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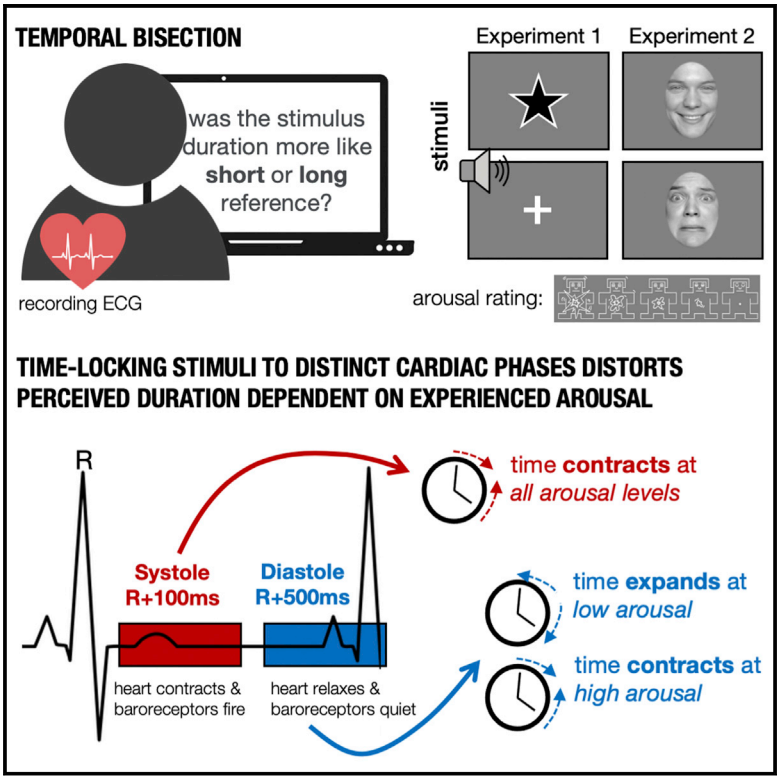
Report

Current Biology

Perceived time expands and contracts within each heartbeat

Graphical abstract



Highlights

- Time-locking identical stimuli to distinct cardiac phases distorts perceived duration
- The cardiac-led time distortion is modulated by experienced arousal
- At low arousal, systolic time contraction is counteracted by diastolic time expansion
- At high arousal, diastolic time expansion shifts toward time contraction

Authors

Irena Arslanova, Vassilis Kotsaris, Manos Tsakiris

Correspondence

irena.arslanova@rhul.ac.uk

In brief

Arslanova et al. show that cardiac signals arising from the heart distort experienced time. Durations of non-arousing stimuli are contracted during systole but expanded during diastole. This balance is disrupted when arousal increases. The work provides causal evidence for the involvement of interoceptive processes in human time perception.

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Current Biology

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Report

Perceived time expands and contracts within each heartbeat

Irena Arslanova,[1,4,5,*] Vassilis Kotsaris,[2] and Manos Tsakiris[1,3]
[1]Department of Psychology, Royal Holloway, University of London, Egham TW20 0EY, UK
[2]School of Psychology, University of Kent, Canterbury CT2 7NP, UK
[3]Centre for the Politics of Feeling, School of Advanced Study, University of London, London WC1E 7HU, UK
[4]Twitter: @irena_arslanova
[5]Lead contact
*Correspondence: irena.arslanova@rhul.ac.uk
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SUMMARY

Perception of passing time can be distorted.[1] Emotional experiences, particularly arousal, can contract or expand experienced duration via their interactions with attentional and sensory processing mechanisms.[2,3] Current models suggest that perceived duration can be encoded from accumulation processes[4,5] and from temporally evolving neural dynamics.[6,7] Yet all neural dynamics and information processing ensue at the backdrop of continuous interoceptive signals originating from within the body. Indeed, phasic fluctuations within the cardiac cycle impact neural and information processing.[8–15] Here, we show that these momentary cardiac fluctuations distort experienced time and that their effect interacts with subjectively experienced arousal. In a temporal bisection task, durations (200–400 ms) of an emotionally neutral visual shape or auditory tone (experiment 1) or of an image displaying happy or fearful facial expressions (experiment 2) were categorized as short or long.[16] Across both experiments, stimulus presentation was time-locked to systole, when the heart contracts and baroreceptors fire signals to the brain, and to diastole, when the heart relaxes, and baroreceptors are quiescent. When participants judged the duration of emotionally neutral stimuli (experiment 1), systole led to temporal contraction, whereas diastole led to temporal expansion. Such cardiac-led distortions were further modulated by the arousal ratings of the perceived facial expressions (experiment 2). At low arousal, systole contracted while diastole expanded time, but as arousal increased, this cardiac-led time distortion disappeared, shifting duration perception toward contraction. Thus, experienced time contracts and expands within each heartbeat—a balance that is disrupted under heightened arousal.

RESULTS

Across two experiments, participants first learned to discriminate a short (200 ms) from a long (400 ms) reference duration and were then asked to judge whether intermediate test durations (200, 250, 300, 350, and 400 ms) were more like the short or the long reference[16] (Figure 1A; STAR Methods). Across both experiments, stimulus presentation was time-locked to either the systolic (R + 100 ms) or the diastolic (R + 500 ms) cardiac phase (Figure 1B). In experiment 1, participants (n = 28) performed the task for visual and auditory stimuli in separate blocks, judging the duration of emotionally neutral visual images or auditory tones. In experiment 2, a new group of participants (n = 39) judged the duration of images depicting happy or fearful facial expressions presented in a random order. In experiment 2, after the temporal bisection task, participants were presented with each face again for 300 ms and were asked to rate how aroused it made them feel on an adapted 5-point self-assessment mannequin (SAM) scale from calm (1) to aroused (5). The averaged arousal ratings are shown in Figure 1A.

Cardiac systole contracts while diastole expands the experienced duration of emotionally neutral auditory and visual stimuli

Participants' performance on the duration bisection task was modeled with psychometric functions, where the point of subjective equality (PSE) reflects the stimulus duration at which the participant is equally likely to respond "short" or "long." Thus, shifts in PSE indicate relative under- or overestimation of stimulus durations (Figures 2A and 2B). In experiment 1, repeated-measures ANOVA with factors modality (auditory, visual) and cardiac phase (diastole, systole) on PSE values yielded a significant main effect of cardiac phase ($F(1,27) = 8.1$, $p = 0.01$, $\eta 2p = 0.23$), with stimuli presented at diastole judged, on average, 7 ms longer (M = 290, SD = 23) than those presented at systole (M = 297, SD = 26). The main effect of modality was also significant ($F(1,27) = 5.7$, $p = 0.02$, $\eta 2p = 0.17$) with tones judged, on average, 13 ms longer (M = 287, SD = 15) than visual stimuli (M = 300, SD = 30). The interaction between modality and cardiac phase was not statistically significant ($F(1,27) = 1.9$, $p = 0.18$, $\eta 2p = 0.06$), suggesting that the same temporal distortions occurred in both visual and auditory modalities. In addition to

