

1 **Active vision varies across the cardiac cycle**

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3 Stella Kunzendorf^{1,2}, Felix Klotzsche³, Mert Akbal², Arno Villringer^{1,2,3,6}, Sven Ohl^{4,5}, & Mi-
4 chael Gaebler^{2,3}

5

6 **Affiliations:**

7 ¹ Charité – Universitätsmedizin Berlin

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

9 ³ MindBrainBody Institute at Berlin School of Mind and Brain

10 ⁴ Bernstein Center of Computational Neuroscience, Berlin

11 ⁵ Humboldt-Universität zu Berlin

12 ⁶ Dept. of Cognitive Neurology, University Hospital Leipzig

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21 **Corresponding author:**

22 Stella Kunzendorf

23 stella.kunzendorf@charite.de

24

1 **Abstract**

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

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

15

1 **Introduction**

2 We perceive and act upon the world while our brain continuously integrates exteroceptive
3 and interoceptive information, that is, information received from external (e.g., through vision
4 and touch) and internal sources (e.g., through viscerosensation and proprioception), respec-
5 tively (Barrett & Simmons, 2015; Kleckner et al., 2017). Through the fine-tuned interplay of
6 brain and body, we are able to react to changes in the external and the internal environment
7 to maintain or restore our bodily integrity and well-being. Via feedback loops, the brain there-
8 by receives afferent information about bodily states to regulate and adjust bodily activity ac-
9 cordingly (Craig, 2002; Critchley & Harrison, 2013; Mayer, 2011; Saper, 2002). To fully cap-
10 ture the bi-directionality of brain-body interactions and their association with mental process-
11 es, it is essential to investigate if and how such afferent bodily information modulates our
12 thoughts, feelings, and behaviour.

13 One approach to study bodily influences on cognition and behaviour exploits natural
14 physiological fluctuations. Such fluctuations occur at multiple time scales—ranging from milli-
15 seconds to weeks (e.g., brain oscillations, heartbeats, the circadian rhythm, or the menstrual
16 cycle)—and they dynamically interact with each other as well as with the environment (Glass,
17 2001). How such natural physiological variability is processed in the brain remains poorly
18 understood. However, it has been shown that brain and beyond-brain organ systems (e.g.,
19 the cardiorespiratory or the gastrointestinal system) co-vary in their oscillatory activity (Fan et
20 al., 2012; Luft & Bhattacharya, 2015; Richter, Babo-Rebelo, Schwartz, & Tallon-Baudry,
21 2017; Thayer, Åhs, Fredrikson, Sollers, & Wager, 2012).

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

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

22 However, these studies investigating cardiac influences on perception and cognition
23 have only employed passive stimulus presentation, which ignores *self-initiated action* as a
24 crucial dimension of sensory and particularly visual processing. Mediating our engagement
25 with a visual scene, motor actions dynamically orchestrate incoming sensory data and thus
26 strongly influence visual perception—selecting what information is preferentially processed
27 (Benedetto, Spinelli, & Morrone, 2016; Tomassini, Spinelli, Jacono, Sandini, & Morrone,
28 2015). Sensorimotor coupling has also been linked to periodic attentional fluctuations
29 (Hogendoorn, 2016; Morillon, Schroeder, & Wyart, 2014). For example in the visual domain,
30 saccadic eye movements are preceded by a shift of attention to the saccade target resulting
31 in strongly improved visual performance (Deubel & Schneider, 1996; Kowler, Anderson,
32 Doshier, & Blaser, 1995; Li, Barbot, & Carrasco, 2016; Ohl, Kuper, & Rolfs, 2017) and
33 memory performance at the saccade target location (Hanning, Jonikaitis, Deubel, & Szinte,
34 2016; Ohl & Rolfs, 2017) with corresponding neural enhancement in early visual cortex
35 (Merrikhi et al., 2017; Moore, Tolia, & Schiller, 1998). There is sparse evidence that con-
36 nects the heartbeat to general action generation and the few studies that investigated if

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

5 Based on findings of facilitated processing for visual stimuli (Azevedo, Badoud, et al.,
6 2017; Azevedo, Garfinkel, et al., 2017; Garfinkel et al., 2014; Pramme et al., 2016, 2015) and
7 increased oculomotor activity (Ohl et al., 2016) during early phases of the cardiac cycle, we
8 here hypothesized that *active vision* (i.e., self-initiated action towards a visual stimulus)
9 shows periodic variations with the phase of our heartbeat. To investigate perception and ac-
10 tion within a comprehensive framework of mind-brain-body interactions, we here studied car-
11 diac-related sensorimotor processing in a self-paced visual sampling paradigm, in which par-
12 ticipants decide when to press a key to see a task-relevant visual stimulus. Extending studies
13 that emphasize a selectivity of this effect for motivationally salient, passively presented
14 stimuli (Azevedo, Badoud, et al., 2017; Azevedo, Garfinkel, et al., 2017; Garfinkel et al.,
15 2014), we predicted that observers implicitly act upon a relevant visual stimulus such that it is
16 received (and perceived) during preferred cardiac phases. More specifically, we hypothe-
17 sized that visual sampling would be biased towards processing task-relevant pictures during
18 systole.

