



The impact of cardiac phases on multisensory integration

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ABSTRACT

The brain continuously processes information coming from both the external environment and visceral signals generated by the body. This constant information exchange between the body and the brain allows signals originating from the oscillatory activity of the heart, among others, to influence perception. Here, we investigated how the cardiac phase modulates multisensory integration, which is the process that allows information from multiple senses to combine non-linearly to reduce environmental uncertainty. Forty healthy participants completed a Simple Detection Task with unimodal (Auditory, Visual, Tactile) and bimodal (Audio-Tactile, Audio-Visual, Visuo-Tactile) stimuli presented 250 ms and 500 ms after the R-peak of the electrocardiogram, that is, systole and diastole, respectively. First, we found a nonspecific effect of the cardiac cycle phases on detection of both unimodal and bimodal stimuli. Reaction times were faster for stimuli presented during diastole, compared to systole. Then, applying the Race Model Inequality approach to quantify multisensory integration, Audio-Tactile and Visuo-Tactile, but not Audio-Visual stimuli, showed higher integration when presented during diastole than during systole. These findings indicate that the impact of the cardiac phase on multisensory integration may be specific for stimuli including somatosensory (i.e., tactile) inputs. This suggests that the heartbeat-related noise, which according to the interoceptive predictive coding theory suppresses somatosensory inputs, also affects multisensory integration during systole. In conclusion, our data extend the interoceptive predictive coding theory to the multisensory domain. From a more mechanistic view, they may reflect a reduced optimization of neural oscillations orchestrating multisensory integration during systole.

1. Introduction

Interoception is defined as the brain's capacity to represent the organism's internal state and includes the processes by which it senses, interprets, integrates, and regulates signals from within the body (Chen et al., 2021; Khalsa et al., 2018). One of the most studied sources of interoceptive signals is the heart, whose physiological cycle consists of two phases: systole and diastole. At ventricular systole, the heart contracts and ejects blood into the arteries, leading to an increase in firing rate of stretch-responsive baroreceptors in the arterial vessel walls (Lacey & Lacey, 1978; Landgren, 1952; Motyka et al. 2019; Rau & Elbert, 2001; Skora et al., 2022), which carry information about the strength and timing of each heartbeat (Critchley & Garfinkel, 2018). In contrast, during ventricular diastole, the heart fills with blood (i.e., blood is not being ejected) and baroreceptors significantly reduce their

firing rate (Lacey & Lacey, 1978; Landgren, 1952; Motyka et al., 2019; Rau & Elbert, 2001). The baroreceptor-mediated signals are transmitted through the glosso-pharyngeal and vagus nerves to the brainstem nuclei, reaching the nucleus tractus solitarius (NTS) and the parabrachial nucleus (PBN), where they are involved in the homeostatic control of blood pressure and heart rate. Finally, the signals are further relayed to distributed subcortical and cortical regions via thalamic projections with the hippocampus and the insular, anterior cingulate cortex (ACC), medial prefrontal and somatosensory cortices receiving the inputs, as well as other subcortical structures, including the cerebellum, hypothalamus, striatum, and the amygdala, which project to further cortical regions (Larra et al., 2020; Skora et al., 2022). Interestingly, research on interoception has shown that visceral signals, besides their role in homeostatic regulation, can also influence how we process exteroceptive sensory information (Al et al., 2020; Al et al., 2021; Ambrosini et al.,

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2019; Azevedo, Garfinkel et al., 2017; Azzalini et al., 2019; Critchley & Garfinkel, 2015, 2018; Galvez-Pol et al., 2020; Galvez-Pol et al., 2022; Garfinkel et al. 2014; Leganes-Fonteneau et al., 2021; Salomon et al., 2016). In particular, according to the so-called “baroreceptor hypothesis” (Lacey & Lacey, 1958), afferent neural signals from arterial baroreceptors occurring at systole induce changes in cortical inhibition (Duschek et al., 2013). This hypothesis has been validated using neck suction techniques, showing that baroreceptors’ stimulation leads to a globally reduced cortical excitability (Bonvallet et al., 1954; Rau et al., 1993; Skora et al., 2022), and consequently to dampened pain sensitivity (Droste et al. 1994; Suarez-Roca et al., 2021), decreased muscle tone (Dworkin et al., 1994) and reduced startle reflex (Nyklíček et al., 2005).

The timing of stimuli presentation along the cardiac cycle (i.e., systole vs. diastole) impacts perceptual accuracy of visual, auditory, and tactile stimuli (Al et al., 2020, 2021; Grund et al., 2022; Motyka et al., 2019; Park et al., 2014; Salomon et al., 2016; Sandman, 1984; Sandman et al., 1977; Saxon, 1970). For example, within the somatosensory domain, detection of near-threshold stimuli was more accurate towards the diastolic phase of the cardiac cycle, compared to systole (Al et al., 2020, 2021; Grund et al., 2022; Motyka et al., 2019). Moreover, reaction times and performance accuracy for auditory (Birren et al., 1963; Yang et al., 2017) and visual stimuli (Ren et al., 2022; Sandman et al., 1977) depended upon the cardiac phase in which the stimuli were presented with diastole improving accuracy and reaction time compared to systole. Altogether, these findings indicate that sensory performance is enhanced during the cardiac diastole for both exteroceptive modalities (Birren et al., 1963; Ren et al., 2022; Sandman et al., 1977; Yang et al., 2017). Likewise, neural responses to somatosensory stimuli are modulated across the cardiac cycle. Recently, late EEG somatosensory evoked potentials were found to be higher during diastole than systole, and inversely related to the amplitude of the heartbeat-evoked potential (HEP) (Al et al., 2020, 2021), an electrophysiological marker of cardiac interoception (Coll et al., 2021; Park & Blanke, 2019). Similarly, auditory stimuli presentation synchronized with the diastolic phase produced a higher N1 component compared to systole, suggesting increased auditory sensory-perceptual processing (Sandman, 1984; van Elk et al., 2014).

Recently, the abovementioned findings have been interpreted following the predictive coding framework, according to which perception arises from dynamic interactions between incoming sensory inputs from the external world and the brain’s formed hypotheses about their hidden causes (Clark, 2013; Friston, 2010). In this way, the brain works as an active inference generator minimizing the difference between priors (or predictions) and incoming sensation (i.e., prediction error) (Clark, 2013; Friston, 2010). According to the interoceptive predictive coding account (Barrett & Simmons, 2015; Pezzulo, 2014; Seth, 2013; Seth & Friston, 2016), the representation of the world includes also interoceptive signals (e.g., the heartbeat), which can modulate the degree to which sensory evidence is accumulated during perception via changes in the precision of prediction errors (Allen et al., 2022). Therefore, it has been proposed that the same brain mechanism that predicts interoceptive bodily changes related to systole can dampen the perception of exteroceptive stimuli occurring in the same time window (Al et al., 2020, 2021; Allen et al., 2022; Grund et al., 2022).

