuli, we conducted two experiments. We used the Necker Lattice in Experiment 1 and set out to replicate the results in an additional experiment using Rubin's Face-Vase (Experiment 2).

The results were similar across both experiments. We found that the RN was present in all conditions and was unaffected by response demands and which task was completed. This means that the RN could not be accounted for by task and response related differences between reversal and stable trials. Previous studies have also suggested that the RN is insensitive to response action (e.g. Kornmeier & Bach, 2004). In contrast, although the RP was not affected by task, it was only present on trials in which participants made a manual response. However, here there were some differences between the results for the two different ambiguous stimuli. In Experiment 1, non-response trials (the response style where participants had to withhold a response) showed no evidence of a significant RP component. In contrast, in Experiment 2, non-response trials showed a significant difference between reversal and stable trials during the latency of the RP but with an opposite polarity (i.e., stable > reversal) to the RP that was present on response trials. We conducted an overall analysis combining both datasets from the two experiments and found that there was no interaction with the experiment factor. We cannot account for this minor discrepancy between the RP results in Experiments 1 and 2. Nonetheless, it is clear that the RP is sensitive to response action instructions.

Although the RP is uniquely present for endogenous reversals, our results suggest that it is not a pure measure of perceptual processing related to reversals (e.g., Kornmeier & Bach, 2012). Instead, our results support the idea that the RP reflects response-related processes. It is possible, however, that reversal-related perceptual processes are different between response and non-response trials and that the observed differences in the RP reflect this. In this case, the RP would still reflect perceptual processes involved in generating reversals but there presumably would then be another ERP correlate of the perceptual processes generating reversals on non-response trials as we found in Experiment 2. Further work will be necessary to confirm whether this is robust and whether it can be attributed to perceptual or non-perceptual processing.

Alternatively, the RP may arise from response-dependent, non-perceptual processes that are not directly involved in generating the reversals themselves but instead only co-occur with reversal processes. Other researchers have suggested that the RP may be a marker of the detection of ambiguity/disambiguation process (e.g., Kornmeier & Bach, 2012; Kornmeier, Pfäffle, & Bach, 2011). If this is an accurate description of the source of the RP, then our results suggest that this ambiguity/conflict signal is modulated by whether the trial requires a response or not.

On the other hand, all the evidence suggests that the RN could potentially be a pure and more reliable marker of perceptual reversals. This component is present for both exogenous and endogenous reversals. It can be measured regardless of stimulus, task or response action. However, there is some risk that our task manipulation may not have been completely effective. For instance, although we intended the identity task to better equate task and response factors between reversal and stable trials, this was not complete. The percentage of reversals (~33%) was equal in the two tasks and thus, there is potential for reversal trials to stand out as rare oddballs even in the identity task. This could account for the similarity of our RN results between the identity and reversal tasks. However, we would argue that the rarity of reversals was less salient in the identity task than in the reversal task because the task did not explicitly require monitoring for them. One way to address this issue would be to test whether the RN/RP differs depending on reversal rate. Unfortunately, we did not have sufficient data to compute the RN/RP for different reversal rates across our participants, but future research should explore this. Reversal and stable trials also differed in their response actions in the identity task. Specifically, reversal trials in the identity task always required a change in response action relative to the previous trial whereas stable trials had the same response action as the preceding trial. Thus, a reversal trial in the identity task necessarily involved a task-relevant change in motor behavior that was not required for stable trials. This was not the case for the reversal task. Reversal and stable trials could require a response action change or no change depending on the preceding trial type.

Overall, our results in Chapter 3 demonstrate that response arrangements must be considered carefully when studying the RP. In particular, collapsing across response and non-response can hide a significant source of variability in the data even in relatively early latency ERP components.

6.2.2. What patterns of post-stimulus activity are associated with perceptual reversals of an ambiguous figure? Are these the same across Necker Lattice and Rubin's Face-Vase perception?