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

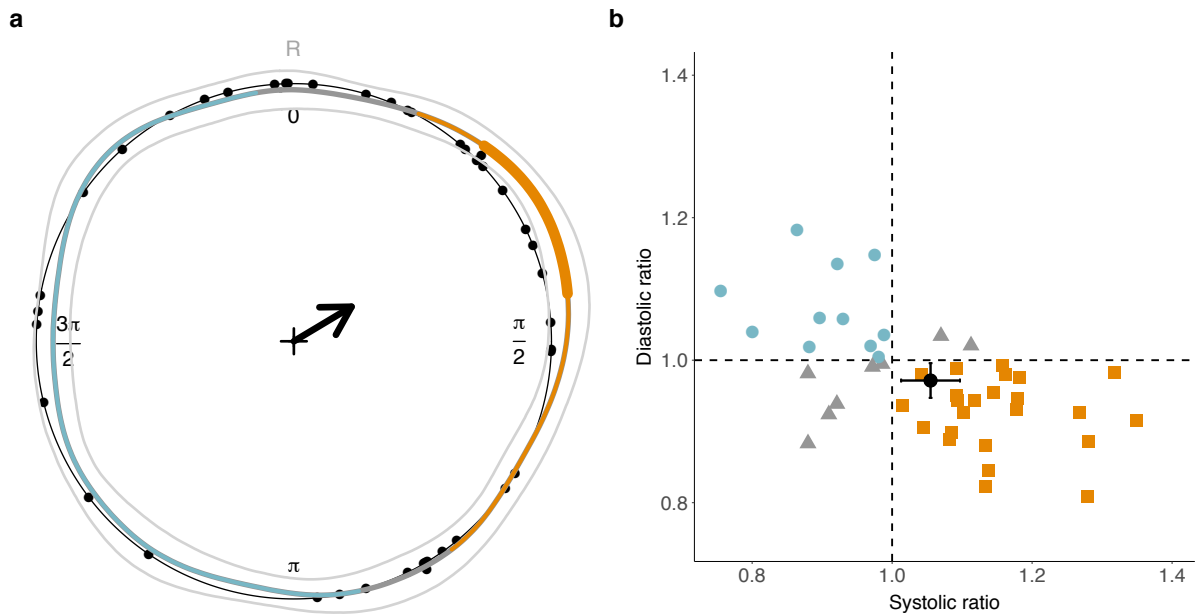
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1 **Results**

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

9 *Encoding:* The distribution of self-paced picture onsets relative to the cardiac R-R
10 interval showed an overall increase in early phases of the cardiac cycle ($M = 0.33\pi$, $SD =$
11 0.52π , $\rho = 0.26$, cf. **Fig. 1a**). This observation was supported by inferential circular statistics
12 indicating a non-significant trend that the self-paced key presses in the present experiment
13 are unlikely to be uniformly distributed (Rayleigh test statistics $R_0 = 0.26$, $p = .053$). Of note,
14 the same analysis with our preregistered sample size (i.e., the first 40 healthy subjects of $N =$
15 43 ; cf. <https://osf.io/5z8rx/>) showed a significant deviation from a uniform distribution ($R_0 =$
16 0.28 , $p = .039$), that is due to a significant increase in self-paced key presses in the interval
17 from 0.24 to 0.44π (**Fig. 1a**) as revealed by nonparametric bootstrapping (performed on the
18 original participant pool, $N = 43$). Although this circular statistics can infer that the distribution
19 of relative picture onsets deviates from a uniform distribution, it cannot pinpoint the transition
20 from systole to diastole – particularly in the presence of varying heartbeat lengths, for which
21 the same section of the circular distribution can be associated with different cardiac phases.

22 Accounting for the bi-phasic nature of cardiac activity in the binary analysis, we com-
23 puted the number of key presses during cardiac systole and diastole, normalised by the pro-
24 portion of the systole vs. diastole in the whole cardiac cycle. We found a significantly larger
25 ($t(42) = 2.76$, $p = .009$, Cohen's $d = 0.42$) ratio of picture onsets in the systole ($M = 1.05$, SD
26 $= 0.14$) as compared to diastole ($M = 0.97$, $SD = 0.081$), corroborating our finding of an in-
27 crease in self-paced visual sampling during cardiac systole (cf. **Fig. 1b**). Similar results were
28 obtained for the preregistered sample size ($n = 40$), showing a significantly larger ($t(39) =$
29 2.70 , $p = .01$, Cohen's $d = 0.43$) systolic ($M = 1.05$, $SD = 0.14$) than diastolic ratio ($M = 0.97$,
30 $SD = 0.079$).



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

21
22 *Recognition:* We also investigated the association between the cardiac cycle and
23 memory processing: In a circular analysis, we tested whether the distribution of onset times
24 during stimulus encoding differed for pictures that were correctly remembered (hits) or erro-
25 neously identified as new pictures (miss). Overall, picture onset times during the encoding

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

3 We further investigated the influence of cardiac phase (systole, diastole) and picture
 4 valence on recognition memory. A LMM (cf. **Table 1**) with contrast-coded picture valence
 5 (negative-neutral, positive-neutral) revealed a significant memory benefit for negative vs.
 6 neutral stimuli ($b = 0.37$, $SE = 0.12$, $z = 3.11$, $p = .002$), as well as for positive vs. neutral
 7 stimuli ($b = 0.29$, $SE = 0.12$, $z = 2.43$, $p = .015$). More specifically, memory performance for
 8 negative pictures ($M = 0.80$, $SD = 0.13$) and for positive pictures ($M = 0.78$, $SD = 0.16$) signif-
 9 icantly exceeded memory performance for neutral pictures ($M = 0.73$, $SD = 0.18$). Critically,
 10 including cardiac phase (systole, diastole) did not improve the model fit: Neither phase ($b = -$
 11 0.17 , $SE = 0.19$, $z = -0.89$, $p = .37$) nor the interaction of picture valence and phase (nega-
 12 tive-neutral X phase: $b = 0.30$, $SE = 0.27$, $z = 1.11$, $p = .27$; positive-neutral X phase: $b =$
 13 0.16 , $SE = 0.27$, $z = 0.61$, $p = .54$) significantly accounted for variation in recognition memory
 14 (cf. **Table 1**).

15

| | 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 |

16

17 **Table 1.** Linear mixed model (LMM) with recognition memory (hit = 1, miss = 0) relative to picture va-
 18 lence (negative-neutral, positive-neutral) ($m_0 = \text{memory} \sim \text{picture valence} + (1|vp)$), cardiac phase,
 19 and their interaction ($m_1 = \text{memory} \sim \text{picture valence} \times \text{cardiac phase} + (1|vp)$). Valenced pictures
 20 (negative and positive) showed a significant memory benefit compared to neutral pictures. Neither
 21 cardiac phase, nor its interaction with picture valence significantly accounted for variation in visual
 22 memory performance.