Despite the extensive body of literature on the influence of cardiac phases on sensory perception, all the studies carried out so far have focused on single modalities, neglecting multisensory perception, rendering these findings far from everyday life perception. Indeed, our exteroceptive perception relies on multiple senses, hence it is often the result of multisensory integration, which is defined as the ability to synthesize information arriving from cross-modal stimuli (Stein, 1998; Stein & Stanford, 2008). Multisensory integration generates a facilitatory effect on both perception and action, reducing environmental uncertainty (Driver & Noesselt, 2008; Meredith & Stein, 1986; Vastano et al., 2022). At the behavioral level, this facilitatory effect is reflected in faster reaction times (RTs) for multisensory pair, compared to the most

effective of its component stimuli (multisensory enhancement) (Stein & Stanford, 2008). Indeed, this multisensory enhancement speeds sensory processing shortening the interval between stimuli encoding and overt behavior (Bell et al., 2005; Rowland et al., 2007). At the neural level, multisensory perception is supported by the coherence of oscillatory neural signals (Keil & Senkowski, 2018; Senkowski et al., 2008). In particular, inter-trial coherence (ITC) increase in neural activity follows the impact of a sensory stimulus on spontaneous activity in the brain (Kanayama et al., 2015; Mercier et al., 2013; Thorne et al., 2011).

For the first time, our work investigated the influence of cardiac cycle phases on a fundamental property of exteroception, namely multisensory integration. It also aimed at exploring whether the cardiac modulation of multisensory integration was specific for those bimodal combinations containing tactile inputs, as somatosensory signals are thought to be tightly linked to heartbeat-related activity. Here, we time-locked the presentation of unimodal and cross-modal stimuli (multisensory pairs) to systole and diastole in a Simple Detection Task paradigm. The main aim of the study was to assess the influence of the cardiac phase on multisensory perception, identifying two cardiac phase-related phenomena. First, based on previous studies suggesting a more efficient sensory processing during minimal baroreceptor stimulation at diastole compared to systole across all sensory modalities, we predicted that RTs to unimodal and multimodal stimuli would vary depending on the phase of the cardiac cycle: responses would be slower at systole and faster at diastole. Second, considering recent findings highlighting the relevance of heartbeat-related activity on somatosensory perception as both arising from the body, then we hypothesized that the cardiac cycle phases would specifically impact the integration of multimodal stimuli containing tactile inputs, leading to higher integration at diastole compared to systole.

Overall, our research investigated the impact of cardiac phases on multisensory integration, expanding the interoceptive predictive coding framework to encompass multimodal perception. Previous studies have predominantly focused on individual sensory modalities, overlooking the significance of multisensory integration. By specifically examining multisensory integration, our study aimed to provide a more comprehensive understanding of how sensory information from the environment is processed and integrated with the fluctuating cardiac activity. This approach allows for a more ecologically valid exploration of the topic, aligning with our everyday perception. Furthermore, our research offers a fresh and ecologically grounded approach to comprehending the fundamental mechanisms that underlie brain-body-perception coupling. As a result, it may yield valuable insights for clinical populations affected by conditions like schizophrenia and autism, which exhibit abnormal multisensory integration and disrupted interoceptive systems (Di Cosmo et al., 2021; Ferri et al., 2017; Quattrocki & Friston, 2014; Stevenson et al., 2014; Yao & Thakkar, 2022).

2. Materials and methods

2.1. Participants

Forty healthy participants (27 females; 8 left-handed; mean age = 25.9 years, SD = 4.2) participated in the study. All participants had normal or corrected-to-normal vision, no history of hearing loss, and neither mental nor neurological disorders, as self-reported. We estimated the sample size with an a-priori power analysis for paired t-test through the G*Power 3 software (Version 3.1.9.6, Düsseldorf, Germany) (Faul et al., 2007), based on previous literature on multisensory integration showing medium-to-large effect sizes (Barutcu & Spence, 2020; Tong et al., 2021). The power analysis indicated a sample size of 34 participants to detect significant within-subjects effects, with a medium effect size (Cohen’s $d = 0.5$) and a statistical power of 0.8. Ethical approval from the local ethics board was obtained (Institutional Review Board of Psychology – IRBP, Department of Psychological, Health and Territorial Sciences, University “G. d’Annunzio”, Chieti-Pescara,

Protocol Number 20015). The experiment was conducted in accordance with the Declaration of Helsinki and its later amendments. Before the experiment, participants gave written informed consent.

2.2. Stimuli and procedure

Participants were presented with three types of unimodal stimuli (Auditory - A, Tactile - T, and Visual - V) and their bimodal combinations (Audio-Visual - AV, Audio-Tactile - AT, and Visuo-Tactile - VT). The A stimulus consisted of a pure tone (1000 Hz; 30 ms of duration) presented approximately at 60 dB using a buzzer; the V stimulus (30 ms of duration) was delivered through a light-emitting diode (LED) (5 mm diameter; 200 mcd); the T stimulus consisted of a suprathreshold electrical pulse (duration of 100 μ s), delivered on the middle finger of the right hand using a Digitimer (model DS7A, Digitimer Ltd., Welwyn Garden City, UK). A and V stimuli were delivered through an in-house box containing a fixation cross, the buzzer, and the LED (Fig. 1). All stimuli were administered using the E-Prime 3.0 software (Psychology Software Tools, Pittsburgh, PA, USA) connected to a TriggerStation™ (BRAINTRENDS LTD 2010, Rome, Italy).

Individual thresholds for the tactile stimulus were determined for each participant with the method of the limits (Gerr & Letz, 1988; Vastano et al., 2022). Before starting the experiment, the intensity of the stimulator was set to 0 mA, and then progressively increased by 1 mA until the participant reported to clearly perceive the stimulation (i.e., suprathreshold stimulation). Then, the participant was additionally stimulated 5 times: if only one of the additional stimuli was not detected, the intensity was increased by 1 mA, and the procedure was repeated (Vastano et al., 2022). Unbeknownst to the participants, stimuli were presented with timings that allowed synchronization with phases of the cardiac cycle (i.e., systole or diastole). To this purpose, 3 ECG electrodes (Ag/AgCl) were placed in a II-Lead chest configuration: two electrodes were positioned on the left side and right side of the participant's lower

abdomen, and another electrode was located underneath the right collarbone. The cardiac signal was continuously recorded with a BIOPAC MP160 System (BIOPAC System, Inc., Goleta, CA, USA) (low-pass filter: 35 Hz; high-pass filter: 0.05 Hz; notch filter: 50 Hz; sampling rate: 2000 Hz) using the AcqKnowledge software (version 5.0.5, BIOPAC System, Inc., Goleta, CA, USA). The occurrence of the R-peaks in the ECG signal was identified online through a Digital Trigger Unit (DTU100, BIOPAC System, Inc., Goleta, CA, USA).

