Active vision varies across the cardiac cycle

Stella Kunzendorf[1,2] , Felix Klotzsche[3] , Mert Akbal[2] , Arno Villringer[1,2,3,6], Sven Ohl[4,5], & Michael Gaebler[2,3]

Affiliations:

[1] Charité – Universitätsmedizin Berlin

[2] Dept. of Neurology, Max Planck Institute for Human Cognitive and Brain Sciences

[3] MindBrainBody Institute at Berlin School of Mind and Brain

[4] Bernstein Center of Computational Neuroscience, Berlin

[5] Humboldt-Universität zu Berlin

[6] Dept. of Cognitive Neurology, University Hospital Leipzig

Acknowledgments:

We would like to thank all those who participated in and advanced this study. This research was supported by a DFG research grant to S.O. (OH 274/2-1).

Competing interests:

The authors declare that they have no competing financial interests.

Corresponding author:

Stella Kunzendorf

stella.kunzendorf@charite.de

Abstract

Perception and cognition oscillate with fluctuating bodily states. For example, visual processing has been shown to change with alternating cardiac phases. Here, we study the heartbeat's role for active information sampling—testing whether humans implicitly act upon their environment so that relevant signals appear during preferred cardiac phases.

During the encoding period of a visual memory experiment, participants clicked through a set of emotional pictures to memorize them for a later recognition test. By self-paced key press, they actively prompted the onset of shortly (100-ms) presented pictures. Simultaneously recorded electrocardiograms allowed us to analyse the self-initiated picture onsets relative to the heartbeat. We find that self-initiated picture onsets vary across the cardiac cycle, showing an increase during cardiac systole, while memory performance was not affected by the heartbeat. We conclude that active information sampling integrates heart-related signals, thereby extending previous findings on the association between body-brain interactions and behaviour.

Introduction

We perceive and act upon the world while our brain continuously integrates exteroceptive and interoceptive information, that is, information received from external (e.g., through vision and touch) and internal sources (e.g., through viscerosensation and proprioception), respectively (Barrett & Simmons, 2015; Kleckner et al., 2017). Through the fine-tuned interplay of brain and body, we are able to react to changes in the external and the internal environment to maintain or restore our bodily integrity and well-being. Via feedback loops, the brain thereby receives afferent information about bodily states to regulate and adjust bodily activity accordingly (Craig, 2002; Critchley & Harrison, 2013; Mayer, 2011; Saper, 2002). To fully capture the bi-directionality of brain-body interactions and their association with mental processes, it is essential to investigate if and how such afferent bodily information modulates our thoughts, feelings, and behaviour.

One approach to study bodily influences on cognition and behaviour exploits natural physiological fluctuations. Such fluctuations occur at multiple time scales—ranging from milliseconds to weeks (e.g., brain oscillations, heartbeats, the circadian rhythm, or the menstrual cycle)—and they dynamically interact with each other as well as with the environment (Glass, 2001). How such natural physiological variability is processed in the brain remains poorly understood. However, it has been shown that brain and beyond-brain organ systems (e.g., the cardiorespiratory or the gastrointestinal system) co-vary in their oscillatory activity (Fan et al., 2012; Luft & Bhattacharya, 2015; Richter, Babo-Rebelo, Schwartz, & Tallon-Baudry, 2017; Thayer, Åhs, Fredrikson, Sollers, & Wager, 2012).

Particularly the heart, as a fundamental internal oscillator, has been the target of a growing body of research that investigates how cardiac fluctuations are integrated with the processing of external stimuli (for a review see Critchley & Garfinkel, 2018). Cardiac activity occurs in a cycle of two phases: During diastole, the ventricles relax to be filled with blood; during systole, the ventricles contract and eject blood into the arteries, while visceral pathways send information about each heartbeat to the brain (Critchley & Harrison, 2013). Such natural phasic changes of the cardiovascular state have been mainly associated with variations in perception: For sensory processing, which is typically measured with detection tasks or reaction time tasks, response to passively presented stimuli has been shown to be attenuated during early cardiac phases (i.e., during systole) or relatively enhanced at later time points in the cardiac cycle (i.e., at diastole; Birren, Cardon, & Phillips, 1963; Callaway & Layne, 1964; Edwards, Ring, McIntyre, Carroll, & Martin, 2007; Lacey & Lacey, 1974; McIntyre, Ring, Edwards, & Carroll, 2008; Réquin & Brouchon, 1964; Saari & Pappas, 1976; Sandman, McCanne, Kaiser, & Diamond, 1977; Wilkinson, McIntyre, & Edwards, 2013).

A growing number of more recent findings, however, suggests *facilitated* processing during systole, specifically for task- or context-relevant stimuli. While enhanced processing during systole was also reported for non-emotional visual stimuli (Pramme, Larra, Schächinger, & Frings, 2016; Pramme, Schächinger, & Frings, 2015), an emotional specificity of this effect was observed when testing neutral stimuli vs. valenced stimuli like emotional faces—particularly for emotionally arousing fear or threat stimuli (Azevedo, Badoud, & Tsakiris, 2017; Azevedo, Garfinkel, Critchley, & Tsakiris, 2017; Garfinkel et al., 2014). Thus pointing towards an increase in emotional salience through interoceptive channels (Critchley & Harrison, 2013), these findings correspond with evidence for preferential stimulus processing (e.g., enhanced perception and memory) fostered by states of general psychophysiological arousal (Cahill & McGaugh, 1998; Mather, Clewett, Sakaki, & Harley, 2016; Mather & Sutherland, 2011; McGaugh, 2015; Tambini, Rimmele, Phelps, & Davachi, 2017). At the same time, phasic cardiac modulation of stimulus processing has been associated with altered memory formation and retrieval (Fiacconi, Peter, Owais, & Köhler, 2016; Garfinkel et al., 2013)—also in the context of respiratory oscillations (Zelano et al., 2016). Taken together, sensory processing is differentially modulated during early cardiac phases, indicating a selective processing benefit for relevant (e.g., emotionally arousing) stimuli, while other perceptual processes are attenuated (for a review see Garfinkel & Critchley, 2016). This suggests that cardiac (or cardio-respiratory) fluctuations not only are an important target of efferent arousal regulation but contribute to afferent signalling of bodily arousal states to the brain (Critchley & Harrison, 2013).

However, these studies investigating cardiac influences on perception and cognition have only employed passive stimulus presentation, which ignores *self-initiated action* as a crucial dimension of sensory and particularly visual processing. Mediating our engagement with a visual scene, motor actions dynamically orchestrate incoming sensory data and thus strongly influence visual perception—selecting what information is preferentially processed (Benedetto, Spinelli, & Morrone, 2016; Tomassini, Spinelli, Jacono, Sandini, & Morrone, 2015). Sensorimotor coupling has also been linked to periodic attentional fluctuations (Hogendoorn, 2016; Morillon, Schroeder, & Wyart, 2014). For example in the visual domain, saccadic eye movements are preceded by a shift of attention to the saccade target resulting in strongly improved visual performance (Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995; Li, Barbot, & Carrasco, 2016; Ohl, Kuper, & Rolfs, 2017) and memory performance at the saccade target location (Hanning, Jonikaitis, Deubel, & Szinte, 2016; Ohl & Rolfs, 2017) with corresponding neural enhancement in early visual cortex (Merrikhi et al., 2017; Moore, Tolias, & Schiller, 1998). There is sparse evidence that connects the heartbeat to general action generation and the few studies that investigated if

movements are modulated across the cardiac cycle indicate that systole provides a facilitating time window for spontaneous motor activity—both in the somatomotor (Mets, Konttinen, & Lyytinen, 2007) as well as in the oculomotor domain (Ohl, Wohltat, Kliegl, Pollatos, & Engbert, 2016).

Based on findings of facilitated processing for visual stimuli (Azevedo, Badoud, et al., 2017; Azevedo, Garfinkel, et al., 2017; Garfinkel et al., 2014; Pramme et al., 2016, 2015) and increased oculomotor activity (Ohl et al., 2016) during early phases of the cardiac cycle, we here hypothesized that *active vision* (i.e., self-initiated action towards a visual stimulus) shows periodic variations with the phase of our heartbeat. To investigate perception and action within a comprehensive framework of mind-brain-body interactions, we here studied cardiac-related sensorimotor processing in a self-paced visual sampling paradigm, in which participants decide when to press a key to see a task-relevant visual stimulus. Extending studies that emphasize a selectivity of this effect for motivationally salient, passively presented stimuli (Azevedo, Badoud, et al., 2017; Azevedo, Garfinkel, et al., 2017; Garfinkel et al., 2014), we predicted that observers implicitly act upon a relevant visual stimulus such that it is received (and perceived) during preferred cardiac phases. More specifically, we hypothesized that visual sampling would be biased towards processing task-relevant pictures during systole.

We assessed the emotional specificity of cardiac-phase effects (Garfinkel et al., 2014; for a review see Garfinkel & Critchley, 2016) by presenting negative, positive, and neutral pictures (cf. **Methods**). To further induce stimulus relevance, participants were instructed to memorize the pictures during sampling and their recognition memory was tested after a delay of several minutes. This enabled us to also address the previously reported link between memory performance and the cardiac cycle: Based on the abovementioned systolic modulation of memory formation (Garfinkel et al., 2013), we expected recognition performance to be modulated by the cardiac timing of memory probes during encoding. Specifically, we hypothesized that memory performance for pictures encoded at different time points of the cardiac cycle is not equally distributed, but varies across the cardiac cycle.

Results

We tested whether self-paced visual sampling and visual memory encoding fluctuate across the cardiac cycle. Based on previous studies that demonstrated facilitated visual processing (Pramme et al., 2016, 2015) and increased oculomotor activity (Ohl et al., 2016) during the early phase of the cardiac cycle, we hypothesized that participants prefer to prompt a visual stimulus during early phases of the cardiac cycle. In addition, we hypothesized memory performance to be influenced by the cardiac time point of memory probes during encoding (Garfinkel et al., 2013).

Encoding: The distribution of self-paced picture onsets relative to the cardiac R-R interval showed an overall increase in early phases of the cardiac cycle (M = 0.33π, SD = 0.52π, ϱ = 0.26, cf. **Fig. 1a**). This observation was supported by inferential circular statistics indicating a non-significant trend that the self-paced key presses in the present experiment are unlikely to be uniformly distributed (Rayleigh test statistics R_0 = 0.26, p = .053). Of note, the same analysis with our preregistered sample size (i.e., the first 40 healthy subjects of N = 43; cf. https://osf.io/5z8rx/) showed a significant deviation from a uniform distribution (R_0 = 0.28, p = .039), that is due to a significant increase in self-paced key presses in the interval from 0.24 to 0.44π (**Fig. 1a**) as revealed by nonparametric bootstrapping (performed on the original participant pool, N = 43). Although this circular statistics can infer that the distribution of relative picture onsets deviates from a uniform distribution, it cannot pinpoint the transition from systole to diastole – particularly in the presence of varying heartbeat lengths, for which the same section of the circular distribution can be associated with different cardiac phases.

Accounting for the bi-phasic nature of cardiac activity in the binary analysis, we computed the number of key presses during cardiac systole and diastole, normalised by the proportion of the systole vs. diastole in the whole cardiac cycle. We found a significantly larger (t(42) = 2.76, p = .009, Cohen's d = 0.42) ratio of picture onsets in the systole (M = 1.05, SD = 0.14) as compared to diastole (M = 0.97, SD = 0.081), corroborating our finding of an increase in self-paced visual sampling during cardiac systole (cf. **Fig. 1b**). Similar results were obtained for the preregistered sample size (n = 40), showing a significantly larger (t(39) = 2.70, p = .01, Cohen's d = 0.43) systolic (M = 1.05, SD = 0.14) than diastolic ratio (M = 0.97, SD = 0.079).