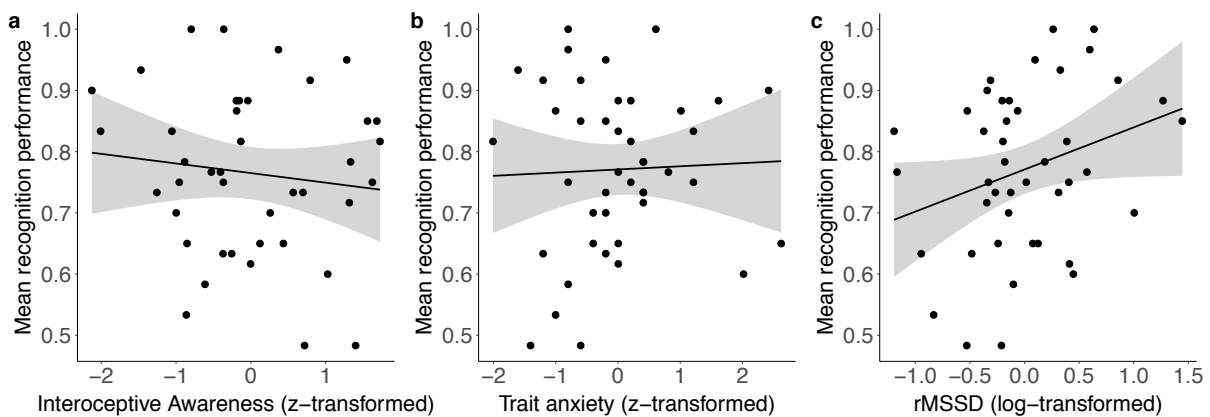
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24 **Supplementary results**

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

1 *Recognition memory varies with resting heart rate variability.* We investigated the role
2 of inter-individual variables (i.e., interoceptive awareness, trait anxiety, resting heart rate var-
3 iability) for memory performance with correlation analyses (cf. **Supplementary Methods**).
4 Neither differences in interoceptive accuracy ($r(39) = -.12, p = .46$), nor in trait anxiety ($r(41)$
5 $= .039, p = .80$) were associated with mean recognition performance (**Supplementary Fig.**
6 **1a, 1b**). However, there was a non-significant trend of resting heart rate variability (i.e., rest-
7 ing rMSSD) to be positively correlated with mean recognition performance ($r(41) = .29, p =$
8 $.056$), that is, recognition memory increased with higher resting heart rate variability (**Sup-**
9 **plementary Fig. 1c**).

10

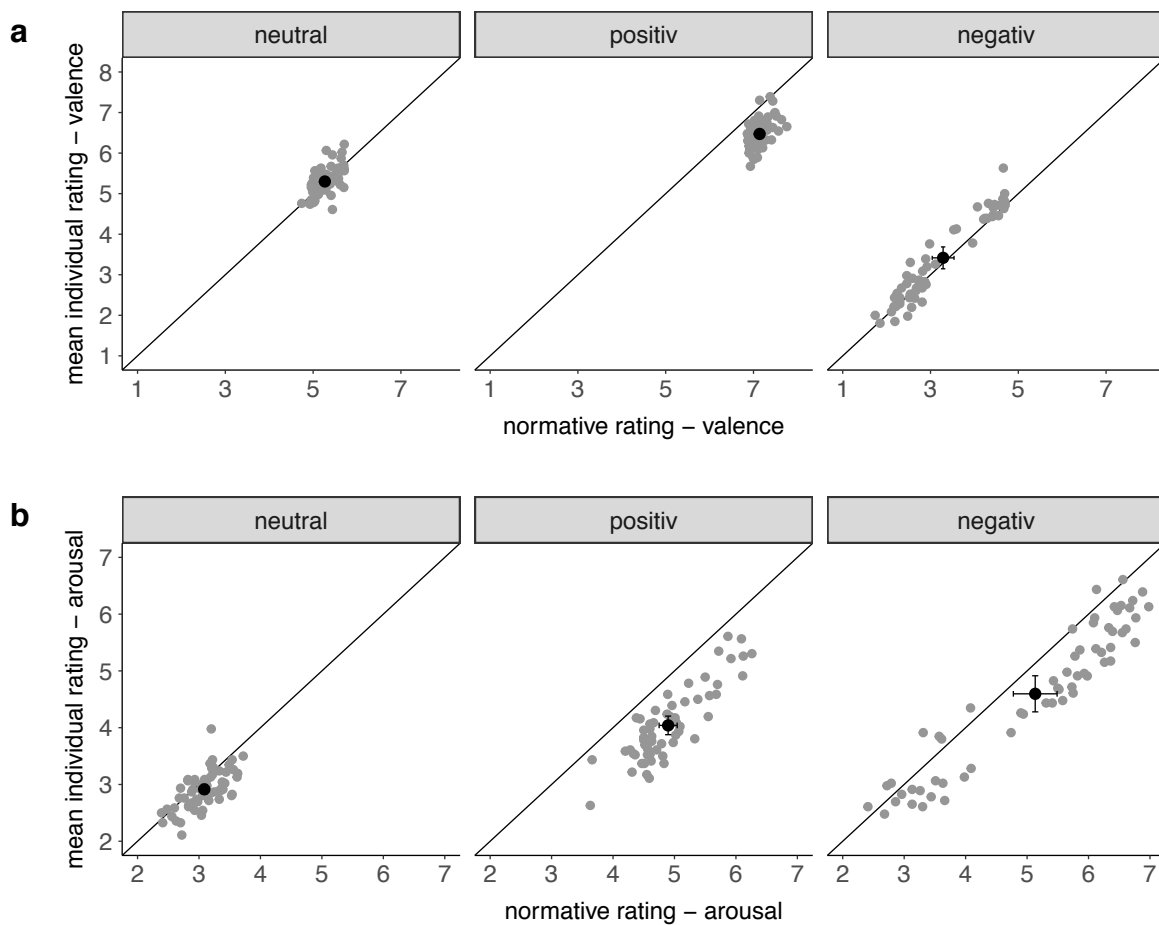


11
12 **Supplementary Figure 1.** Correlation of mean recognition performance with **a**, interoceptive aware-
13 ness, **b**, trait anxiety, and **c**, heart rate variability (resting rMSSD). Grey areas are the 95% confidence
14 intervals of the linear model (black line).

