University of Kent

Kent Academic Repository

Weick, Mario, Allen, John, Vasiljevic, Milica and Yao, Bo (2015) *Walking blindfolded unveils unique contributions of behavioural approach and inhibition to lateral spatial bias.* Cognition, 147 . pp. 106-112. ISSN 0010-0277.

Downloaded from
https://kar.kent.ac.uk/51736/ The University of Kent's Academic Repository KAR

The version of record is available from
https://doi.org/10.1016/j.cognition.2015.11.006

This document version
Publisher pdf

DOI for this version

Licence for this version
CC BY (Attribution)

Additional information

Versions of research works

Versions of Record
If this version is the version of record, it is the same as the published version available on the publisher's web site. Cite as the published version.

Author Accepted Manuscripts
If this document is identified as the Author Accepted Manuscript it is the version after peer review but before type setting, copy editing or publisher branding. Cite as Surname, Initial. (Year) 'Title of article'. To be published in ***Title of Journal*** , Volume and issue numbers [peer-reviewed accepted version]. Available at: DOI or URL (Accessed: date).

Enquiries
If you have questions about this document contact ResearchSupport@kent.ac.uk. Please include the URL of the record in KAR. If you believe that your, or a third party's rights have been compromised through this document please see our Take Down policy (available from https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies).

Cognition 147 (2016) 106–112

Contents lists available at ScienceDirect

Cognition

journal homepage: www.elsevier.com/locate/COGNIT

Walking blindfolded unveils unique contributions of behavioural approach and inhibition to lateral spatial bias

Mario Weick [a,*], John A. Allen [a], Milica Vasiljevic [b], Bo Yao [c]

[a] School of Psychology, University of Kent, UK
[b] Behaviour and Health Research Unit, University of Cambridge, UK
[c] School of Psychological Sciences, University of Manchester, UK

ARTICLE INFO

Article history:
Received 7 January 2015
Revised 2 November 2015
Accepted 11 November 2015

Keywords:
Approach (BAS)
Inhibition (BIS)
Spatial bias
Lateralization
Motion tracking

ABSTRACT

Healthy individuals display a tendency to allocate attention unequally across space, and this bias has implications for how individuals interact with their environments. However, the origins of this phenomenon remain relatively poorly understood. The present research examined the joint and independent contributions of two fundamental motivational systems – behavioural approach and inhibition systems (BAS and BIS) – to lateral spatial bias in a locomotion task. Participants completed self-report measures of trait BAS and BIS, then repeatedly traversed a room, blindfolded, aiming for a straight line. We obtained locomotion data from motion tracking to capture variations in the walking trajectories. Overall, walking trajectories deviated to the left, and this tendency was more pronounced with increasing BIS scores. Meanwhile, BAS was associated with relative rightward tendencies when BIS was low, but not when BIS was high. These results demonstrate for the first time an association between BIS and lateral spatial bias independently of variations in BAS. The findings also contribute to clarify the circumstances in which BAS is associated with a rightward bias. We discuss the implications of these findings for the neurobiological underpinnings of BIS and for the literature on spatial bias.
© 2015 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

1. Introduction

Striving for outcomes that benefit the organism, and being vigilant for threats, are two fundamental survival strategies in many species (Wilson, Coleman, Clark, & Biederman, 1993). The behavioural approach system (BAS; Gray, 1972) and the behavioural inhibition system (BIS; Gray, 1975, 1990) are two analogous regulatory mechanisms that are manifested in affective, cognitive, and behavioural traits (Carver & White, 1994; Fowles, 1980). Activation of BAS is linked to the experience of positive affect and goal-directed behaviour. In contrast, activation of BIS is linked to the experience of anxiety, increased sensitivity to threatening cues, and disruption of ongoing processes. The aim of the present research is to probe the independent and joint associations of these motivational orientations with spatial attention.

1.1. Lateral bias and BAS

Activation in the contralateral cerebral hemisphere modulates the orientation of attention (e.g., Kinsbourne, 1970; Milner, Brechmann, & Pagliarini, 1992). Accordingly, temporal or enduring shifts in the balance of activation in the two hemispheres are associated with a bias in attention to the left or to the right side of space. Researchers often employ the line-bisection task to examine such shifts in hemispatial attention (for review see Jewell & McCourt, 2000). The task requires individuals to segment lines into two equidistant elements. The magnitude and the extent of bisection errors correlate with lateralised neural activity (Nash, McGregor, & Inzlicht, 2010).

Approach motivation is associated with greater relative left (vs. right) prefrontal brain activation (see Coan & Allen, 2003a; Harmon-Jones & Allen, 1997), reflecting asymmetries in dopaminergic signalling (Berridge, España, & Stalnaker, 2003). Several studies have linked approach motivation to right-oriented lateral bias. For example, Tomer (2008) observed a strong association between lateral bias assessed using a greyscale task (Nicholls, Bradshaw, & Mattingley, 1999) and self-reported novelty seeking – a construct that correlates with self-reported approach motivation (Carver & White, 1994; Mardaga & Hansenne, 2007). Employing an

* Corresponding author at: School of Psychology, University of Kent, Keynes College, Canterbury, Kent CT2 7NP, UK.
E-mail address: m.weick@kent.ac.uk (M. Weick).

http://dx.doi.org/10.1016/j.cognition.2015.11.006
0010-0277/© 2015 The Authors. Published by Elsevier B.V.
This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

experimental manipulation of approach motivation, Friedman and Förster (2005, Study 3) found a greater right-oriented bias relative to participants in a neutral state of mind.

The circumstances in which approach motivation induces a shift in attention have come under scrutiny. Roskes, Sligte, Shalvi, and De Dreu (2011) argued that the right-oriented bias observed in approach-motivated individuals only arises under high time pressure. In their analysis of Fédération Internationale de Football Association (FIFA) World Cup penalty shootouts, Roskes and colleagues found that goalkeepers were more likely to dive to the right than to the left in penalty shootouts, but only when their team was behind. Following a failed attempt to replicate these results in other major football tournaments (Price & Wolfers, 2014), Roskes, Sligte, Shalvi, and De Dreu (2014) conceded that it remains unclear under which circumstances approach-motivation is linked with a right-oriented bias. Their remark dovetails the findings of Nash et al. (2010, Study 2), who found that people with high self-esteem are more oriented to the right than people with low self-esteem, but this discrepancy only emerged after people re-lived a personal dilemma.

