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Interactions between cardiac activity and conscious somatosensory perception

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Abstract

Fluctuations in the heart's activity can modulate the access of external stimuli to consciousness. The link between perceptual awareness and cardiac signals has been investigated mainly in the visual and auditory domain. Here, we investigated whether the phase of the cardiac cycle and the prestimulus heart rate influence conscious somatosensory perception. We also tested how conscious detection of somatosensory stimuli affects the heart rate. Electrocardiograms (ECG) of 33 healthy volunteers were recorded while applying near-threshold electrical pulses at a fixed intensity to the left index finger. Conscious detection was not uniformly distributed across the cardiac cycle but significantly higher in diastole than in systole. We found no evidence that the heart rate before a stimulus influenced its detection, but hits (correctly detected somatosensory stimuli) led to a more pronounced cardiac deceleration than misses. Our findings demonstrate interactions between cardiac activity and conscious somatosensory perception, which highlights the importance of internal bodily states for sensory processing beyond the auditory and visual domain.

KEYWORDS

cardiac cycle, heart rate, interoception, perceptual awareness, somatosensory perception

1 | INTRODUCTION

The internal state of the body is continuously monitored by interoceptive regions and networks in the brain (Barrett & Simmons, 2015; Craig, 2009; Kleckner et al., 2017). Besides their well-described role in homeostatic regulation, visceral signals have been argued to contribute to a wide range of psychological phenomena, including emotions (Critchley & Garfinkel, 2017; Wiens, 2005), empathy (Fukushima, Terasawa, & Umeda, 2011; Grynberg & Pollatos, 2015), time perception (Di Lernia et al., 2018; Meissner & Wittmann, 2011), self-consciousness (Craig, 2009; Park & Tallon-Baudry, 2014), and decision making (Gu & Fitzgerald, 2014; Seth, 2014). At the perceptual level, it remains unclear to what extent signals from visceral organs can modulate the conscious access to exteroceptive (e.g., visual, auditory, somatosensory) input. Here, we examined the interactions between perceptual awareness for somatosensory stimuli and cardiac activity, that is, the phase of the cardiac cycle and the heart rate.

The cardiac cycle from one heartbeat to the next can be divided into two phases: systole, when the heart contracts and ejects blood into the arteries—leading to activation of pressure-sensitive baroreceptors in arterial vessel walls—and diastole, when the cardiac muscle relaxes, the heart refills with blood, and baroreceptors remain quiescent (Landgren, 1952; Mancia & Mark, 2011). Baroreceptor activity signals the strength and timing of each heartbeat to the nuclei in the

lower brain stem, where the signal is relayed to subcortical and cortical brain regions (Dampney, 2016). In studies with noninvasive baroreceptor stimulation, their activity was found to decrease the BOLD signal (Makovac et al., 2015) and ERP amplitudes (Rau & Elbert, 2001; Rau, Pauli, Brody, Elbert, & Birbaumer, 1993) in cortical regions. Baroreceptor firing is thought to underlie cardiac cycle effects on behavior and cognition (Duschek, Werner, & Reyes Del Paso, 2013; Garfinkel & Critchley, 2016), like decreased intensity ratings for acoustic (Cohen, Lieb, & Rist, 1980; Schulz et al., 2009) or painful stimulation (Wilkinson, McIntyre, & Edwards, 2013) as well as higher reaction times to stimuli (Birren, Cardon, & Phillips, 1963; Edwards, Ring, McIntyre, Carroll, & Martin, 2007; McIntyre, Ring, Edwards, & Carroll, 2008) during early (i.e., at systole) compared to later phases (i.e., at diastole) of the cardiac cycle.

There are conflicting findings as to what extent the cardiac cycle modulates the access of exteroceptive information to perceptual awareness. Earlier studies reported that the detection of visual (Réquin & Brouchon, 1964; Sandman, McCanne, Kaiser, & Diamond, 1977) and auditory signals (Saxon, 1970) vary for different points of the cardiac cycle. However, other studies in the visual (Elliott & Graf, 1972) and auditory domain (Delfini & Campos, 1972; Velden & Juris, 1975) did not find such variations. More recently, an enhanced detection selectively for fearful faces was observed during cardiac systole (Garfinkel et al., 2014). As almost all studies in that field involved visual or auditory stimuli, it remains unclear whether cardiac phase-related fluctuations occur in other sensory modalities. The only previous study in the somatosensory domain with a behavioral measure of perception reported lower detection thresholds for electrical stimulation at systole compared to diastole (Edwards, Ring, McIntyre, Winer, & Martin, 2009). As in most studies of cardiac phase effects, the detection performance was sampled only at fixed time points (R+0, R+300, and R+600 ms), which may have missed perceptual changes at other parts of the cardiac cycle.

In the present study, we examined fluctuations in conscious somatosensory perception across the entire cardiac cycle. Given the variations in cortical excitability over the cardiac cycle, we hypothesized that detection of near-threshold electrical stimuli is not equally distributed but varies over the interval between one heartbeat and the next. We also aimed to explore associations between conscious somatosensory perception and the heart rate. The bidirectional information flow between the heart and the brain (Faes et al., 2017; Lin, Liu, Bartsch, & Ivanov, 2016; Valenza, Toschi, & Barbieri, 2016) implies that cardiac activity may not only impact perception but is also influenced by it. Therefore, we tested whether the prestimulus heart rate influences conscious perception and, in turn, whether perception changes the (poststimulus) heart rate.