15

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

1 for multiple comparisons with Bonferroni correction: positive (individual: $M=4.04$, $SD=0.65$;
2 normative: $M=4.90$, $SD=0.58$) arousal ratings differed significantly larger from each other
3 ($t(59) = 20.2$, $p < .001$, Cohen's $d = 1.39$) than both neutral (individual: $M=2.91$, $SD=0.34$;
4 normative: $M=3.09$, $SD=0.32$) ($t(59) = 4.77$, $p < .001$, Cohen's $d = 0.52$) and negative (indi-
5 vidual: $M=4.60$, $SD=1.26$; normative: $M=5.13$, $SD=1.41$) arousal ratings ($t(59) = 9.32$, $p <$
6 $.001$, Cohen's $d = 0.40$). Furthermore, while normative arousal ratings did not differ signifi-
7 cantly between positive and negative pictures (cf. **Methods**), individual arousal ratings were
8 significantly higher for negative compared to positive pictures ($t(88.3) = 3.05$, $p = .003$, Co-
9 hen's $d = 0.56$).



10
11 **Supplementary Figure 2. a, Valence ratings and b, Arousal ratings** were both significantly lower for
12 individual compared to normative ratings (overall mean in black with standard error bars). For arousal
13 but not for valence ratings there was a significant interaction effect between rating category and pic-
14 ture valence.
15

1 **Discussion**

2 We studied the association between the cardiac cycle and self-paced visual sampling as well
3 as visual recognition memory for pictures of different emotional valence. We hypothesized
4 that facilitated visual processing (Pramme et al., 2016, 2015)—observed specifically for rele-
5 vant or emotionally salient stimuli (Azevedo, Badoud, et al., 2017; Azevedo, Garfinkel, et al.,
6 2017; Garfinkel et al., 2014)—as well as facilitated oculomotor processing during systole (Ohl
7 et al., 2016) guides active perception in the shape of a preference to prompt a relevant visual
8 stimulus during early phases of the cardiac cycle. We observed a significant accumulation of
9 key presses (i.e., prompted picture onsets) during systole, thereby showing for the first time a
10 coupling between self-paced visual sampling and the heartbeat. Memory performance, how-
11 ever, was only influenced by picture valence, replicating a significant memory benefit for
12 emotional content (Hamann, 2001; Kensinger, 2006; Kensinger & Corkin, 2003; LaBar &
13 Cabeza, 2006), but not further modulated by the cardiac phase in which targets were encod-
14 ed (Garfinkel et al., 2013). The association between the cardiac cycle and self-initiated ac-
15 tions complements findings of facilitated visual processing during systole, thereby proposing
16 a link between the heartbeat and active perception.

17 Sensorimotor processing of passively presented stimuli has been shown to be de-
18 creased during early cardiac phases (Birren et al., 1963; Callaway & Layne, 1964; Edwards
19 et al., 2007; Lacey & Lacey, 1974; McIntyre et al., 2008; Saari & Pappas, 1976), but evi-
20 dence is mixed, including some earlier null findings (Jennings & Wood, 1977; Salzman &
21 Jaques, 1976; Thompson & Botwinick, 1970). However, which processing stages are modu-
22 lated by the heartbeat has long remained unclear. More fine-grained decomposition of reac-
23 tion time into central (sensory, pre-motor) and peripheral (motor) processes has indicated
24 that the response inhibition during early cardiac phases was confined to central (pre-motor)
25 levels of stimulus processing, whereas the motor component remained unaffected (Edwards
26 et al., 2007; McIntyre et al., 2008; Saari & Pappas, 1976) or even accelerated (Schulz et al.,
27 2009). This differential effect could also underlie findings that report an increased tendency to
28 act during systole such as fire a virtual (Azevedo, Garfinkel, et al., 2017) or an actual weapon
29 (Mets et al., 2007) during early cardiac phases. Our results of facilitated spontaneous actions
30 during systole when engaging with a visual stimulus furthermore add to results from oculo-
31 motor behaviour: Ohl et al. (2016) reported involuntarily occurring oculomotor activity (i.e.,
32 microsaccade generation) to be heightened during early cardiac phases. Hence, for both
33 somatomotor and oculomotor processes, our readiness to act upon an external stimulus fluc-
34 tuates with our (internal) cardiac rhythm, being relatively increased during the phase of sys-
35 tolic blood ejection.