Univariate analyses do not take full advantage of the multivariate nature of EEG data. This means that there could be reversal-related activity that is not picked up in time and frequency domains when using these analyses. In particular, complex patterns of activity across the scalp are typically not considered. In Chapter 4, I used Multi-Variate Pattern Analysis (MVPA) in order to investigate the post-stimulus period in Experiments 1 (Necker Lattice) and 2 (Face-Vase) in full without any a priori spatial regions of interest. This allowed me to isolate in time and to certain frequency bands, patterns of activity that are predictive of a reversal or stability trial that might have been lost in univariate analyses. I used MVPA in both the time and frequency domains (separately). This “decoding” analysis was done in two ways: identity and reversal decoding. In identity decoding MVPA, the classifier was trained to distinguish different perceptual outcomes (e.g., face vs. vase) based on the pattern of brain activity. This approach does not isolate activity linked to reversals but does give an indication of activity which is linked to determining which interpretation is seen in a trial. In reversal decoding MVPA, the classifier was trained to distinguish between perceptual reversal and perceptual stability based on the pattern of brain activity. Unlike identity decoding, this allowed us to isolate activity linked to reversals in a single trial.

In Experiment 1 (Necker Lattice), MVPA in the time domain successfully distinguished reversal from stable trials. Notably, periods of significant reversal decoding were consistent with the established timing of the RP, RN and other electrophysiological correlates (e.g. Frontopolar Positivity) linked to perceptual reversals. This was also observed in the frequency domain decoding of these data. These results showed a single significant cluster that included, but was not restricted to, frequencies modulated by reversals in previous univariate findings. This is also true for both time and frequency domain decoding run separately on the Response and No Response conditions as well. The findings in this experiment further previous findings by showing that activity related to perceptual reversals can be decoded early on in the post-stimulus period, starting right after stimulus onset. Previous findings in the ERP literature identified several ERP components in the post-stimulus period with the earlier reversal related component (the RP) starting at around 130ms. Our findings suggest that the earliest reversal related activity could be detected very close to stimulus onset.

Moreover, MVPA in the frequency domain reveals that this activity spans throughout the majority of the frequency bands included in our analyses. This has not been shown before either. Previous findings have shown a chain of frequency modulations occurring at different times, whereas our findings reveal that several frequency modulations occur at the same time that are related to perceptual reversals. However, it is unclear whether clusters comprise one single mechanism across their span or contain several mechanisms that are directly adjacent in time or frequency and connect to form one cluster. This is also true for the findings from Experiment 2.

In MVPA analyses of the Experiment 2 (Face-Vase) data, results in the frequency domain revealed a significant time-frequency cluster with significant decoding accuracy values at several frequency bands that spans throughout the post-stimulus period included in our analyses (until ~540ms). This is also true for the individual analyses conducted on the two response conditions (i.e. response and non response). However, unlike Experiment 1, time domain MVPA results reveal that decoding of the overall trials, the response only trials and the non-response trials, each, identified one time cluster that overlaps with the latencies of the RP and the RN only. The time domain MVPA analyses in Experiment 2 revealed that a substantially shorter time window was identified as significant compared to the one in Experiment 1. The time domain findings in Experiment 2 suggest that during the latencies of the RP and the RN, the activity is related to perceptual reversals. However, as was mentioned previously, pattern classification integrates information for the entire scalp. Thus, it is not necessarily the case that the classifier was picking on patterns associated with these

ERP components. It could be that, in addition to these components, other patterns of activity at different electrode sites drive accurate classification.

The smaller significant time-window in Experiment 2 seems to suggest that the reversal related activity for Faces-Vase is different from the reversal related activity for the Necker Lattice. This difference is not observed during the latency of the RP and RN. That this difference would not be observed during that time window, are in line with the results from our combined analysis in Chapter 3 (section 3.4), where there was no significant interaction between ambiguous figure presented (Face-Vase or Necker Lattice) and the effects observed for the RP and the RN.

However, there is a similarity of the effects in the frequency domain in both experiments suggesting that these differences might be due to some effects being hidden in the time domain in Experiment 2. Future experiments designed to allow for a cross decoding analysis of the results would allow the investigation of whether these differences are indicative of differences in reversal related activity between the two stimuli. It is possible that the absence of an effect at later time points could be due to phase incoherence (i.e. oscillations are not phase aligned across trials) seeing as the MVPA results in the frequency domain reveal significant effects at later time points for Experiment 2 similar to Experiment 1.