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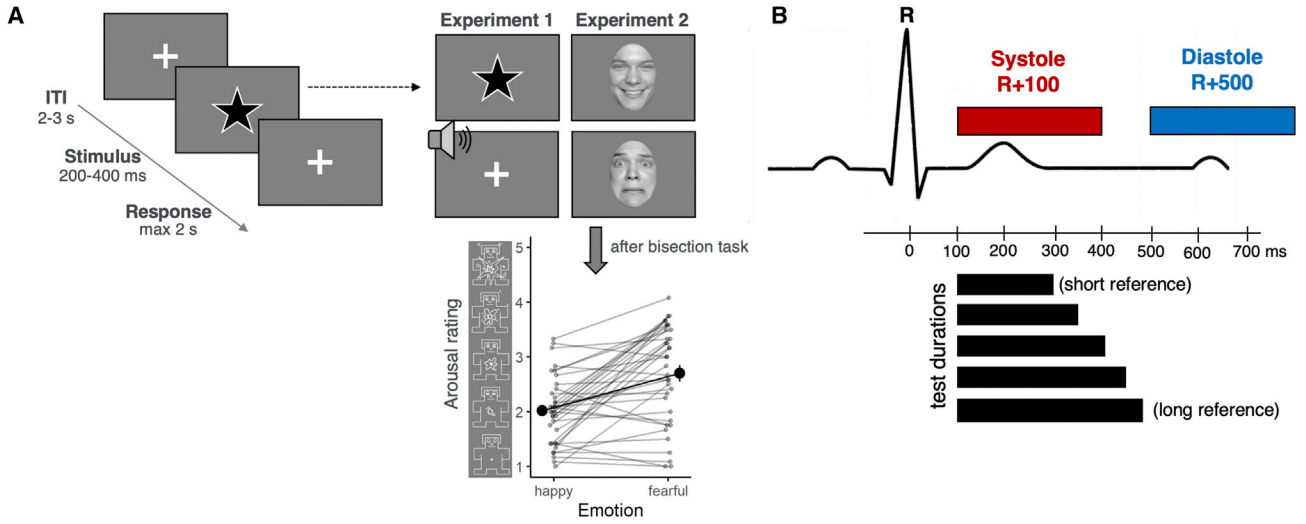

Figure 1. Task design

(A) Schematic trial structure. A stimulus was presented on the screen, and participants judged whether the presented stimulus was long or short. In experiment 1, we manipulated the stimulus modality (auditory or visual), whereas in experiment 2, the emotional valence of the stimulus (happy or fearful face). At the end of experiment 2, participants rated the level of arousal they experienced in response to each presented face on a scale from 1 to 5. The plot shows individual and group-level ratings (mean and SEM).

(B) Schematic task design. Stimulus onset was time-locked to distinct cardiac phases: systole (red) and diastole (blue). The figure shows how the most ambiguous duration (300 ms) did not overlap across the phases. The black bars represent stimulus durations. Participants first learned to discriminate between the short (200 ms) and the long (400 ms) reference, and during bisection, they were presented with additional intermediate test durations.

PSE, just noticeable difference (JND) reflects temporal sensitivity, where smaller values indicate better discriminability of changes in stimulus durations (Figure 2C). In experiment 1, the cardiac phase did not have a significant effect ($F(1,27) = 1.5$, $p = 0.24$, $\eta 2p = 0.05$), but JND values were significantly affected by modality ($F(1,27) = 100.0$, $p < 0.001$, $\eta 2p = 0.79$) with higher sensitivity for tone durations ($M = 22$, $SD = 8$) as compared with visual durations ($M = 46$, $SD = 17$). That auditory stimuli are perceived to last longer and result in more precise duration representation than visual stimuli is a common finding.[17] The interaction between cardiac phase and modality was not statistically significant ($F(1,27) = 0.001$, $p = 0.94$, $\eta 2p < 0.001$).

Because we observed heart rate changes over the course of the trial, in particular, heart deceleration before and during the stimulus presentation, we tested whether the cardiac phase effect was independent from the effects arising from the heart rate changes. For that reason, we ran a mixed linear model (MLL) on PSE and JND values with predictors coding for cardiac phase and modality while controlling for heart deceleration just before and during the stimulus presentation (STAR Methods). The magnitude of heart deceleration did not affect PSE values (beta = −0.1, SE = 2.2, $\chi^2 = 0.0$, $p = 0.96$). Cardiac phase retained its effect when heart deceleration was added into the model (beta = 6.8, SE = 2.4, $\chi^2 = 7.7$, $p = 0.006$) and so did the effect of modality (beta = 12.7, SE = 5.3, $\chi^2 = 5.3$, $p = 0.02$). The interaction between cardiac phase and modality remained statistically not significant (beta = 6.6, SE = 4.8, $\chi^2 = 1.9$, $p = 0.17$). Heart deceleration did not affect JND values either (beta = 0.6, SE = 1.5, $\chi^2 = 0.2$, $p = 0.66$). When heart deceleration was added into the model, cardiac phase effect remained statistically not significant (beta = 1.9, SE = 1.9, $\chi^2 = 1.0$, $p = 0.31$) as well as its interaction with modality (beta = −0.3, SE = 3.8, $\chi^2 = 0.0$, $p = 0.93$). Modality retained its statistically significant effect (beta = 24.1, SE = 2.4, $\chi^2 = 48.7$, $p < 0.001$). Thus, the effect of the cardiac phase on duration perception was independent from heart rate changes.

Cardiac distortion of experienced duration extends to low arousal stimuli but disappears when subjective arousal increases

First, experiment 2 (Figure 2D) was analyzed like experiment 1, with a repeated-measures ANOVA coding for the cardiac phase (diastole, systole) and the emotional valence of the presented face (happy, fearful). There was a significant main effect of cardiac phase on PSE values ($F(1,38) = 20.9$, $p < 0.001$, $\eta 2p = 0.35$), with stimuli presented at diastole judged, on average, 9 ms longer ($M = 305$, $SD = 25$) than those at systole ($M = 314$, $SD = 26$). The effect of valence was not statistically significant ($F(1,38) = 1.3$, $p = 0.27$, $\eta 2p = 0.03$) and neither was the cardiac phase by valence interaction ($F(1,38) = 1.3$, $p = 0.26$, $\eta 2p = 0.03$; Figure 2E). In contrast to experiment 1, the cardiac phase extended a small but statistically significant influence on JND values ($F(1,38) = 4.5$, $p = 0.04$, $\eta 2p = 0.14$) with sensitivity being higher during the diastolic ($M = 42$, $SD = 17$) than during the systolic phase ($M = 45$, $SD = 17$). There was no interaction ($F(1,38) < 0.001$, $p = 1.0$, $\eta 2p < 0.001$) and no main effect of valence ($F(1,38) = 0.58$, $p = 0.45$, $\eta 2p = 0.001$; Figure 2F).

Second, we considered the arousal ratings given to each presented face (Figure 1A) because such ratings can capture the variance in people's affective response to the stimuli and consequently in the arousal-led effects on time perception.[2,3] For that reason, we included arousal ratings for each stimulus, independently of its valence, into the LMM model and controlled for the heart deceleration like in experiment 1 (STAR Methods). PSE values were significantly affected by an interaction between