1 Although underlying heart-brain pathways remain unclear, systolic influences on per-
2 ception and cognition have often been attributed to the phasic nature of cardio-afferent sig-
3 nalling, which is triggered with the heartbeat (Koriath & Lindholm, 1986; Lacey & Lacey,
4 1978). More specifically, stretch-responsive baroreceptors located in arterial walls respond to
5 transient pressure rises at each blood ejection and communicate the current cardiovascular
6 state (i.e., the heartbeat's strength and timing) to the brain. Thus, baroreceptor-transmitted
7 cardiac signals, which are phasically registered by central processing systems, have been
8 proposed to induce a general suppression of cortical excitability, converging with earlier find-
9 ings of sensory inhibition (Dembrowsky & Seller, 1995; Rau & Elbert, 2001). Formulated in
10 terms of the *interoceptive predictive coding* framework (Barrett & Simmons, 2015; Seth,
11 2013), which extends the *free-energy principle* (Friston, 2010) to interoceptive processes and
12 connects them to consciousness and emotion, this periodic—and thus predictable—
13 ascending baroreceptor input to central structures is anticipatorily cancelled out by top-down
14 interoceptive predictions, thereby minimizing its influence on perception (Critchley &
15 Garfinkel, 2018; Salomon et al., 2016). Besides modulating arterial baroreceptor discharge,
16 heartbeat-related pressure fluctuations generate periodic sensory influences throughout the
17 body—affecting for example the discharge of tactile (Macefield, 2003) or muscle spindle af-
18 ferents (Birznieks, Boonstra, & Macefield, 2012)—which are predicted and normally do not
19 enter perceptual awareness. In our constant attempt to minimize sensory uncertainty (Peters,
20 McEwen, & Friston, 2017), inhibition of such predictable cardiac-induced sensory effects has
21 been argued to reduce—potentially distracting—self-related sensory noise (Salomon et al.,
22 2016) at the benefit of our processing of the outside world, for example by increasing the
23 signal-to-noise ratio of external stimuli. Correspondingly, stimuli presented simultaneously
24 with the heartbeat are interpreted as sensory consequences of the organism's own (internal)
25 cardiac activity and thus perceptually attenuated (Salomon et al., 2016). Our finding that par-
26 ticipants implicitly act upon a visual stimulus during the phase of heartbeat-related (barore-
27 ceptor-mediated) central inhibition could indicate a short-term benefit: As argued by Pramme
28 et al. (2016), the impact of baroreceptor-mediated central influences may depend on context-
29 or task-specific processing demands. In other words, extraction of behaviourally relevant
30 external stimuli from a distracting sensory scene might be facilitated during inhibition of irrel-
31 evant (e.g., cardiac-related) sensory information (Pramme et al., 2016). Accordingly, predict-
32 able phases of attenuated heartbeat-related noise might provide a short-term window to facil-
33 itate active engagement towards an external relevant stimulus.

34 Such differential processing during transient cardiac signalling converges with the ob-
35 served specificity of cardiac effects when using valenced stimuli, in particular selectively facil-
36 itated processing of threat stimuli during systole (Garfinkel & Critchley, 2016). The notion that

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

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

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

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

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

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

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

17

1 **Methods**

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

4
5 *Participants.* 47 (23 female) healthy, young, right-handed subjects (age: 18 – 34 years, M =
6 25.8 years, SD = 4.31) with normal or corrected-to-normal vision participated in this study.
7 Four subjects were excluded due to deviant cardiovascular parameters: two subjects with
8 tachycardic mean resting heart rates (> 100 bpm), one subject with hypertonic blood pres-
9 sure (171/89 mmHg), one subject with numerous ventricular extrasystoles during the experi-
10 mental period (> 10 per minute). The sample size was based on previous cardiac cycle stud-
11 ies (mainly Fiacconi et al., 2016): We aimed for a net sample size of 40 to enter the analyses
12 (cf. <https://osf.io/5z8rx/>) expecting 10% participant exclusions. Participants were recruited
13 through the ORSEE-based (Greiner, 2015) participant database of the Berlin School of Mind
14 and Brain and received a monetary compensation of 9 €/h for their participation. All partici-
15 pants were naïve regarding the purpose of the study and signed informed consent before
16 participation. The study followed the Declaration of Helsinki and was approved by the Ethics
17 Committee of the Department of Psychology at the Humboldt-Universität zu Berlin.

18
19 *Setup and experimental task.* (cf. **Fig. 2a**) Participants were seated in a dimly lit room in front
20 of a gamma-linearized 19-inch Cathode ray tube (CRT) monitor (Samsung Syncmaster
21 959NF, Suwong, Korea) with a refresh rate of 100 Hz and a spatial resolution of 1280x1024
22 pixels. Their head was positioned on a chin rest at a distance of 50 cm from the screen. The
23 participants' task comprised two parts: During the *encoding* period, participants were asked
24 to click through a picture set (800x600 pixels) in self-paced speed and to memorize the pic-
25 tures for a subsequent memory test. By button press, they prompted the immediate onset of
26 the next picture, which appeared for 100 ms. In between self-chosen key presses (i.e. picture
27 onsets), a central fixation cross was presented. After a break of five minutes, they completed
28 the *recognition* period, during which they indicated for each picture whether or not they had
29 seen it before. Here, pictures were passively presented for 100 ms, followed by a centrally
30 presented fixation cross until participants entered their recognition response (“old”, “new”) via
31 key press.

32
33 *Stimuli.* The picture set consisted of 180 coloured photographs (60 pictures with positive, 60
34 with negative, and 60 with neutral content) of humans in various life situations, selected from
35 a collection of standardized and validated affective picture material (EmoPicS, Wessa et al.,
36 2010). In addition to physical image statistics (i.e., luminance, contrast, RGB values, visual

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

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

14

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

21

22 *Additional measures of inter-individual differences.* Previous studies suggest that the influ-
23 ence of cardiac signals on perception and behaviour varies with interoceptive accuracy, that
24 is, the ability to consciously perceive signals originating in the body (Dunn et al., 2010;
25 Garfinkel et al., 2013). We determined inter-individual differences in interoceptive accuracy
26 with a heartbeat perception task (Schandry, 1981), in which participants were asked to esti-
27 mate the number of their heartbeats in five intervals of different length (25, 45, 15, 55, and 35
28 s). As inter-individual differences in anxiety have been proposed to moderate the behavioural
29 effect of autonomic signalling (Garfinkel et al., 2014; Pollatos, Schandry, Auer, & Kaufmann,
30 2007), we also acquired participants' trait anxiety using the State-Trait Anxiety Inventory
31 (STAI-T; Laux et al., 1981; Spielberger et al., 1983). Resting heart rate variability (HRV)
32 measures inter-individual differences in brain-heart interaction and particularly in parasympa-
33 thetic cardiorespiration (Task Force, 1996). HRV can be quantified through changes in the
34 beat-to-beat intervals of the ECG (Task Force, 1996). We calculated the root mean square of
35 successive differences (rMSSD) during the 7-minute baseline ECG.