Regarding the relation between the heart rate and perception, an early theory suggested that a decreased heart rate increases sensitivity to sensory stimulation by directing attention to external rather than internal signals (Graham & Clifton, 1966; Lacey, 1967; Lacey, Kagan, Lacey, & Moss, 1963; Sandman, 1986). The evidence for this hypothesis is mixed and comes only from studies in the auditory and visual domain: For auditory thresholds, there were no differences between transient periods of low and high heart rate (Edwards & Alsip, 1969) unless the procedure involved exercise-induced changes in heart rate (Saxon & Dahle, 1971). In addition to such heart rate variations over longer periods of time, quick changes from one heartbeat to the next were suggested to modulate perception (Lacey & Lacey, 1974; Sandman et al., 1977). In general, cardiac deceleration (i.e., a lengthening of the period between consecutive heartbeats) is known to occur in anticipation of a (cued) stimulus or in reaction to a salient stimulus (Lacey & Lacey, 1970, 1977; Simons, 1988), and it is typically followed by cardiac acceleration after the behavioral response (e.g., Börger & van Meere, 2000; Park, Correia, Ducorps, & Tallon-Baudry, 2014). While both spontaneous (Sandman et al., 1977) and conditioned (McCanne & Sandman, 1974) cardiac deceleration coincident with a visual stimulus was found to increase its detection, other—more recent—studies did not show a modulation of visual awareness by heart rate changes prior to and coincident with a near-threshold stimulus (Cobos, Guerra, Vila, & Chica, 2018; Park et al., 2014).

For heart rate changes after stimulus presentation, earlier studies found a cardiac deceleration in response to suprathreshold visual (Davis & Buchwald, 1957), auditory (Davis, Buchwald, & Frankmann, 1955; Uno & Grings, 1965; Wilson, 1964), tactile (Davis et al., 1955), and olfactory stimuli (Gray & Crowell, 1968). Additionally, cardiac deceleration was found to be more pronounced after viewing unpleasant compared to pleasant or neutral scenes (Bradley, Cuthbert, & Lang, 1990; Greenwald, Cook, & Lang, 1989; Hare, 1973; Libby, Lacey, & Lacey, 1973; Walker & Sandman, 1977). Most importantly in the context of this work, recent studies using near-threshold visual stimuli showed that hits resulted in increased cardiac deceleration compared to misses (Cobos et al., 2018; Park et al., 2014). This suggests that not only the physical characteristics of a stimulus determine the cardiac response but also the level of its processing (i.e., conscious vs. nonconscious).

The association between cardiac activity and perception was also related to cardiac-phase independent variations in arterial pressure after changes in heart rate (Sandman et al., 1977). In this view, the late phase of the cardiac cycle (i.e., diastole) and cardiac deceleration result in—similar but not identical—transient decreases in blood pressure, thus facilitating the access of external stimuli to consciousness by decreasing the inhibitory effects of baroreceptor activity on the

brain (Sandman, 1986; Sandman et al., 1977). Notably, even though higher mean arterial blood pressure has been associated with higher resting heart rate (Christofaro, Casonatto, Vanderlei, Cucato, & Dias, 2017; Mancia et al., 1983), increases in blood pressure after cardiac deceleration (i.e., decreases in heart rate) were observed during experimental tasks (Otten, Gaillard, & Wientjes, 1995; Wölk, Velden, Zimmermann, & Krug, 1989). In addition, animal studies showed that, also with constant mean arterial pressure, the heart rate elevation leads to an increased discharge of arterial baroreceptors (Abboud & Chapleau, 1988; Barrett & Bolter, 2006). Taken together, these findings suggest that the heart rate contributes to cortical excitability through a transient modulation of baroreceptor activity.

Furthermore, we aimed to test whether the influence of cardiac signals on perception varies with interindividual differences in interoceptive accuracy, that is, the ability to consciously perceive signals originating from the body (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015). Given that the capacity to detect one's own heartbeat has been repeatedly shown to modulate (usually strengthen) cardiac effects on perception and behavior (Critchley & Garfinkel, 2018; Dunn et al., 2010; Suzuki, Garfinkel, Critchley, & Seth, 2013), we hypothesized that the link between conscious somatosensory perception and cardiac activity would be stronger for participants with higher interoceptive accuracy (measured with the heartbeat counting task; Schandry, 1981).

In sum, given that baroreceptor activity, which is thought to suppress the processing of external input, varies both across the cardiac cycle and with the heart rate, we hypothesized that perceptual awareness for somatosensory stimuli increases at the later phases of the cardiac cycle (at diastole) and with greater cardiac deceleration. Also, we explored whether a consciously detected somatosensory stimulus affects the heart rate differently compared to a nondetected stimulus and whether cardiac effects on conscious somatosensory perception vary with the capacity to consciously perceive one's heartbeat.

2 | METHOD

2.1 | Participants

Thirty-three healthy volunteers (17 female, mean age = 25.9, *SD* = 4.1, range: 19–36 years, right-handed) were recruited from the database of the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig, Germany. The procedure was approved by the ethics committee of the Medical Faculty at the University of Leipzig. All participants gave written informed consent before taking part in the study and were financially compensated for their participation.