In sum, converging evidence suggests that approach-motivation is associated with a right-oriented bias, but little is known about the circumstances that engender the bias. In the present research we sought to address this, separating the contributions of BAS and BIS to lateral bias.

1.2. Lateral bias and BIS

Compared to BAS, the neurological underpinnings of BIS have been elusive and subject to conceptual disagreements (see Amodio, Master, Yee, & Taylor, 2008, for a review). Some researchers conceptualised BIS as behavioural avoidance, anatomically linked to right-sided activity in the prefrontal cortex. However, this conceptualisation ignores the fact that the motivation to escape harm (withdrawal) is *not* mediated by BIS in Gray's framework (Gray & McNaughton, 2003). Furthermore, a number of studies failed to establish a link between BIS and frontal asymmetry, casting further doubt on the lateralisation of BIS (e.g., Coan & Allen, 2003b; De Pascalis, Cozzuto, Caprara, & Alessandri, 2013; Harmon-Jones & Allen, 1997; Wacker, Heldmann, & Stemmler, 2003; but see Peterson, Gable, & Harmon-Jones, 2008).

According to Heller (1993), threatening conditions prime the right hemisphere and trigger higher activity in right posterior areas. This anxiety/arousal function is consistent with a right-sided orienting network for attention, which responds to novel and unexpected events and acts as a "circuit breaker" for focal processing (Corbetta & Shulman, 2002, p. 212). Increased activation in BIS mediates the experience of anxiety and facilitates the disruption of ongoing behaviour (Carver & White, 1994; Fowles, 1980, 1988; Gray, 1982). Thus, there are strong grounds to assume an association between BIS and posterior hemisphericity. This assumption has received preliminary support in EEG studies (Balconi, Brambilla, & Falbo, 2009; Hewig, Hagemann, Seifert, Naumann, & Bartussek, 2006).

To date, little is known about the independent association between BIS and orientating bias. Some studies examined the consequences of behavioural avoidance for performance on the line bisection task (Friedman & Förster, 2005; Roskes et al., 2011). However, since avoidance was conceptualised as withdrawal in these studies, which as discussed above is not mediated by BIS, the findings have limited relevance. In another line of work, Wilkinson, Guinote, Weick, Molinari, and Graham (2010), found that inducing a sense of powerlessness experimentally fostered a left-oriented bias in two motor tasks. Whilst consistent with the framework discussed here, one can only speculate about the involvement of BIS in the effects of powerlessness. It is important to note that experimental manipulations aimed at increasing activation in BIS may also inadvertently reduce activation in BAS, thus confounding the individual contributions of the two motivational systems to lateral bias.

Garner et al. (2012) found that individuals scoring simultaneously high on BIS *and* low on BAS exhibited a stronger leftward bias in visual orienting than individuals scoring simultaneously high on BAS *and* low on BIS. These results are consistent with a right-sided specialisation for BIS (inducing a leftward attentional bias). However, grouping participants into two quadrants – high BIS/low BAS and low BIS/high BAS – creates a perfect correlation between BIS and BAS. Consequently it remains unknown whether Garner and colleagues' findings speak to an effect of BIS that occurs independently of variation of BAS, an effect of BAS that occurs independently of variation in BIS, or an effect that derives from an interaction of the two motivational systems.

To summarise, the cognitive neuroscience literature points to a right hemisphere specialisation for BIS. However, compared to BAS, the hemisphericity of BIS is less well understood. Importantly, at present there is no conclusive evidence that activation in BIS fosters a left-oriented bias in attention independently of variation in BAS.

1.3. The present research

In the present research, we sought to probe the individual and joint contributions of BAS and BIS to lateral spatial bias. Doing so provides the first empirical test of an independent association between BIS and lateral spatial bias, and furthers our understanding of how individual differences are manifested in neurobiological processes. It also sheds light on the circumstances in which activation in BAS is associated with a right-oriented bias (cf. Price & Wolfers, 2014; Roskes et al., 2014).

In order to probe spatial bias in a task that is sufficiently demanding for self-regulatory dispositions to manifest (see Coan, Allen, & McKnight, 2006), we asked participants to walk across a room in a straight line, blindfolded, aiming for a target on the other side. This task capitalises on the fact that the orientation bias manifests itself in mental representations of space (see Brooks, Della Sala, & Darling, 2014, for a review). In absence of visual feedback, people often depart from a straight trajectory and deviate to either side (e.g., Boyadjian, Marin, & Danion, 1999; Vuillerme, Nougier, & Camicioli, 2002). We expected individual differences in self-reported BIS and BAS to uniquely account for variations in participants' walking trajectories. We used motion tracking to capture participants' locomotion during task performance.

2. Method

2.1. Participants

Eighty right-handed students at a British University participated for course credits. Locomotion data from two participants were lost due to a technical error, thus leaving a final sample of 78 participants (60 females, 17 males, 1 other gender; M_{Age} = 20.15, SD_{Age} = 4.15). All participants had normal or corrected-to-normal vision, and none reported any history of motor problems or neurological disease.

2.2. Materials

2.2.1. Individual difference measures

Participants completed the trait BAS/BIS inventory (Carver & White, 1994), embedded in a battery of unrelated questionnaires.

They also provided information on demographic background and handedness.

2.2.2. Locomotion task

Participants were asked to walk up to a target (an 'X' marked on the floor), 6 metres away from the starting position, along an imaginary straight line perpendicular to the boundaries of a rectangular room (8.25 m (L) × 4.2 m (W) × 2.37 m (H)). They did this wearing dedicated blindfold goggles, and with an optical marker affixed midline at the top of the head. Walking trajectories were digitised with a WorldViz PPT-H camera system using three degrees of freedom position tracking.