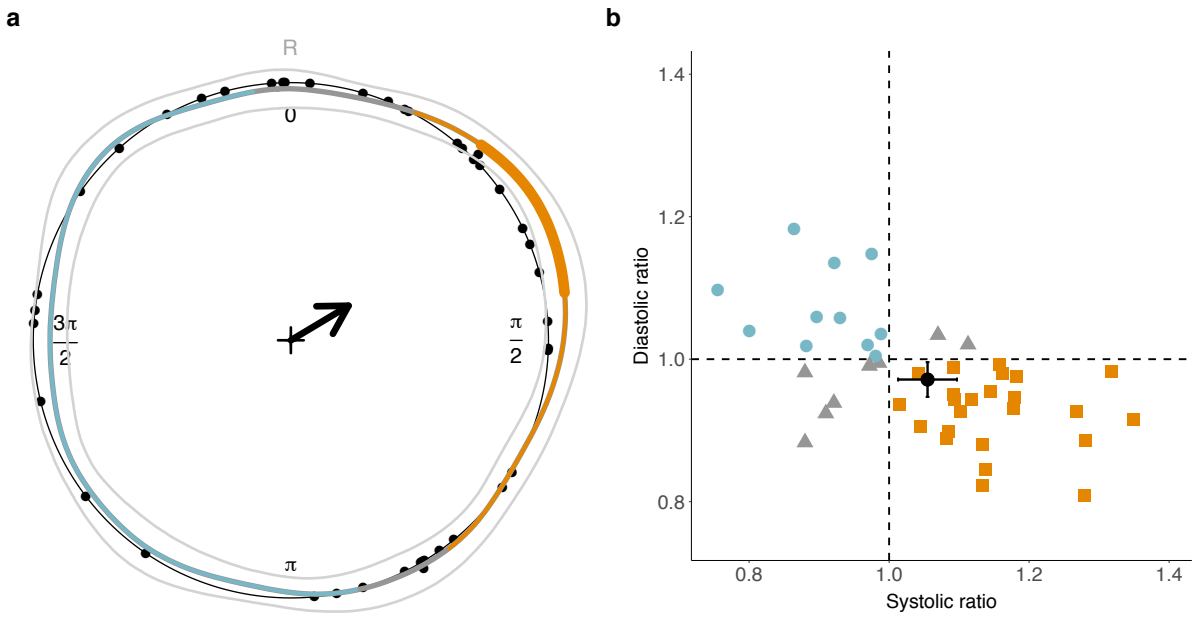


Figure 1. ***a,*** *Circular analysis.* Circular distribution of individual mean picture onsets (black dots, N = 43) across the cardiac cycle (from R-peak to R-peak). We observed a trend for increased self-prompted stimulus presentations (weighted overall mean as black arrow) in early phases of the cardiac cycle (Rayleigh test statistic R_0= 0.26, p = .053). Based on a bootstrapping procedure, we computed the mean circular density of picture onsets (middle thicker line), as well as a 95% confidence interval (CI, within inner and outer thin grey lines). Segments of the cardiac cycle are determined as statistically significant (thick orange segment) when the circular density significantly differs from the circular uniform (i.e. the lower bound of the CI is outside of the black uniform circle). To relate segments of the cardiac cycle to the two cardiac phases (systole = orange, diastole = blue, non-defined = grey), overall mean systole and diastole lengths were obtained, showing, that the significant density segment falls into systole. ***b***, *Binary analysis*. Most subjects (24/43) preferred to prompt pictures during their systole (orange/square). Fewer subjects (11/43) chose to prompt them during their diastole (blue/dot) or did not show a preference in any of the two defined phases (8/43; grey/triangle). The phase-specific proportion of key presses (relative to all 120 trials) was normalized by the proportion of the cardiac phase (systole, diastole) in the entire R-R interval. A ratio >1 thus indicates that the number of prompted picture onsets during systole or diastole exceeds the number that would be expected if they were uniformly distributed (resulting in a ratio = 1, dashed line). The group-level mean (black dot with standard error bars) shows an over-proportional accumulation of picture onsets during individual systole relative to individual diastole (t(42) = 2.76, p = .009, Cohen's d = 0.42).

Recognition: We also investigated the association between the cardiac cycle and memory processing: In a circular analysis, we tested whether the distribution of onset times during stimulus encoding differed for pictures that were correctly remembered (hits) or erroneously identified as new pictures (miss). Overall, picture onset times during the encoding

period did not significantly deviate from a uniform distribution over the cardiac cycle for hits (R_0 = 0.20, p = .21) and misses (R_0 = 0.16, p = .36).

We further investigated the influence of cardiac phase (systole, diastole) and picture valence on recognition memory. A LMM (cf. **Table 1**) with contrast-coded picture valence (negative-neutral, positive-neutral) revealed a significant memory benefit for negative vs. neutral stimuli (b = 0.37, SE = 0.12, z = 3.11, p = .002), as well as for positive vs. neutral stimuli (b = 0.29, SE = 0.12, z = 2.43, p = .015). More specifically, memory performance for negative pictures (M = 0.80, SD = 0.13) and for positive pictures (M = 0.78, SD = 0.16) significantly exceeded memory performance for neutral pictures (M = 0.73, SD = 0.18). Critically, including cardiac phase (systole, diastole) did not improve the model fit: Neither phase (b = -0.17, SE = 0.19, z = -0.89, p = .37) nor the interaction of picture valence and phase (negative-neutral X phase: b = 0.30, SE = 0.27, z = 1.11, p = .27; positive-neutral X phase: b = 0.16, SE = 0.27, z = 0.61, p = .54) significantly accounted for variation in recognition memory (cf. **Table 1**).

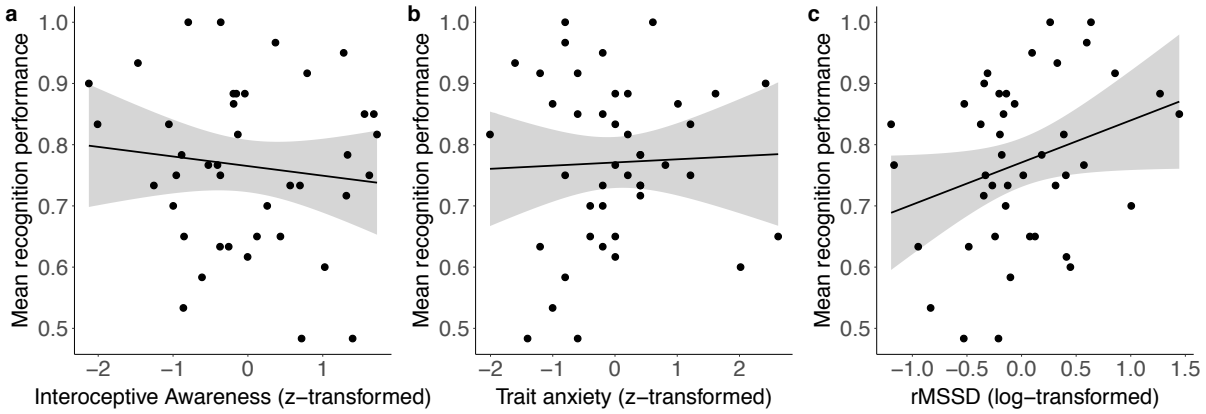
	Coefficient	**SE**	**z-Value**	**p-Value**
m0 (~ picture valence)				
Intercept	1.17	0.15	7.71	< .001
negative vs. neutral (neg-neu)	0.37	0.12	3.11	.002
positive vs. neutral (pos-neu)	0.29	0.12	2.43	.015
m1 (~ picture valence X cardiac phase)				
Intercept	1.24	0.17	7.14	< .001
cardiac phase (0 = diastole, 1 = systole)	-0.17	0.19	-0.89	.37
phase X neg-neu	0.30	0.27	1.11	.27
phase X pos-neu	0.16	0.27	0.61	.54

Table 1. Linear mixed model (LMM) with recognition memory (hit = 1, miss = 0) relative to picture valence (negative-neutral, positive-neutral) (m0 = memory ~ picture valence + (1|vp)), cardiac phase, and their interaction (m1 = memory ~ picture valence X cardiac phase + (1|vp)). Valenced pictures (negative and positive) showed a significant memory benefit compared to neutral pictures. Neither cardiac phase, nor its interaction with picture valence significantly accounted for variation in visual memory performance.

Supplementary results

Beyond our preregistered hypotheses, additional results were obtained by further exploratory analyses.

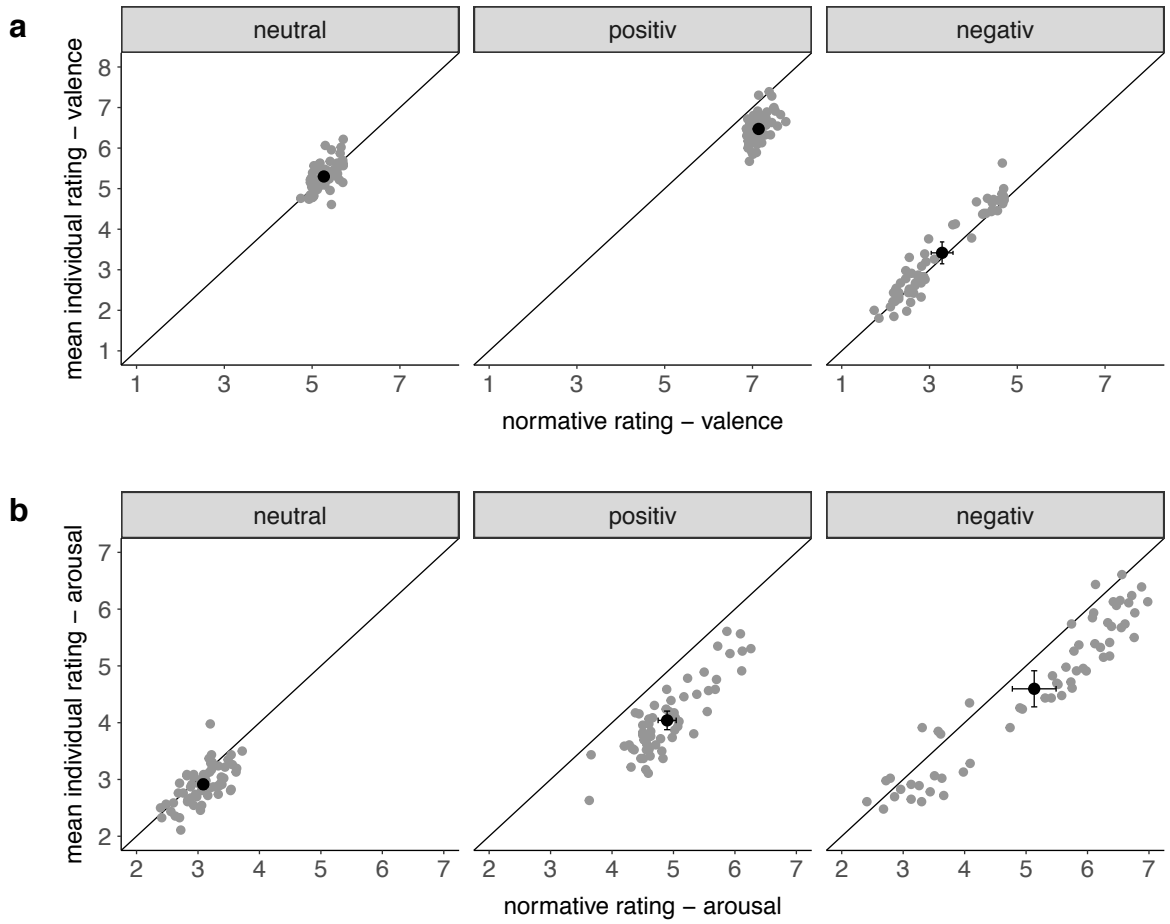
Recognition memory varies with resting heart rate variability. We investigated the role of inter-individual variables (i.e., interoceptive awareness, trait anxiety, resting heart rate variability) for memory performance with correlation analyses (cf. **Supplementary Methods**). Neither differences in interoceptive accuracy (r(39) = -.12, p = .46), nor in trait anxiety (r(41) = .039, p = .80) were associated with mean recognition performance (**Supplementary Fig. 1a, 1b**). However, there was a non-significant trend of resting heart rate variability (i.e., resting rMSSD) to be positively correlated with mean recognition performance (r(41) = .29, p = .056), that is, recognition memory increased with higher resting heart rate variability (**Supplementary Fig. 1c**).