2.2 | Apparatus

Electrocardiography (ECG) was measured while near-threshold electrical finger nerve stimulation was applied. ECG was recorded at a sampling frequency of 1,000 Hz with BrainAmp (Brain Products GmbH, Gilching, Germany). Electrodes were placed on the wrists and the left ankle (ground) according to Einthoven's triangle. Electrical finger nerve stimulation was performed with a constant-current stimulator (DS5; Digitimer) applying single rectangular pulses with a length of 200 μS. A pair of steel wire ring electrodes was attached to the middle (anode) and the proximal (cathode) phalanx of the left index finger. The experiment was programmed, and behavioral data were recorded with MATLAB 8.5.1 (Psychtoolbox 3.0.11, Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

2.3 | Procedure

Each participant was tested individually in a dimly lit experimental chamber seated in a comfortable chair and facing a computer screen. After a brief explanation of the experimental procedure and the attachment of ECG electrodes, the steel wire ring electrodes were attached to the left index finger. The response button box was placed under the right hand. The computer screen indicated when to expect a stimulus and when to respond (Figure 1). Participants responded with *yes* if they felt an electrical stimulus and *no* if not. The left/right button-response mapping (yes-no or no-yes) was pseudorandomized across participants. The experimental session consisted of 360 trials divided into three blocks. Each block included 100 trials with near-threshold stimulation and 20 catch trials without stimulation in pseudorandomized order. The intensity of electrical stimulation was fixed throughout a block. Before each block, the somatosensory perceptual threshold was assessed using an automated staircase procedure to estimate a stimulus intensity that would be equally likely to be felt or not (the 50% detectability level). The applied method combines a coarser staircase procedure (up/down method) and a more fine-grained Bayesian procedure (psi method) of the Palamedes Toolbox (Kingdom & Prins, 2010). The automated threshold assessment resembled the actual experimental design, except for the shorter (500 ms) intertrial interval and the time window in which stimulation could occur (1,000 ms). Thus, before each block, the experimenter made a data-driven decision of the individual sensory threshold ($M = 2.24$, $SD = 0.81$, range = 1–5 milliamperes). At the end of the experimental session and after a short break of approximately 3 min, interindividual differences in interoceptive accuracy (Garfinkel et al., 2015) were assessed with a heartbeat counting task (Schandry, 1981), in which participants were asked to estimate the number of their heartbeats in five intervals of different duration (detailed in the online supporting information, Appendix S1).

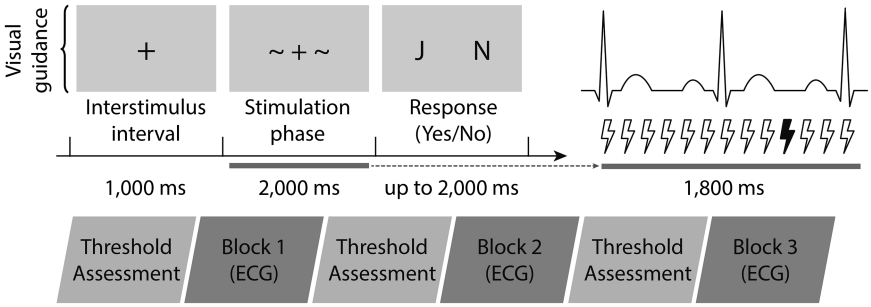

FIGURE 1 Near-threshold somatosensory signal detection task. Upper: Each trial started with a 1,000-ms central fixation cross, followed by the 2,000-ms time window during which the stimulus could occur (except for the first and the last 100 ms of this interval). The stimulation onset was pseudorandomized within this 1,800-ms time window, aiming for a uniform distribution of stimuli over the entire cardiac cycle. Next, the response phase began (cued by displaying *J N*—corresponding to *yes* and *no*, respectively) and lasted until participants gave a response within the maximum time of 2,000 ms. After the button press, the fixation cross was visible for the rest of the 2,000-ms interval so that the total duration of each trial was kept constant at 5,000 ms. The next trial followed immediately so that the duration of each block was fixed (10 min). Lower: An experimental session consisted of three such blocks, which were each preceded by a threshold assessment to estimate stimulus intensities with 50% detection probability

2.4 | Statistical analysis

All statistical analyses were conducted using R version 3.5.1 (R Core Team, 2016) with RStudio version 1.1.453 (RStudio Team, 2016) and the Circular package version 0.4.93 (Agostinelli & Lund, 2013). Kubios 2.2 (Tarvainen, Niskanen, Lipponen, Ranta-aho, & Karjalainen, 2014; Biosignal Analysis and Medical Imaging Group, Department of Applied Physics, University of Eastern Finland, Kuopio, http://kubios.uef.fi/) was used to automatically detect and visually inspect R peaks in the ECG. Falsely detected or missed R peaks (<0.2%) were manually corrected. A two-sided alpha level of 0.05 was used in all statistical analyses. All preprocessed data and the codes used for the main and supplementary analyses are available on GitHub at <https://github.com/Pawel-Motyka/CCSomato>.

2.4.1 | Behavior

Prior to the analysis, the following data were excluded: 191 trials (from 26 participants) with no response within 2 s (1.7% of all trials), 15 trials where the stimulation failed, two trials with the unassigned button pressed, and two trials with physiologically implausible interbeat interval (IBI) lengths (>1,500 ms). Also, one block of one participant was excluded due to data recording failure. Thus, the total number of trials retained for analysis was 11,550 (from 33 participants): 4,530 hits (correctly detected near-threshold stimuli), 5,104 misses (not detected near-threshold stimuli), 81 false alarms (wrongly detected nonstimulation), and 1,835 correct rejections (correctly detected nonstimulation).