2.3. Procedure

Participants volunteered consent and then completed individual difference measures on a PC. The subsequent walking task proceeded as follows: After viewing the target, participants covered their eyes with the goggles. They then walked up to the target until they were stopped by the experimenter and led back to the start position. At this point, participants were allowed to lift the goggles, adjusted their position in preparation for the next trial, took new aim, covered their eyes with the goggles, and then set off. Altogether, participants traversed the room 20 times. At the end, participants were thanked and debriefed.

3. Results

For four participants, the experimenter concluded the walking task prematurely, resulting in the omission of five walking attempts (0.32% of all trials). Altogether, participants made 1555 walking attempts with a combined distance of 8.38 km (see Fig. 1).

We aggregated the items measuring individual differences in behavioural approach (BAS: $\alpha = .85$, $M_{Sum} = 40.81$, $SD_{Sum} = 5.43$) and behavioural inhibition (BIS, $\alpha = .78$, $M_{Sum} = 22.13$, $SD_{Sum} = 3.58$). The correlation between the two items was unreliable, $r(76) = .19$, $p = .10$, 95% CI [−.18, .48]. All analyses reported below were carried using z-standardised BIS and BAS scores.

3.1. Variations in lateral bias

At first, we examined final deviations from the sagittal plane (in cm) captured at the end of each walking attempt before participants were stopped and led back to the starting position. Thus, each data point marks the end-point of a single walking attempt at an average walking distance of 5.39 m ($SD = .40$). Negative values indicate deviations to the left, and positive values indicate deviations to the right. The data revealed a small but robust bias to the left ($M = -8.42$, $SD = 40.69$), $t(1554) = -8.16$, $p < .001$, 95% CI [−10.44, −6.39]. The magnitude of lateral drifts to the left was similar to the magnitude of lateral drifts to the right, although the former was slightly more pronounced (left: $|M| = 34.25$, $SD = 26.41$, |95% CI| [32.53, 35.94], right: $|M| = 29.54$, $SD = 26.17$, |95% CI| [27.54, 31.53], $t_{diff}(1537) = 3.44$, $p = .001$, 95% CI_{diff} [2.02, 7.38]. Overall, 16 trials ended on target, 918 walks concluded with a drift to the left, and 621 walks concluded with a drift to the right (χ^2 (1, $N = 1539$) = 57.32, $p < .001$, for the comparison between left- and right-sided drifts).

For each participant, we also calculated the proportion of trials (out of 20)[1] ending to either side (or on target). Participants exhibited a leftward bias on 60% of trials on average (12 out of 20 trials; $SD = 29\%$). This figure differs significantly from 50% and thus points to the presence of a systematic bias, $t(77) = 3.05$, $p = .003$, 95% CI_{diff} [67%, 53%]. Forty-eight participants (61.5%) concluded their walks more frequently to the left (>10 out of 20 trials), and twenty-three participants (29.5%) more frequently to the right (>10 out of 20 trials). One participant (1.2%) was always biased to the right (20 out of 20 trials), and seven participants (8.9%) always erred to the left (20 out of 20 trials).

3.2. Contributions of BAS/BIS

Finally, we turned our attention to the individual walking trajectories depicted in Fig. 1. Our aim was to see if differences in BIS and BAS relate to differences in the shape, or more precisely the slope of the trajectories ($k = 1555$). In a growth regression, trial-by-trial deviations from the sagittal plane (in cm) at 0, 1, 2, 3, 4, and 5 m displacement (Y) can be described with the equation[2]:

$$Y_t = b_0 + b_1 * P_t + e_t$$

Whereby t denotes the measurement occasion (i.e., displacements) and P is a polynomial that depicts a linear trend ($P = 0, 1, 2, 3, 4, 5$). The constant b_0 indicates the lateral deviation for $P = 0$ (i.e., the start of a trial). Running this initial model confirmed that, overall, the walking trajectories were biased to the left, $B_1 = -1.51$, SE = .14, $p < .001$, 95% CI [−1.78, −1.23]. This becomes especially clear when looking at the predictions for Y: after a distance of 1 m walking, the model predicts an average lateral deviation of −0.67 cm (0.48 + (1 * (−1.15)), −1.82 cm after 2 m ((0.48 + (2 * (−1.15)), −2.97 cm after 3 m (0.48 + (3 * (−1.15)), −4.12 cm after 4 m (0.48 + (4 * (−1.15)), and −5.27 after 5 m (0.48 + (5 * (−1.15)).

Next, we added the effects of BIS and BAS to the model:

$$Y_t = b_0 + b_1 * P_t + b_2 * \text{BIS} + b_3 * \text{BAS} + b_4 * P_t * \text{BIS} + b_5 * P_t * \text{BAS} + e_t$$

The intercept and the unconditional effects of BIS (b_2) and BAS (b_3) were not significant. More importantly, the results showed that both BIS and BAS moderated the linear trend (P). The direction of the effects indicates that walking trajectories were more strongly biased to the left with increasing BIS scores, $B_4 = -.40$, SE = .14, $p = .004$, 95% CI [−.68, −.13], and more strongly biased to the right with increasing BAS scores, $B_5 = .30$, SE = .14, $p = .032$, 95% CI [.03, .58].

In a final step, we also added the interaction between BIS and BAS:

$$Y_t = b_0 + b_1 * P_t + b_2 * \text{BIS} + b_3 * \text{BAS} + b_4 * P_t * \text{BIS} + b_5 * P_t * \text{BAS} + b_6 * \text{BIS} * \text{BAS} + b_7 * P_t * \text{BIS} * \text{BAS} + e_t$$

As can be seen in Table 1, the three-way interaction between P, BIS and BAS was significant, $B_7 = -.24$, SE = .08, $p = .006$, 95% CI [−.40, −.07]. Importantly, controlling for the interaction with BAS, the effects of BIS remained significant, $B_4 = -.51$, SE = .45, $p < .001$, 95% CI [−.80, −.23]. Thus, variations in BAS did not qualify the effects of BIS. However, variations in BIS *did* qualify the effects of BAS (b_5), which were no longer significant when the three-way interaction (b_7) was added to the model.

[1] As indicated earlier, data were unavailable for five trials in all. Thus, for one participant we calculated the proportion on the basis of 17 available trials, and for two participants on the basis of 19 available trials.