The MVPA analyses of Experiments 1 and 2 showed large, continuous time periods of significant decoding accuracy, especially for Experiment 2, we see this effect in both the time and frequency domains. One interpretation of this is that there is one mechanism continuously active across the time course. Alternatively, these large continuous clusters of decoding accuracy could reflect several temporally-overlapping mechanisms operating in sequence. This issue is difficult to resolve with the analyses conducted here. One approach to answering this question with frequency domain decoding is to look at changes in the frequencies across time. For instance, if beta is involved for one time period and then the following time period has a different set of frequencies involved, this might suggest the boundaries between different mechanisms. To our knowledge, there is not an established method for assessing this quantitatively. Alternatively, approaches like temporal generalisation analysis (King & Dahaene, 2014; see General Discussion and Conclusion section 4.4. in Chapter 4 for a definition of the analysis) may be able to address this question.

The results from separate decoding of response and non-response trials suggest that perceptual processes related to reversals differ between response conditions. This is apparent in the paired samples statistics results where the means of successful decoding differ for the two response conditions. The difference between the overall trials and the response and non-response results suggests different patterns of activity associated with perceptual reversals between response conditions. The significant cluster results in both the time and time-frequency domains reveal that the mean differences between response conditions takes place during the latency of the RP for both experiments. Due to the nature of the analysis (in both the time and frequency domains) conducted on the data; the results suggest that the activity during the latency of the RP is predictive of perceptual reversals. In addition to that, these findings reveal that the activity linked to perceptual reversals during that time window is modulated by response. Previous research have suggested that the modulations taking place at the significant frequency bands identified by the classifier during that time window are related to the disambiguation and detection of ambiguity of the ambiguous stimulus (Ehm et al., 2011; Kornmeier & Bach, 2012). Taking this into consideration, our results suggest that this disambiguation process is modulated by response. One way to address this idea is to conduct cross-decoding analyses between response conditions in order to identify whether the reversal related activity in the response condition differs from the reversal related activity in the non-response condition.

Nevertheless, our findings from Chapter 4 are in line with the response effects found in Chapter 3. Further demonstrating that response arrangements need to be carefully considered when investigating reversal related activity. As can be seen from the difference in the results between the separate response conditions and the overall trials results (i.e. when MVPA was conducted on both response and non-response trials collapsed across one another), collapsing across response conditions can hide significant effects. Some of the time-frequency areas that were identified as non-significant for the overall trials came out as significant in the separate results of the response conditions.

Finally, although some similarities between the two experiments (Experiment 1: Necker Lattice; Experiment 2: Face-Vase) are identified in the significant MVPA clusters, there are some differences that were identified that suggest that there are some different electrophysiological mechanisms that underlie perceptual reversals between the two ambiguous images. Future cross-decoding analyses are required in order to explore this relationship further.

We were not able to conduct effective cross-decoding analyses here. Our main goal for these Experiments was to assess the effects of task and response-related factors on the ERPs. Thus, our design focused on ensuring that task and response factors were within-subjects comparisons. With the experiment already involving 45-60 minutes of task time (plus setup time of approx. 40 minutes), it was impractical to double the experiment length to also include stimulus type (Faces-Vase vs. Necker) within the same session. Thus, we ran this factor between-subjects. Cap position, electrode contact quality differences, as well as human state differences (e.g., attention, time of day) can cause large differences in patterns of activity across sessions. These would reduce decoding accuracy when conducting decoding in a between-subjects design. Thus, we have not attempted that here. Instead, we rely on comparing the results of decoding from each on its own. This still allows us to compare whether similar time frames and frequencies are involved in reversals for the two types of stimuli.

Interestingly, the significant clusters indicate that the processes underlying perceptual reversals start early on in the post-stimulus period. This suggests that there is potentially some pre-stimulus activity that also influences the occurrence of an upcoming perceptual reversal.