36

1 *Procedure.* Upon arrival in the lab, participants were equipped with the ECG. Comfortably
2 seated, they were asked to relax for seven minutes and breathe normally. Then, blood pres-
3 sure was measured (twice, if elevated) using a standard sphygmomanometer (OMRON M8
4 Comfort). After a brief training session to familiarize participants with the task, they per-
5 formed the two experimental periods (i.e., encoding and recognition). During a 5-minute
6 break between the two parts, participants completed the Trait Anxiety Inventory (STAI-T;
7 Laux et al., 1981; Spielberger et al., 1983). To assess subjective perception in our sample
8 and compare it to the EmoPicS' normative ratings, all 180 photos were rated after the recog-
9 nition period similarly to the original EmoPicS normative ratings (Wessa et al., 2010): “How
10 do you feel looking at the picture?” was answered for valence (1: sad – 9: happy) and arousal
11 (1: calm – 9: excited) on a 9-level Likert-type scale. For each trial, both rating scales were
12 displayed successively, one above and one below each picture, followed by a 500-ms fixa-
13 tion cross (between trials). Finally, subjects performed the heartbeat perception task
14 (Schandry, 1981) that was presented acoustically.

15

16 *Data analysis.* The timing of behavioural responses was analysed relative to the heartbeats:
17 electrical events indicating the beginning of each cardiac cycle (R peaks) were extracted
18 from the ECG signal with Kubios 2.2 (Tarvainen et al., 2014, <http://kubios.uef.fi/>). Two com-
19plementary analytic approaches—circular and binary analysis—were performed to exploit the
20 oscillatory (repeating cycle of cardiac events) as well as the phasic (two distinct cardiac
21 phases: systole and diastole) nature of cardiac activity, respectively. The code of our analy-
22sis, computed in the R Statistical Environment with RStudio version 1.0.136 (RStudio Team,
23 2016) is available on GitHub (https://github.com/SKunzendorf/0303_INCASI). Graphics were
24 obtained with the circular package (Agostinelli & Lund, 2013) and the ggplot2 package
25 (Wickham, 2009).

26

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

28 *Circular analysis:* For the circular analysis, we computed the relative onset of each key press
29 (prompting picture onset) within the cardiac cycle, which was indicated in the ECG as the
30 interval between the previous and the following R peak (**Fig. 2b**). According to its relative
31 timing within this R-R interval, radian values between 0 and 2π were assigned to each stimu-
32 lus (Ohl et al., 2016; Pikovsky, Rosenblum, & Kurths, 2003; Schäfer, Rosenblum, Kurths, &
33 Abel, 1998). For each participant, we computed the mean of the circular distribution for the
34 120 picture onsets. In a second step, a mean vector of all participants was computed via
35 vector addition of individual means divided by their number, showing the average self-paced
36 picture onset in the cardiac cycle across the group, and weighted by its length (mean result-

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

18 *Binary analysis:* To account for the phasic nature of cardiac activity and to increase
19 comparability to previous cardiac cycle studies, we segmented the cardiac cycle into systole
20 and diastole (**Fig. 2b**). It needs to be noted that systolic phases vary inversely with heart rate
21 (Fridericia, 1920; R. P. Lewis, Rittogers, Froester, & Boudoulas, 1977; Lombard & Cope,
22 1926; Wallace, Mitchell, Skinner, & Sarnoff, 1963; Weissler, Harris, & Schoenfield, 1968):
23 Although the absolute length of systole decreases with a faster heartbeat, its proportionate
24 share of the entire cardiac cycle increases. Such between-subject variation of cardiac phase
25 lengths that arises from differences in heart rate supports the need for more elaborated ana-
26 lytical approaches in cardiac cycle studies. Thus, we did not use absolute systole and diasto-
27 le lengths (e.g., defining systole as the 300 ms following an R peak) but computed partici-
28 pant-specific phases based on cardio-mechanical events related to the ECG (for detailed
29 binning procedure cf. **Supplementary Methods**). This enabled us to extract the phase of
30 systolic blood-ejection for each participant. In the following, we will use the term “systole” to
31 refer to this ejection-phase. The (self-paced) picture onsets were then assigned to the re-
32 spective cardiac phase (i.e., individual systole or diastole). To take into account between-
33 subject differences in heart rate (and thus cardiac phase lengths), the sum of picture onsets
34 per phase (as ratio of all 120 trials) was normalized to the proportion of the subject-specific
35 phase length in the total cardiac cycle, resulting in a value of (picture onsets per cardiac
36 phase / 120) / (individual cardiac phase length / individual mean R-R length) for each cardiac