2.4.2 | ECG data

To investigate cardiac phase-related variations in perceptual awareness for somatosensory stimuli while accounting for both the oscillatory and the biphasic nature of cardiac activity, the distribution of hits and misses were examined (a) over the whole cardiac cycle by means of circular statistics (Pewsey, Neuhäuser, & Ruxton, 2013), and (b) by testing differences in hit rates between the two cardiac phases (systole and diastole), respectively. Furthermore, it was analyzed (c) whether pre- and poststimulus changes in heart period differed between hits and misses.

1. Circular statistics allowed us to analyze the distribution of hits and misses along the entire cardiac cycle (from one R peak to the next). For each participant, the mean phase angle, at which hits or misses occurred on average, was calculated in degrees (see Section 2.5 Determination of stimulus onset distribution across the cardiac cycle). At the group level, it was tested with Rayleigh tests (Pewsey et al., 2013) whether the distributions of hits and misses deviated from the uniform distribution. The Rayleigh test is based on the mean vector length out of a sample of circular data points and specifies the average concentration of these phase values around the circle—ranging from 0 to 1 indicating no to perfect (angular) concentration, respectively. A statistically significant Rayleigh test result indicates that the data are unlikely to be uniformly distributed around the circle (in this case, the cardiac cycle).
2. Binary analysis, based on the segmentation of the cardiac cycle into the two cardiac phases, allowed us to compare our results to previous studies of cardiac effects on perception.

To divide the cardiac cycle into systole and diastole, the trial-specific cardiac phases were computed based on cardio-mechanical events related to the ECG signal (for a description of the applied t-wave end detection algorithm, see Section 2.6 Determination of individual cardiac phases). Given the between-subjects variation of cardiac phase lengths arising, for example, from differences in heart rate (Herzog et al., 2002; Lewis, Rittogers, Froester, & Boudoulas, 1977; Wallace, Mitchell, Skinner, & Sarnoff, 1963), an individualized approach was used—instead of rather arbitrary and fixed systole and diastole intervals (e.g., defining systole as the 300 ms following an R peak). Stimulus onsets were assigned to the corresponding cardiac phase (i.e., systole or diastole) for each trial. Then, for each participant, hit rates were calculated separately for systole and diastole. A paired *t* test was used to determine whether hit rates differed between cardiac phases.

3. To analyze the pre- and poststimulus heart rate for hits and misses, the mean lengths of six consecutive IBIs were computed (with an average IBI of 827 ms, $SD = 119$ ms; these aimed to cover the full trial length of 5,000 ms): two before the stimulation (S-2, S-1), one at which the stimulus occurred (stimulus), and three after the stimulation (S+1, S+2, S+3). To test whether the (changes in) heart period differed between hits and misses, a two-way repeated measures analysis of variance (ANOVA) was used—with perceptual awareness (hits/misses) and time (six IBIs, S-2 to S+3, per trial) as factors—followed by post hoc Bonferroni-corrected paired *t* tests. Furthermore, an association between the extent of cardiac deceleration and the conscious access to somatosensory stimuli was investigated. For each trial, cardiac deceleration was calculated (and *z* scored within participants) as the difference between the lengths of the IBI at which the stimulus occurred (stimulus) and the IBI prior to it (S-1). A paired *t* test was used to examine whether the extent of cardiac deceleration differed between hits and misses.

2.4.3 | Interoceptive accuracy

A score of interoceptive accuracy was calculated for each participant. The closer the estimated number to the number of heartbeats measured by the ECG over five intervals, the higher the interoceptive accuracy score (cf. supporting information, Appendix S1). The sample was then median-split into groups of high and low interoceptive accuracy, which were compared using analyses described in Section 2.4.2.

2.5 | Determination of stimulus onset distribution across the cardiac cycle

In each trial, stimulus onset was pseudorandomized within a 1,800-ms time window. Stimulation at different points of IBI aimed to cover the entire cardiac cycle for each subject. For each stimulus, the time of the previous and the subsequent R peak were extracted from the ECG to calculate the stimulus onset's relative position within the IBI using the following formula: [(onset time − previous R peak time)/(subsequent R peak time − previous R peak time)] × 360, assigning the values from 0 to 360 degrees (with 0 indicating the R peak before the stimulus). The distribution of stimulus onsets was tested separately for each participant with a Rayleigh test for uniformity. One participant was excluded from further circular analyses due to nonuniformly distributed stimulation onsets across the cardiac cycle, $\bar{R} = 0.11$, $p = 0.009$. For the rest of the participants, the assumption of uniform onset distributions was fulfilled (all ps > 0.091).

2.6 | Determination of individual cardiac phases

To account for the biphasic nature of cardiac activity, we encoded the length of individual cardiac phases using the t-wave end detection method (Vázquez-Seisdedos, Neto, Marañón Reyes, Klautau, & Limão de Oliveira, 2011): First, the peak of the t wave was located as a local maximum within a physiologically plausible interval (up to 350 ms after the R peak). Subsequently, a series of trapezes were calculated along the descending part of the t-wave signal, defining the point at which the trapezium's area gets maximal as the t-wave end. Detection performance was visually controlled by overlaying the t-wave ends and the ECG trace from each trial. Twenty-seven trials with extreme systole lengths (more than 4 *SD*s above or below the participant-specific mean) were excluded.