Stimuli were presented 250 ms after the R-peak in the systole condition, and 500 ms after the R-peak in the diastole condition. Such delays were chosen according to a number of several studies, which estimated the maximum peak of arterial baroreceptors activity at R+ 250 ms, and the lowest peak of baroreceptors' activity at R+ 500 ms (Ambrosini et al., 2019; Edwards et al., 2009; Garfinkel et al., 2014; Kroeker & Wood, 1955). Due to high heart rate, the offline control analysis of ECG recordings revealed that very few diastole trials (25 out of 19200: i.e., 0.13%) were presented immediately after the subsequent R-peak. Those trials were not excluded as they were presented only few milliseconds (~15 ms) after the R-peak, within a time lag in which the brain is not yet informed about the heartbeat (i.e., after 250 ms) (Angell James, 1971; Coleridge et al., 1987; Edwards et al., 2007). Despite the individual variability of heart rate that can, in turn, affect the actual time locking at systole and diastole, the presentation of stimuli triggered to the cardiac phases allowed us to have enough trials to perform multisensory integration's analysis (i.e., Race Model Inequality) (Gondan, 2010; Gondan & Minakata, 2016; Kiesel et al., 2007). We presented a total of 480 stimuli to each participant, divided into 2 blocks. In each block, 240 presented stimuli were equally divided for each unimodal and bimodal stimulation (40 A, 40 T, 40 V, 40 AT, 40 AV, 40 VT). Among these, half of the stimuli were presented within the participant's cardiac systole (systole condition), whereas the other half was presented within the cardiac diastole (diastole condition). The number of trials was chosen based on published recommendations (Gondan, 2010; Gondan & Minakata, 2016; Kiesel et al., 2007; Mahoney & Verghese, 2019).

The experiment consisted of a Simple Detection Task. Each trial started with the online R-peak detection performed by the DTU100 (BIOPAC System, Inc., Goleta, CA, USA). After either 250 ms (systole condition) or 500 ms (diastole condition) from the R-peak, either a unimodal (A, T, V) or a bimodal stimulus (AT, AV, VT) was presented in random order. Participants were seated 57 cm from the in-house box and were instructed to respond by pressing a pedal with the right foot as soon as they perceived any stimulus or pair. The allowed maximum response time was set to 2000 ms. After a fixed inter-trial interval (500 ms), the next trial started (Fig. 2). We used fixed inter-trial interval as the jittering of the onset of each trial was guaranteed by the natural occurring variability in inter-beat intervals. The experimental session was preceded by a brief training session to familiarize with the task. RTs were collected using a pedal board connected to the TriggerStation™ (BRAINTRENDS LTD 2010, Rome, Italy). Missed trials were not replaced. To prevent fatigue and maintain focus, participants were allowed to take a break between the two blocks.

2.3. Statistical analyses

We first performed ANOVAs to assess whether the cardiac phase (i.e., systole vs. diastole) affected simple Reaction Times (RTs) to sensory stimuli, and to confirm the well-known redundant signals effect (RSE, i.e., faster RTs to bimodal stimulations than to unimodal ones) (Diederich & Colonius, 2004; Hershenson, 1962; Todd, 1912). A further step was to assess any effect of the cardiac phase on multisensory integration by testing the Race Model Inequality (RMI) (Miller, 1982) separately for systole/diastole and each multisensory combination. RMI rejection accounts for interactions that allow unimodal signals from redundant information sources to integrate or combine non-linearly (Mahoney et al., 2011). As the performance accuracy is expected to be at ceiling with high detection rates and RMI typically works on RTs distributions (Otto

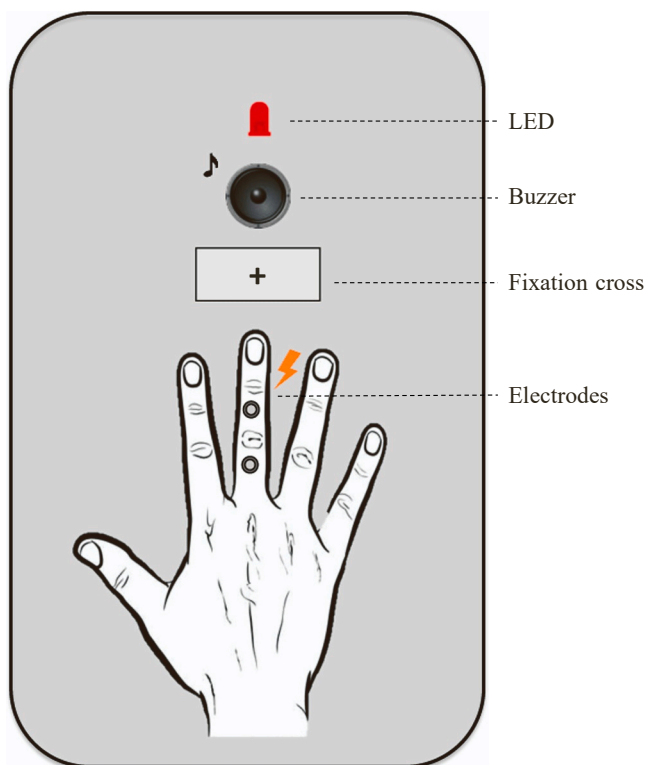


Fig. 1. Stimulus delivery apparatus. The in-house box allowed to present stimuli: electrical pulse on the right middle finger (T), the LED (V), and the buzzer (A), in close spatial proximity.