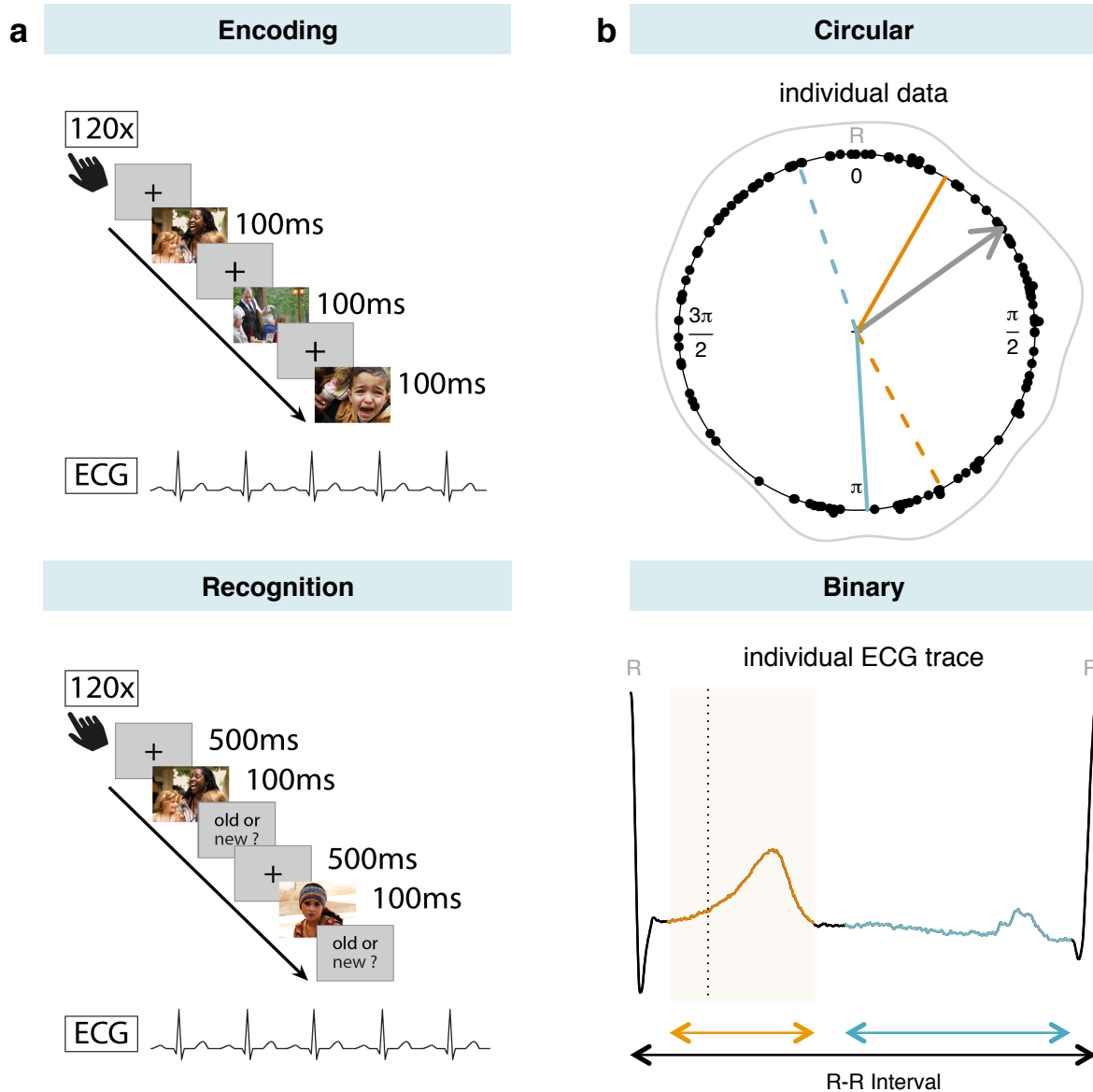
1 phase. With no cardiac effect, button presses (triggering picture onsets) would be randomly
2 distributed across both cardiac phases. That is, the rate of systolic (diastolic) picture onsets
3 should correspond to the proportion of systole (diastole) in the total R-R length, thereby re-
4 sulting in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

7

8 *Recognition period—cardiac modulation of recognition memory.*

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

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



1
2 **Figure 2. a, Experimental setup.** During encoding (top), participants prompted by button press the
3 onset of the next picture, which could be positive, neutral, or negative. In the recognition period (bot-
4 tom), they indicated for each picture (60 old, 60 new) whether or not they had seen it before. Simulta-
5 neous ECG was recorded to analyse behaviour relative to the cardiac cycle: **b, Data analysis.** For
6 circular analysis (top), values between 0 and 2π were assigned to each stimulus onset (black dots),
7 corresponding to its appearance within the cardiac cycle (from the previous to the next R peak in the
8 ECG). Mean (grey arrow) and circular density (grey line) of stimulus onsets were calculated per sub-
9 ject. Individual cardiac phases from the binary analysis (see below) are visualised as circular seg-
10 ments (start: solid, end: dashed): systole (orange) and diastole (blue). For binary analysis (bottom),
11 stimulus onsets (dashed line) were binned into participant-specific systole (orange) and diastole (blue)
12 using a template approach (cf. Supplementary Methods).

13
14
15

1 **Supplementary Methods.**

2 *Detection of individual cardiac phases.* Subject-specific systole and diastole lengths were
3 computed based on cardio-mechanical events that could be related to the ECG trace. Alt-
4 hough mechanical systole cannot be automatically derived from the duration of electrical sys-
5 tole (Fridericia, 1920), both are closely linked under normal conditions (Boudoulas, Geleris,
6 Lewis, & Rittgers, 1981; Coblenz, Harvey, Ferrer, Cournand, & Richards, 1949; Fozzard,
7 1977; Fridericia, 1920; Gill & Hoffmann, 2010; T. Lewis, 1925; Wiggers, 1921, 1923). That is,
8 systolic contraction of the ventricles is preceded by their depolarisation (indicated in the ECG
9 by the QRS complex), while aortic valve closure, marking the end of systolic blood outflow,
10 coincides with ventricular repolarisation, around the end of the t-wave (Gill & Hoffmann,
11 2010). The total ventricular systolic phase (cf. **Supplementary Fig. 3a**) was defined as the
12 time difference between q-wave onset and the t-wave end (QT). For each cardiac cycle, the
13 systolic ejection period was extracted by removing the pre-ejection period (PEP) using re-
14 gression equations (Weissler et al., 1968, see below) that were formerly used in clinical car-
15 diology as a “non-invasive” technique to determine systolic time intervals (R. P. Lewis et al.,
16 1977). Thus, we could more precisely disentangle systolic phases of isovolumetric contrac-
17 tion (no blood outflow, PEP), and ejection phase (blood outflow into the aorta and pulmonary
18 artery, EP). To prevent an overlap of systole and diastole, a window of 50 ms was inserted
19 between both segments. Diastole was defined as the remaining part within the R-R interval
20 ($R-R - QT - 50$ ms).