Supplementary Figure 1. Correlation of mean recognition performance with ***a***, interoceptive awareness, ***b***, trait anxiety, and ***c***, heart rate variability (resting rMSSD). Grey areas are the 95% confidence intervals of the linear model (black line).

Subjective perception of picture emotionality. As a control, we analysed if the subjective valence and arousal ratings in our study differed from the EmoPicS normative ratings (**Supplementary Fig. 2**). For ratings of the two affective dimensions, valence and arousal, mixed-design ANOVAs tested the main and interaction effects of the repeated-measures factor rating category (normative, individual) and the factor picture valence (positive, neutral, negative). We observed a significant main effect of rating category for both, valence and arousal: Mean individual valence ratings (M = 5.06, SD = 1.43) were significantly lower (F(1,352) = 10.1, p = .002) than normative ratings (M = 5.23, SD = 1.69), as were mean individual arousal ratings (M = 3.85, SD = 1.09) compared to normative (M = 4.37, SD = 1.28) ratings (F(1,352) = 27.0, p < .001). However, while valence ratings did not show a significant interaction for rating category X picture valence (F(2,352) = 1.91, p = .15; see **Supplementary Fig. 2a**), the difference between individual and normative arousal ratings was influenced by picture valence (F(2,352) = 5.71, p = .004; see **Supplementary Fig. 2b**). To further examine this interaction, two-sided paired t-tests were calculated and p-values were adjusted

for multiple comparisons with Bonferroni correction: positive (individual: M=4.04, SD=0.65; normative: M=4.90, SD=0.58) arousal ratings differed significantly larger from each other (t(59) = 20.2, p = < .001, Cohen's d = 1.39) than both neutral (individual: M=2.91, SD=0.34; normative: M=3.09, SD=0.32) (t(59) = 4.77, p = < .001, Cohen's d = 0.52) and negative (individual: M=4.60, SD=1.26; normative: M=5.13, SD=1.41) arousal ratings (t(59) = 9.32, p = < .001, Cohen's d = 0.40). Furthermore, while normative arousal ratings did not differ significantly between positive and negative pictures (cf. **Methods**), individual arousal ratings were significantly higher for negative compared to positive pictures (t(88.3) = 3.05, p = .003, Cohen's d = 0.56).



Supplementary Figure 2. ***a,*** *Valence ratings* and ***b,*** *Arousal ratings* were both significantly lower for individual compared to normative ratings (overall mean in black with standard error bars). For arousal but not for valence ratings there was a significant interaction effect between rating category and picture valence.

Discussion

We studied the association between the cardiac cycle and self-paced visual sampling as well as visual recognition memory for pictures of different emotional valence. We hypothesized that facilitated visual processing (Pramme et al., 2016, 2015)—observed specifically for relevant or emotionally salient stimuli (Azevedo, Badoud, et al., 2017; Azevedo, Garfinkel, et al., 2017; Garfinkel et al., 2014)—as well as facilitated oculomotor processing during systole (Ohl et al., 2016) guides active perception in the shape of a preference to prompt a relevant visual stimulus during early phases of the cardiac cycle. We observed a significant accumulation of key presses (i.e., prompted picture onsets) during systole, thereby showing for the first time a coupling between self-paced visual sampling and the heartbeat. Memory performance, however, was only influenced by picture valence, replicating a significant memory benefit for emotional content (Hamann, 2001; Kensinger, 2006; Kensinger & Corkin, 2003; LaBar & Cabeza, 2006), but not further modulated by the cardiac phase in which targets were encoded (Garfinkel et al., 2013). The association between the cardiac cycle and self-initiated actions complements findings of facilitated visual processing during systole, thereby proposing a link between the heartbeat and active perception.

Sensorimotor processing of passively presented stimuli has been shown to be decreased during early cardiac phases (Birren et al., 1963; Callaway & Layne, 1964; Edwards et al., 2007; Lacey & Lacey, 1974; McIntyre et al., 2008; Saari & Pappas, 1976), but evidence is mixed, including some earlier null findings (Jennings & Wood, 1977; Salzman & Jaques, 1976; Thompson & Botwinick, 1970). However, which processing stages are modulated by the heartbeat has long remained unclear. More fine-graded decomposition of reaction time into central (sensory, pre-motor) and peripheral (motor) processes has indicated that the response inhibition during early cardiac phases was confined to central (pre-motor) levels of stimulus processing, whereas the motor component remained unaffected (Edwards et al., 2007; McIntyre et al., 2008; Saari & Pappas, 1976) or even accelerated (Schulz et al., 2009). This differential effect could also underlie findings that report an increased tendency to act during systole such as fire a virtual (Azevedo, Garfinkel, et al., 2017) or an actual weapon (Mets et al., 2007) during early cardiac phases. Our results of facilitated spontaneous actions during systole when engaging with a visual stimulus furthermore add to results from oculomotor behaviour: Ohl et al. (2016) reported involuntarily occurring oculomotor activity (i.e., microsaccade generation) to be heightened during early cardiac phases. Hence, for both somatomotor and oculomotor processes, our readiness to act upon an external stimulus fluctuates with our (internal) cardiac rhythm, being relatively increased during the phase of systolic blood ejection.

Although underlying heart-brain pathways remain unclear, systolic influences on perception and cognition have often been attributed to the phasic nature of cardio-afferent signalling, which is triggered with the heartbeat (Koriath & Lindholm, 1986; Lacey & Lacey, 1978). More specifically, stretch-responsive baroreceptors located in arterial walls respond to transient pressure rises at each blood ejection and communicate the current cardiovascular state (i.e., the heartbeat's strength and timing) to the brain. Thus, baroreceptor-transmitted cardiac signals, which are phasically registered by central processing systems, have been proposed to induce a general suppression of cortical excitability, converging with earlier findings of sensory inhibition (Dembrowsky & Seller, 1995; Rau & Elbert, 2001). Formulated in terms of the *interoceptive predictive coding* framework (Barrett & Simmons, 2015; Seth, 2013), which extends the *free-energy principle* (Friston, 2010) to interoceptive processes and connects them to consciousness and emotion, this periodic—and thus predictable—ascending baroreceptor input to central structures is anticipatorily cancelled out by top-down interoceptive predictions, thereby minimizing its influence on perception (Critchley & Garfinkel, 2018; Salomon et al., 2016). Besides modulating arterial baroreceptor discharge, heartbeat-related pressure fluctuations generate periodic sensory influences throughout the body—affecting for example the discharge of tactile (Macefield, 2003) or muscle spindle afferents (Birznieks, Boonstra, & Macefield, 2012)—which are predicted and normally do not enter perceptual awareness. In our constant attempt to minimize sensory uncertainty (Peters, McEwen, & Friston, 2017), inhibition of such predictable cardiac-induced sensory effects has been argued to reduce—potentially distracting—self-related sensory noise (Salomon et al., 2016) at the benefit of our processing of the outside world, for example by increasing the signal-to-noise ratio of external stimuli. Correspondingly, stimuli presented simultaneously with the heartbeat are interpreted as sensory consequences of the organism's own (internal) cardiac activity and thus perceptually attenuated (Salomon et al., 2016). Our finding that participants implicitly act upon a visual stimulus during the phase of heartbeat-related (baroreceptor-mediated) central inhibition could indicate a short-term benefit: As argued by Pramme et al. (2016), the impact of baroreceptor-mediated central influences may depend on context- or task-specific processing demands. In other words, extraction of behaviourally relevant external stimuli from a distracting sensory scene might be facilitated during inhibition of irrelevant (e.g., cardiac-related) sensory information (Pramme et al., 2016). Accordingly, predictable phases of attenuated heartbeat-related noise might provide a short-term window to facilitate active engagement towards an external relevant stimulus.

Such differential processing during transient cardiac signalling converges with the observed specificity of cardiac effects when using valenced stimuli, in particular selectively facilitated processing of threat stimuli during systole (Garfinkel & Critchley, 2016). The notion that

cardiac signals prioritise the processing of motivationally relevant information suggests a crucial role of cardiac interoceptive information in conveying bodily arousal states to the brain (Critchley & Garfinkel, 2018; Garfinkel & Critchley, 2016). In other studies, states of higher psychophysiological arousal have shown to bias the processing of relevant stimuli, including facilitated memory formation (Cahill & McGaugh, 1998; Mather et al., 2016; Mather & Sutherland, 2011; McGaugh, 2015). However, the pattern of results concerning memory modulation across the cardiac cycle remains fragmented and unclear. Although perceptual sensitivity for emotional stimuli is increased during systole (Garfinkel et al., 2014), affective (positive, negative) and neutral words are recalled less often when they are encoded during systole as compared to diastole (Garfinkel et al., 2013). Furthermore, this cardiac memory effect could only be obtained in subjects with lower interoceptive accuracy, suggesting influences of an individual's access to interoceptive sensations (Pollatos & Schandry, 2008). On the other hand, Fiacconi et al. (2016) found that fearful and neutral faces presented during systole are more likely to be judged as known or old, irrespective of whether they had been shown before or not. In our study, recognition memory was not influenced by the cardiac phase during which a stimulus was encoded—also adding to a recent study reporting a lack of cardiac influences on memory retrieval (Pfeifer et al., 2017)—but only by its valence, showing a significant benefit for negative and positive pictures. This suggests that—at least in our study—the influence of externally-induced emotional arousal states (e.g., by seeing an upsetting negative picture) on memory formation (Tambini et al., 2017) might have exceeded a transient cognitive modulation across the cardiac cycle (Garfinkel et al., 2013). Such reasoning is further supported by a recent study showing that interoceptive cardiac signals can easily be overshadowed by external stimuli or other task-specific influences (Yang, Jennings, & Friedman, 2017).

Our exploratory supplementary finding indicates that inter-individual differences in recognition memory are positively associated with inter-individual differences in resting heart rate variability. Considered a trait marker of autonomic or parasympathetic cardio-regulation and—more generally—of heart-brain coupling (Thayer et al., 2012), variation in beat-to-beat intervals at rest has been associated with cognitive capacities: participants with higher resting heart rate variability performed better in tests of working memory and attention (Hansen, Johnsen, & Thayer, 2003; Luft, Takase, & Darby, 2009). Future studies investigating cardiac influences on cognition could further examine the impact of inter-individual differences in resting heart rate variability.