Although mechanical systole cannot be fully equated with the duration of electrical systole in the ECG (Fridericia, 1920), both are closely tied under normal conditions (Boudoulas, Geleris, Lewis, & Rittgers, 1981; Coblentz, Harvey, Ferrer, Cournand, & Richards, 1949; Fridericia, 1920; Gill & Hoffmann, 2010). Systolic contraction of the ventricles follows from their depolarization (marked in the ECG by the QRS complex), whereas the closure of the aortic valve, terminating the systolic blood outflow, corresponds to ventricular repolarization (around the end of the t wave; Gill & Hoffmann, 2010). In our study, the ventricular systolic phase (further referred to as systole) was defined as the time between the R peak of the QRS complex and the t-wave end, while diastole was defined as the remaining part of the RR interval.

3 | RESULTS

3.1 | Detection rate for near-threshold somatosensory stimuli

On average, 46.7% of the near-threshold somatosensory stimuli were detected (SD = 16.2%, range: 15.1%–79.3%). The false alarm rate was 4.2% (SD = 5.7%, range: 0%–16.6%).

3.2 | Hits concentrated in the late phase of the cardiac cycle

Rayleigh tests were applied to analyze the distribution of hits and misses across the cardiac cycle. Hits were not uniformly distributed across the cardiac cycle, $\bar{R} = 0.32$, $p = 0.034$ (Figure 2a), with their mean angle directing to the later phase of the cardiac cycle (i.e., diastole). Misses showed a nonsignificant tendency to deviate from uniformity, $\bar{R} = 0.30$, $p = 0.060$ (Figure 2b), with their mean angle directing to the earlier phase of the cardiac cycle (i.e., systole). For 14 out of 32 participants, the individual mean angles for hits fell into the last quarter of the cardiac cycle. The individual mean angles for misses accumulated in the second quarter of the cardiac cycle for 13 participants. Distributions of hits or misses across the cardiac cycle did not differ significantly between participants with high or low interoceptive accuracy (see supporting information, Figure S1).

3.3 | Higher hit rates in diastole than in systole

Accounting for the biphasic nature of cardiac activity, differences in hit rates between systole and diastole were examined. Hit rates for near-threshold somatosensory stimuli were significantly higher during diastole (M = 47.9%, SD = 16.5%) than during systole (M = 45.1%, SD = 16.3%), $t(32) = -2.76$, $p = 0.009$, Cohen's $d = 0.48$. Increased hit rate during diastole was observed for 25 out of 33 participants (Figure 3). This mirrors the concentration of hits in the later phase of the cardiac cycle (see circular statistics, Figure 2). Hit rates at different cardiac phases did not differ significantly between the groups with high and low interoceptive accuracy (see Figure S2). Further, to allow a more direct comparison with the previous study by Edwards et al. (2009), hit rates were analyzed across the three 100-ms intervals of the cardiac cycle centered around the time points used therein: R+0 ms; R+300 ms, R+600 ms. Hit rates were significantly higher during the R+600 ms (at diastole) than during the R+300 ms interval (at systole), with no other significant differences between intervals (see supporting information, Appendix S1, for details and Figure S3).

3.4 | Pre- and poststimulus heart rate (changes) for hits and misses

To investigate how the heart rate interacts with conscious somatosensory perception, pre- and poststimulus IBIs (factor: time) were analyzed separately for hits and misses (factor: detection). The analysis showed significant main effects of time (Greenhouse-Geisser corrected; $F(5, 160) = 57.9$, $p < 0.001$, $\varepsilon = 0.299$, $\eta^2_G = 0.008$) and detection, $F(1, 32) = 6.37$, $p = 0.020$, $\eta^2_G = 0.0004$, as well as their significant interaction (Greenhouse-Geisser corrected, $F(5, 160) = 13.5$, $p < 0.001$, $\varepsilon = 0.399$, $\eta^2_G = 0.0003$; Figure 4a). IBIs prior to the stimulus (S-1, S-2) did not differ significantly between hits and misses. IBIs concurrent with the stimulus were significantly longer for hits than for misses (stimulus: $t(32) = 4.21$,

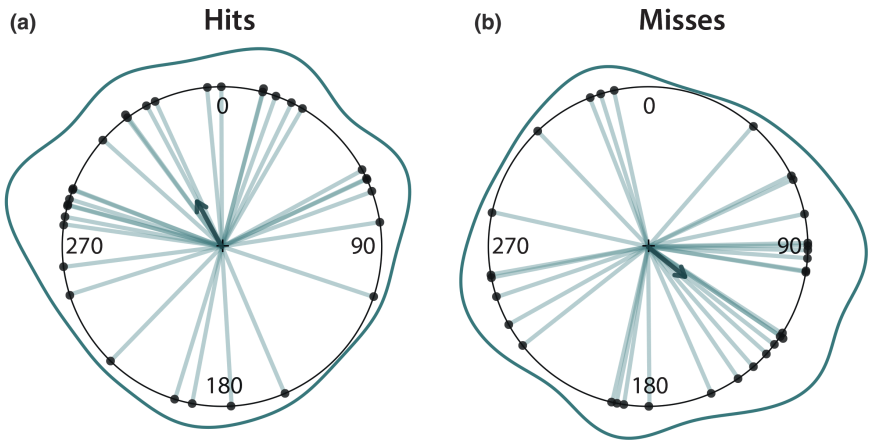

FIGURE 2 Distribution of (a) hits, and (b) misses across the cardiac cycle (i.e., the interval between two R peaks; at 0/360°). Rayleigh tests showed a significant deviation from a uniform distribution for hits ($\bar{R} = 0.32$, $p = 0.034$) and a nonsignificant trend for misses ($\bar{R} = 0.30$, $p = 0.060$). Each dot (and line) indicates one participant's mean phase angle. The annular line depicts the distribution of individual means. The darker arrows represent the directions of the group means for hits (331°) and misses (129°), with their length indicating the concentration of individual means across the cardiac cycle (hits: 0.32; misses: 0.30—with 1 indicating perfect angular concentration)