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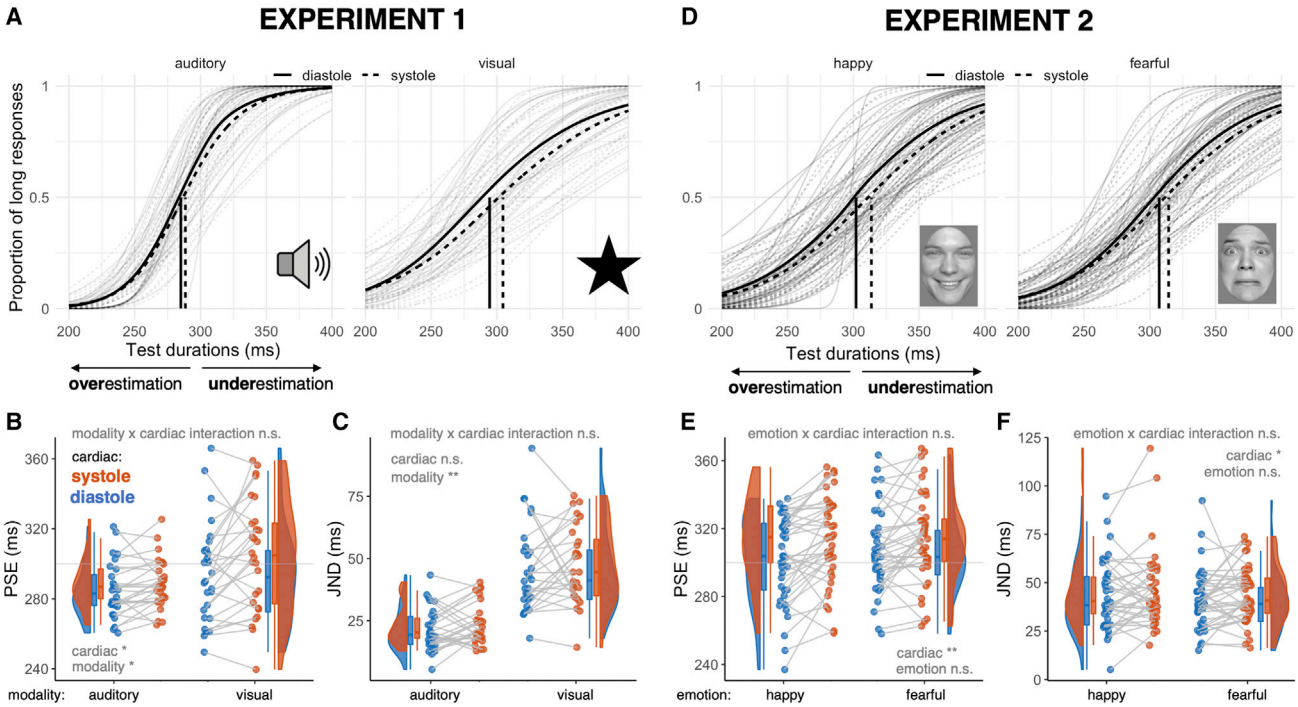

Figure 2. PSE and JND values estimated from the psychometric functions as a function of cardiac phase, modality (experiment 1), or emotion (experiment 2)

(A) Fitted individual (gray) and group-level (black) cumulative Gaussian functions showing the proportion of long responses as a function of test durations across modality (auditory, visual) by cardiac (systole, diastole) conditions in experiment 1. The vertical lines show the average PSE.

(B) PSE values in experiment 1 from systolic (red) and diastolic (blue) conditions, across modality conditions. Labels in gray indicate the main effects and interactions of the repeated-measures ANOVA, n = 28. The cardiac phase influenced PSEs without interaction by modality. Systolic durations were underestimated, whereas diastolic durations overestimation. The dots represent individual data while the boxplots reprsent group-level data (median and quartiles). Distribution plots were created with "raincloud" R package.[18,19]

(C) Same for JND values. Only modality influenced JNDs.

(D) Fitted individual (gray) and group-level (black) cumulative Gaussian functions showing the proportion of long responses as a function of test durations across emotion (happy, fearful) by cardiac (systole, diastole) conditions in experiment 2.

(E) PSE values in experiment 2 from systolic (red) and diastolic (blue) conditions, across emotion conditions. Labels in gray indicate the main effects and interactions of the repeated-measures ANOVA, n = 39. The cardiac phase influenced the PSEs in the same way as in experiment 1 without an interaction by emotion.

(F) Same for the JND values. The cardiac phase influenced JNDs without interaction by emotion. Participants were more sensitive to duration differences at diastole compared with systole. n.s., non-significant; **p < 0.001; *p < 0.05.

cardiac phase and arousal ratings (beta = −5.2, SE = 2.3, χ^2 = 5.3, p = 0.02). The main effect of arousal ratings was not significant (beta = 0.9, SE = 1.7, χ^2 = 0.3, p = 0.59), but the cardiac phase retained its statistical significance (beta = 9.2, SE = 2.3, χ^2 = 16.1, p < 0.001). A significant cardiac phase by arousal interaction was followed up with simple slopes analysis (Figure 3), which showed that the opposing effects of systole and diastole on time perception were present for low and average arousal ratings (beta = 14.4, SE = 3.2, t = 4.5, p < 0.001 and beta = 9.2, SE = 2.3, t = 4.1, p < 0.001, respectively) but disappeared when arousal ratings increased (beta = 4.1, SE = 3.2, t = 1.3, p = 0.21). For JND values, none of the predictors and their interactions made a statistically significant contribution. The main effect of the cardiac phase was no longer significant (beta = 2.8, SE = 2.1, χ^2 = 1.8, p = 0.18).

DISCUSSION

Experiment 1 showed that when timing emotionally neutral auditory and visual stimuli, cardiac systole contracted the experienced duration, while diastole expanded it. Experiment 2 replicated the observed cardiac-led temporal distortion and showed that it was further modulated by the subjectively experienced arousal in response to the presented facial expressions. As the experienced arousal increased, the relative cardiac-led temporal contraction-expansion was disrupted, biasing duration perception toward contraction.

There has been a growing interest in the idea of embodied time, according to which experienced time is influenced by physiological, interoceptive, signals from the body.[20,21] For example, past studies have examined interoceptive attention effects,[22] the cortical processing of cardiac signals,[23] and heart rate changes.[24–27] Specifically, asking participants to focus on bodily sensations exaggerates the emotional distortions of time so that negative experiences seem to last even longer and positive ones seem to pass even quicker compared with when participants focus externally.[22] In addition, the strength of cortical processing of afferent cardiac signals indexed by heart-evoked potential (HEP) is modulated by the over- and underestimation of elapsed

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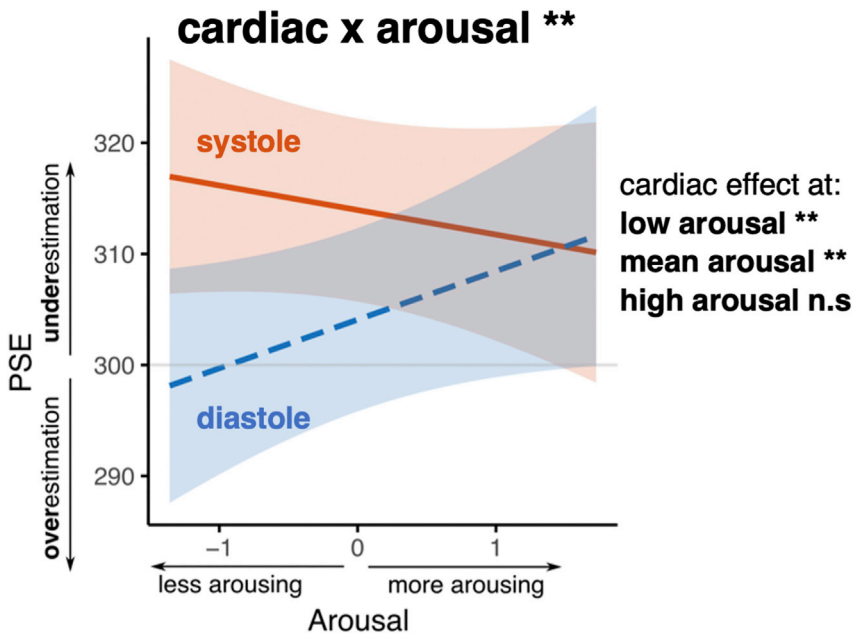

Figure 3. Simple slopes analysis breaking down the cardiac phase by subjective arousal interaction on PSE values in experiment 2

A linear mixed model was run on the PSE values modeling the effects of the cardiac phase (systole, diastole), subjective arousal, and changes in heart rate. The cardiac effect on PSEs was concentrated at low and mean levels of arousal but disappeared at high arousal levels. Arousal ratings were mean-centered. The lines represent the slopes and the shading represents the 95% confidence band. n.s., non-significant; **p < 0.001; *p < 0.05.

time so that lower amplitude in HEPs accompany duration overestimation.[23] Furthermore, when performing daily activities participants tend to report quicker passage of time during periods of heightened heart rate[25] (but not all studies have found significant influence of heart rate on temporal judgments[26,27]).