Taken together, cardiac phase effects on perception, cognition, and behaviour might constitute a non-functional epiphenomenon emerging from transient physiological changes, which set the context for heart-brain interactions: As baroreceptor-transmitted afferent sig-

nals (Critchley & Harrison, 2013) occur with every systolic pressure wave and reflect momentary states of increased blood pressure, they constitute a fine-tuned reference of cardiovascular arousal. Although autonomously generated, cardiac fluctuations are integrated in multiple feedback loops to react to environmental challenges such as exercise, body position, or stress (Dampney et al., 2002; Glass, 2001; Saper, 2002). Cardiovascular arousal is thus directly encoded via frequency (e.g., increased heart rate) and waveform (e.g., increased amplitude in elevated blood pressure) (Dampney et al., 2002; Schächinger, Weinbacher, Kiss, Ritz, & Langewitz, 2001), which reciprocally affect afferent baroreceptor stimulation (Chapleau, Li, Meyrelles, Ma, & Abboud, 2001). Influences of the cardiovascular state on sensory processing might thus subtly emerge with heartbeat-related pressure fluctuations, but are only fully expressed under a sustained shift of our bodily state beyond physiological variability; for example, under stress, when the whole spectrum of adaptive brain-body responses is activated (e.g., elevated blood pressure and accelerated heart rate) and the afferent cardiac signalling increases. Correspondingly, Luft and Bhattacharya (2015) found that the representation of cardiac signals in the brain, as measured by EEG-derived heartbeat-evoked potentials, differs between states of high vs. low emotional arousal. Besides increased amplitudes in arterial blood pressure waves, it could be argued that a faster heartbeat during stressful situations—next to providing metabolic support for action requirements to re-stabilize our homeostatic integrity (Gianaros & Wager, 2015)—results in relatively increased systolic signalling (as raises in heart rate occur mainly at the expense of diastole length) and thereby generates more time windows of selectively facilitated sensory processing. Evidence for this proposal comes from a recent study that associated experimentally increased heart rates (Pezzulo et al., 2018) with prioritized fear processing across different measures (reaction time, peak velocity, response acceleration, choice uncertainty). Hence, increased signalling of cardiovascular states under conditions of higher bodily arousal and heart rates might more strongly modulate cognition and behaviour (e.g., active perception and self-paced action), thereby supporting what information is preferentially processed.

Our experiment has several limitations: While linking active perception and the cardiac cycle, our design does not allow to decompose cardiac influences at the levels of somatomotor, sensory, and cognitive processing. A control condition to dissociate cardiac-related motor activity from visual processing could rule out a pure motor effect, for example by testing spontaneous motor actions that are not explicitly coupled to perception of (relevant) stimuli. The hypothesis would be that button presses that do not prompt relevant sensory input would be randomly (i.e., uniformly) distributed across the cardiac cycle. An essential step to investigate the role of cardiac activity as bodily reference would be to test cardiac coupling of stimulus processing under conditions of altered cardiac activity (e.g., increased heart rate),

for example by inducing stress through increased sensory uncertainty (e.g., by manipulating stimulus predictability). In addition, measurements of cardiac representations in the brain (e.g., using EEG) would extend our understanding of the central integration and modulation of cardiac signals, for example, in the context of self-paced visual sampling and visual memory processing.

In conclusion, our findings imply that the heartbeat constitutes a crucial bodily signal that is integrated in our active engagement with the external world. Specifically, they suggest that we tend to act in a phase of inhibited cardiac- and thus self-related sensory processing (namely cardiac systole) when extracting relevant information from our environment. Subtly emerging under normal conditions, this influence might become functionally relevant in states of high arousal (e.g., in stressful situations). Extending previous frameworks of mind-brain-body interactions (Park & Tallon-Baudry, 2014), we propose that we implicitly exploit internal ongoing bodily fluctuations as a predictable reference frame from which interaction with our ever-changing and often unpredictable environment can arise. When initiating actions to sample the noisy world around us, we relate them to the rhythm we know best—our own heartbeat.

Methods

Preregistration. The protocol and the hypotheses of our study were pre-registered prior to the data acquisition using the Open Science Framework (https://osf.io/5z8rx/).

Participants. 47 (23 female) healthy, young, right-handed subjects (age: 18 – 34 years, M = 25.8 years, SD = 4.31) with normal or corrected-to-normal vision participated in this study. Four subjects were excluded due to deviant cardiovascular parameters: two subjects with tachycardic mean resting heart rates (> 100 bpm), one subject with hypertonic blood pressure (171/89 mmHg), one subject with numerous ventricular extrasystoles during the experimental period (> 10 per minute). The sample size was based on previous cardiac cycle studies (mainly Fiacconi et al., 2016): We aimed for a net sample size of 40 to enter the analyses (cf. https://osf.io/5z8rx/) expecting 10% participant exclusions. Participants were recruited through the ORSEE-based (Greiner, 2015) participant database of the Berlin School of Mind and Brain and received a monetary compensation of 9 €/h for their participation. All participants were naïve regarding the purpose of the study and signed informed consent before participation. The study followed the Declaration of Helsinki and was approved by the Ethics Committee of the Department of Psychology at the Humboldt-Universität zu Berlin.

Setup and experimental task. (cf. **Fig. 2a**) Participants were seated in a dimly lit room in front of a gamma-linearized 19-inch Cathode ray tube (CRT) monitor (Samsung Syncmaster 959NF, Suwong, Korea) with a refresh rate of 100 Hz and a spatial resolution of 1280x1024 pixels. Their head was positioned on a chin rest at a distance of 50 cm from the screen. The participants' task comprised two parts: During the *encoding* period, participants were asked to click through a picture set (800x600 pixels) in self-paced speed and to memorize the pictures for a subsequent memory test. By button press, they prompted the immediate onset of the next picture, which appeared for 100 ms. In between self-chosen key presses (i.e. picture onsets), a central fixation cross was presented. After a break of five minutes, they completed the *recognition* period, during which they indicated for each picture whether or not they had seen it before. Here, pictures were passively presented for 100 ms, followed by a centrally presented fixation cross until participants entered their recognition response ("old", "new") via key press.

Stimuli. The picture set consisted of 180 coloured photographs (60 pictures with positive, 60 with negative, and 60 with neutral content) of humans in various life situations, selected from a collection of standardized and validated affective picture material (EmoPicS, Wessa et al., 2010). In addition to physical image statistics (i.e., luminance, contrast, RGB values, visual

complexity; cf. Wessa et al., 2010), two independent observers matched the three sets for (1) number of people shown, (2) number of images with social interactions, (3) number of images with close-ups, and (4) number of images showing eye contact with the observer. Notably, positive and negative images were matched for (normative) arousal ratings and did not significantly differ ($t(78.6) = 1.20$, $p = .23$, Cohen's $d = 0.22$). Stimuli were displayed using MATLAB version 7.8.0.347 (The MathWorks Inc., Natick, MA, USA) with the Psychophysics Toolbox 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

For each participant, stimuli were randomly selected and presented in randomized order: For encoding, a subset of 120 pictures with 40 pictures of each picture valence (positive, neutral, negative) was sampled from the whole set of 180. The second picture set, shown during the recognition period, consisted of the 60 yet unused pictures (20 per picture valence)—serving as distractors—as well as 60 memory probes (20 per picture valence) that were sampled from the encoded picture set.

ECG recording. ECG was recorded at 2048 Hz using an ActiveTwo AD amplifier (Biosemi, Amsterdam, Netherlands). Three electrodes were attached according to an adapted limb lead configuration at the right and left lower coastal arch as well as the left medial ankle. Participants were told that the ECG is to measure their general bodily state without mentioning details regarding the experimental conditions (cf. Fiacconi et al., 2016). The ECG lead most clearly displaying the onset of ventricular depolarisation (lead II) was used for analysis.

Additional measures of inter-individual differences. Previous studies suggest that the influence of cardiac signals on perception and behaviour varies with interoceptive accuracy, that is, the ability to consciously perceive signals originating in the body (Dunn et al., 2010; Garfinkel et al., 2013). We determined inter-individual differences in interoceptive accuracy with a heartbeat perception task (Schandry, 1981), in which participants were asked to estimate the number of their heartbeats in five intervals of different length (25, 45, 15, 55, and 35 s). As inter-individual differences in anxiety have been proposed to moderate the behavioural effect of autonomic signalling (Garfinkel et al., 2014; Pollatos, Schandry, Auer, & Kaufmann, 2007), we also acquired participants' trait anxiety using the State-Trait Anxiety Inventory (STAI-T; Laux et al., 1981; Spielberger et al., 1983). Resting heart rate variability (HRV) measures inter-individual differences in brain-heart interaction and particularly in parasympathetic cardioregulation (Task Force, 1996). HRV can be quantified through changes in the beat-to-beat intervals of the ECG (Task Force, 1996). We calculated the root mean square of successive differences (rMSSD) during the 7-minute baseline ECG.

Procedure. Upon arrival in the lab, participants were equipped with the ECG. Comfortably seated, they were asked to relax for seven minutes and breathe normally. Then, blood pressure was measured (twice, if elevated) using a standard sphygmomanometer (OMRON M8 Comfort). After a brief training session to familiarize participants with the task, they performed the two experimental periods (i.e., encoding and recognition). During a 5-minute break between the two parts, participants completed the Trait Anxiety Inventory (STAI-T; Laux et al., 1981; Spielberger et al., 1983). To assess subjective perception in our sample and compare it to the EmoPicS' normative ratings, all 180 photos were rated after the recognition period similarly to the original EmoPicS normative ratings (Wessa et al., 2010): "How do you feel looking at the picture?" was answered for valence (1: sad – 9: happy) and arousal (1: calm – 9: excited) on a 9-level Likert-type scale. For each trial, both rating scales were displayed successively, one above and one below each picture, followed by a 500-ms fixation cross (between trials). Finally, subjects performed the heartbeat perception task (Schandry, 1981) that was presented acoustically.

Data analysis. The timing of behavioural responses was analysed relative to the heartbeats: electrical events indicating the beginning of each cardiac cycle (R peaks) were extracted from the ECG signal with Kubios 2.2 (Tarvainen et al., 2014, http://kubios.uef.fi/). Two complementary analytic approaches—circular and binary analysis—were performed to exploit the oscillatory (repeating cycle of cardiac events) as well as the phasic (two distinct cardiac phases: systole and diastole) nature of cardiac activity, respectively. The code of our analysis, computed in the R Statistical Environment with RStudio version 1.0.136 (RStudio Team, 2016) is available on GitHub (https://github.com/SKunzendorf/0303_INCASI). Graphics were obtained with the circular package (Agostinelli & Lund, 2013) and the ggplot2 package (Wickham, 2009).

Encoding period—cardiac modulation of self-paced visual sampling.