6.2.3. What patterns of pre-stimulus activity are associated with perceptual reversals of an ambiguous figure? Are these the same across Necker Lattice and Rubin's Face-Vase perception?

In Chapter 5, I used the same MVPA analyses as Chapter 4 in order to investigate perceptual reversals of ambiguous stimuli (Experiment 3: Face-Vase; Experiment 4: Necker Lattice) but now with a focus on brain activity in the pre-stimulus period. Successful time domain reversal decoding occurred between 96 ms before stimulus onset until stimulus onset. This is temporally close to Britz et al (2009)'s findings. They found significant differences in pre-stimulus activity between reversal and stable trials 50ms before stimulus. Using source localisation, they observed this in the right inferior parietal lobe. Our findings do support the evidence that activity occurring right before stimulus onset is predictive of an upcoming reversal and that significant decoding during that time window might have been driven by activity occurring in the right inferior parietal lobe. However, in addition to the findings from Britz et al. (2009)'s study, the findings from the time domain MVPA suggest that the difference between the pattern of activity representing reversal coded trials and the one representing stability coded trials starts at an earlier time window in the pre-stimulus period than the window they identified. Therefore suggesting that the momentary fluctuations of baseline activity that influence perceptual reversals start at an earlier time point than what has been previously identified in the univariate literature.

This idea is furthered by frequency domain reversal decoding in Experiment 3 where the significant cluster of above chance decoding accuracy occurred between 485 ms to 355 ms before stimulus onset and falls in the beta band. This frequency band has been previously associated with perceptual reversals in previous findings in the univariate literature (e.g. Ehm et al., 2011; Engel & Fries, 2010). Specifically, the beta band was found to be related to the destabilization process in ambiguous figure perception in the pre-stimulus period (Ehm et al., 2011) and to be involved in the endogenous regulation of perceptual states (Engel & Fries, 2010). These oscillations have been identified at around 200ms before stimulus onset and found that they only occur in the pre-stimulus period preceding reversal reported trials (Ehm et al., 2011). The beta band significant decoding accuracies from our classifier occur at an earlier time window and stop before the activity identified by Ehm et al. (2011). This could be because the frequency range included in our analyses does not include the gamma frequency band. Ehm et al. (2011) found a decrease of higher gamma activity (35-55Hz) at around 160 ms before stimulus onset. Future analyses using a wider range of frequencies would be necessary to either support or disprove this idea.

Unfortunately, no results can be discussed with regards to Reversal Decoding in Experiment 4 due to the small sample size that was included in the analysis. The exclusion criteria and pre-processing of the data resulted in a low number of Reversal Coded trials for the majority of the participants which resulted in their data being excluded from the analysis. The idea behind conducting Identity and Reversal Decoding on the same data set was to make the data underlying these two analyses maximally comparable. The limitation of doing such a thing is discussed below in the 'Limitations and Future Directions' section (section 6.6).

Overall, pattern classification of the reversal coded trials have furnished significant results that demonstrate that pre-stimulus oscillatory activity is related to whether or not a perceptual reversal is going to occur. I was able to isolate in time and frequency the activity that predicts the upcoming perceptual changes in perceptual experience in the absence of changes in sensory input. This is novel decoding work as existing EEG studies of ambiguous figures (e.g., Rassi, et al) focused on identity decoding rather than reversal decoding or used univariate methods.

6.2.4. What patterns of pre-stimulus activity are associated with each perceptual outcome of an ambiguous figure? Are these the same across Necker Lattice and Rubin's Face-Vase perception?

In Chapter 5, I also performed Identity Decoding on Experiment 3 (Face-Vase) and Experiment 4 (Necker Lattice). I found that the results in the time and frequency domains for both experiments are similar across both experiments.