[2] Readers familiar with multi-level modelling will note that measurement occasions are nested within trials (k), which in turn are nested within individuals (i). We also used multi-level growth models to explore the contributions of BIS and BAS to the walking trajectories. The random intercepts for level 2 and 3 were significant, but the models did not converge when adding random slopes. The conclusions derived from the multi-level model with random intercepts were the same as the conclusions derived from a regression model with no random effects. In light of this, we chose to report the results of the latter statistical technique.

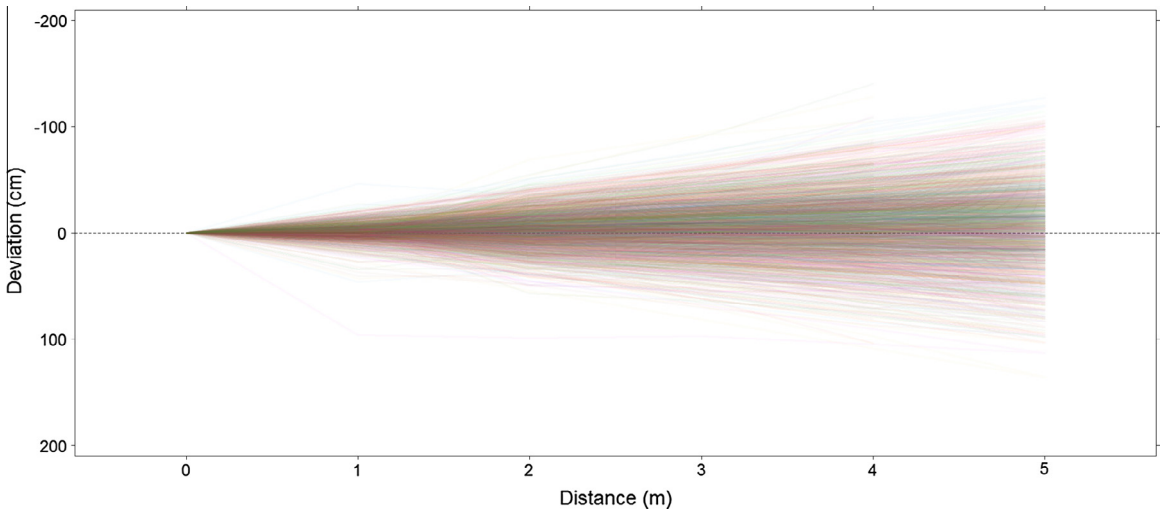


Fig. 1. Spaghetti plot of walking trajectories observed in the locomotion task. Negative values on the *y*-axis indicate a bias to the left, and positive deviations indicate a bias to the right.

Table 1
Parameter estimates of growth regressions predicting lateral deviations (in cm) in the walking task.

Effect	Model 1					Model 2					Model 3				
	B	SE	*p*	95% CI		*B*	SE	*p*	95% CI		*B*	SE	*p*	95% CI	
Intercept	0.49	0.42	.244	−0.33	1.30	0.49	0.42	.239	−0.33	1.30	0.47	0.42	.266	−0.35	1.28
P (linear slope)	−1.51	0.14	<.001	−1.78	−1.23	−1.51	0.14	<.001	−1.78	−1.24	−1.46	0.14	<.001	−1.74	−1.19
BIS						0.33	0.42	.429	−0.49	1.15	0.39	0.43	.372	−0.46	1.24
BAS						−0.22	0.42	.605	−1.04	0.61	−0.13	0.45	.767	−1.02	0.75
P ∗ BIS						−0.40	0.14	.004	−0.68	−0.13	−0.51	0.15	<.001	−0.80	−0.23
P ∗ BAS						0.30	0.14	.032	0.03	0.58	0.15	0.15	.338	−0.15	0.44
BIS ∗ BAS											0.12	0.25	.625	−0.37	0.62
P ∗ BIS ∗ BAS											−0.24	0.08	.006	−0.40	−0.07

To illuminate the interaction, we carried out further analyses probing the simple effects of BAS at high (+1SD) and low (−1SD) levels of BIS. These analyses showed that BAS was only associated with rightward tendencies when combined with low levels of BIS, B_5 = .38, SE = .14, p = .008, 95% CI [.10, .66], but not when combined with high levels of BIS, B_5 = −.09, SE = .20, p = .650, 95% CI [−.48, .30].

To gain a better understanding of these results, we examined participants' predicted walking trajectories at different levels of BAS and BIS. As can be seen in Fig. 2, all combinations of BIS and BAS yield a bias to the left, with the strongest bias predicted for individuals high on BIS irrespective of the levels of BAS. Meanwhile, higher levels of BAS are associated with an increased (relative) rightward bias at low and medium levels of BIS. As expected, the weakest (absolute) bias to the left is evident for the combination of low levels of BIS and high levels of BAS.

Finally, we were curious to see what combinations of BIS and BAS would trigger an absolute bias to the right. To this end, we examined the combination of extremely high levels of BAS ($\bar{x}$ + 2.5SD) and low levels of BIS ($\bar{x}$ − 1SD), which yields a straight trajectory, B_1 = −.00, p = .997, 95% CI [−.87, .87]. The combination of extremely high levels of BAS ($\bar{x}$ + 2.5SD) and extremely low levels BIS ($\bar{x}$ − 2.5SD) does translate into a rightward bias, B_1 = 1.65, p = .028, 95% CI [.18, 3.12].

Taken together, these results lend support to the conclusion that BIS is associated with a leftward bias independently of variation in BAS, and further suggest that (relative) rightward tendencies associated with BAS only emerge when BIS is low.

4. Discussion

Behavioural approach and inhibition are two fundamental motivational systems manifested in affective, cognitive, and behavioural traits. The aim of the present research was to examine the individual and joint associations of these systems with lateral spatial bias. Blindfolded participants traversed a room aiming for a straight line. Locomotion data obtained from motion tracking revealed systematic lateral biases in participants' walking trajectories. Overall, participants exhibited a reliable leftward bias, consistent with past research on spatial attention (for reviews see Brooks et al., 2014; Jewell & McCourt, 2000). Importantly, this bias was moderated by motivational dispositions, such that walking trajectories deviated more to the left with increasing BIS scores, and (relatively) more to the right with increasing BAS scores.