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

29 Q-wave onsets (or, if not clearly discernable, R-peak onsets), demarcating the onset
30 of ventricular systole, served as a starting point for the regression equations (Weissler et al.,
31 1968). Similarly computed within an averaged template, they were determined as the first
32 prominent negative deflection from baseline (or, if replaced by R-peak onset, the first domi-
33 nant upward deflection), preceding the R-peak in the ECG trace (Sherwood et al., 1990).
34 Thereby, a template-based systole length (QT) was obtained for each participant.

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

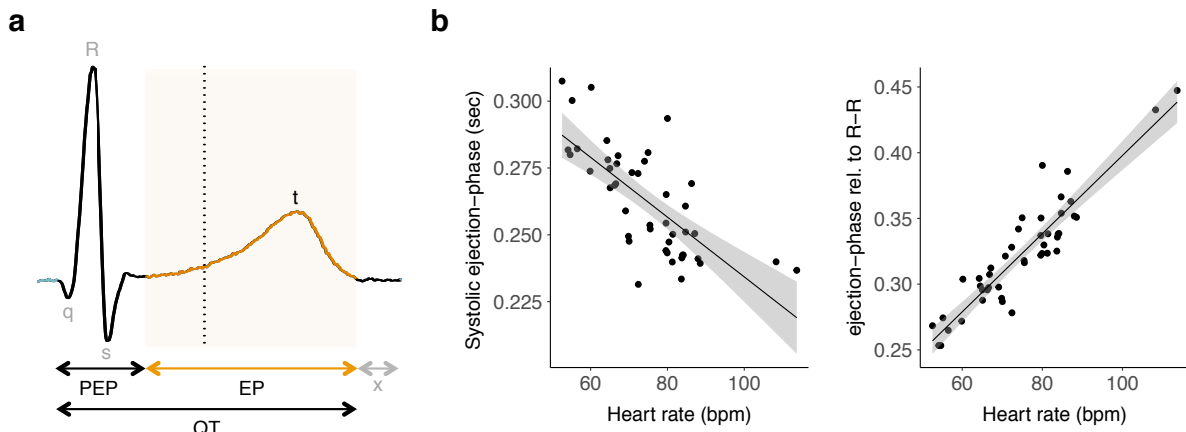
1 pant's mean heart rate (HR), and is corrected for slight differences between male (M) and
2 female (F) ($PEP(M) = -0.4 HR + 131$, $PEP(F) = -0.4 HR + 133$) (Weissler et al., 1968). The
3 PEP was then subtracted from the whole QT-Interval, which determined the EP within each
4 cardiac cycle. We visually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

8
9 *Inter-individual variation of cardiac intervals.* To illustrate the heart rate-dependent variation
10 of cardiac intervals, the two tachycardic subjects were included in this control analysis (sam-
11 ple size: $N = 45$, including 21 female; age: 18 – 34 years, $M = 25.9$ years, $SD = 4.38$). Mean
12 heart rates varied from 52.6 to 113.7 bpm ($M = 74.7$, $SD = 12.9$), with mean R-R intervals
13 ranging from 0.53 s to 1.15 s ($M = 0.83$, $SD = 0.14$).

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

18 In line with earlier research (Boudoulas et al., 1981; R. P. Lewis et al., 1977; Lombard
19 & Cope, 1926; Wallace et al., 1963; Weissler, Harris, & Schoenfeld, 1969; Weissler et al.,
20 1968), we observed an inverse correlation of EP length and mean individual heart rate
21 (Pearson's $r(43) = -.72$, $p < .001$), confirming that heart rate is an important determinant of
22 EP. As shown in **Supplementary Fig. 3b left**, absolute EP duration decreased with higher
23 resting heart rates, ranging from 0.23 s to 0.31 s ($M = 0.26$, $SD = 0.020$), with a total systolic
24 QT interval between 0.32 s and 0.42 s ($M = 0.36$, $SD = 0.024$). However, the proportion of
25 EP relative to the whole cardiac cycle (from one R peak to the next) increased with rising
26 mean heart rate (Pearson's $r(43) = .92$, $p < .001$), comprising between 0.25 up to 0.45 ($M =$
27 0.33 , $SD = 0.042$) of the total mean R-R interval (**Supplementary Fig. 3b right**). This non-
28 proportional shrinking of systolic intervals at higher heart rates underpins the crucial physio-
29 logical role of systole within the cardiac cycle: Cardiac cycle lengths shorten mainly at cost of
30 diastole to ensure sufficient blood ejection at higher heart rates.

31



1
2 **Supplementary Figure 3. a**, The total systolic interval (onset q-wave until t-wave end, QT) was divid-
3 ed into pre-ejection period (PEP) and ejection phase (EP). To prevent an overlap of systole and dias-
4 tole, a window of 50 ms was inserted after t-wave end (indicated by an “x”). Diastole was defined as
5 the remaining part within the R-R interval ($R-R - QT - 50$ ms). **b, left:** Between subjects, the absolute
6 duration of systolic EP decreased with increasing mean heart rate (Pearson’s $r(43) = -0.72$, $p < .001$)
7 while **right:** the systolic proportion within the total cardiac cycle (R-R interval) increased (Pearson’s r
8 $(43) = 0.92$, $p < .001$). That is, cardiac phase lengths shrink disproportionately with faster heartbeats.
9 Grey areas represent the 95% confidence intervals.

10
11 *Supplementary analysis of recognition memory and inter-individual differences.* In an addi-
12 tional analysis, participants’ overall mean recognition performance (i.e., the percentage of
13 correctly recognised pictures) was correlated with variables of inter-individual differences:
14 Interoceptive accuracy (centred via z-transformation), trait anxiety (centred via z-
15 transformation), and resting heart rate variability/ rMSSD (log-transformed to mitigate
16 skewedness and centred to the mean). For measures of interoceptive accuracy, two partici-
17 pants with lacking information in the heartbeat perception task were excluded from the analy-
18 sis ($n = 41$).

19

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