Although these findings correlate interoceptive processes in time perception, these studies demonstrated in a more mechanistic way how common time distortions[1–3]—the contraction and the expansion of time—arise from the phasic modulations within each heartbeat. Ascending cardiac signals from the baroreceptors provide the brain with continuous information about the heart rate and blood pressure changes. However, baroreceptor activity is maximal during the systolic period of the cardiac cycle, and although some baroceptor activity may still be present during the diastolic period, it is reduced or ceased relative to the systolic period.[28] Thus, the method of time-locking stimulus presentation to specific cardiac phases, while not necessarily reflecting real life perception, can be used to approximate the causal role of ascending cardiac signals in shaping temporal perception, as the only factor that varies across the two conditions is the timing of identical stimuli relative to the ECG R-wave.

A fundamental question pertains to how temporal distortions can arise from the ascending cardiac signals. One potential explanation stems from the observation that non-affective sensory processing is generally attenuated during the systole due to the neural noise produced by the baroreceptor output.[8–10,29] According to the coding efficiency accounts of temporal processing[30] more efficient or enhanced sensory processing predicts temporal dilation, whereas suppressed sensory processing predicts temporal contraction. On this view, experienced time is encoded from the evolving neural networks during perception.[6,7] Accordingly, temporal contraction during the systole may have resulted from a periodic sensory attenuation. The relative temporal expansion during the diastole may then act as a compensating mechanism that counteracts the systolic time contraction, similar to how time dilates post-saccade to compensate for the contraction caused by the saccade.[31]

However, beyond this sensory modulation account, it is also possible that cardiac signals directly affect the temporal accumulation processes[5] via the physiological arousal they convey. Classical pacemaker-accumulation models conceptualize timing as an accumulation of internally produced ticks.[32,33] To highlight the embodied nature of such temporal accumulation, the insular cortex, considered the main interoceptive hub in the brain,[34] has been found to be consistently engaged during duration perception tasks[35,36] and is argued to underpin the accumulation of "how do I feel" moments across time, essentially defining the subjective passage of time.[20,21] Importantly, the rate of such accumulation can be influenced by arousal.[2] It is often assumed that the systolic phase of the cardiac cycle represents a state of simulated heightened arousal, in contrast to the diastole.[37] On that account, the neural encoding of cardiac signals could directly affect temporal accumulation processes, as the encoding of arousing physiological states at the systole would lead to temporal contraction, followed by a temporal elongation during the diastolic phase. This is consistent with the finding that a reduction in sympathetic tone induced by clonidine injection resulted in a subjective slowing of time.[38] Combining the present paradigm with electroencephalography (EEG) methods could distinguish between these two accounts. Specifically, sensory modulation accounts would predict that cardiac signals attenuate the amplitude of sensory event-related potentials (ERPs),[8–10] whereas temporal accumulation accounts would predict that cardiac signals either attenuate the amplitude of the contingent negative variation (CNV)[39] or enhance the ERP response at the offset of the stimulus.[5] While the two accounts are not mutually exclusive, meaning that cardiac signals likely affect a range of components, it would be important to examine which of these modulations (sensory ERP, CNV, or offset ERP) is ultimately predictive of the subjective contraction of the stimulus duration.[39]

Interestingly, the opposing temporal distortions—contraction and expansion—within each heartbeat imply that over multiple heartbeats, such distortions would average out to produce a duration estimate that is close to the veridical duration of the stimulus. We show that the opposing effect of systole and diastole on duration perception breaks down, however, as the subjectively experienced arousal increased, skewing the duration

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representation toward contraction. Although arousal has been associated with temporal dilation,[27,40–43] some studies find that if arousal arises due to anxiety or uncertainty it can lead to temporal contraction.[44,45] Notably, we did not observe a main effect of arousal or valence on perceived stimulus durations in experiment 2. Rather, we show that subjectively felt arousal modulated how the cardiac effects shaped perceived stimulus durations, biasing temporal representation at the diastolic phase toward contraction. Static facial stimuli do not always induce temporal distortions,[46] thus future studies could use more arousal-inducing paradigms involving, for example, unexpected painful stimulation.[44]

This study demonstrated how fluctuations within the cardiac phases together with the subjectively experienced arousal affect perceptual temporal performance. Yet unexpected arousal can also reduce the metacognitive confidence in perceptual decisions.[47] A recent computational model of phasic cardiac influences on perception suggests that systole reduces the confidence in exteroceptive sensory channels.[48] However, direct evidence as to whether the ascending cardiac signals directly impact metacognitive processing is still lacking. Incorporating confidence judgements within the current paradigm would thus be a fruitful avenue for future studies to help disentangle the cardiac-driven temporal perceptual distortions from distortions in metacognition.

Overall, our findings are in line with recent research showing that interoceptive signals, particularly cardiac signals from the heart, shape neural activity and perception[8–15] and that the intricate interplay between the brain and the heart maintains our emotional experiences,[49] which in turn modulate how time is experienced.[2,3] Thus, the current results strengthen the view that time processing is an embodied process that arises from the continuous integration between exteroceptive and interoceptive processes.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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AUTHOR CONTRIBUTIONS

Conceptualization, M.T., V.K., and I.A.; methodology, M.T. and V.K.; formal analysis, I.A.; investigation, I.A.; data curation, I.A.; writing – original draft, I.A.; writing – review & editing, I.A. and M.T.; visualization, I.A.; supervision, M.T.; project administration, I.A.; funding acquisition, M.T.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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REFERENCES