The present data demonstrate for the first time an association between BIS and lateral bias independently of variations in BAS. Whilst several attempts have been made to demonstrate the association between BAS and spatial bias, the evidence for lateral asymmetries in BIS is limited. Previous experimental studies manipulated *avoidance* (Friedman & Förster, 2005; Roskes et al., 2011) or *powerlessness* (Wilkinson et al., 2010), raising questions about the conceptual overlap between these constructs and BIS. Measuring individual differences in BIS and BAS, Garner et al. (2012) observed a leftward bias in people scoring simultaneously high on BIS *and* low on BAS. The present findings echo Garner and colleagues' results but also demonstrate that the association between BIS and lateral bias does not depend on, and cannot be explained by, variations in BAS.

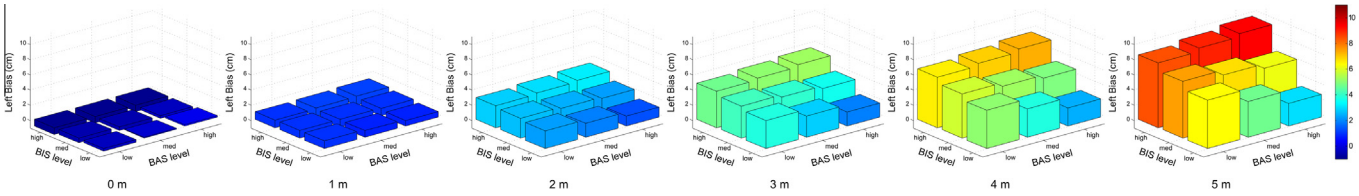


Fig. 2. Predicted walking trajectories at different levels of BIS and BAS. The simple effect of *P* (linear slope) indicates the extent to which trajectories are biased; a significant negative weight ($b_1 < 0$) implies a bias to the left, a significant positive weight ($b_1 > 0$) a bias to the right, and a non-significant weight ($b_1 = 0$) implies no lateral deviation. The results are as follows: BIS low ($\bar{x} - 1SD$) and BAS high ($\bar{x} + 1SD$): $B_1 = -.57$, $p = .034$, 95% CI [−1.10, −.04]; BIS medium ($\bar{x}$) and BAS high ($\bar{x} + 1SD$): $B_1 = -1.32$, $p < .001$, 95% CI [−1.71, −.92]; BIS high ($\bar{x} + 1SD$) and BAS high ($\bar{x} + 1SD$): $B_1 = -2.07$, $p < .001$, 95% CI [−2.62, −1.52]; BIS low ($\bar{x} - 1SD$) and BAS medium ($\bar{x}$): $B_1 = -.95$, $p < .001$, 95% CI [−1.35, −.55]; BIS medium ($\bar{x}$ and BAS medium ($\bar{x}$: $B_1 = -1.46$, $p < .001$, 95% CI [−1.74, −1.19]; BIS high ($\bar{x} + 1SD$) and BAS medium ($\bar{x}$: $B_1 = -1.98$, $p < .001$, 95% CI [−2.37, −1.59]; BIS low ($\bar{x} - 1SD$) and BAS low ($\bar{x} - 1SD$): $B_1 = -1.33$, $p < .001$, 95% CI [−1.78, −.88]; BIS medium ($\bar{x}$ and BAS low ($\bar{x} - 1SD$): $B_1 = -.1.61$, $p < .001$, 95% CI [−2.02, −1.20]; BIS high ($\bar{x} + 1SD$) and BAS low ($\bar{x} - 1SD$): $B_1 = -1.89$, $p < .001$, 95% CI [−2.44, −1.33].

The present data corroborate previous studies showing an association between approach motivation and rightward attentional bias. This is in line with evidence derived from EEG studies (e.g., Coan & Allen, 2003a; Harmon-Jones & Allen, 1997). However, to the best of our knowledge, the present data present the first attempt to 'partial out' the effects of inhibition in the relationship between approach and lateral bias. Tomer (2008) reported an association between individual differences in novelty seeking and lateral bias, whilst Nash et al. (2010) found that in some circumstances individuals with high self-esteem exhibit a stronger rightward bias than individuals with low self-esteem. Neither of these studies controlled for variations in behavioural inhibition. This is important because higher levels of novelty seeking and self-esteem are not only associated with increased approach motivation, but also with reduced inhibition (e.g., Caseras, Avila, & Torrubia, 2003; Erdle & Rushton, 2010). Thus, variations in BIS may have contributed to effects observed in Tomer's (2008) and Nash et al. (2010) studies. Similarly, it cannot be ruled out that by manipulating approach motivation previous experiments did not also decrease inhibition tendencies (e.g., Friedman & Förster, 2005).

Whilst BIS was associated with a leftward bias in walking trajectories irrespective of variations in BAS, we observed that BAS was only associated with a relative rightward bias when BIS was low, but not when BIS was high. In other words, BIS moderated the link between BAS and the orienting bias. This pattern of results could be explained by asymmetries in antagonistic links between the two motivational systems, in line with the notion of BIS acting as a 'circuit breaker' (cf. Corbetta & Shulman, 2002). This interpretation is tentative and further research is needed to explore the interplay between BIS and BAS (see also Corr, 2002). It stands to reason that behavioural inhibition has a more central role in the orienting bias than previously assumed.

The present findings advance our understanding of circumstances in which approach motivation biases attention and ensuing behaviour to the right (Price & Wolfers, 2014; Roskes et al., 2011). In our study, (relative) rightward tendencies associated with approach-motivation were countered by leftward tendencies associated with behavioural inhibition. All combinations of BIS and BAS within a 'normal' range ($\bar{x} - 1SD$ to $\bar{x} + 1SD$) yielded a bias to the left. In order to elicit an *absolute* bias to the right, it would appear that very high levels of approach-motivation have to be accompanied by very low levels of inhibition. This suggests that a rightward bias may only occur when individuals are not apprehensive about the prospect of negative outcomes. Future studies may benefit from examining spatial bias in situations that vary the salience of appetitive and aversive stimuli, or probe hemispatial bias in relevant clinical populations (see Waldie & Hausmann, 2010, for an example).