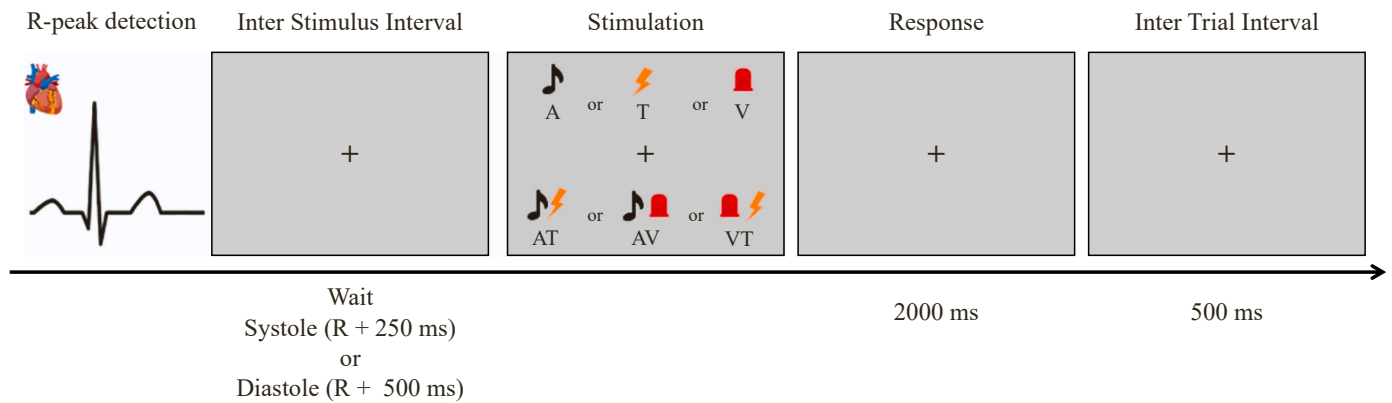


Fig. 2. Timeline of the experimental trials. Each trial started with online detection of the R-peak. After either 250 ms (systole condition) or 500 ms (diastole condition) from the R-peak, either unimodal (Auditory, Tactile, Visual) or bimodal (Audio-Tactile, Audio-Visual, Visuo-Tactile) stimuli were presented. Participants had to respond by pressing a pedal within 2000 ms. There was a fixed inter-trial interval (500 ms) before the subsequent trial.

& Mamassian, 2017), we did not analyze it further.

2.3.1. Effect of the cardiac phase on reaction times

The following adjustments of RTs were performed before entering them into the ANOVA models. First, RTs faster than 120 ms were considered fast guesses and were removed from the analysis (Couth et al., 2017). Next, as RTs distributions violated the assumption of normality (K-S normality test, $d = 0.12$, $p < .01$; Lilliefors $p < .01$), they were normalized using a log-transformation. Finally, for each stimulus type and participant, we trimmed all log-transformed RTs falling outside 2 SD from the mean. Adjusted RTs were entered into three separate 3×2 repeated-measure ANOVAs with the Heart (i.e., systole vs. diastole) and Modality (i.e., A/T/AT or A/V/AV or V/T/VT) as within-subject factors (Vastano et al., 2022). These analyses allowed us to verify the influence of the cardiac phase on RTs. In addition, they were also used to confirm the well-known RSE (i.e., faster RTs to bimodal stimulations than to unimodal ones) (Diederich & Colonius, 2004; Hershenson, 1962; Todd, 1912). Post-hoc analyses were run, when necessary, using the Tukey test.

2.3.2. Race model inequality

Multisensory integration in bimodal stimulations was assessed with the RMI (Miller, 1982). In brief, typically participants exhibit shorter RTs in bimodal stimulations than in unimodal ones, and several models have been proposed to explain this effect, known as RSE (Diederich & Colonius, 2004; Hershenson, 1962; Todd, 1912). In general, Race Model approaches consider the redundancy gain as a mere consequence of statistical facilitation (Raab, 1962), which does not reflect multisensory integration processes. In other words, according to Race Model approaches, components of the two unimodal stimuli would be processed in separate sensory channels, and the fastest one would trigger the response (i.e., “wins the race”). The RMI is used to rule out the possibility that RTs facilitation could be explained by separate processing (i.e., Race Model). It states that the cumulative RTs distribution for the redundant stimuli never exceeds the sum of the RTs distribution for the unimodal stimuli (Gondan, 2010; Gondan & Minakata, 2016), while the rejection of this possibility reflects multisensory interactions.

To assess multisensory integration, the RMI was performed separately for each modality combination (i.e., A/T/AT, A/V/AV, V/T/VT). Following the procedure proposed by Mahoney & Verghese (2019), we clustered raw RTs into 21 progressively increasing time-bins, by first identifying a specific RT range for each participant, obtained by subtracting its slowest RT from the fastest RT, and then by gradually adding the 5% of this range to each time-bin. Next, we created the cumulative distribution frequency (CDF) by summing the total probabilities across the quantized bins, obtaining 11-time bins (0%, 0% + 10%, 0% + 10% + 20%, etc.) for each of the three multisensory pair. The CDF of the

multisensory pair (i.e., AT, AV, VT) represents the observed CDF, whereas the predicted CDF corresponds to the independent version of the Race Model (Fig. 3) (Stevenson et al., 2014) calculated across each of the 11-time bins using the following formula:

$$\text{CDF}(\text{Uni}_x) + \text{CDF}(\text{Uni}_y) - \text{CDF}(\text{Uni}_x) * \text{CDF}(\text{Uni}_y)$$

To test for significant violations of the RMI, while controlling for Type I error (Kiesel et al., 2007), we conducted a series of permutation tests (Gondan, 2010; Mahoney & Verghese, 2019, 2020) over group averaged RMI data within the violated portion of the CDF (i.e., those portions where differences between observed CDF and predicted CDF were positive). The RMI permutation test provides a T_{\max} value, a T_{critic} value, the 95% criterion, and a p-value, representing the significance level. If the observed CDF was significantly greater than the predicted CDF, the RMI was rejected (or violated) and RTs facilitation in multimodal stimuli was considered dependent on multisensory integration, and not on redundancy gain (Mahoney & Verghese, 2019, 2020).

To assess the influence of the cardiac phase on multisensory integration, we first performed the RMI in each participant separately for each cardiac phase and stimulus combination (e.g., A/T/AT systole, A/T/AT diastole, A/V/AV systole, A/V/AV diastole, etc.), then we calculated the area-under-the-curve (AUC) of the difference wave (i.e., observed CDF minus predicted CDF) for each stimulus combination and each cardiac phase. The AUC quantifies the magnitude of multisensory integration as it provides the accumulated probability of the RMI violation over consecutive time bins, allowing us to disentangle the impact of cardiac phases (Mahoney & Verghese, 2019, 2020). Consequently, we performed a series of paired t-tests between systole AUC vs. diastole AUC, for each time-bin and bimodal stimulation (e.g., AUC 0.1 – 0.2 AT systole vs. AUC 0.1 – 0.2 AT diastole, etc.). Obtained p-values were adjusted for multiple comparisons with the Benjamini & Hochberg procedure (False Discovery Rate – FDR) (Benjamini & Hochberg, 1995). Following previous literature, we determined that at least two consecutive t-tests have to reach the significance level to indicate violations of the RMI (Senkowski et al., 2011).