Circular analysis: For the circular analysis, we computed the relative onset of each key press (prompting picture onset) within the cardiac cycle, which was indicated in the ECG as the interval between the previous and the following R peak (**Fig. 2b**). According to its relative timing within this R-R interval, radian values between 0 and 2π were assigned to each stimulus (Ohl et al., 2016; Pikovsky, Rosenblum, & Kurths, 2003; Schäfer, Rosenblum, Kurths, & Abel, 1998). For each participant, we computed the mean of the circular distribution for the 120 picture onsets. In a second step, a mean vector of all participants was computed via vector addition of individual means divided by their number, showing the average self-paced picture onset in the cardiac cycle across the group, and weighted by its length (mean result-

ant length ϱ) to reflect the spread of individual means around the circle. As a measure of concentration of circular data, ϱ was integrated in a subsequent Rayleigh test for uniformity (Pewsey, Neuhäuser, & Ruxton, 2013): if ϱ gets sufficiently high to exceed a threshold value (i.e., the set of individual means is not spread evenly across the cardiac cycle), the data can be interpreted as too locally clustered to be consistent with a uniform distribution that served as null hypothesis (Pewsey et al., 2013). The code for individual and group-level circular analysis can be found on GitHub (https://github.com/SKunzendorf/0303_INCASI). Confidence intervals and significance were non-parametrically calculated through bootstrapping based on analyses from a previous study (Ohl et al., 2016): From the original pool of 43 participants, we drew a random bootstrap sample of 43 participants with replacement. For each participant in the bootstrap sample, we first computed a circular density (bandwidth = 20) of picture onsets, and then computed the mean circular density across the 43 participants in the bootstrap sample. Confidence intervals (95%) were determined as 2.5% and 97.5% percentiles from the distribution of mean circular densities obtained by repeating the bootstrap procedure 10000 times. Deviation from the circular uniform was considered as significant when the 95% confidence interval determined by the bootstrapping is outside the circular density of a uniform distribution.

Binary analysis: To account for the phasic nature of cardiac activity and to increase comparability to previous cardiac cycle studies, we segmented the cardiac cycle into systole and diastole (**Fig. 2b**). It needs to be noted that systolic phases vary inversely with heart rate (Fridericia, 1920; R. P. Lewis, Rittogers, Froester, & Boudoulas, 1977; Lombard & Cope, 1926; Wallace, Mitchell, Skinner, & Sarnoff, 1963; Weissler, Harris, & Schoenfield, 1968): Although the absolute length of systole decreases with a faster heartbeat, its proportionate share of the entire cardiac cycle increases. Such between-subject variation of cardiac phase lengths that arises from differences in heart rate supports the need for more elaborated analytical approaches in cardiac cycle studies. Thus, we did not use absolute systole and diastole lengths (e.g., defining systole as the 300 ms following an R peak) but computed participant-specific phases based on cardio-mechanical events related to the ECG (for detailed binning procedure cf. **Supplementary Methods**). This enabled us to extract the phase of systolic blood-ejection for each participant. In the following, we will use the term “systole” to refer to this ejection-phase. The (self-paced) picture onsets were then assigned to the respective cardiac phase (i.e., individual systole or diastole). To take into account between-subject differences in heart rate (and thus cardiac phase lengths), the sum of picture onsets per phase (as ratio of all 120 trials) was normalized to the proportion of the subject-specific phase length in the total cardiac cycle, resulting in a value of (picture onsets per cardiac phase / 120) / (individual cardiac phase length / individual mean R-R length) for each cardiac

phase. With no cardiac effect, button presses (triggering picture onsets) would be randomly distributed across both cardiac phases. That is, the rate of systolic (diastolic) picture onsets should correspond to the proportion of systole (diastole) in the total R-R length, thereby resulting in a ratio of 1. A ratio >1 thus reflects an over-proportional accumulation of picture onsets in the respective cardiac phase. In the group-level analysis, normalized systolic and diastolic ratios were tested against each other with a two-sided paired t-test.

Recognition period—cardiac modulation of recognition memory.

Circular analysis: To relate memory performance in the recognition period and stimulus onset in the encoding period, we analysed—for each participant—the stimulus subset of memory probes (i.e., pictures in the recognition period that had already been shown during the encoding phase) with respect to their cardiac onset during encoding. Parallel to the circular analysis regarding visual sampling during encoding (see above), we computed the self-paced onset of memory probes during encoding across the participant's cardiac cycle (**Fig. 2b**). To correct for a possible bias due to self-paced memory probe distributions, three subjects with non-uniform circular distributions of memory probes (indicated by significant Rayleigh tests) were excluded from further analysis. At the group level, we then analysed circular distributions of onset times for memory probes that were correctly remembered (hits) or erroneously identified as new pictures (miss). To that aim, sets of individual mean onsets for hits and misses were tested against the circular uniform distribution using Rayleigh tests.

Binary analysis: The hypothesized association between cardiac phase and memory performance was further analysed by determining the stimulus' phasic timing during encoding, that is, whether it had been presented in individual systole or diastole (for detailed binning procedure cf. **Supplementary Methods**), relative to its recognition performance. To predict the binary recognition outcome (miss = 0, hit = 1), we computed linear mixed regression models (LMM) for binomial data, with subjects as random factor. The first model (m0) was fitted for the overall fixed effect of valence, with the three picture valence levels (positive, negative, neutral) contrast-coded against neutral picture valence as baseline condition. The second model (m1) included picture valence (negative-neutral, positive-neutral), cardiac phase (diastole = 0, systole = 1), and their interaction as fixed effects. NB: For m1, the data included only pictures encoded in individual systole or diastole (i.e., pictures encoded in non-defined cardiac intervals were excluded from analysis). For the regression analysis, we used the lme4 package (Bates, Mächler, Bolker, & Walker, 2015) in the R Statistical Environment.

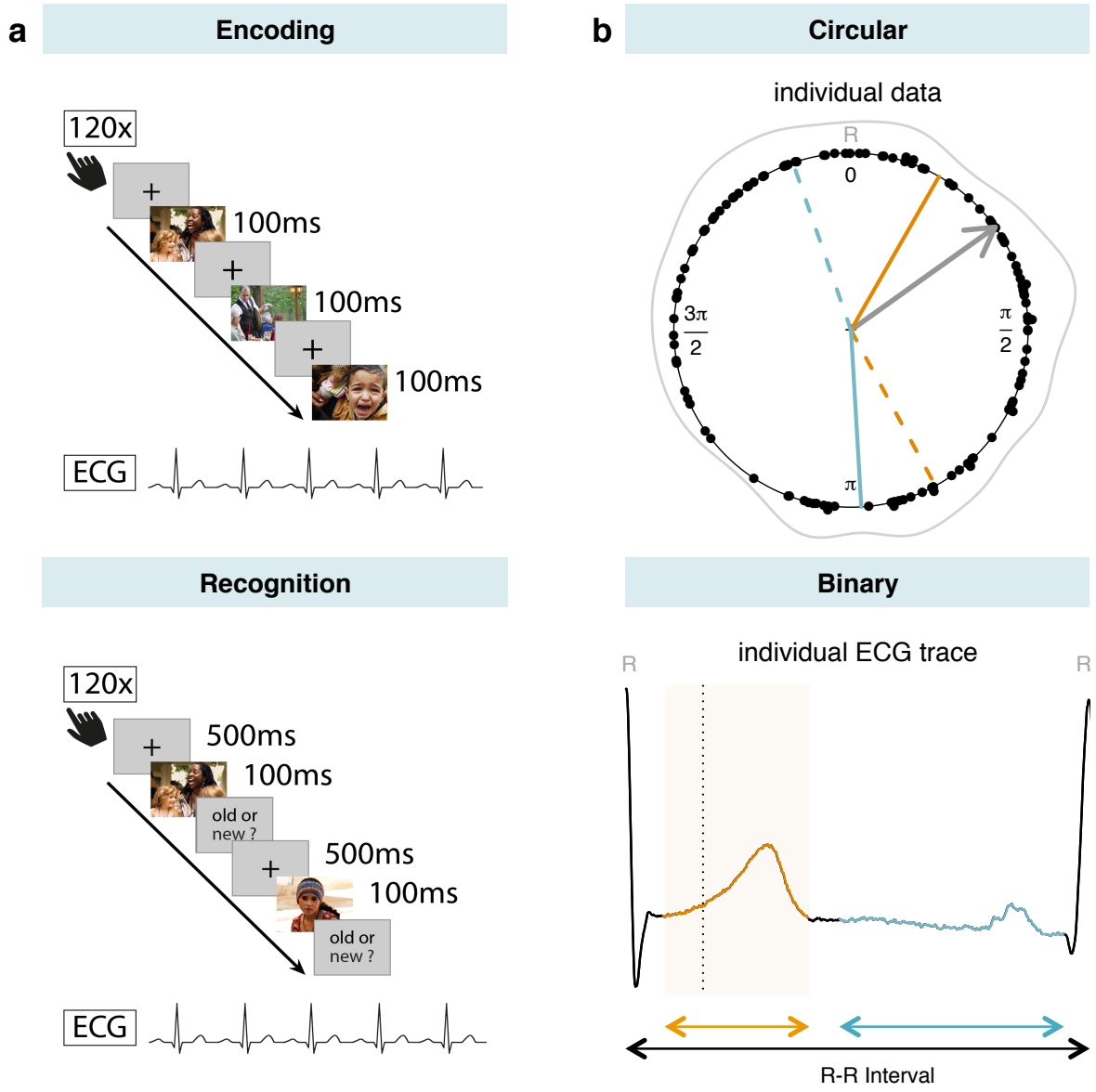


Figure 2. ***a,*** *Experimental setup*. During encoding (top), participants prompted by button press the onset of the next picture, which could be positive, neutral, or negative. In the recognition period (bottom), they indicated for each picture (60 old, 60 new) whether or not they had seen it before. Simultaneous ECG was recorded to analyse behaviour relative to the cardiac cycle: **b,** *Data analysis.* For circular analysis (top)**,** values between 0 and 2π were assigned to each stimulus onset (black dots), corresponding to its appearance within the cardiac cycle (from the previous to the next R peak in the ECG). Mean (grey arrow) and circular density (grey line) of stimulus onsets were calculated per subject. Individual cardiac phases from the binary analysis (see below) are visualised as circular segments (start: solid, end: dashed): systole (orange) and diastole (blue). For binary analysis (bottom), stimulus onsets (dashed line) were binned into participant-specific systole (orange) and diastole (blue) using a template approach (cf. Supplementary Methods).

Supplementary Methods.

Detection of individual cardiac phases. Subject-specific systole and diastole lengths were computed based on cardio-mechanical events that could be related to the ECG trace. Although mechanical systole cannot be automatically derived from the duration of electrical systole (Fridericia, 1920), both are closely linked under normal conditions (Boudoulas, Geleris, Lewis, & Rittgers, 1981; Coblentz, Harvey, Ferrer, Cournand, & Richards, 1949; Fozzard, 1977; Fridericia, 1920; Gill & Hoffmann, 2010; T. Lewis, 1925; Wiggers, 1921, 1923). That is, systolic contraction of the ventricles is preceded by their depolarisation (indicated in the ECG by the QRS complex), while aortic valve closure, marking the end of systolic blood outflow, coincides with ventricular repolarisation, around the end of the t-wave (Gill & Hoffmann, 2010). The total ventricular systolic phase (cf. **Supplementary Fig. 3a**) was defined as the time difference between q-wave onset and the t-wave end (QT). For each cardiac cycle, the systolic ejection period was extracted by removing the pre-ejection period (PEP) using regression equations (Weissler et al., 1968, see below) that were formerly used in clinical cardiology as a "non-invasive" technique to determine systolic time intervals (R. P. Lewis et al., 1977). Thus, we could more precisely disentangle systolic phases of isovolumetric contraction (no blood outflow, PEP), and ejection phase (blood outflow into the aorta and pulmonary artery, EP). To prevent an overlap of systole and diastole, a window of 50 ms was inserted between both segments. Diastole was defined as the remaining part within the R-R interval (R-R – QT – 50 ms).

T-wave end detection followed a two-step procedure: First, a t-wave template was computed for every participant by averaging 1000 ECG trace snippets from the experimental period, which encompassed a—physiologically plausible—time interval to contain the t-wave: up to 390 ms following each R peak. Subsequently, the Trapez area algorithm (Vázquez-Seisdedos et al., 2011) was applied to compute the t-wave end in each subject-specific template: Having located the t-peak as local maximum within the template, the algorithm computes a series of trapezes along the descending part of the t-wave signal, defining the t-wave end as the point where the trapezium's area gets maximal.