The present research sheds some light on the hemisphericity of BIS, which is poorly understood, perhaps in part due to conceptual disagreements (see Amodio et al., 2008). Hemispatial bias provides an indication of cortical activation. Thus, the present results point to a right hemisphere specialisation for BIS, consistent with the framework proposed by Heller (1993). This finding holds relevance for our understanding of how individual differences are manifested in neurobiological processes. Gaining an understanding of the neurological underpinnings of motivational processes is important and can have implications for the treatment of unilateral neglect. For example, individuals suffering from right-sided neglect may benefit from interventions to reduce anxiety (the affective component of BIS). Conversely, elevated anxiety may ameliorate spatial bias in individuals suffering from left-sided neglect – a common debilitating condition following right-sided brain damage. This is in line with the findings of Robertson, Mattingley, Rorden, and Driver (1998), who observed that administering a sudden sound burst improved spatial awareness in left-neglect patients.

Recent studies have shown that a heightened state of alertness biases attention to the left, whereas a reduced state of alertness biases attention to the right (e.g., Manly, Dobler, Dodds, & George, 2005; Newman, O'Connell, & Bellgrove, 2013). For example, Linnell, Caparos, and Davidoff (2014) reported that urbanised people have a left spatial bias whereas people living in remote areas have no significant bias. The authors attributed this effect to differences in alertness. The present findings complement these streams of inquiry and further suggest a critical role of negative or anxious arousal, as opposed to positive arousal triggered by excitement or elation, in the alertness/spatial attention relationship. Future research should examine in more detail how different *types* of arousal (i.e., positive vs. negative) modulate spatial bias.

Previous studies examined walking trajectories in neglect patients (Huitema et al., 2006), and lateral collisions in healthy individuals performing a locomotion task (e.g., Nicholls, Loftus, Mayer, & Mattingley, 2007). However, very few studies examined spatial bias in blind-folded walking tasks. Paquet and colleagues did not find any evidence for a systematic leftward bias in forward locomotion (Paquet, Lajoie, Rainville, & Sabagh-Yazdi, 2008; Paquet, Rainville, Lajoie, & Tremblay, 2007). In contrast, Mohr and colleagues observed more frequent left-sided drifts (Mohr, Brugger, Bracha, Landis, & Viaud-Delmon, 2004), while Kennedy and colleagues reported a small left-sided bias using motion tracking (Kennedy et al., 2003). Neither of these effects was significant, however, perhaps due to a relatively small number of observations. Using a larger sample of participants, data derived from a much larger number of trials, and motion tracking to minimise measurement error, we found evidence for a small but reliable leftward bias in individuals' walking trajectories. This is noteworthy as the consensus in the literature has been that individuals do not show a systematic lateral bias when advancing blindfolded towards a

previously seen target.[3] Thus, the present research contributes to reconcile the literature on walking trajectories and the literature on spatial representations (see Brooks et al., 2014, for a review).

It is also interesting to ask why previous studies often failed to observe evidence for the lateralisation of BIS. Studies examining the neurological underpinnings of motivational dispositions often measure cortical activity *at rest* (e.g., Coan & Allen, 2003b; Harmon-Jones & Allen, 1997; Hewig et al., 2006; Sutton & Davidson, 1997; but see Amodio et al., 2008; De Pascalis, Varriale, & D'Antuono, 2010). This is problematic because individual differences in cortical activity are more likely to emerge in situations where underlying dispositions are relevant for the demands of the situation (see Coan et al., 2006). Participants in the present walking task experienced a *motivated performance situation* (Blascovich & Tomaka, 1996), and this enabled us to elicit evidence for the lateralisation of BIS. The present findings demonstrate that novel insights can be gained from methods that enable individuals to actively engage with their environments. Virtual Reality (VR) applications afford such a high degree of involvement, and we anticipate that this technology will soon provide novel insights into the neurobiological correlates of human motivation.

To conclude, using a blindfolded walking task we found evidence that behavioural inhibition is associated with a leftward spatial bias independently of variations in BAS. This finding points to a right hemisphere specialisation for BIS. As expected, BAS was associated with (relative) rightward tendencies, but this effect only emerged when combined with low levels of BIS. This finding adds to the literature on spatial bias suggesting that overt shifts to the right (i.e., absolute rightward tendencies) may only be observed in certain circumstances when levels of inhibition are very low.

Acknowledgements

The present research was supported by the Economic and Social Research Council (ESRC) grant PTA-026-27-1908 to the first author. We would like to thank Nicole van der Veen for assistance with data collection.

References

Amodio, D. M., Master, S. L., Yee, C. M., & Taylor, S. E. (2008). Neurocognitive components of the behavioral inhibition and activation systems: Implications for theories of self-regulation. *Psychophysiology, 45*, 11–19. http://dx.doi.org/10.1111/j.1469-8986.2007.00609.x.

Balconi, M., Brambilla, E., & Falbo, L. (2009). BIS/BAS, cortical oscillations and coherence in response to emotional cues. *Brain Research Bulletin, 80*, 151–157. http://dx.doi.org/10.1016/j.brainresbull.2009.07.001.

Berridge, C. W., España, R. A., & Stalnaker, T. A. (2003). Stress and coping: Asymmetry of dopamine efferents within the prefrontal cortex. In K. Hugdahl & R. J. Davidson (Eds.), *The asymmetrical brain* (pp. 59–63). Cambridge, MA: MIT Press.

Blascovich, J., & Tomaka, J. (1996). The biopsychosocial model of arousal regulation. *Advances in Experimental Social Psychology, 28*, 1–51.

Boyadjian, A., Marin, L., & Danion, F. (1999). Veering in human locomotion: The role of the effectors. *Neuroscience Letters, 265*, 21–24. http://dx.doi.org/10.1016/S0304-3940(99)00198-6.

Brooks, J. L., Della Sala, S., & Darling, S. (2014). Representational pseudoneglect: A review. *Neuropsychology Review, 24*, 148–165. http://dx.doi.org/10.1007/s11065-013-9245-2.

Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS scales. *Journal of Personality and Social Psychology, 67*, 319–333. http://dx.doi.org/10.1037/0022-3514.67.2.319.

Caseras, X., Avila, C., & Torrubia, R. (2003). The measurement of individual differences in behavioural inhibition and behavioural activation systems: A comparison of personality scales. *Personality and Individual Differences, 34*, 999–1013. http://dx.doi.org/10.1016/S0191-8869(02)00084-3.

Coan, J. A., & Allen, J. J. B. (2003a). The state and trait nature of frontal EEG asymmetry in emotion. In K. Hugdahl & R. J. Davidson (Eds.), *The asymmetrical brain* (pp. 565–615). Cambridge, MA: MIT Press.

Coan, J. A., & Allen, J. J. B. (2003b). Frontal EEG asymmetry and the behavioral activation and inhibition systems. *Psychophysiology, 40*, 106–114. http://dx.doi.org/10.1111/1469-8986.00011.

Coan, J. A., Allen, J. J. B., & McKnight, P. E. (2006). A capability model of individual differences in frontal EEG asymmetry. *Biological Psychology, 72*, 198–207. http://dx.doi.org/10.1016/j.biopsycho.2005.10.003.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3*, 201–215. http://dx.doi.org/10.1038/nrn755.

Corr, P. J. (2002). J.A. Gray's reinforcement sensitivity theory: Tests of the joint subsystems hypothesis of anxiety and impulsivity. *Personality and Individual Differences, 33*, 511–532. http://dx.doi.org/10.1016/S0191-8869(01)00170-2.

De Pascalis, V., Cozzuto, G., Caprara, G. V., & Alessandri, G. (2013). Relations among EEG-alpha asymmetry, BIS/BAS, and dispositional optimism. *Biological Psychology, 94*, 198–209. http://dx.doi.org/10.1016/j.biopsycho.2013.05.016.

De Pascalis, V., Varriale, V., & D'Antuono, L. (2010). Event-related components of the punishment and reward sensitivity. *Clinical Neurophysiology, 121*, 60–76. http://dx.doi.org/10.1016/j.clinph.2009.10.004.

Erdle, S., & Rushton, J. P. (2010). The general factor of personality, BIS–BAS, expectancies of reward and punishment, self-esteem, and positive and negative affect. *Personality and Individual Differences, 48*, 762–766. http://dx.doi.org/10.1016/j.paid.2010.01.025.

Fowles, D. C. (1980). The three arousal model: Implications of Gray's two-factor learning theory for heart rate, electrodermal activity, and psychopathy. *Psychophysiology, 17*, 87–104. http://dx.doi.org/10.1111/j.1469-8986.1980.tb00117.x.

Fowles, D. C. (1988). Psychophysiology and psychopathology: A motivational approach. *Psychophysiology, 25*, 373–391. http://dx.doi.org/10.1111/j.1469-8986.1988.tb01873.x.

Friedman, R. S., & Förster, J. (2005). Effects of motivational cues on perceptual asymmetry: Implications for creativity and analytical problem solving. *Journal of Personality and Social Psychology, 88*, 263–275. http://dx.doi.org/10.1037/0022-3514.88.2.263.

Garner, K. G., Dux, P. E., Wagner, J., Cummins, T. D., Chambers, C. D., & Bellgrove, M. A. (2012). Attentional asymmetries in a visual orienting task are related to temperament. *Cognition & Emotion, 26*, 1508–1515. http://dx.doi.org/10.1080/02699931.2012.666205.

Gray, J. A. (1975). *Elements of a two-process theory of learning*. London: Academic Press.

Gray, J. A. (1982). *The neuropsychology of anxiety: An enquiry into the functions of the septo-hippocampal system*. London: Oxford University Press.

Gray, J. A. (1990). Brain systems that mediate both emotion and cognition. *Cognition & Emotion, 4*, 269–288. http://dx.doi.org/10.1080/02699939008410799.

Gray, J. A., & McNaughton, N. (2003). *The neuropsychology of anxiety: An enquiry into the function of the septo-hippocampal system*. Oxford, UK: Oxford University Press.

Gray, J. A. (1972). The psychophysiological basis of introversion–extraversion: A modification of Eysenck's theory. In V. D. Nebylitsyn & J. A. Gray (Eds.), *The biological bases of individual behaviour* (pp. 182–205). San Diego, CA: Academic Press.

Harmon-Jones, E., & Allen, J. J. B. (1997). Behavioral activation sensitivity and resting frontal EEG asymmetry: Covariation of putative indicators related to risk of mood disorders. *Journal of Abnormal Psychology, 106*, 159–163. http://dx.doi.org/10.1037/0021-843X.106.1.159.

Heller, W. (1993). Neuropsychological mechanisms of individual differences in emotion, personality, and arousal. *Neuropsychology, 7*, 476–489. http://dx.doi.org/10.1037/0894-4105.7.4.476.

Hewig, J., Hagemann, D., Seifert, J., Naumann, E., & Bartussek, D. (2006). The relation of cortical activity and BIS/BAS on the trait level. *Biological Psychology, 71*, 42–53. http://dx.doi.org/10.1016/j.biopsycho.2005.01.006.

Huitema, R. B., Brouwer, W. H., Hof, A. L., Dekker, R., Mulder, T., & Postema, K. (2006). Walking trajectory in neglect patients. *Gait & Posture, 23*, 200–205. http://dx.doi.org/10.1016/j.gaitpost.2005.02.003.

Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia, 38*, 93–110. http://dx.doi.org/10.1016/S0028-3932(99)00045-7.

Kennedy, P. M., Carlsen, A. N., Inglis, J. T., Chow, R., Franks, I. M., & Chua, R. (2003). Relative contributions of visual and vestibular information on the trajectory of human gait. *Experimental Brain Research, 153*, 113–117. http://dx.doi.org/10.1007/s00221-003-1633-z.

Kinsbourne, M. (1970). The cerebral basis of lateral asymmetries in attention. *Acta Psychologica, 33*, 193–201. http://dx.doi.org/10.1016/0001-6918(70)90132-0.