Overall, time domain results showed that the subjective interpretation of participants could be accurately decoded early on in the pre-stimulus time window at around 950 ms before stimulus onset. This early time window has not been previously identified by studies investigating the pre-stimulus period (e.g. Hesselmann et al., 2008; Rassi et al., 2019). This early time window suggests that there are ongoing oscillations in the gap between the significant cluster and stimulus onset that is related to the perceptual outcome (e.g. face or vase). This idea is furthered by the time domain MVPA results in Experiment 4 (Necker Lattice) where two other significant time clusters were identified later in the pre-stimulus period. These subsequent time windows have not been previously identified in studies investigating the activity occurring in the period before the onset of the Necker Lattice. Moreover, the studies who have investigated the role of pre-stimulus activity on the perceptual outcome of the Necker Lattice, have focused on the reversal event itself and have used univariate approaches. This means that these studies might have missed effects in the pre-stimulus period that influence the perceptual outcome of Necker Lattice perception as indexed by our pre-stimulus time domain findings. The presence of several clusters in the pre-stimulus period suggests that there are ongoing oscillations that influence the perceptual outcome of Necker Lattice perception.

However, as was mentioned in the ‘General Discussion and Conclusion’ section in Chapter 5 (section 5.4), causality cannot be inferred from these results alone. Stimulation via Transcranial Magnetic Stimulation during those early time windows (e.g. at 950 ms before stimulus onset) could be performed in order to investigate the effects that this significant pre-stimulus window possesses over the perceptual outcome.

In addition to the results from MVPA in the time-domain, MVPA in the frequency domain of the Identity Coded trials in both experiments (3&4) revealed that the reported interpretation of the upcoming reported stimulus identity could be successfully decoded from the ongoing pre-stimulus oscillation within the beta band between -745 and -95 ms before stimulus onset for the Face-Vase experiment (Experiment 3) and between - 745 ms and stimulus onset for the Necker Lattice experiment (Experiment 4). These results renewed previous evidence (e.g. Castelhano et al., 2013; Ehm et al., 2011; Engel & Fries, 2010; Richter et al., 2018) of a relationship between beta oscillations and perceptual outcome (face or vase). Previous findings have suggested that beta oscillations in the pre-stimulus period are involed in the endogenous regulation of perceptual states (Engel & Fries, 2010) and that they carry category information (Richter et al., 2018). Our classifier in the frequency domain furthers these findings because we can now isolate them in time and at certain frequency levels. Future analyses involving cross-decoding are necessary in order to determine whether the neural activity underlying both ambiguous figures are the same or different between the two.

In summary, pattern classification for Identity Decoding can successfully decode the identities of an ambiguous stimulus in both Experiments 3 and 4 in the pre-stimulus period at the beta frequency band. The activity observed suggests ongoing oscillatory activity throughout the pre-stimulus period that is related to subsequent percept choice. The effects observed are necessarily related to spontaneous fluctuations. These findings are new in that they allow us to isolate in time and frequency the exact clusters during which the pattern of activity representing one interpretation is distinguishable from the pattern of activity representing the other interpretation.

6.6. Limitations and Future Directions

In this thesis, different experimental paradigms were used in order to investigate the activity in the pre- and post-stimulus period related to perceptual reversals and the perceptual outcomes of ambiguous figures like the Necker Lattice (Experiments 1 and 4) and the Face-Vase (Experiments 2 and 3). Limitations and recommendations for future research that are specific to each study were discussed in the relevant chapter discussions. Here, I will discuss some of the more general limitations of this thesis and the possible future directions of this research.