Q-wave onsets (or, if not clearly discernable, R-peak onsets), demarcating the onset of ventricular systole, served as a starting point for the regression equations (Weissler et al., 1968). Similarly computed within an averaged template, they were determined as the first prominent negative deflection from baseline (or, if replaced by R-peak onset, the first dominant upward deflection), preceding the R-peak in the ECG trace (Sherwood et al., 1990). Thereby, a template-based systole length (QT) was obtained for each participant.

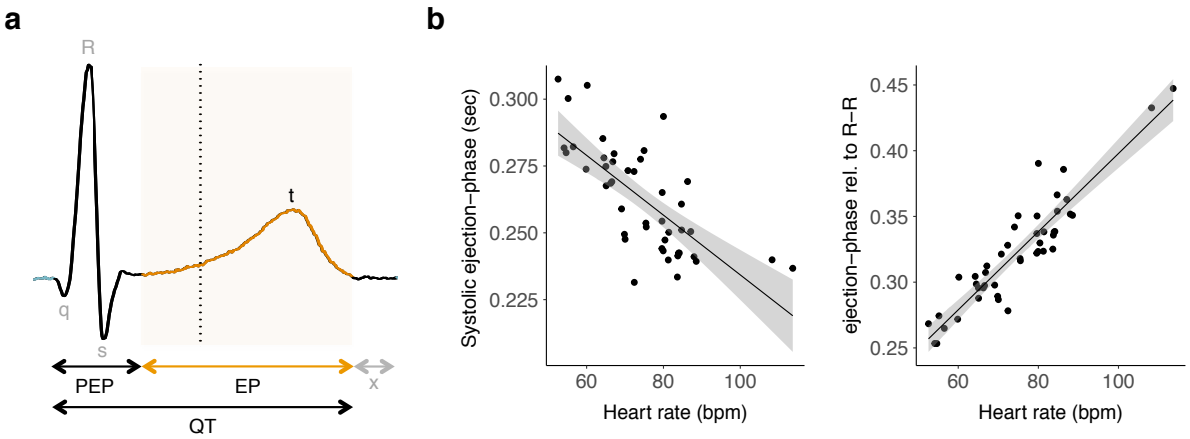
To extract PEP intervals from participants' total systole length (QT), a regression equation was applied to each cardiac cycle, which relates the duration of PEP to the partici-

pant's mean heart rate (HR), and is corrected for slight differences between male (M) and female (F) (PEP (M) = -0.4 HR + 131, PEP (F) = -0.4 HR+ 133) (Weissler et al., 1968). The PEP was then subtracted from the whole QT-Interval, which determined the EP within each cardiac cycle. We visually checked the fit of individual cardiac intervals, visualizing them on the actual ECG trace (in the encoding period) of each subject (cf. **Supplementary Fig. 3a)**. The code for detection of individual cardiac intervals (in R) is available on GitHub (https://github.com/SKunzendorf/0303_INCASI).

Inter-individual variation of cardiac intervals. To illustrate the heart rate-dependent variation of cardiac intervals, the two tachycardic subjects were included in this control analysis (sample size: N = 45, including 21 female; age: 18 – 34 years, M = 25.9 years, SD = 4.38). Mean heart rates varied from 52.6 to 113.7 bpm (M = 74.7, SD = 12.9), with mean R-R intervals ranging from 0.53 s to 1.15 s (M = 0.83, SD = 0.14).

Visualization of subject-specific systolic templates within their individual ECG trace indicated that under the present experimental conditions, within-subject systole lengths stay rather constant. However, between subjects, systolic intervals do differ together with differences in mean individual heart rates.

In line with earlier research (Boudoulas et al., 1981; R. P. Lewis et al., 1977; Lombard & Cope, 1926; Wallace et al., 1963; Weissler, Harris, & Schoenfeld, 1969; Weissler et al., 1968), we observed an inverse correlation of EP length and mean individual heart rate (Pearson's $r(43) = -.72$, $p < .001$), confirming that heart rate is an important determinant of EP. As shown in **Supplementary Fig. 3b left**, absolute EP duration decreased with higher resting heart rates, ranging from 0.23 s to 0.31 s (M = 0.26, SD = 0.020), with a total systolic QT interval between 0.32 s and 0.42 s (M = 0.36, SD = 0.024). However, the proportion of EP relative to the whole cardiac cycle (from one R peak to the next) increased with rising mean heart rate (Pearson's $r(43) = .92$, $p < .001$), comprising between 0.25 up to 0.45 (M = 0.33, SD = 0.042) of the total mean R-R interval (**Supplementary Fig. 3b right**). This non-proportional shrinking of systolic intervals at higher heart rates underpins the crucial physiological role of systole within the cardiac cycle: Cardiac cycle lengths shorten mainly at cost of diastole to ensure sufficient blood ejection at higher heart rates.



Supplementary Figure 3. ***a,*** The total systolic interval (onset q-wave until t-wave end, QT) was divided into pre-ejection period (PEP) and ejection phase (EP). To prevent an overlap of systole and diastole, a window of 50 ms was inserted after t-wave end (indicated by an "x"). Diastole was defined as the remaining part within the R-R interval (R-R – QT – 50 ms). ***b*, left:** Between subjects, the absolute duration of systolic EP decreased with increasing mean heart rate (Pearson's r (43) = -0.72, p <.001) while **right:** the systolic proportion within the total cardiac cycle (R-R interval) increased (Pearson's r (43) = 0.92, p < .001). That is, cardiac phase lengths shrink disproportionally with faster heartbeats. Grey areas represent the 95% confidence intervals.

Supplementary analysis of recognition memory and inter-individual differences. In an additional analysis, participants' overall mean recognition performance (i.e., the percentage of correctly recognised pictures) was correlated with variables of inter-individual differences: Interoceptive accuracy (centred via z-transformation), trait anxiety (centred via z-transformation), and resting heart rate variability/ rMSSD (log-transformed to mitigate skewedness and centred to the mean). For measures of interoceptive accuracy, two participants with lacking information in the heartbeat perception task were excluded from the analysis (n = 41).

References.

Agostinelli, C., & Lund, U. (2013). R package “circular”: Circular Statistics (version 0.4-7). CA: Department of Environmental Sciences, Informatics and Statistics, Ca’ Foscari University, Venice, Italy. UL: Department of Statistics, California Polytechnic State University, San Luis Obispo, California, USA. Retrieved from https://r-forge.r-project.org/projects/circular/

Azevedo, R. T., Badoud, D., & Tsakiris, M. (2017). Afferent cardiac signals modulate attentional engagement to low spatial frequency fearful faces. *Cortex*, (July), 1–9. https://doi.org/https://doi.org/10.1016/j.cortex.2017.06.016

Azevedo, R. T., Garfinkel, S. N., Critchley, H. D., & Tsakiris, M. (2017). Cardiac afferent activity modulates the expression of racial stereotypes. *Nature Communications*, *8*, 13854. https://doi.org/10.1038/ncomms13854

Barrett, L. F., & Simmons, W. K. (2015). Interoceptive predictions in the brain. *Nature Reviews Neuroscience*, *16*(7), 419. https://doi.org/10.1038/nrn3950

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Benedetto, A., Spinelli, D., & Morrone, M. C. (2016). Rhythmic modulation of visual contrast discrimination triggered by action. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1831), 20160692. https://doi.org/10.1098/rspb.2016.0692

Birren, J. E., Cardon, P. V, & Phillips, S. L. (1963). Reaction Time as a Function of the Cardiac Cycle in Young Adults. *Science*, *140*(3563), 195–196. Retrieved from http://science.sciencemag.org/content/140/3563/195.2.abstract

Birznieks, I., Boonstra, T. W., & Macefield, V. G. (2012). Modulation of human muscle spindle discharge by arterial pulsations - functional effects and consequences. *PLoS ONE*, *7*(4), e35091. https://doi.org/10.1371/journal.pone.0035091

Boudoulas, H., Geleris, P., Lewis, R. P., & Rittgers, S. E. (1981). Linear relationship between electrical systole, mechanical systole, and heart rate. *Chest*, *80*(5), 613–617. https://doi.org/10.1378/chest.80.5.613

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10.1163/156856897X00357

Cahill, L., & McGaugh, J. L. (1998). Mechanisms of emotional arousal and lasting declarative memory. *Trends in Neurosciences*, *21*(7), 294–299. https://doi.org/10.1016/S0166-2236(97)01214-9

Callaway, E., & Layne, R. S. (1964). Interaction between the visual evoked response and two spontaneous biological rhythms: the EEG alpha cycle and the cardiac arousal cycle. *Annals of the New York Academy of Sciences*, *112*(1), 421–431. https://doi.org/10.1111/j.1749-6632.1964.tb26762.x

Chapleau, M. W., Li, Z., Meyrelles, S. S., Ma, X., & Abboud, F. M. (2001). Mechanisms determining sensitivity of baroreceptor afferents in health and disease. *Annals of the New York Academy of Sciences*, *940*(1), 1–19. https://doi.org/10.1111/j.1749-6632.2001.tb03662.x

Coblentz, B., Harvey, R. M., Ferrer, M. I., Cournand, A., & Richards, D. W. (1949). the Relationship Between Electrical and Mechanical Events in the Cardiac Cycle of Man. *British Heart Journal*, *11*(1), 1–22. https://doi.org/10.1136/hrt.11.1.1

Craig, A. D. B. (2002). How do you feel? Interoception: the sense of the physiological condition of the body. *Nature Reviews Neuroscience*, *3*(8), 655–666. https://doi.org/10.1038/nrn894

Critchley, H. D., & Garfinkel, S. N. (2018). The influence of physiological signals on cognition. *Current Opinion in Behavioral Sciences*, *19*, 13–18. https://doi.org/10.1016/j.cobeha.2017.08.014

Critchley, H. D., & Harrison, N. A. (2013). Visceral Influences on Brain and Behavior. *Neuron*, *77*(4), 624–638. https://doi.org/10.1016/j.neuron.2013.02.008

Dampney, R. A. L., Coleman, M. J., Fontes, M. A. P., Hirooka, Y., Horiuchi, J., Li, Y.-W. W., … Tagawa, T. (2002). Central mechanisms underlying short- and long-term regulation of the cardiovascular system. *Clinical and Experimental Pharmacology & Physiology*, *29*(4), 261–268. https://doi.org/10.1046/j.1440-1681.2002.03640.x

Dembrowsky, K., & Seller, H. (1995). Arterial baroreceptor reflexes. In *Vaitl D. & Schandry R. (Eds.): From the heart to the brain: The psychophysiology of circulation-brain interaction* (pp. 35–60). Europäischer Verlag der Wissenschaften Frankfurt aM.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837. https://doi.org/10.1016/0042-6989(95)00294-4

Dunn, B. D., Galton, H. C., Morgan, R., Evans, D., Oliver, C., Meyer, M., … Dalgleish, T. (2010). Listening to your heart: How interoception shapes emotion experience and intuitive decision making. *Psychological Science*, *21*(12), 1835–1844. https://doi.org/10.1177/0956797610389191

Edwards, L., Ring, C., McIntyre, D., Carroll, D., & Martin, U. (2007). Psychomotor speed in hypertension: Effects of reaction time components, stimulus modality, and phase of the cardiac cycle. *Psychophysiology*, *44*(3), 459–468. https://doi.org/10.1111/j.1469-8986.2007.00521.x