Linnell, K. J., Caparos, S., & Davidoff, J. (2014). Urbanization increases left-bias in line-bisection: An expression of elevated levels of intrinsic alertness? *Frontiers in Psychology, 5*, 1127. http://dx.doi.org/10.3389/fpsyg.2014.01127.

Manly, T., Dobler, V. B., Dodds, C. M., & George, M. A. (2005). Rightward shift in spatial awareness with declining alertness. *Neuropsychologia, 43*, 1721–1728. http://dx.doi.org/10.1016/j.neuropsychologia.2005.02.009.

Mardaga, S., & Hansenne, M. (2007). Relationships between Cloninger's biosocial model of personality and the behavioral inhibition/approach systems (BIS/BAS). *Personality and Individual Differences, 42*, 715–722. http://dx.doi.org/10.1016/j.paid.2006.08.013.

Milner, A. D., Brechmann, M., & Pagliarini, L. (1992). To halve and to halve not: An analysis of line bisection judgements in normal subjects. *Neuropsychologia, 30*, 515–526. http://dx.doi.org/10.1016/0028-3932(92)90055-Q.

Mohr, C., Brugger, P., Bracha, H. S., Landis, T., & Viaud-Delmon, I. (2004). Human side preferences in three different whole-body movement tasks. *Behavioural Brain Research, 151*, 321–326. http://dx.doi.org/10.1016/j.bbr.2003.09.006.

[3] We thank an anonymous reviewer for pointing this out to us.

Nash, K., McGregor, I., & Inzlicht, M. (2010). Line bisection as a neural marker of approach motivation. *Psychophysiology, 47*, 979–983. http://dx.doi.org/10.1111/j.1469-8986.2010.00999.x.

Newman, D. P., O'Connell, R. G., & Bellgrove, M. A. (2013). Linking time-on-task, spatial bias and hemispheric activation asymmetry: A neural correlate of rightward attention drift. *Neuropsychologia, 51*, 1215–1223. http://dx.doi.org/10.1016/j.neuropsychologia.2013.03.027.

Nicholls, M. E., Bradshaw, J. L., & Mattingley, J. B. (1999). Free-viewing perceptual asymmetries for the judgement of brightness, numerosity and size. *Neuropsychologia, 37*, 307–314. http://dx.doi.org/10.1016/S0028-3932(98)00074-8.

Nicholls, M. E., Loftus, A., Mayer, K., & Mattingley, J. B. (2007). Things that go bump in the right: The effect of unimanual activity on rightward collisions. *Neuropsychologia, 45*, 1122–1126.

Paquet, N., Lajoie, Y., Rainville, C., & Sabagh-Yazdi, F. (2008). Effect of navigation direction on the dual-task of counting backward during blind navigation. *Neuroscience Letters, 442*, 148–151. http://dx.doi.org/10.1016/j.neulet.2008.07.002.

Paquet, N., Rainville, C., Lajoie, Y., & Tremblay, F. (2007). Reproducibility of distance and direction errors associated with forward, backward, and sideway walking in the context of blind navigation. *Perception, 36*, 525–536. http://dx.doi.org/10.1068/p5532.

Peterson, C. K., Gable, P., & Harmon-Jones, E. (2008). Asymmetrical frontal ERPs, emotion, and behavioral approach/inhibition sensitivity. *Social Neuroscience, 3*, 113–124. http://dx.doi.org/10.1080/17470910701612736.

Price, J., & Wolfers, J. (2014). Right-oriented bias: A comment on Roskes, Sligte, Shalvi, and De Dreu (2011). *Psychological Science, 25*, 2109–2111. http://dx.doi.org/10.1177/0956797614536738.

Robertson, I. H., Mattingley, J. B., Rorden, C., & Driver, J. (1998). Phasic alerting of neglect patients overcomes their spatial deficit in visual awareness. *Nature, 395*, 169–172. http://dx.doi.org/10.1038/25993.

Roskes, M., Sligte, D., Shalvi, S., & De Dreu, C. K. W. (2011). The right side? Under time pressure, approach motivation leads to right-oriented bias. *Psychological Science, 22*, 1403–1407. http://dx.doi.org/10.1177/0956797611418677.

Roskes, M., Sligte, D., Shalvi, S., & De Dreu, C. K. W. (2014). Does approach motivation induce right-oriented bias? Reply to Price and Wolfers (2014). *Psychological Science, 25*, 2112–2115. http://dx.doi.org/10.1177/0956797614547919.

Sutton, S. K., & Davidson, R. J. (1997). Prefrontal brain asymmetry: A biological substrate of the behavioral approach and inhibition systems. *Psychological Science, 8*, 204–210. http://dx.doi.org/10.1111/j.1467-9280.1997.tb00413.x.

Tomer, R. (2008). Attentional bias as trait: Correlations with novelty seeking. *Neuropsychologia, 46*, 2064–2070. http://dx.doi.org/10.1016/j.neuropsychologia.2008.02.005.

Vuillerme, N., Nougier, V., & Camicioli, R. (2002). Veering in human locomotion: Modulatory effect of attention. *Neuroscience Letters, 331*, 175–178. http://dx.doi.org/10.1016/S0304-3940(02)00876-5.

Wacker, J., Heldmann, M., & Stemmler, G. (2003). Separating emotion and motivational direction in fear and anger: Effects on frontal asymmetry. *Emotion, 3*, 167–193. http://dx.doi.org/10.1037/1528-3542.3.2.167.

Waldie, K. E., & Hausmann, M. (2010). Right fronto-parietal dysfunction in children with ADHD and developmental dyslexia as determined by line bisection judgements. *Neuropsychologia, 48*, 3650–3656. http://dx.doi.org/10.1016/j.neuropsychologia.2010.08.023.

Wilkinson, D., Guinote, A., Weick, M., Molinari, R., & Graham, K. (2010). Feeling socially powerless makes you more prone to bumping into things on the right and induces leftward line bisection error. *Psychonomic Bulletin & Review, 17*, 910–914.

Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology, 107*, 250–260. http://dx.doi.org/10.1037/0735-7036.107.3.250.