1. Eagleman, D.M. (2008). Human time perception and its illusions. Curr. Opin. Neurobiol. *18*, 131–136. https://doi.org/10.1016/j.conb.2008.06.002.
2. Lake, J.I., LaBar, K.S., and Meck, W.H. (2016). Emotional modulation of interval timing and time perception. Neurosci. Biobehav. Rev. *64*, 403–420. https://doi.org/10.1016/j.neubiorev.2016.03.003.
3. Droit-Volet, S., and Meck, W.H. (2007). How emotions colour our perception of time. Trends Cogn. Sci. *11*, 504–513. https://doi.org/10.1016/j.tics.2007.09.008.
4. Roseboom, W., Fountas, Z., Nikiforou, K., Bhowmik, D., Shanahan, M., and Seth, A.K. (2019). Activity in perceptual classification networks as a basis for human subjective time perception. Nat. Commun. *10*, 267. https://doi.org/10.1038/s41467-018-08194-7.
5. Ofir, N., and Landau, A.N. (2022). Neural signatures of evidence accumulation in temporal decisions. Curr. Biol. *32*, 4093–4100.e6. https://doi.org/10.1016/j.cub.2022.08.006.
6. Zhou, S., Masmanidis, S.C., and Buonomano, D.V. (2020). Neural sequences as an optimal dynamical regime for the readout of time. Neuron *108*, 651–658.e5. https://doi.org/10.1016/j.neuron.2020.08.020.
7. Tsao, A., Yousefzadeh, S.A., Meck, W.H., Moser, M.B., and Moser, E.I. (2022). The neural bases for timing of durations. Nat. Rev. Neurosci. *23*, 646–665. https://doi.org/10.1038/s41583-022-00623-3.
8. Schulz, A., Vögele, C., Bertsch, K., Bernard, S., Münch, E.E., Hansen, G., Naumann, E., and Schächinger, H. (2020). Cardiac cycle phases affect auditory-evoked potentials, startle eye blink and pre-motor reaction times in response to acoustic startle stimuli. Int. J. Psychophysiol. *157*, 70–81. https://doi.org/10.1016/j.ijpsycho.2020.08.005.
9. Al, E., Iliopoulos, F., Forschack, N., Nierhaus, T., Grund, M., Motyka, P., Gaebler, M., Nikulin, V.V., and Villringer, A. (2020). Heart–brain interactions shape somatosensory perception and evoked potentials. Proc. Natl. Acad. Sci. USA *117*, 10575–10584. https://doi.org/10.1073/pnas.1915629117.
10. Al, E., Iliopoulos, F., Nikulin, V.V., and Villringer, A. (2021). Heartbeat and somatosensory perception. Neuroimage *238*, 118247. https://doi.org/10.1016/j.neuroimage.2021.118247.
11. Gray, M.A., Beacher, F.D., Minati, L., Nagai, Y., Kemp, A.H., Harrison, N.A., and Critchley, H.D. (2012). Emotional appraisal is influenced by cardiac afferent information. Emotion *12*, 180. https://doi.org/10.1037/a0025083.
12. Garfinkel, S.N., Minati, L., Gray, M.A., Seth, A.K., Dolan, R.J., and Critchley, H.D. (2014). Fear from the heart: sensitivity to fear stimuli depends on individual heartbeats. J. Neurosci. *34*, 6573–6582. https://doi.org/10.1523/JNEUROSCI.3507-13.2014.
13. Salomon, R., Ronchi, R., Dönz, J., Bello-Ruiz, J., Herbelin, B., Martet, R., Faivre, N., Schaller, K., and Blanke, O. (2016). The insula mediates access to awareness of visual stimuli presented synchronously to the heartbeat.

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J. Neurosci. *36*, 5115–5127. https://doi.org/10.1523/JNEUROSCI.4262-15.2016.

14. Ren, Q., Marshall, A.C., Kaiser, J., and Schütz-Bosbach, S. (2022). Multisensory integration of anticipated cardiac signals with visual targets affects their detection among multiple visual stimuli. NeuroImage *262*, 119549. https://doi.org/10.1016/j.neuroimage.2022.119549.
15. Marshall, A.C., Gentsch-Ebrahimzadeh, A., and Schütz-Bosbach, S. (2022). From the inside out: interoceptive feedback facilitates the integration of visceral signals for efficient sensory processing. NeuroImage *251*, 119011. https://doi.org/10.1016/j.neuroimage.2022.119011.
16. Kopec, C.D., and Brody, C.D. (2010). Human performance on the temporal bisection task. Brain Cogn. *74*, 262–272. https://doi.org/10.1016/j.bandc.2010.08.006.
17. Grondin, S. (2010). Timing and time perception: a review of recent behavioral and neuroscience findings and theoretical directions. Atten. Percept. Psychophys. *72*, 561–582. https://doi.org/10.3758/APP.72.3.561.
18. Allen, M., Poggiali, D., Whitaker, K., Marshall, T.R., and Kievit, R.A. (2021). Raincloud plots: a multi-platform tool for robust data visualization. Wellcome Open Res. *4*, 63. https://doi.org/10.12688/wellcomeopenres.15191.2.
19. Allen, M., Poggiali, D., Whitaker, K., Marshall, T.R., and Kievit, R. (2018). RainCloudPlots Tutorials and Codebase, Version V1.1. Zenodo. https://doi.org/10.5281/zenodo.3368186.
20. Wittmann, M. (2013). The inner sense of time: how the brain creates a representation of duration. Nat. Rev. Neurosci. *14*, 217–223. https://doi.org/10.1038/nrn3452.
21. Craig, A.D. (2009). Emotional moments across time: a possible neural basis for time perception in the anterior insula. Philos. Trans. R. Soc. Lond. B Biol. Sci. *364*, 1933–1942. https://doi.org/10.1098/rstb.2009.0008.
22. Pollatos, O., Laubrock, J., and Wittmann, M. (2014). Interoceptive focus shapes the experience of time. PLoS ONE *9*, e86934. https://doi.org/10.1371/journal.pone.0086934.
23. Richter, F., and Ibáñez, A. (2021). Time is body: multimodal evidence of crosstalk between interoception and time estimation. Biol. Psychol. *159*, 108017. https://doi.org/10.1016/j.biopsycho.2021.108017.
24. Meissner, K., and Wittmann, M. (2011). Body signals, cardiac awareness, and the perception of time. Biol. Psychol. *86*, 289–297. https://doi.org/10.1016/j.biopsycho.2011.01.001.
25. Ogden, R.S., Dobbins, C., Slade, K., McIntyre, J., and Fairclough, S. (2022). The psychophysiological mechanisms of real-world time experience. Sci. Rep. *12*, 12890. https://doi.org/10.1038/s41598-022-16198-z.
26. Suárez-Pinilla, M., Nikiforou, K., Fountas, Z., Seth, A.K., and Roseboom, W. (2019). Perceptual content, not physiological signals, determines perceived duration when viewing dynamic, natural scenes. Collabra Psychol. *5*, 55. https://doi.org/10.1525/collabra.234.
27. Schwarz, M.A., Winkler, I., and Sedlmeier, P. (2013). The heart beat does not make us tick: the impacts of heart rate and arousal on time perception. Atten. Percept. Psychophys. *75*, 182–193. https://doi.org/10.3758/s13414-012-0387-8.
28. Bronk, D.W., and Stella, G. (1932). Afferent impulses in the carotid sinus nerve I. The relation of the discharge from single end organs to arterial blood pressure. J. Cell. Comp. Physiol. *1*, 113–130. https://doi.org/10.1002/jcp.1030010110.
29. Skora, L.I., Livermore, J.J.A., and Roelofs, K. (2022). The functional role of cardiac activity in perception and action. Neurosci. Biobehav. Rev. *137*, 104655. https://doi.org/10.1016/j.neubiorev.2022.104655.
30. Kruijne, W., Olivers, C.N.L., and van Rijn, H. (2021). Neural repetition suppression modulates time perception: evidence from electrophysiology and pupillometry. J. Cogn. Neurosci. *33*, 1230–1252. https://doi.org/10.1162/jocn_a_01705.
31. Yarrow, K., Haggard, P., Heal, R., Brown, P., and Rothwell, J.C. (2001). Illusory perceptions of space and time preserve cross-saccadic perceptual continuity. Nature *414*, 302–305. https://doi.org/10.1038/35104551.
32. Treisman, M. (1963). Temporal discrimination and the indifference interval. Implications for a model of the "internal clock". Psychol. Monogr. *77*, 1–31. https://doi.org/10.1037/h0093864.
33. Ivry, R.B., and Schlerf, J.E. (2008). Dedicated and intrinsic models of time perception. Trends Cogn. Sci. *12*, 273–280. https://doi.org/10.1016/j.tics.2008.04.002.
34. Craig, A.D. (2009). How do you feel—now? The anterior insula and human awareness. Nat. Rev. Neurosci. *10*, 59–70. https://doi.org/10.1038/nrn2555.
35. Nani, A., Manuello, J., Liloia, D., Duca, S., Costa, T., and Cauda, F. (2019). The neural correlates of time: a meta-analysis of neuroimaging studies. J. Cogn. Neurosci. *31*, 1796–1826. https://doi.org/10.1162/jocn_a_01459.
36. Wittmann, M., Simmons, A.N., Aron, J.L., and Paulus, M.P. (2010). Accumulation of neural activity in the posterior insula encodes the passage of time. Neuropsychologia *48*, 3110–3120. https://doi.org/10.1016/j.neuropsychologia.2010.06.023.
37. Critchley, H.D., and Garfinkel, S.N. (2017). Interoception and emotion. Curr. Opin. Psychol. *17*, 7–14. https://doi.org/10.1016/j.copsyc.2017.04.020.
38. Coull, J.T. (2004). fMRI studies of temporal attention: allocating attention within, or towards, time. Brain Res. Cogn. Brain Res. *21*, 216–226. https://doi.org/10.1016/j.cogbrainres.2004.02.011.
39. Damsma, A., Schlichting, N., and van Rijn, H. (2021). Temporal context actively shapes EEG signatures of time perception. J. Neurosci. *41*, 4514–4523. https://doi.org/10.1523/JNEUROSCI.0628-20.2021.
40. Ogden, R.S., Henderson, J., McGlone, F., and Richter, M. (2019). Time distortion under threat: sympathetic arousal predicts time distortion only in the context of negative, highly arousing stimuli. PLoS ONE *14*, e0216704. https://doi.org/10.1371/journal.pone.0216704.
41. Appelqvist-Dalton, M., Wilmott, J.P., He, M., and Simmons, A.M. (2022). Time perception in film is modulated by sensory modality and arousal. Atten. Percept. Psychophys. *84*, 926–942. https://doi.org/10.3758/s13414-022-02464-9.
42. Mella, N., Conty, L., and Pouthas, V. (2011). The role of physiological arousal in time perception: psychophysiological evidence from an emotion regulation paradigm. Brain Cogn. *75*, 182–187. https://doi.org/10.1016/j.bandc.2010.11.012.
43. Harjunen, V.J., Spapé, M., and Ravaja, N. (2022). Anticipation of aversive visual stimuli lengthens perceived temporal duration. Psychol. Res. *86*, 1230–1238. https://doi.org/10.1007/s00426-021-01559-6.
44. Sarigiannidis, I., Grillon, C., Ernst, M., Roiser, J.P., and Robinson, O.J. (2020). Anxiety makes time pass quicker while fear has no effect. Cognition *197*, 104116. https://doi.org/10.1016/j.cognition.2019.104116.
45. Cui, Q., Liu, M., Liu, C.H., Long, Z., Zhao, K., and Fu, X. (2021). Unpredictable fearful stimuli disrupt timing activities: evidence from event-related potentials. Neuropsychologia *163*, 108057. https://doi.org/10.1016/j.neuropsychologia.2021.108057.
46. Fayolle, S.L., and Droit-Volet, S. (2014). Time perception and dynamics of facial expressions of emotions. PLoS One *9*, e97944. https://doi.org/10.1371/journal.pone.0097944.
47. Allen, M., Frank, D., Schwarzkopf, D.S., Fardo, F., Winston, J.S., Hauser, T.U., and Rees, G. (2016). Unexpected arousal modulates the influence of sensory noise on confidence. eLife *5*, e18103. https://doi.org/10.7554/eLife.18103.
48. Allen, M., Levy, A., Parr, T., and Friston, K.J. (2022). In the body's eye: the computational anatomy of interoceptive inference. PLoS Comput. Biol. *18*, e1010490. https://doi.org/10.1371/journal.pcbi.1010490.
49. Candia-Rivera, D., Catrambone, V., Thayer, J.F., Gentili, C., and Valenza, G. (2022). Cardiac sympathetic-vagal activity initiates a functional brain–body response to emotional arousal. Proc. Natl. Acad. Sci. USA *119*. e2119599119. https://doi.org/10.1073/pnas.2119599119.
50. Brainard, D.H. (1997). The psychophysics toolbox. Spat. Vis. *10*, 433–436.
51. Ebner, N.C., Riediger, M., and Lindenberger, U. (2010). FACES—A database of facial expressions in young, middle-aged, and older women and