Fan, J., Xu, P., Van Dam, N. T., Eilam-Stock, T., Gu, X., Luo, Y. J., & Hof, P. R. (2012). Spontaneous brain activity relates to autonomic arousal. *Journal of Neuroscience*, *32*(33), 11176–11186. https://doi.org/10.1523/JNEUROSCI.1172-12.2012

Fiacconi, C. M., Peter, E. L., Owais, S., & Köhler, S. (2016). Knowing by heart: Visceral feedback shapes recognition memory judgments. *Journal of Experimental Psychology*, *145*(5), 559–572. https://doi.org/10.1037/xge0000164

Fozzard, H. A. (1977). Heart: excitation-contraction coupling. *Annual Review of Physiology*, *39*(1), 201–220. https://doi.org/10.1146/annurev.ph.39.030177.001221

Fridericia, L. S. (1920). Die Systolendauer im Elektrokardiogramm bei normalen Menschen und bei Herzkranken. *Journal of Internal Medicine*, *53*(1), 469–486. https://doi.org/10.1111/j.0954-6820.1920.tb18266.x

Friston, K. (2010). The free-energy principle: A unified brain theory? *Nature Reviews Neuroscience*, *11*(2), 127–138. https://doi.org/10.1038/nrn2787

Garfinkel, S. N., Barrett, A. B., Minati, L., Dolan, R. J., Seth, A. K., & Critchley, H. D. (2013). What the heart forgets: Cardiac timing influences memory for words and is modulated by metacognition and interoceptive sensitivity. *Psychophysiology*, *50*(6), 505–512. https://doi.org/10.1111/psyp.12039

Garfinkel, S. N., & Critchley, H. D. (2016). Threat and the Body: How the Heart Supports Fear Processing. *Trends in Cognitive Sciences*, *20*(1), 34–46.

https://doi.org/10.1016/j.tics.2015.10.005

Garfinkel, S. N., Minati, L., Gray, M. A., Seth, A. K., Dolan, R. J., & Critchley, H. D. (2014). Fear from the Heart: Sensitivity to Fear Stimuli Depends on Individual Heartbeats. *Journal of Neuroscience*, *34*(19), 6573–6582. https://doi.org/10.1523/JNEUROSCI.3507-13.2014

Gianaros, P. J., & Wager, T. D. (2015). Brain-Body Pathways Linking Psychological Stress and Physical Health. *Current Directions in Psychological Science*, *24*(4), 313–321. https://doi.org/10.1177/0963721415581476

Gill, H., & Hoffmann, A. (2010). The timing of onset of mechanical systole and diastole in reference to the QRS-T complex: A study to determine performance criteria for a non-invasive diastolic timed vibration massage system in treatment of potentially unstable cardiac disorders. *Cardiovascular Engineering*, *10*(4), 235–245. https://doi.org/10.1007/s10558-010-9108-x

Glass, L. (2001). Synchronization and rhythmic processes in physiology. *Nature*, *410*(6825), 277–284. https://doi.org/10.1038/35065745

Greiner, B. (2015). Subject pool recruitment procedures: organizing experiments with ORSEE. *Journal of the Economic Science Association*, *1*(1), 114–125. https://doi.org/10.1007/s40881-015-0004-4

Hamann, S. (2001). Cognitive and neural mechanisms of emotional memory. *Trends in Cognitive Sciences*, *5*(9), 394–400. https://doi.org/10.1016/S1364-6613(00)01707-1

Hanning, N. M., Jonikaitis, D., Deubel, H., & Szinte, M. (2016). Oculomotor selection underlies feature retention in visual working memory. *Journal of Neurophysiology*, *115*(2), 1071–1076. https://doi.org/10.1152/jn.00927.2015

Hansen, A. L., Johnsen, B. H., & Thayer, J. F. (2003). Vagal influence on working memory and attention. *International Journal of Psychophysiology*, *48*(3), 263–274. https://doi.org/10.1016/S0167-8760(03)00073-4

Hogendoorn, H. (2016). Voluntary Saccadic Eye Movements Ride the Attentional Rhythm. *Journal of Cognitive Neuroscience*, *28*(10), 1625–1635. https://doi.org/10.1162/jocn_a_00986

Jennings, J. R., & Wood, C. C. (1977). Cardiac Cycle Time Effects on Performance, Phasic Cardiac Responses, and Their Intercorrelation in Choice Reaction Time. *Psychophysiology*, *14*(3), 297–307. https://doi.org/10.1111/j.1469-8986.1977.tb01179.x

Kensinger, E. A. (2006). Amygdala Activity Is Associated with the Successful Encoding of Item, But Not Source, Information for Positive and Negative Stimuli. *Journal of Neuroscience*, *26*(9), 2564–2570. https://doi.org/10.1523/JNEUROSCI.5241-05.2006

Kensinger, E. A., & Corkin, S. (2003). Memory enhancement for emotional words: Are emotional words more vividly remembered than neutral words? *Memory & Cognition*, *31*(8), 1169–1180. https://doi.org/10.3758/BF03195800

Kleckner, I. R., Zhang, J., Touroutoglou, A., Chanes, L., Xia, C., Simmons, W. K., … Feldman Barrett, L. (2017). Evidence for a large-scale brain system supporting allostasis and interoception in humans. *Nature Human Behaviour*, *1*(5), 69. https://doi.org/10.1038/s41562-017-0069

Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in Psychtoolbox-3? *Perception*, *36*(14), 1–16. https://doi.org/10.1068/v070821

Koriath, J. J., & Lindholm, E. (1986). Cardiac-related cortical inhibition during a fixed foreperiod reaction time task. *International Journal of Psychophysiology*, *4*(3), 183–195. https://doi.org/10.1016/0167-8760(86)90014-0

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, *35*(13), 1897–1916. https://doi.org/10.1016/0042-6989(94)00279-U

LaBar, K. S., & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nature Reviews Neuroscience*, *7*(1), 54–64. https://doi.org/10.1038/nrn1825

Lacey, B. C., & Lacey, J. I. (1974). Studies of heart rate and other bodily processes in sensorimotor behavior. In *In P. A. Obrist, A. H. Black, J. Brener, & L. V. DiCara (Eds.), Cardiovascular psychophysiology: Current issues in response mechanisms, biofeedback and methodology.* (pp. 538–564). New Brunswick, NJ, US: AldineTransaction. Retrieved from http://ezproxy.net.ucf.edu/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=psyh&AN=2007-11499-026&site=ehost-live

Lacey, B. C., & Lacey, J. I. (1978). Two-way communication between the heart and the brain. Significance of time within the cardiac cycle. *American Psychologist*, *33*(2), 99–113. https://doi.org/10.1037/0003-066X.33.2.99

Laux, L., Glanzmann, P., Schaffner, P., & Spielberger, C. D. (1981). *State-Trait Anxiety Inventory (Spielberger, C.D., Gorsuch, R.L., Lushene, R.E., 1970) - Deutsche Version. Das State Trait Angstinventar (Testmappe mit Handanweisung, Fragebogen STAI G Form X 1 und Fragebogen STAI G Form X 2)*. Weinheim: Beltz.

Lewis, R. P., Rittogers, S. E., Froester, W. F., & Boudoulas, H. (1977). A critical review of the systolic time intervals. *Circulation*, *56*(2), 146–158. https://doi.org/10.1161/01.CIR.56.2.146

Lewis, T. (1925). The Mechanism and Graphic Registration of the Heart Beat. *JAMA: The Journal of the American Medical Association*, *85*(23), 1832. https://doi.org/10.1001/jama.1925.02670230064033

Li, H. H., Barbot, A., & Carrasco, M. (2016). Saccade Preparation Reshapes Sensory Tuning. *Current Biology*, *26*(12), 1564–1570. https://doi.org/10.1016/j.cub.2016.04.028

Lombard, W. P., & Cope, O. M. (1926). The duration of the systole of the left ventricle of man. *American Journal of Physiology--Legacy Content*, *77*(2), 263–295. https://doi.org/10.1159/000165005

Luft, C. D. B., & Bhattacharya, J. (2015). Aroused with heart: Modulation of heartbeat evoked potential by arousal induction and its oscillatory correlates. *Scientific Reports*, *5*(1), 15717. https://doi.org/10.1038/srep15717

Luft, C. D. B., Takase, E., & Darby, D. (2009). Heart rate variability and cognitive function: Effects of physical effort. *Biological Psychology*, *82*(2), 196–201. https://doi.org/10.1016/j.biopsycho.2009.07.007

Macefield, V. G. (2003). Cardiovascular and respiratory modulation of tactile afferents in the human finger pad. *Experimental Physiology*, *88*(5), 617–625. https://doi.org/10.1113/eph8802548

Mather, M., Clewett, D., Sakaki, M., & Harley, C. W. (2016). Norepinephrine ignites local hotspots of neuronal excitation: How arousal amplifies selectivity in perception and memory. *Behavioral and Brain Sciences*, *39*, 1–75.

https://doi.org/10.1017/S0140525X15000667

Mather, M., & Sutherland, M. R. (2011). Arousal-biased competition in perception and memory. *Perspectives on Psychological Science*, *6*(2), 114–133. https://doi.org/10.1177/1745691611400234

Mayer, E. A. (2011). Gut feelings: The emerging biology of gut-brain communication. *Nature Reviews Neuroscience*, *12*(8), 453–466. https://doi.org/10.1038/nrn3071

McGaugh, J. L. (2015). Consolidating Memories. *Annual Review of Psychology*, *66*(1), 1–24. https://doi.org/10.1146/annurev-psych-010814-014954

McIntyre, D., Ring, C., Edwards, L., & Carroll, D. (2008). Simple reaction time as a function of the phase of the cardiac cycle in young adults at risk for hypertension. *Psychophysiology*, *45*(2), 333–336. https://doi.org/10.1111/j.1469-8986.2007.00619.x

Merrikhi, Y., Clark, K., Albarran, E., Parsa, M., Zirnsak, M., Moore, T., & Noudoost, B. (2017). Spatial working memory alters the efficacy of input to visual cortex. *Nature Communications*, *8*, 15041. https://doi.org/10.1038/ncomms15041

Mets, T., Konttinen, N., & Lyytinen, H. (2007). Shot placement within cardiac cycle in junior elite rifle shooters. *Psychology of Sport and Exercise*, *8*(2), 169–177. https://doi.org/10.1016/j.psychsport.2006.02.002

Moore, T., Tolias, A. S., & Schiller, P. H. (1998). Visual representations during saccadic eye movements. *Proceedings of the National Academy of Sciences*, *95*(15), 8981–8984. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=9671790

Morillon, B., Schroeder, C. E., & Wyart, V. (2014). Motor contributions to the temporal precision of auditory attention. *Nature Communications*, *5*, 5255. https://doi.org/10.1038/ncomms6255

Ohl, S., Kuper, C., & Rolfs, M. (2017). Selective enhancement of orientation tuning before saccades. *Journal of Vision*, *17*(13), 1–11. https://doi.org/10.1167/17.13.2

Ohl, S., & Rolfs, M. (2017). Saccadic eye movements impose a natural bottleneck on visual short-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *43*(5), 736–748. https://doi.org/10.1037/xlm0000338

Ohl, S., Wohltat, C., Kliegl, R., Pollatos, O., & Engbert, R. (2016). Microsaccades Are Coupled to Heartbeat. *Journal of Neuroscience*, *36*(4), 1237–1241. https://doi.org/10.1523/JNEUROSCI.2211-15.2016

Park, H.-D., & Tallon-Baudry, C. (2014). The neural subjective frame: from bodily signals to perceptual consciousness. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1641), 20130208–20130208. https://doi.org/10.1098/rstb.2013.0208