One of the challenges of this thesis is comparing findings across different ambiguous stimuli. In order to be able to properly compare the neural activity across stimuli (e.g. cross-decoding in pattern classification in order to compare Face-Vase decoding and Necker Lattice decoding), a within subjects design is preferred. This means that the same group of participants would need to complete both experiments with the two different ambiguous stimuli. This would allow us to compare the neural activity associated with Necker Lattice perception and the neural activity associated with Face-Vase perception. Therefore, we would be able to identify whether the mechanisms underlying perception of an ambiguous figure that involves figure ground reversals are the same as or different from the mechanisms underlying perception of one that involves depth perception reversals. I did ensure that the settings and parameters between participants are the same (e.g. lighting in the room, luminance on the screen, instructions, etc…). However, although occurring for all observers, multistability and its neural bases vary across individuals (Kleinschmidt et al., 2012). This variability makes it difficult to compare different stimulus presentations across individuals. Therefore, any similarities or differences identified between the stimuli would not be purely related to perceptual processing of these stimuli, but to individual differences between individuals as well. However, as was mentioned previously, the choices made with regards to presenting only one type of ambiguous stimulus with its unambiguous variants per experiment was because it would have been impractical to double the length of the experiments within the same session. This is because the duration of the experiment is already quite long, lasting for about two hours on average per participant. Moreover, conducting cross-decoding on the available data in a between-subjects design would affect the decoding accuracy values and reduce them. This is due to a multitude of factors that have been mentioned previously (e.g. cap position, electrode contact quality differences, human state differences). Instead, we relied on comparing the results of decoding from each on its own. This still allowed us to compare whether similar time and frequency clusters are involved in reversals and perceptual outcomes for the two types of stimuli used in our experiments.

Another challenge in conducting this type of experiment is that participants can get quite bored and tired while performing these experiments, which could influence the results identified. Although I tried to control for this by introducing breaks between blocks, the length of which were determined by the participants themselves, these breaks still required participants to sit still, because they were still wearing the EEG cap, in a dimly lit room. These experiments were relatively long, lasting for almost 2 hours. Considering the tasks that the participants had to complete and that they were testing the whole time, this can be quite tiring. Experiment 1 and 2 involved repeatedly presenting the same stimulus for 1200 (90% ambiguous, 10% unambiguous) trials. In Experiments 3 and 4, the same stimulus was presented for 350 trials in total. However, the ITIs were long and stimulus presentation time were short, which means participants were required to sit in place and stare at a blank black screen for a relatively long period of time. In total, out of 107 participants, data from 72 of these participants were included in our analyses. This was due to a multitude of factors, including 7 of these participants dropping out because they were tired. Setting up an EEG cap takes a long time (up to 30-40 minutes in some cases). Typically, in the types of experiments that we conducted, participants completed a practice test or a pre-test during the setup of the EEG cap in order to familiarize themselves with the task of the main experiment or to determine certain parameters that are necessary for the main experiment (e.g. Inter-Edge Distance and Frame Width of the ambiguous Face-Vase). Following the practice test/pre-test, participants would then complete the main experiment. As was mentioned previously, for the experiments conducted in this thesis, one session would last around two hours on average. Therefore, with the type of experiments used in this thesis, it is challenging to gather enough data without risking having very long experimental sessions which could impact participant performance on the tasks and the EEG signal (e.g. more alpha oscillations which could potentially lead to long periods of stable percepts; Piantoni et al., 2017).

A third challenge I faced is with needing to discard a substantial amount of data. As was mentioned earlier, out of 107 participants, data from 72 participants were included in the analyses. Although some of these participants were excluded because they dropped out, and others were excluded as a result of experimenter mistakes (e.g. data not being recorded or EEG recording stopping halfway), some of these participants were excluded because of the low number of trials in some of the conditions. These low numbers were a result of artefact rejections and/or participant response patterns. In Experiments 1 and 2, we followed the previous protocols used in Kornmeier and Bach (2004a)'s experiment. On average, we achieved similar percentages of reversals as they did. However, there was some variability across participants. For Experiments 3 and 4, the experiments followed previous literature (e.g. Hesselmann et al., 2008) but these were optimised for identity coding. The pre-test measures adopted were used to balance identities. Reversal coding of these data produced highly variable trial numbers across participants and led to significant data loss in Experiment 4. We conducted reversal and identity decoding on the same data sets for efficiency as well as to make the data underlying these two analyses maximally comparable. However, to avoid data loss, it may be sensible to try conducting separate experiments for reversal and identity decoding so that parameters can be adjusted to optimise trial numbers for both types of analyses.