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men: development and validation. Behav. Res. Methods *42*, 351–362. https://doi.org/10.3758/BRM.42.1.351.

52. Penney, T.B., and Cheng, X. (2018). Duration bisection: a user's guide. In Timing and Time Perception: Procedures, Measures, & Applications (Brill), pp. 98–127.
53. DeBruine, L. (2021). faux: simulation for Factorial Designs R package version 1.1.0. Zenodo. https://doi.org/10.5281/zenodo.2669586.
54. Azevedo, R.T., Garfinkel, S.N., Critchley, H.D., and Tsakiris, M. (2017). Cardiac afferent activity modulates the expression of racial stereotypes. Nat. Commun. *8*, 13854. https://doi.org/10.1038/ncomms13854.
55. Bradley, M.M., and Lang, P.J. (1994). Measuring emotion: the self-assessment manikin and the semantic differential. J. Behav. Ther. Exp. Psychiatry *25*, 49–59. https://doi.org/10.1016/0005-7916(94)90063-9.
56. Linares, D., and López-Moliner, J. (2016). quickpsy: an R package to fit psychometric functions for multiple groups. R J. *8*, 122–131. https://doi.org/10.32614/RJ-2016-008.
57. Park, H.D., Correia, S., Ducorps, A., and Tallon-Baudry, C. (2014). Spontaneous fluctuations in neural responses to heartbeats predict visual detection. Nat. Neurosci. *17*, 612–618. https://doi.org/10.1038/nn.3671.
58. Motyka, P., Grund, M., Forschack, N., Al, E., Villringer, A., and Gaebler, M. (2019). Interactions between cardiac activity and conscious somatosensory perception. Psychophysiology *56*, e13424. https://doi.org/10.1111/psyp.13424.
59. Lawrence, M.A. (2016). ez: easy analysis and visualization of factorial experiments. R package, version 4.4-0. https://CRAN.R-project.org/package=ez.
60. Glass, G.V., Peckham, P.D., and Sanders, J.R. (1972). Consequences of failure to meet assumptions underlying the fixed effects analyses of variance and covariance. Rev. Educ. Res. *42*, 237–288. https://doi.org/10.3102/00346543042003237.
61. Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. J. Stat. Softw. *67*, 1–48. https://doi.org/10.18637/jss.v067.i01.
62. Kuznetsova, A., Brockhoff, P.B., and Christensen, R.H.B. (2017). lmerTest package: tests in linear mixed effects models. J. Stat. Softw. *82*, 1–26. https://doi.org/10.18637/jss.v082.i13.
63. Singmann, H., Bolker, B., Westfall, J., Aust, F., and Ben-Shachar, M. (2022). afex: analysis of factorial experiments. R package version 1.1-1. https://CRAN.R-project.org/package=afex.
64. Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., and Makowski, D. (2021). performance: an R package for assessment, comparison and testing of statistical models. J. Open Source Softw. *6*, 3139. https://doi.org/10.21105/joss.03139.
65. Bauer, D.J., and Curran, P.J. (2005). Probing interactions in fixed and multilevel regression: inferential and graphical techniques. Multivariate Behav. Res. *40*, 373–400. https://doi.org/10.1207/s15327906mbr4003_5.
66. Long, J.A. (2019). interactions: comprehensive, user-friendly toolkit for probing interactions. R package version 1.1.0. https://cran.r-project.org/package=interactions.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw behavioral data	This paper	https://osf.io/4dn6q/
Participant-level visualizations	This paper	https://osf.io/4dn6q/
Software and algorithms		
MATLAB 2019B	The MathWorks	http://www.mathworks.com/products/matlab/; RRID: SCR_001622
Psychtoolbox	Breinard[50]	http://psychtoolbox.org/; RRID: SCR_002881
Labchart 8 Pro	AD Instruments	https://www.adinstruments.com/products/labchart; RRID: SCR_017551
Experiment code	This paper	https://osf.io/4dn6q/
R version 4.2.1 (2022 - 06 - 26)	R project	http://www.r-project.org/; RRID: SCR_001905
R Studio version 2022.07.2 Build 576	RStudio	http://www.rstudio.com/; RRID: SCR_000432
Analysis code	This paper	https://osf.io/4dn6q/
Other		
FACES database	Ebner et al.[51]	https://faces.mpdl.mpg.de/imeji/
Chosen and processed stimuli from the FACES database	Ebner et al.[51]	https://osf.io/4dn6q/
Auditory stimuli	Penney & Cheng[52]	https://osf.io/4dn6q/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Irena Arslanova (irena.arslanova@rhul.ac.uk).