3. Results

3.1. Reaction Times

Repeated-measures ANOVAs were performed on 40 participants, after excluding 3 participants due to excessive missing responses ($> 50\%$ in any condition). Performance accuracy was high across all unimodal and multimodal stimulations (A/Sys = 99%, AT/Sys = 99%, AV/Sys = 99%, T/Sys = 91%, V/Sys = 98%, VT/Sys = 98%, A/Dia = 99%, AT/Dia

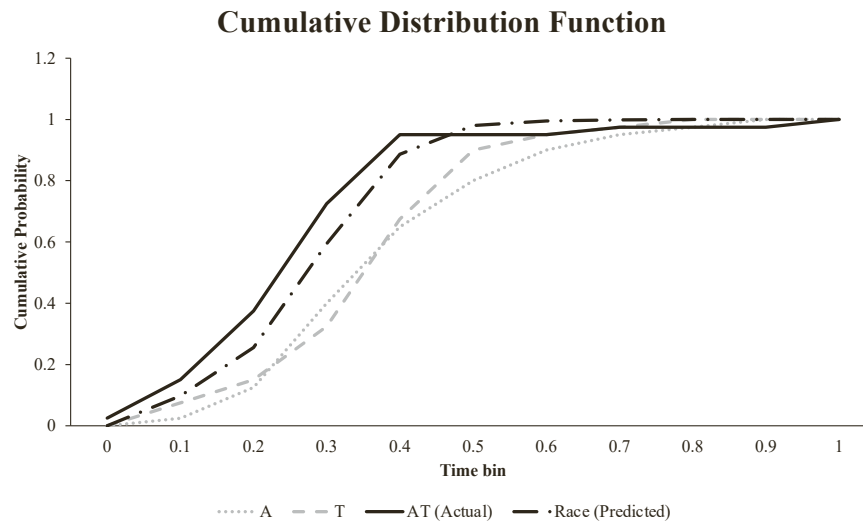


Fig. 3. A single participant example of cumulative distribution function (CDF). CDF of auditory (A), tactile (T), and audio-tactile (AT), as well as the Independent Race Model (Race). According to the Race Model Inequality, AT should always be below the Race (i.e., never exceeds the sum of the distribution of unimodal stimuli). Here, the violation of the RMI occurs within the range 0–0.4 time bins.

= 99%, AV/Dia = 98%, T/Dia = 92%, V/Dia = 98%, VT/Dia = 99%). Results from A/T/AT repeated-measures ANOVA showed the main effect of Modality ($F(2, 78) = 25.62$; $p < .001$; $\eta^2 = .387$) with detection accuracy lower for T stimuli (Mean = 91.41; SD = 9.73) compared to A stimuli (Mean = 98.56; SD = 2.46; $t = -4.92$; $p_{\text{Tukey}} < .001$) and AT stimuli (Mean = 98.88; SD = 1.94; $t = -5.10$; $p_{\text{Tukey}} < .001$). Similarly, results from V/T/VT repeated-measures ANOVA showed the main effect of Modality ($F(2, 78) = 24.01$; $p < .001$; $\eta^2 = .381$) with detection accuracy lower for T stimuli (Mean = 91.41; SD = 9.73) compared to V stimuli (Mean = 98.13; SD = 3.07; $t = -4.64$; $p_{\text{Tukey}} < .001$) and VT stimuli (Mean = 98.88; SD = 1.98; $t = -5.23$; $p_{\text{Tukey}} < .001$).

For reaction time, results from repeated-measures ANOVA for the A/T/AT modalities showed a significant main effect of Modality ($F(2, 78) = 142.05$; $p < .001$; $\eta^2 = .785$; Fig. 4, Panel A). Post hoc tests showed faster RTs for bimodal stimulation (AT Mean = 5.81; AT SD = 0.20) compared to unimodal stimulation (A Mean = 5.89; A SD = 0.20; $t = -10.09$, $p_{\text{Tukey}} < .001$; T Mean = 6.03; T SD = 0.18; $t = -15.95$, $p_{\text{Tukey}} < .001$) and faster responses to A stimuli than to T stimuli ($t = -8.51$, $p_{\text{Tukey}} < .001$). The main effect of Heart was also significant ($F(1, 39) = 17.33$; $p < .001$; $\eta^2 = .308$) with faster RTs at diastole (Mean = 5.89; SD = 0.19) as compared to systole (Mean = 5.91; SD = 0.18; Fig. 4, Panel B).

The ANOVA on V/T/VT modalities showed a significant main effect of Modality ($F(2, 78) = 112.15$; $p < .001$; $\eta^2 = .742$; Fig. 4, Panel C). Post hoc tests showed faster RTs for bimodal stimulation (VT Mean = 5.86; VT SD = 0.17) compared to unimodal stimulation (V Mean = 5.94; V SD = 0.16; $t = -13.70$, $p_{\text{Tukey}} < .001$; T Mean = 6.03; T SD = 0.18; $t = -14.29$, $p_{\text{Tukey}} < .001$). Also, responses to V stimuli were faster than to T stimuli ($t = -5.88$, $p_{\text{Tukey}} < .001$). The main effect of Heart was also significant ($F(1, 39) = 29.52$; $p < .001$; $\eta^2 = .431$) with faster RTs at diastole (Mean = 5.93; SD = 0.17) compared to systole (Mean = 5.96; SD = 0.16; Fig. 4, Panel D).

Finally, results from A/V/AV modalities showed a significant main effect of Modality ($F(2, 78) = 103.53$; $p < .001$; $\eta^2 = .726$; Fig. 4, Panel E). Post hoc tests showed faster RTs to bimodal stimuli (AV Mean = 5.81; AV SD = 0.20) compared to unimodal stimuli (A Mean = 5.89; A SD = 0.20; $t = -10.02$, $p_{\text{Tukey}} < .001$; V Mean = 5.94; V SD = 0.16; $t = -14.96$, $p_{\text{Tukey}} < .001$). Furthermore, responses to A stimuli were faster than to V stimuli ($t = -4.97$, $p_{\text{Tukey}} < .001$). The main effect of Heart was also significant ($F(1, 39) = 13.32$; $p < .001$; $\eta^2 = .255$) with faster RTs at diastole (Mean = 5.87; SD = 0.19) compared to systole (Mean = 5.89; SD = 0.18; Fig. 4, Panel F). Although we did not have a

specific hypothesis on the interaction effects, here we reported the result for completeness. The interaction Modality x Heart was significant ($F(2, 78) = 5.05$; $p = .01$; $\eta^2 = .115$). Post hoc tests showed faster responses for AV stimuli at diastole (Mean = 5.79; SD = 0.20) compared to AV stimuli at systole (Mean = 5.82; SD = 0.19; $t = -5.23$; $p_{\text{Tukey}} < .001$).