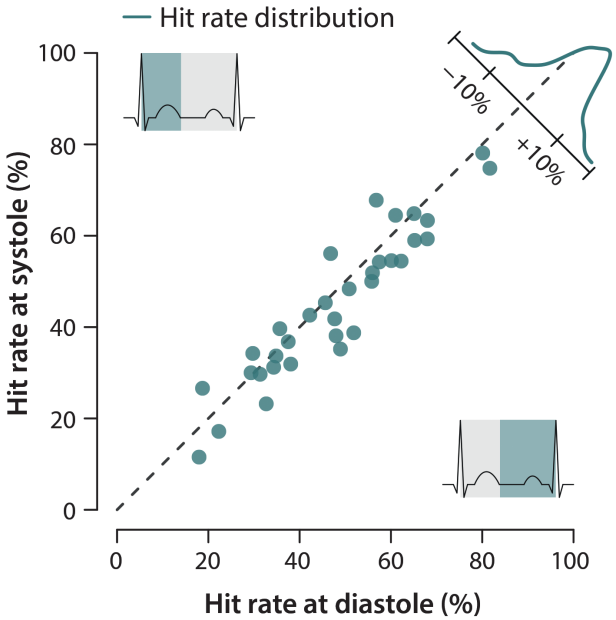

FIGURE 3 Significantly higher hit rates in diastole than in systole. Coordinates of each dot represent a participant's mean hit rate at systole (*x* axis) and diastole (*y* axis). Dashed lines mark the identity line in hit rate between cardiac phases. The distribution in the upper right corner aggregates the frequency across participants. The probability distribution was shifted toward diastole indicating significantly higher hit rates during the later phase (i.e., diastole) than the earlier phase (i.e., systole) of the cardiac cycle, $t(32) = -2.76$, $p = 0.009$, Cohen's $d = 0.48$

$p = 0.006$). This effect was also observed for IBIs right after the stimulus (S+1: $t(32) = 5.22$, $p < 0.001$) but not for subsequent IBIs (S+2, S+3). For both hits and misses, a significant cardiac deceleration was found between the IBIs before and during the stimulus (from/S to stimulus, hits: $t(32) = -7.28$, $p < 0.001$, misses: $t(32) = -4.96$, $p < 0.001$) as well as between the IBIs during and after the stimulus (from stimulus to S+1, hits: $t(32) = -5.95$, $p < 0.001$, misses: $t(32) = -5.00$, $p < 0.001$). Cardiac deceleration was followed by an immediate acceleration for hits (from S+1 to S+2: $t(32) = 4.93$, $p < 0.001$), which was not observed for misses (from S+1 to S+2: $t(32) = 1.28$, $p_{corrected} = 1.000$). In the later phase of the trials (from S+2 to S+3), cardiac acceleration was present after both hits, $t(32) = 7.50$, $p < 0.001$, and misses, $t(32) = 5.67$, $p < 0.001$.

To further explore the association between cardiac deceleration and conscious somatosensory perception, the "slopes" of the stimulus-induced heartbeat deceleration (stimulus − S-1) were compared between hits and misses. Consciously perceiving the stimulus was accompanied by larger cardiac deceleration ($M = 0.07$, $SD = 0.08$) than missing the stimulus ($M = -0.08$, $SD = 0.07$), $t(32) = 6.97$, $p < 0.001$, Cohen's $d = 1.21$ (Figure 4b).

4 | DISCUSSION

In this study, we investigated if conscious somatosensory perception varies across the cardiac cycle and how it interacts with the heart rate. In line with our main hypothesis of an increased somatosensory sensitivity during the later phase of the cardiac cycle, we found that the detection of near-threshold electrical finger nerve stimulation is significantly increased during diastole compared to systole. We also found