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442. https://doi.org/10.1163/156856897X00366

Peters, A., McEwen, B. S., & Friston, K. J. (2017). Uncertainty and stress: Why it causes diseases and how it is mastered by the brain. *Progress in Neurobiology*, *156*, 164–188. https://doi.org/10.1016/j.pneurobio.2017.05.004

Pewsey, A., Neuhäuser, M., & Ruxton, G. D. (2013). *Circular Statistics in R*. Oxford University Press. Retrieved from https://global.oup.com/academic/product/circular-

statistics-in-r-9780199671137?cc=de&lang=en&

Pezzulo, G., Iodice, P., Barca, L., Chausse, P., Monceau, S., & Mermillod, M. (2018). Increased heart rate after exercise facilitates the processing of fearful but not disgusted faces. *Scientific Reports*, *8*(1), 398. https://doi.org/10.1038/s41598-017-18761-5

Pfeifer, G., Garfinkel, S. N., Gould van Praag, C. D., Sahota, K., Betka, S., & Critchley, H. D. (2017). Feedback from the heart: Emotional learning and memory is controlled by cardiac cycle, interoceptive accuracy and personality. *Biological Psychology*, *126*, 19–29. https://doi.org/10.1016/j.biopsycho.2017.04.001

Pikovsky, A., Rosenblum, M., & Kurths, J. (2003). *Synchronization: A Universal Concept in Nonlinear Sciences*. *Cambridge Nonlinear Science Series 12*. Cambridge: Cambridge University Press. https://doi.org/10.1063/1.1554136

Pollatos, O., & Schandry, R. (2008). Emotional processing and emotional memory are modulated by interoceptive awareness. *Cognition and Emotion*, *22*(2), 272–287. https://doi.org/10.1080/02699930701357535

Pollatos, O., Schandry, R., Auer, D. P., & Kaufmann, C. (2007). Brain structures mediating cardiovascular arousal and interoceptive awareness. *Brain Research*, *1141*, 178–187. https://doi.org/10.1016/j.brainres.2007.01.026

Pramme, L., Larra, M. F., Schächinger, H., & Frings, C. (2016). Cardiac cycle time effects on selection efficiency in vision. *Psychophysiology*, *53*(11), 1702–1711. https://doi.org/10.1111/psyp.12728

Pramme, L., Schächinger, H., & Frings, C. (2015). Baroreceptor activity impacts upon controlled but not automatic distractor processing. *Biological Psychology*, *110*, 75–84. https://doi.org/10.1016/j.biopsycho.2015.06.006

Rau, H., & Elbert, T. (2001). Psychophysiology of arterial baroreceptors and the etiology of hypertension. *Biological Psychology*, *57*(1–3), 179–201. https://doi.org/10.1016/S0301-0511(01)00094-1

Réquin, J., & Brouchon, M. (1964). Mise en évidence chez l' homme d'une fluctuation des seuils perceptifs visuels dans la période cardiaque. *Comptes Rendus Des Séances de La Société de Biologie et de Ses Filiales*, *158*(10), 1891.

Richter, C. G., Babo-Rebelo, M., Schwartz, D., & Tallon-Baudry, C. (2017). Phase-amplitude coupling at the organism level: The amplitude of spontaneous alpha rhythm fluctuations varies with the phase of the infra-slow gastric basal rhythm. *NeuroImage*, *146*, 951–958. https://doi.org/10.1016/j.neuroimage.2016.08.043

RStudio Team. (2016). RStudio: Integrated Development Environment for R. Boston, MA: RStudio, Inc. Retrieved from http://www.rstudio.com/

Saari, M. J., & Pappas, B. A. (1976). Cardiac cycle phase and movement and reaction times. *Perceptual and Motor Skills*, *42*(3), 767–770.

Salomon, R., Ronchi, R., Dönz, J., Bello-Ruiz, J., Herbelin, B., Martet, R., … Blanke, O. (2016). The Insula Mediates Access to Awareness of Visual Stimuli Presented Synchronously to the Heartbeat. *Journal of Neuroscience*, *36*(18), 5115–5127. https://doi.org/10.1523/JNEUROSCI.4262-15.2016

Salzman, L. F., & Jaques, N. (1976). Heart Rate and Cardiac Cycle Effects on Reaction Time. *Perceptual and Motor Skills*, *42*(3_suppl), 1315–1321. https://doi.org/10.2466/pms.1976.42.3c.1315

Sandman, C. A., McCanne, T. R., Kaiser, D. N., & Diamond, B. (1977). Heart rate and cardiac phase influences on visual perception. *Journal of Comparative and Physiological Psychology*, *91*(1), 189–202. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/838914%5Cnhttp://search.proquest.com/docview/614323373/fulltextPDF?accountid=14182

Saper, C. B. (2002). The Central Autonomic Nervous System: Conscious Visceral Perception and Autonomic Pattern Generation. *Annual Review of Neuroscience*, *25*(1), 433–469. https://doi.org/10.1146/annurev.neuro.25.032502.111311

Schächinger, H., Weinbacher, M., Kiss, A., Ritz, R., & Langewitz, W. (2001). Cardiovascular indices of peripheral and central sympathetic activation. *Psychosomatic Medicine*, *63*(5), 788–796. https://doi.org/10.1097/00006842-200109000-00012

Schäfer, G., Rosenblum, M. G., Kurths, J., & Abel, H. H. (1998). Heartbeat synchronized with ventilation. *Nature*, *392*(6673), 239–240. https://doi.org/10.1038/32567

Schandry, R. (1981). Heart Beat Perception and Emotional Experience. *Psychophysiology*, *18*(4), 483–488. https://doi.org/10.1111/j.1469-8986.1981.tb02486.x

Schulz, A., Reichert, C. F., Richter, S., Lass-Hennemann, J., Blumenthal, T. D., & Schächinger, H. (2009). Cardiac modulation of startle: Effects on eye blink and higher cognitive processing. *Brain and Cognition*, *71*(3), 265–271. https://doi.org/10.1016/j.bandc.2009.08.002

Seth, A. K. (2013). Interoceptive inference, emotion, and the embodied self. *Trends in Cognitive Sciences*, *17*(11), 565–573. https://doi.org/10.1016/j.tics.2013.09.007

Sherwood, A., Allen, M. T., Fahrenberg, J., Kelsey, R. M., Lovallo, W. R., & van Doornen, L. J. P. (1990). Methodological Guidelines for Impedance Cardiography. *Psychophysiology*, *27*(1), 1–23. https://doi.org/10.1111/j.1469-8986.1990.tb02171.x

Spielberger, C. D., Gorsuch, R. L., Lushene, P. R., Vagg, P. R., & Jacobs, A. G. (1983). *Manual for the State-Trait Anxiety Inventory (Form Y)*. Palo Alto, CA: Consulting Psychologists Press. https://doi.org/10.1007/978-1-4419-9893-4

Tambini, A., Rimmele, U., Phelps, E. A., & Davachi, L. (2017). Emotional brain states carry over and enhance future memory formation. *Nature Neuroscience*, *20*(2), 271–278. https://doi.org/10.1038/nn.4468

Tarvainen, M. P., Niskanen, J.-P., Lipponen, J. A., Ranta-aho, P. O., & Karjalainen, P. A. (2014). Kubios HRV – Heart rate variability analysis software. *Computer Methods and Programs in Biomedicine*, *113*(1), 210–220. https://doi.org/10.1016/j.cmpb.2013.07.024

Task Force of the European Society of Cardiology and the North American Society of Pacing and Electrophysiology (1996). Heart rate variability; Standards of measurements, physiological interpretation and clinical use. (1996). *Circulation*, *93*, 1043–1065. Retrieved from http://circ.ahajournals.org/content/93/5/1043.abstract

Thayer, J. F., Åhs, F., Fredrikson, M., Sollers, J. J., & Wager, T. D. (2012). A meta-analysis of heart rate variability and neuroimaging studies: Implications for heart rate variability as a marker of stress and health. *Neuroscience and Biobehavioral Reviews*, *36*(2), 747–756. https://doi.org/10.1016/j.neubiorev.2011.11.009

Thompson, L. W., & Botwinick, J. (1970). Stimulation in different phases of the cardiac cycle and reaction time. *Psychophysiology*, *7*(1), 57–65. https://doi.org/10.1111/j.1469-8986.1970.tb02276.x

Tomassini, A., Spinelli, D., Jacono, M., Sandini, G., & Morrone, M. C. (2015). Rhythmic

Oscillations of Visual Contrast Sensitivity Synchronized with Action. *Journal of Neuroscience*, *35*(18), 7019–7029. https://doi.org/10.1523/JNEUROSCI.4568-14.2015

Vázquez-Seisdedos, C. R., Neto, J. E., Marañón Reyes, E. J., Klautau, A., de Oliveira, R. C., & Limão de Oliveira, R. C. (2011). New approach for T-wave end detection on electrocardiogram: Performance in noisy conditions. *BioMedical Engineering OnLine*, *10*(1), 77. https://doi.org/10.1186/1475-925X-10-77

Wallace, A. G., Mitchell, J. H., Skinner, N. S., & Sarnoff, S. J. (1963). Duration of the Phases of Left Ventricular Systole. *Circulation Research*, *12*(6), 611–619. https://doi.org/10.1161/01.RES.12.6.611

Weissler, A. M., Harris, W. S., & Schoenfeld, C. D. (1969). Bedside technics for the evaluation of ventricular function in man. *American Journal of Cardiology*, *23*(4), 577–583. https://doi.org/10.1016/0002-9149(69)90012-5

Weissler, A. M., Harris, W. S., & Schoenfield, C. D. (1968). Systolic Time Intervals in Heart Failure in Man. *Circulation*, *37*(2), 149–159. Retrieved from http://circ.ahajournals.org/cgi/content/abstract/37/2/149

Wessa, M., Kanske, P., Neumeister, P., Bode, K., Heissler, J., & Schönfelder, S. (2010). EmoPics: Subjektive und psychophysiologische Evaluation neuen Bildmaterials für die klinisch-biopsychologische Forschung. *Zeitschrift Für Klinische Psychologie Und Psychotherapie*, *39*(Suppl. 1/11), 77.

Wickham, H. (2009). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. Retrieved from http://ggplot2.org

Wiggers, C. J. (1921). Studies on the consecutive phases of the cardiac cycle: II. The laws governing the relative durations of ventricular systole and diastole. *American Journal of Physiology--Legacy Content*, *56*(3), 439–459.

Wiggers, C. J. (1923). Modern Aspects of the Circulation in Health and Disease. *The Journal of the American Medical Association*, *81*(15), 1305. https://doi.org/10.1001/jama.1923.02650150059033

Wilkinson, M., McIntyre, D., & Edwards, L. (2013). Electrocutaneous pain thresholds are higher during systole than diastole. *Biological Psychology*, *94*(1), 71–73. https://doi.org/10.1016/j.biopsycho.2013.05.002

Yang, X., Jennings, J. R., & Friedman, B. H. (2017). Exteroceptive stimuli override interoceptive state in reaction time control. *Psychophysiology*, *54*(12), 1940–1950. https://doi.org/10.1111/psyp.12958

Zelano, C., Jiang, H., Zhou, G., Arora, N., Schuele, S., Rosenow, J., & Gottfried, J. A. (2016). Nasal Respiration Entrains Human Limbic Oscillations and Modulates Cognitive Function. *Journal of Neuroscience*, *36*(49), 12448–12467. https://doi.org/10.1523/JNEUROSCI.2586-16.2016