Taken together, results from ANOVAs indicated faster RTs to multisensory as well as unisensory stimuli delivered at diastole compared to systole. Moreover, they confirmed faster RTs to bimodal stimulations than unimodal ones (i.e., RSE). All these effects were found for each stimulus combination (A/T/AT, V/T/VT, A/V/AV). These main effects motivated a further analysis, using the RMI, to understand, first, whether the RSE was due to multisensory integration, second and most important if the cardiac cycle modulated such multisensory integration processes.

3.2. Race model inequality

To investigate the presence of multisensory integration in bimodal stimulations, we performed a series of RMI permutation tests (Gondan, 2010) for each multisensory pair and cardiac phase. We found significant violations of the RMI, showing multisensory integration in all the conditions. In particular, for the AT stimulation, we found a significant violation of the RMI at systole within time bins ranging from 0.1 to 0.3 ($T_{\text{max}} = 3.96$, $T_{\text{critic}} = 2.04$, $p = .001$), and at diastole on time bins from 0.1 to 0.4 ($T_{\text{max}} = 5.31$, $T_{\text{critic}} = 2.06$, $p < .001$). Multisensory integration occurred also for AV stimuli in both systole (time bins 0.1–0.2, $T_{\text{max}} = 3.31$, $T_{\text{critic}} = 1.89$, $p = .002$) and diastole (time bins 0.1–0.3, $T_{\text{max}} = 3.97$, $T_{\text{critic}} = 2.01$, $p = .001$). Similarly, for the VT stimulation, RMI permutation tests indicated significant integration in both cardiac phases: systole (time bins 0.1–0.2, $T_{\text{max}} = 4.26$, $T_{\text{critic}} = 1.88$, $p < .001$), and diastole (time bins 0.1–0.4, $T_{\text{max}} = 5.95$, $T_{\text{critic}} = 2.11$, $p < .001$).

Crucially, when we focused on the role of the cardiac phase on multisensory integration, paired sample t-test between AUC belonging to systole and diastole showed a significantly larger violation at diastole compared to systole for the AT and the VT stimulation (AT, time bins 0–0.3, Table 1; Fig. 5, Panel A; VT, time bins 0.2–0.4, Table 1; Fig. 5, Panel C), indicating a different impact of the cardiac phases on multisensory integration, specifically for AT and VT. In contrast, we found no differences in multisensory integration among cardiac phases for AV stimulations, as the criterion of at least two significant consecutive time bins was not fulfilled (see Section 2.3.2) (Table 1, Fig. 5, Panel B). Indeed, as indicated in Table 1, AUC in the time bin 0.3–0.4 for AV

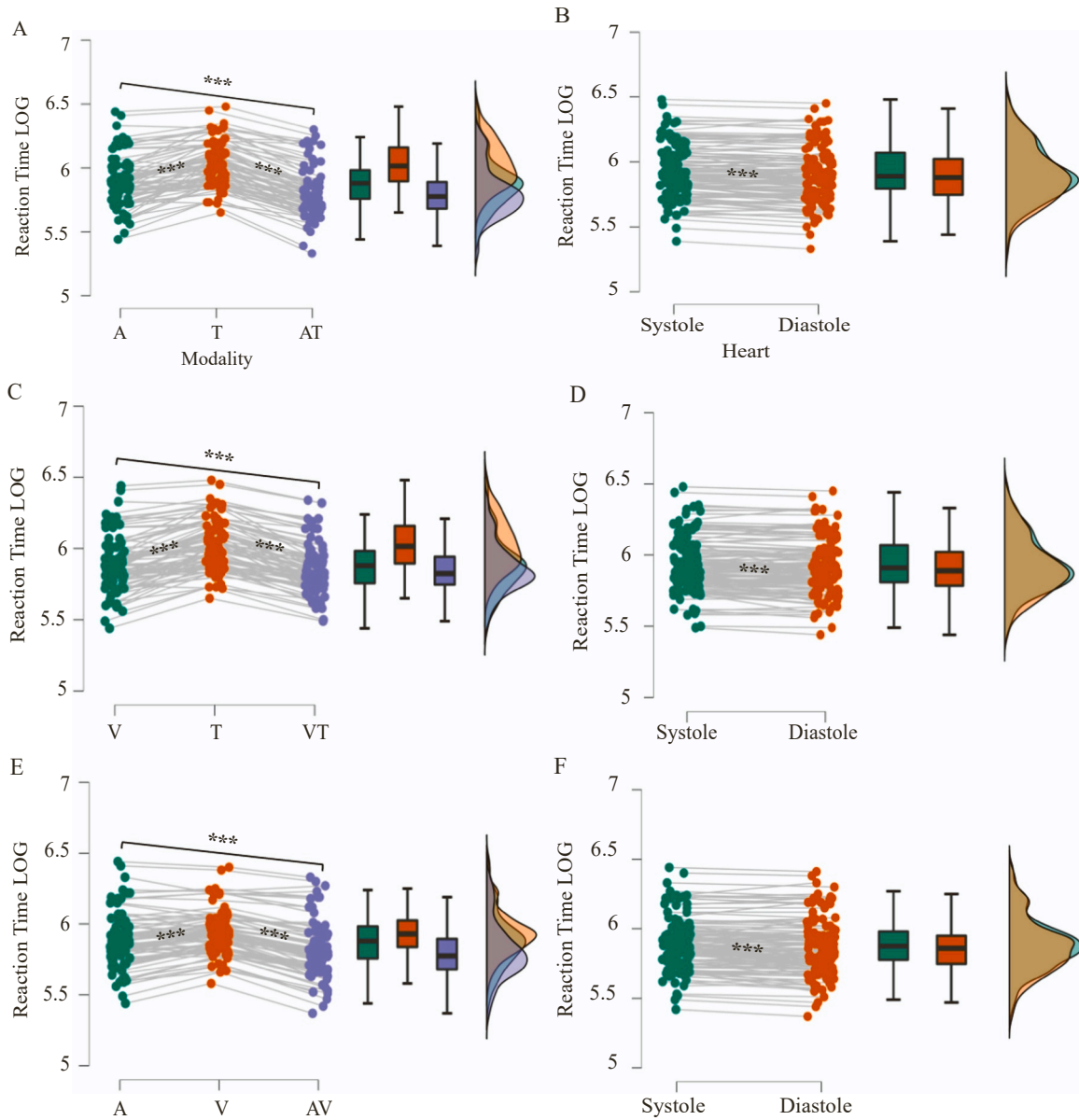


Fig. 4. Effects of stimulus type and cardiac phase on Reaction Times (RTs). Raincloud plots from 3×2 repeated measures ANOVA A/T/AT (A – B), 3×2 repeated measures ANOVA V/T/VT. (C – D), 3×2 repeated measures ANOVA A/V/AV (E – F). *** represents $p_{\text{Tukey}} < .001$.