Materials availability

This study did not generate new materials.

Data and code availability

- De-identified behavioral data have been deposited at OSF. They are publicly available as of the date of publication. DOIs are listed in the key resources table.
- All original code for running the experiments as well as the analysis reported in this paper has been deposited at OSF and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

For Experiment 1, 36 participants were recruited. Data from 8 participants was excluded from the final analysis, resulting in n = 28 (5 men, aged between 18 to 40, average age 22).

For Experiment 2, 45 participants were recruited. Data from 6 participants was excluded from the final analysis, resulting in n = 39 (4 men, aged between 18 to 40, average age 23). Psychometric fits and timing of the stimuli relative to cardiac phase for each participant (including those that were excluded from the analysis) can be found at the DOI listed in the key resources table. The criterion for participant exclusion was as follows:

(1) More than 20% of trials were flagged in one cardiac phase condition relative to the other. The trial was flagged if: (a) Inter-beat interval (IBI) was less than 500 ms or more than 1200 ms, which indicated impossibly low or high heart rate. (b) The actual start of the stimulus was considerably displaced relative to the systolic or diastolic phase. (c) A wrong key was pressed, or no

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response was given within the 2 second time limit. (d) The stimuli presented at the diastole exceeded the IBI by at least 200 ms, which made it overlap with the systolic phase of the next R wave. This happened if the IBI was too short.

(2) The psychometric function fit to behavioral data did not reach a above chance level (50%) performance in any one of the conditions

However, a re-analysis of the data with the excluded participants did not change the main inferences of the paper.

The sample size for Experiment 1 was based on previous studies examining heart-related effects on time perception[24] and cardiac phase effects on perception.[12]

The sample size for Experiment 2 was based on the effect sizes obtained in the visual task of the Experiment 1. The prediction was that the valence of the visual stimulus (happy vs. fearful face) will modulate the cardiac phase effect. Specifically, that the fearful face will reverse the cardiac effect relative to the happy face. We simulated data within a 2 (cardiac phase: systole, diastole) by 2 (emotion: happy, fear) within-subject ANOVA using the "faux" package[53] in R. We assumed that the cardiac effect under happy condition will be equivalent to the one in the Experiment 1 (PSE = 290 ms at diastole, PSE = 300 ms at systole). Thus, we estimated the sample size required to find an interaction, whereby PSE under fearful condition will be smaller by 10 ms at systole (PSE = 280 ms at systole) compared to the diastole (PSE = 290 ms at diastole). SDs were kept at 30 ms and correlations at 0.5. Simulations (1000 iterations) were run with sample sizes of 30, 35, 40, 45, 50, 55, and 60 until the power of 80% was achieved. At n = 40, we reached a power of.83 (η^2_p =.20).

Participants were recruited from the Royal Holloway's community and were compensated for their time with either money (£10 per hour) or class credit. The study was approved by Royal Holloway's Ethics Committee in accordance with the 1964 Declaration of Helsinki, and signed informed consents were obtained from all participants.

METHOD DETAILS

Design and Procedure

The task was identical across the two experiments, but the presented stimuli differed (see Stimuli). The task was a temporal bisection task.[16] Participants first learned to distinguish between the short (200 ms) and the long (400 ms) stimulus duration with feedback provided after each trial (20 trials). After completing the learning phase with less than 6 errors (in case error rate was higher than 6, they repeated 10 learning trials), participants were presented with 5 test durations (200, 250, 300, 350, 400 ms) and, on each trial, were asked to judge whether the presented test duration was more like the short or the long reference presented during the learning. They responded by pressing A or K keyboard keys with the left and right index fingers, respectively. The correspondence between the A/K keys and SHORT/LONG response was counterbalanced across participants. Participants had 2 seconds to respond. In each condition, test durations were repeated 8, 16, 24, 16, and 8 times, respectively, so that a third of trials was at the bisection point (300 ms). Stimulus durations were controlled with Psychophysics Toolbox MATLAB extension.[50]

The onset of test durations was time-locked to either the systolic or the diastolic cardiac phases. Specifically, an electrocardiogram (ECG) was recorded throughout the experiment with three disposable ECG electrodes placed in a modified lead I chest configuration: two electrodes were positioned underneath the left and right collarbone and another on the participant's lower back on the left side. The ECG signal was recorded with a Powerlab 8/35 (Powerlab, ADInstruments, http://www.adinstruments.com/) using Labchart 8 Pro software. The sampling rate was 1,000 Hz and a hardware band-pass filter (Bio Amp 132) between 0.3 and 1,000 Hz was applied. Heartbeats were detected online with a hardware-based function (fast output response), which identifies the ECG R-wave with a delay smaller than 1 ms by detecting when the amplitude exceeds an individually defined threshold. The stimuli were time-locked in a way that at least 50% of the longest stimulus (400 ms) was contained within the respective cardiac phase. The systolic phase is typically defined from approximately 200 to 400 ms post R-wave while the diastolic phase from approximately 500 to 800 ms post R-wave.[54] Thus, our stimuli were presented at 100 ms post R-wave in systolic condition, and at 500 ms post R-wave in diastolic condition. To account for the fact that wait times in the diastolic condition were always longer than systolic condition, 400 ms was removed from the inter-trial-interval (ITI) preceding the diastolic condition. The total ITI ranged randomly between 2 to 3 seconds.

In Experiment 1, participants performed the task in two modalities – visual and auditory – in a counterbalanced order, so that half of the participants performed the visual task first and the other half performed the auditory task first. Both tasks started with a separate learning phase. Both tasks were divided into 4 successive blocks with breaks in-between. The reference short and long durations were presented again (3 times each) at the beginning of each block to reduce memory demands. The cardiac phase condition was randomized within each block.

In Experiment 2, instead of the modality manipulation, the valence of the visual stimuli was manipulated, so that participants judged the duration of faces showing happy or fearful expressions. In the learning phase, a scrambled face served as a timed stimulus. Both valence and cardiac phase conditions were randomized across 6 blocks with reference short and long durations presented again (for 3 times each) at the beginning of each block to reduce memory demands. After temporal bisection task, participants were presented with each of 12 faces from the experiment for 300 ms. For each face they rated how aroused it made them feel on an adapted 5-point Self-Assessment Mannequin (SAM)[55] from calm (1) to aroused (5).