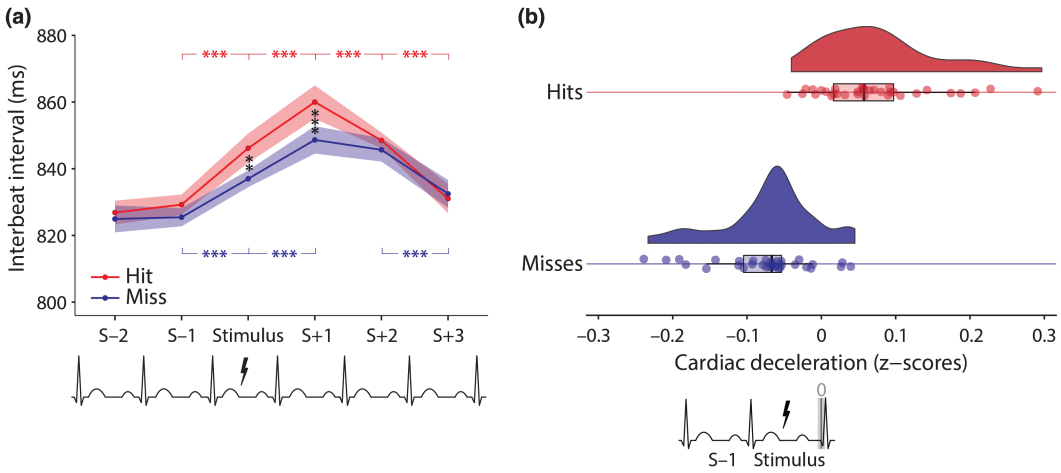

FIGURE 4 Association between heart rate and perceptual performance over the course of a trial. (a) Mean interbeat intervals (IBIs) for hits and misses: two IBIs before (S-1, S-2) and three IBIs after (S+1, S+2, S+3) the stimulus onset (stimulus). In sum, the previously found deceleration-acceleration pattern was observed during the detection task, with more pronounced cardiac deceleration after hits than after misses. Vertical and horizontal bars with asterisks indicate significant pairwise post hoc comparisons. (b) The extent of cardiac deceleration as a correlate of conscious perception, visualized using raincloud plots (Allen, Poggiali, Whitaker, Marshall, & Kievit, 2019). The standardized slope of cardiac deceleration (i.e., the difference between stimulus and S-1) was greater for hits than for misses. Colored bands indicate 95% within-participant confidence intervals (Morey, 2008). $^{**}p < 0.01$; $^{***}p < 0.001$

(a) no evidence that the heart rate before a stimulus influenced perceptual performance, (b) that conscious detection was significantly associated with a stronger cardiac deceleration in the IBI during and after a stimulus, and (c) that the heart rate significantly accelerated with a delay after nondetected compared to detected stimuli. Taken together, these results indicate that conscious access to somatosensory signals varies across the cardiac cycle and transiently decreases the heart rate.

The difference between our findings and a previous study, which reported increased somatosensory sensitivity during systole (R+300 ms) compared to diastole (R+600 ms; Edwards et al., 2009), may have several—also methodological—reasons: (a) Edwards et al. (2009) assessed perceptual thresholds at different time points within the cardiac cycle, whereas we used stimuli of constant intensity distributed across the entire cardiac cycle; (b) the stimuli in the previous study consisted of 1-ms square wave pulses at 250 Hz for 60 ms, while we used single rectangular pulses with a length of 200 μS; (c) in our analysis of detection across the cardiac cycle, perceptual performance was highest in the last quarter of the cardiac cycle. This period was not necessarily covered in the study by Edwards et al. (2009), in which the latest stimulation after the R peak occurred at R+600 ms. We conducted an additional analysis of our data to facilitate the comparison with Edwards et al. (2009), detailed in the supporting information. It might also be worth pointing out that our findings are in line with the original hypothesis of Edwards et al. (2009) that perceptual sensitivity is higher (and sensory thresholds are lower) at diastole than at systole.

A possible physiological mechanism for the relatively increased detection during diastole is the baroreceptor-driven inhibition of sensory neural systems during systole (Critchley & Garfinkel, 2015; Duschek et al., 2013). This is consistent with previous findings in which baroreceptor activity has been related to lower intensity ratings for acoustic (Cohen et al., 1980; Schulz et al., 2009) and painful stimuli (Wilkinson et al., 2013) as well as longer reaction times (Birren, Cardon, & Phillips, 1963; Edwards et al., 2007; McIntyre et al., 2008) for stimuli presented early (i.e., at systole) compared to late (i.e., at diastole) in the cardiac cycle. However, there is also evidence that specifically threatening visual stimuli are perceived more easily and rated as more intense during systole (Garfinkel et al., 2014). Yet, the faint electrical stimulation in our study does not qualify as a threat signal but is rather an emotionally neutral stimulus, as they are typically used in studies of cardiac effects on conscious perception.

More broadly, it is not clear whether perceptual fluctuations related to rhythmic activity of the body and the brain (such as the heartbeat and respiration and various forms of brain rhythms) come with an overall "functional advantage" or whether they are just an epiphenomenal consequence of physiological and anatomical constraints. For neural oscillations (e.g., alpha band-related variations in visual perception; Busch, Dubois, & VanRullen, 2009; Dugué, Marque, & VanRullen, 2011), it remains a matter of debate how perception benefits from inherent rhythmicity (VanRullen, 2016). It has been proposed that brain oscillations serve the effective communication between neurons (Fries, 2015) and enable the simultaneous encoding of multiple stimulus features (Lisman, 2005; VanRullen, Guyonneau, & Thorpe, 2005). However, perceptual rhythms in the brain have also been suggested to not have any functional role but result from satisfying biological constraints (VanRullen, 2016). A similar point could be made about the role of cardiac-related fluctuations in perception—especially because both are likely to be linked (Klimesch, 2013, 2018).