Table 1

T-test results between systole and diastole for AT, AV, and VT (for AT $*p < .05$; for VT $*p < .025$, 5 t-tests FDR corrected). Only those time bins containing violation of the Race Model Inequality are reported. Differences in multisensory integration were considered only if the criterion of at least two significant consecutive time bins was fulfilled. AUC = Area Under the Curve.

AUC	Audio-Tactile			Audio-Visual			Visuo-Tactile		
	Systole	Diastole	p-value	Systole	Diastole	p-value	Systole	Diastole	p-value
0–0.1	0.01(0.05)	0.04(0.06)	.035 *	0.02(0.06)	0.03(0.05)	.442	0.03(0.05)	0.02(0.05)	.559
0.1–0.2	0.03(0.07)	0.07(0.09)	.005 *	0.03(0.09)	0.04(0.09)	.431	0.03(0.06)	0.05(0.08)	.126
0.2–0.3	0.02(0.09)	0.05(0.08)	.040 *	-0.02(0.09)	0.01(0.11)	.033	0.00(0.07)	0.04(0.08)	.019 *
0.3–0.4	0.00(0.08)	0.01(0.06)	.223	-0.06(0.09)	-0.01(0.09)	.007	-0.02(0.06)	0.01(0.06)	.014 *
Total	0.05(0.25)	0.17(0.24)	.004 *	-0.03(0.25)	0.06(0.30)	.015	0.05(0.19)	0.13(0.21)	.030

stimulations are both negative (systole and diastole), so they cannot be considered as multisensory integration.

4. Discussion

The fundamental impact of cardiac activity has been reported for a

wide variety of perceptual and cognitive processes (Azzalini et al., 2019; Critchley & Garfinkel, 2018; Edwards et al., 2001, 2009; Garfinkel et al. 2013, 2014; Park & Tallon-Baudry, 2014; Rae et al., 2018; Skora et al., 2022). However, its role in modulating the perception of external sensory stimuli has not been fully described so far. The aim of the present study was to investigate the influence of cardiac phases on multisensory

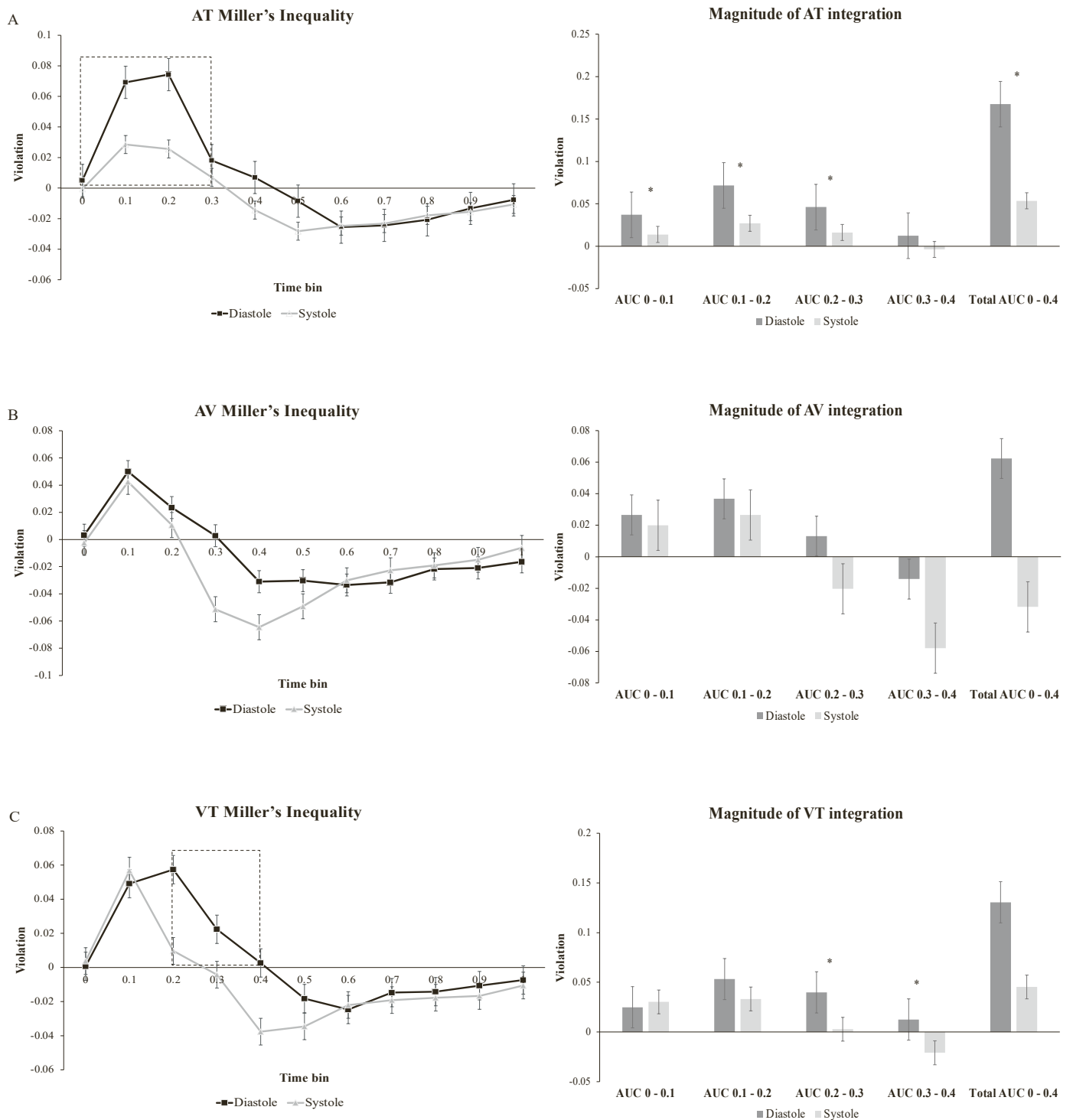


Fig. 5. Miller's inequality for multisensory pairs. Figures show violations in Audio-Tactile (A), Audio-Visual (B), and Visuo-Tactile (C) measured as difference in CDFs between bimodal and the correspondent race (positive values indicate violation). The dashed contour lines represent areas with significant differences between diastole and systole. Histograms on the right side show AUC values which serve as the magnitude of multisensory integration. The asterisks represent significant t-tests between diastole and systole (reported in Table 1).