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Stimuli

In Experiment 1, the auditory stimuli comprised of 300 Hz (4410 sampling Hz) neutral tones with rising and falling phases of 10 ms, played at a 70% volume via headphones. The tones were created with *audiowrite* function in MATLAB according to the script provided by Penney and Cheng.[52] The resulting tones can be found at the DOI listed in the key resources table. The visual stimulus was a black star shape with a white outline presented at the center of the screen. The stimuli can be found at the DOI listed in the key resources table.

In Experiment 2, the stimuli were grayscaled and cropped images of 6 people (3 men, 3 women) chosen from validated FACES database.[51] Each person was presented with either a happy or a fearful expression. The stimuli can be found at the DOI listed in the key resources table.

QUANTIFICATION AND STATISTICAL ANALYSIS

For each participant, the proportion of "long" responses as a function of test durations was fitted with Gaussian cumulative psychometric functions using the "quickpsy" R package,[56] separately for each condition (in Experiment 1: modality & cardiac phase; in Experiment 2: emotion & cardiac phase). The goodness of fits was evaluated with deviance. By re-fitting the psychometric functions with 1000 bootstrap samples, we used the distribution of bootstrapped deviances to calculate the p-value of obtaining a deviance greater than that of the original data. In Experiment 1, none of the participants in any of the conditions showed a statistically significant deviance (mean p =.83, SD =.23). In Experiment 2, three participants (P24, P27, P39) showed a significant deviance in one of the conditions, but none of the other participants showed significant deviance (mean p =.76, SD =.26). However, the results remain the same if those participants were excluded from the analyses. We decided to retain these three participants in the analysis because they reached a sufficient performance (i.e., above a chance level) and thus were capable of distinguishing between the stimulus durations.

Once fitted, the point of subjective equality (PSE) and the just noticeable difference (JND) were extracted. The PSE is the duration value at which the participant is equally likely to classify the duration as short or long. Thus, shifts in PSE indicate temporal under- or overestimation. For example, lower PSE values suggest temporal overestimation, because participants would be predicted to begin responding long during physically short test durations. The JND reflects the temporal sensitivity, whereby smaller values indicate better discriminability of changes in stimulus durations.

ECG processing

The timepoints of R-wave peaks were recorded online with a hardware-based function (fast output response), which identifies the ECG R-wave with a delay smaller than 1 ms by detecting when the amplitude exceeds an individually defined threshold. These timepoints were plotted onto the raw ECG signal for visual checks. The R-peak segments were divided into their respective trials. For each trial, the correspondence between the stimulus onset and the R peak onset was checked, so that trials where the stimulus occurred outside the predefined cardiac phase time-window were flagged. In addition, a trial was flagged if the inter-beat-interval (IBI) between any of the R-peaks was less than 500 ms or more than 1200 ms, which indicated impossibly low or high heart rate. These flagged trials were excluded from the analysis. Further, we flagged additional trials where the duration of the stimulus exceeded the average IBI on that trial by more than 200 ms, which indicated a considerable overlap with the systolic phase of the next R-wave. For most participants, this affected only the longest stimuli (400 ms), and thus were retained for the analysis, because removing these trials distorted the psychometric fitting. If anything, the fact that some diastolic trials may have not been purely diastolic would result in underestimation of the true cardiac effect.

To ensure that the cardiac phase influence on duration perception was independent of any heart rate changes over the course of a trial, IBI lengths at five consecutive IBIs – two prior the stimulus presentation (during ITI: S-2 & S-1), during the stimulus presentation (S), and two after the stimulus (during the response: S+1, S+2) – were calculated.[57,58] For both experiments, across all conditions, the heart decelerated prior and during the stimulus presentation (from S-2 to S+1), followed by a short acceleration during the response (from S+1 to S+2). For each trial, we took the IBI length difference between S-2 and S+1, which indexed the magnitude of the heart's deceleration during the stimulus presentation. We averaged heart's deceleration for each duration and response category and added it as a control variable in the linear mixed models (see Linear mixed model (LMM) analyses below).

ANOVA analyses

First, PSE and JND values were analyzed with a type-3 repeated-measures ANOVA using the *ezANOVA()* function from "ez" R package.[59] In Experiment 1, the repeated factors were: modality (auditory, visual) and cardiac phase (diastole, systole). In Experiment 2, the repeated factors were: emotion (happy, fear) and cardiac phase (diastole, systole). The residual plots of the two ANOVA models were visually inspected to detect violations of normality. However, given that ANOVA with a balanced design is considered robust even with normality violations[60] and that alternative non-parametric Friedman test cannot be done for factorial designs, parametric ANOVA was used in both cases.

Linear mixed model (LMM) analyses

Second, PSE and JND values were modelled with linear mixed models (LMM), using "lme4"[61] and "lmerTest"[62] R packages.

In Experiment 1, the model structure was as follows

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outcome variable ~ cardiac phase * modality + heart deceleration + (1 | participant) + (1 | cardiac phase : participant) + (1 | modality : participant)

Heart deceleration (see ECG processing above) was added as a control variable because we were not interested in its interaction with our main predictors. Categorical variables (cardiac phase and modality) were sum-coded, while continuous variables (heart deceleration) were mean-centered and standardized. Separate intercept was added for each participant to account for repeated measures. In addition, we specified that random effect of "participant" was fully crossed within both cardiac phase and modality conditions – each participant appears at each level of cardiac phase and modality. Statistical significance was evaluated with likelihood ratio tests using the *mixed()* function from the "afex" package.[63]

Initial run of both PSE and JND models produced a singular fit warning, suggesting that the random effect structure did not explain sufficient variance to warrant its inclusion. We checked the proportion of variance explained by each of the random effects with *rePCA()* function from the "lme4" package,[61] which showed that (1 | cardiac phase : participant) random effect explained 0 variance. Thus, in the final models that random effect was removed. However, the removal of that random effect led to equivalent statistical significance of the fixed effects as for the models with the full random effect structure. Model assumptions were checked by plotting the model residuals with *check_model()* function from "performance" R package.[64] Both PSE and JND models did not reveal any clear violations.

In Experiment 2, the LMM model coded for subjective arousal ratings given to the happy and fearful images, which were added irrespective of the stimulus valence (i.e., each participant had 2 arousal ratings per cardiac phase). Due to a coding error, ratings from three participants were missing, thus the models were run on the remaining participants (n = 36). The model structure was as follows:

outcome variable ~ cardiac phase * arousal rating + heart deceleration + (1 | participant) + (1 | cardiac phase : participant)

Categorical variables (cardiac phase) were sum-coded, while continuous variables (arousal rating & heart deceleration) were mean-centered and standardized. Initial run of both PSE and JND models produced a singular fit warning, suggesting that the random effect structure did not explain sufficient variance to warrant its inclusion. We checked the proportion of variance explained by each of the random effects with *rePCA()* function from the "lme4" package,[61] which showed that (1 | cardiac phase : participant) random effect explained 0 variance. Thus, in the final models that random effect was removed. However, the removal of that random effect led to equivalent statistical significance of the fixed effects as for the models with the full random effect structure. Diagnostic plots did not show any clear assumption violations.

Statistically significant interactions were followed up by a simple slopes analysis,[65] whereby the effect of one continuous variable was examined when the interacting continuous variable was either low (-1 SD from the mean), at its mean value, or high (+1 SD from the mean). We used *sim_slopes()* function from the "interactions" package[66] in R.