The present findings could also be understood as suppressing weak and nonsalient somatosensory signals from reaching consciousness during baroreceptor firing. Given the enhanced processing of threat stimuli (Garfinkel et al., 2014) and pain inhibition during systole (Wilkinson et al., 2013), it has been proposed that baroreceptor signals promote a fight-or-flight mode of behavior (Garfinkel & Critchley, 2016). In line with this interpretation, Pramme, Larra, Schächinger, and Frings (2016) reported enhanced visual selection during systole. Hence, baroreceptor-mediated inhibition of cortical activation might facilitate the allocation of attention to situationally relevant stimuli (Pramme et al., 2016). It could be hypothesized that a stressor-evoked heart rate increase facilitates the processing of situation-relevant information in the external world; by shortening diastole rather than systole (Herzog et al., 2002), this results in proportionally longer periods during which nonsalient stimuli are inhibited. Future studies could explore the functional role of perceptual periodicity, for example, by manipulating the salience of the near-threshold signals through different task requirements or an association with threatening stimuli (e.g., declaring or animating near-threshold somatosensory stimuli as bites from malaria-infected mosquitoes).

Further, accounting for the bidirectional information flow between the heart and the brain (Faes et al., 2017; Lin et al., 2016), we investigated the influence of the (prestimulus) heart rate on perception and, in turn, the influence of perception on (poststimulus) heart rate changes. Even though it was early hypothesized that cardiac deceleration enhances perceptual sensitivity (Graham & Clifton, 1966; Lacey, 1967; Lacey et al., 1963; Sandman, 1986; but see also Elliott, 1972), results are inconsistent in the auditory (Edwards & Alsip, 1969; Saxon & Dahle, 1971) or visual (Cobos et al., 2018; McCanne & Sandman, 1974; Park et al., 2014; Sandman et al., 1977) and outright lacking in the somatosensory modality. Our findings match reports in the visual domain (Cobos et al., 2018; Park et al., 2014) with respect to (a) the lack of evidence for the influence of the prestimulus heart rate on detection, and (b) a more pronounced cardiac deceleration after

detecting (relative to not detecting) near-threshold stimuli. In addition, we found that also the interbeat interval length during the somatosensory stimulation differed between hits and misses and that the extent of cardiac deceleration coincident with the stimulation was higher for detected compared to nondetected stimuli. Moreover, for nondetected stimuli, we observed a delayed cardiac acceleration, which might be a side effect of less pronounced deceleration after misses but has been also reported to occur after an incorrect visual stimuli discrimination (Łukowska, Sznajder, & Wierzchoń, 2018) and, more broadly, is thought to reflect the processing of erroneous responses (Crone et al., 2003; Danev & de Winter, 1971; Fiehler, Ullsperger, Grigutsch, & von Cramon, 2004; Hajcak, McDonald, & Simons, 2003).

This lengthening of the IBI reflects the rapid autonomic (i.e., parasympathetic) response to the consciously perceived stimulus (Barry, 2006; Knippenberg, Barry, Kuniecki, & van Luijtelaar, 2012). Due to its speed, it is likely to also affect the duration of the IBI, during which the stimulus is presented (Jennings & van der Molen, 1993; Jennings, van der Molen, Somsen, & Brock, 1991; Lacey & Lacey, 1977; Velden, Barry, & Wölk, 1987; Zimmerman, Velden, & Wölk, 1991; but see also Barry, 1993). It could also be that both cardiac deceleration and enhanced detection are the result of the central processes responsible for attentional preparation, which involve the activity of inhibitory brain circuits (Aron et al., 2007). Particularly subthalamic nuclei have been proposed to regulate the extent of (preparatory) cardiac deceleration (Jennings, van der Molen, & Tanase, 2009), which—as a marker of increased vigilance (Barry, 1988, 1996)—has also been shown to predict accuracy in tasks requiring skilled motor performance (Fahimi & Vaezmousavi, 2011; Tremayne & Barry, 2001). Even though our design minimized the influence of preparation attempts by randomizing stimulus onsets, it cannot be ruled out that the concomitant increases in cardiac deceleration and conscious detection were both caused by coincident peaks of attentional engagement (Fiebelkorn & Kastner, 2018).

The present study has several limitations: First, as baroreceptor or brain activity were not directly measured, we can only speculate about the baroreceptor influences on (central) sensory processing. Peripheral processes like pulse wave-related sensations may equally contribute to changes in perceptual sensitivity. Second, the lack of significant differences in cardiac effects on somatosensory perception between the groups with high and low interoceptive accuracy might be due to the limited sample sizes or the insufficient validity of the heartbeat counting task itself (Brener & Ring, 2016). Third, to apply signal detection theory measures (Green & Swets, 1966), future studies should allow to temporally locate false alarms within the cardiac cycle. In the current design, we used a noncued stimulus onset within a 1,800-ms time window. This precluded determination of the position of false alarms within the cardiac phases. Visual or acoustic cues for stimulus onsets would suffice for this purpose but may themselves introduce crossmodal interactions (Dionne, Meehan, Legon, & Staines, 2010), for which the influence of the cardiac cycle remains unknown. Future research could also consider including a graded measure of stimulus awareness (Ramsøy & Overgaard, 2004; Sandberg, Timmermans, Overgaard, & Cleeremans, 2010) to parametrically assess the effects of (un) conscious sensory processing on cardiac activity.

In sum, we find that conscious perception of somatosensory stimuli varies across the cardiac cycle and is associated with increased cardiac deceleration. This highlights the importance of activity in the autonomic nervous system for perceptual awareness. Our findings emphasize the irreducible relevance of bodily states for sensory processing and suggest a more holistic picture of an organism's cognition, for which contributions from the brain and from the rest of the body cannot be clearly separated.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1
Figure S1
Figure S2
Figure S3

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