Another issue that was not directly addressed in this thesis is the issue of eye position and movement influences on ambiguous perception. Participants were instructed to fixate throughout the experiment and the experimenter was able to observe the participant's eyes with a camera focused on them throughout the experiment. Participants generally followed the instructions. Moreover, during the pre-processing stage of the raw EEG data, I removed all amplitude excursions exceeding ±100 mV, manually checked for artefacts from eye movements and performed an ocular correction Independent Components Analysis. Thus, I have relatively strong confidence that our decoding algorithms were not picking up on eye movement signals in the EEG rather than neural signals. However, findings have shown that eye movements influence the recorded EEG signal in a way that cannot be detected via standard neuronal processing and pre-processing (Plochl et al., 2012). Microsaccadic artefacts (i.e. very small, involuntary flicks in eye position) are too small (2.3 μV) to exceed the EOG-based rejection thresholds applied to single-trial EEG data (here 100 μV). These artefacts cannot be detected by artefact rejection methods, as they reflect cortical activity with no topographical resemblance to typical EEG artefacts (Dimigen et al., 2009). For instance, Dimigen et al. (2009) found that microsaccades, occurring when participants were fixating on a central point, generate a spike potential over the occipital cortex and mid-central scalp sites 100-140ms after the first microsaccade onset. This effect was not detected for slower eye movements (saccades). However, Dimigen et al. (2009) found that, for the standard oddball detection task, the microsaccades did not substantially change the overall pattern of results measured in their experiment.

Relying on artefact rejection methods alone would mean to ignore the fact that eye movements do not only introduce artefacts to the EEG signal but that they also go along with neural activity, which when overlooked may lead to misinterpretation of the data and therefore may not provide adequate information about neural processing under natural conditions (Plochl et al., 2012). Eye movements during EEG recordings should not necessarily be considered as interferences but as a part of natural human behaviour. A previous study by Wilbertz et al. (2018) combined fMRI and Eye tracking data in their decoding analyses of bistable plaid motion perception and found that while fMRI and Eye tracking individually already yielded high decoding accuracies, classification based on the two measures together further improved the accuracy. Therefore, a future study decoding the different perceptual states associated with ambiguous figure perception from eye tracking data would also give us further insight into the underlying mechanisms of ambiguous figure perception. Furthermore, combining EEG data and Eye tracking data might help us identify more mechanisms that have not been previously identified.

Seeing as the findings from the studies used were focused on investigating endogenous perceptual reversals, participants were required to fixate on a central fixation cross. Future studies involving eye-tracking are required to further control for eye movements and to study the predictability of a perceptual interpretation and a perceptual reversal from participants' eye positions and movements (if any).

6.7. Conclusions

In conclusion, I used psychophysical tools and investigated electrophysiological recordings in this thesis to investigate the underlying mechanisms of ambiguous figure perception. In particular, I investigated the underlying mechanisms of perception of Rubin's Face-Vase and the Necker Lattice. Overall, the results demonstrated that there are several factors that come into play when it comes to ambiguous figure perception. Firstly, the findings demonstrated that reversal related electrophysiological components are sensitive to a multitude of factors (e.g. trial numbers, ambiguous stimulus used, etc…) . Here, I demonstrated that response arrangements must also be considered carefully when studying reversal related components (RN and RP). In particular, collapsing across response and non-response can hide significant effects in the data even in relatively early latency ERP components. Furthermore, other findings in this thesis have demonstrated that activity linked to perceptual reversals, in both ambiguous stimuli used in this thesis, is not indexed by isolated electrophysiological phenomena but is an ongoing process that involves several frequency bands (1-30Hz) and spans over the majority of stimulus presentation time. This activity was found to start at stimulus onset, suggesting that there is pre-stimulus activity. This suggestion was confirmed by further analyses in my thesis where a link between pre-stimulus neural oscillations and ambiguous figure perception was identified. I was able to precisely isolate, given the time window and frequency ranges included in the analyses, pre-stimulus effects underlying perceptual reversals in the time and frequency domains, as well as the particular identity experienced when viewing an ambiguous stimulus. The pre-stimulus findings also show that a broad range of frequencies are informative, further suggesting that the effects influencing ambiguous figure perception are not isolated, independent events. These findings support the idea that brief pre-stimulus spontaneous fluctuations influence post-stimulus activity and outcomes.

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