integration, i.e., the mechanism that allows a coherent perception of the external environment by synthesizing information from multiple senses (Stein & Stanford, 2008). Here, we presented unimodal and bimodal stimuli to shed light on the process underlying the interplay between interception and exteroception. In a Simple Detection Task paradigm, we assessed the influence of the cardiac phase on multisensory integration by analyzing and modeling reaction times to unimodal and

bimodal stimuli presented at each cardiac phase. Our results indicated that responses to multisensory pairs (AT, AV, VT) were faster than those to unimodal stimuli (A, T, V). That is the demonstration of the redundant signal effect, according to which redundant conditions (two sensory signals) elicit quicker reaction times compared to the single sensory condition (Diederich & Colonius, 2004; Hershenson, 1962; Miller, 1982; Otto & Mamassian, 2017; Todd, 1912). To confirm our first hypothesis,

the presentation of stimuli time-locked to each cardiac phase significantly affected behavioral performance, resulting in faster responses to unimodal and bimodal stimuli during diastole, compared to systole. This is consistent with previous studies on cardiac interoception reporting enhanced stimulus detection during diastole rather than systole due to interoceptive feedback from baroreceptors (Al et al., 2020, 2021; Birren et al., 1963; Motyka et al., 2019; Sandman, 1984; Sandman et al., 1977), which affects brain activity specifically during systole (Critchley & Garfinkel, 2015; Duschek et al., 2013; Rau et al., 1993). These results are also in agreement with the interoceptive predictive coding account, according to which bodily consequences of biorhythms, such as the heartbeat, are actively predicted and suppressed from entering conscious perception by the same top-down suppression mechanism that inhibits the detection of external stimuli when presented in the time window of baroreceptors firing (i.e., the systolic phase) (Al et al., 2021; Salomon et al., 2016). Thus, the cardiac systole can be regarded as a period of perceptual uncertainty in which the differentiation between “internal noise” and exteroceptive stimuli becomes more difficult (Barrett & Simmons, 2015; Seth & Friston, 2016).

Crucially, here we demonstrated a specific effect of the cardiac phase on multisensory perception, providing support to our second hypothesis. Despite multisensory integration occurred in all bimodal pairs and cardiac phases, it was significantly stronger at diastole compared to systole only for Audio-Tactile and Visuo-Tactile pairs, but not for Audio-Visual pair. This specific involvement of the tactile input can be partially explained by the shared physiological pathways between somatosensory processing (i.e., tactile perception) and heartbeat-related sensations (i.e., the ability to detect one’s own heartbeats) (Khalsa et al., 2009; Knapp-Kline et al., 2021). Indeed, the somatosensory cortex has been mentioned among the relay stations of cardiac sensory information, as well as among the cortical sources of the heartbeat evoked potential (Coll et al., 2021; Park & Blanke, 2019). Therefore, it might be possible that the decreased multisensory integration at cardiac systole is due to a less efficient interaction of tactile stimuli with auditory and visual stimuli. In particular, the tactile stimulus weakened by the top-down predictive suppression related to the systolic interference (Al et al., 2021) would not be able to optimize the response to the auditory or visual stimulus, and this would result in a reduction of early multisensory integration.

This hypothesis is based on a large body of evidence from both animal and human studies. Generally, multisensory integration refers to the process by which a behavioral response, or the activity elicited by one stimulus, can be modulated (enhanced or depressed) by a stimulus from another sensory modality (Kayser & Logothetis, 2007). Contrasting a traditional view that posits a hierarchical structure of sensory processing ranging from low-level unimodal areas to higher-level multimodal or associative areas, compelling anatomical, physiological and neuroimaging evidence suggests that cross-modal interactions occur even earlier at the primary stages of sensory cortical processing (Cappe & Barone, 2005; Foxe et al., 2002; Foxe & Schroeder, 2005; Ghazanfar & Schroeder, 2006). From an electrophysiological standpoint, recording laminar current source density and multiunit activity directly from macaques’ brain, Lakatos et al. (2007) outlined the mechanisms by which co-presentation of somatosensory and auditory stimuli results in a super-additive multisensory interaction at the level of the primary auditory cortex (Lakatos et al., 2007). Later animal studies confirmed that the integration of other multisensory stimuli, such as Audio-Visual and Visuo-Tactile pairs, occurred at the level of the primary sensory cortices (Kambe et al., 2015; King & Walker, 2012; Sieben et al., 2013). In humans, increases in the stimulus-locked inter-trial coherence of spontaneous activity of the brain, which is generally considered to result from the phase-reset of ongoing neural oscillation following sensory stimulation (Kanayama et al., 2015; Mercier et al., 2013; Thorne et al., 2011), has been reported to support multisensory perception (Keil & Senkowski, 2018; Senkowski et al., 2008). In general, during a multisensory stimulation, the first stimulus induces the phase-reset of ongoing

spontaneous neural oscillations, while the second stimulus, arriving during this ideal high excitability phase, leads to an enhanced response to multisensory pairs (Lakatos et al., 2007). Consequently, we interpreted our findings of reduced multisensory integration during systole following this mechanistic explanation, according to which the tactile stimulus is weakened by the predictive top-down suppression related to the “systolic interference” and hence would not be able to optimize the response to the auditory or visual stimuli, resulting in a reduction of early sensory integration.

Another possible contribution to the weakening of the tactile stimuli may be due to bottom-up (peripheral) influences of the cardiac systole. The discharge of tactile mechanoreceptors afferents in the fingers has been shown to be modulated by the cardiac pulse wave arriving immediately after each heartbeat (Macefield, 2003). This pulse can be considered by the central nervous system as an “additive noise” that would decrease the resolution of the tactile stimulus, hence it must be filtered out (Macefield, 2003). However, the lowest tactile detection rate for near-threshold stimuli has been located 250–300 ms after the R-peak, that is before the pulse wave peak (at 405 ms post R-peak) (Grund et al., 2022). Thus, this suggests that tactile perception is unlikely influenced by the peripheral influences of the cardiac systole. Rather, it seems to interact with the above mentioned higher-level predictive suppressive mechanism (Grund et al., 2022).

However, the existence of such predictive suppressive mechanism has been proposed also for other sensory modalities. For example, in the auditory domain, the brain can distinguish sounds in-sync with the heartbeat from sounds not in-sync, via a sensory suppression process reflected in a reduced auditory N1 component in the former condition (van Elk et al., 2014). Similarly, integration of the systolic signal with simultaneous visual stimulation reduces the detection of a target among distractors, as indexed by prolonged reaction times as well as by inhibitory modulations in event-related potential amplitude (Ren et al., 2022). In line with these findings, we found a general increase in the reaction times during systole for all the sensory modalities; only the impact on multisensory integration was specific for the tactile domain.

Our findings also shed light on the interaction between interoception and multisensory representations of the bodily self (Ardizzi & Ferri, 2018; Azzalini et al., 2019; Tsakiris et al., 2011), such as the sense of body ownership, as investigated by the rubber hand illusion and full-body illusion. Both these body illusions are induced by multisensory conflicts between exteroceptive sensory modalities, such as vision and touch (Blanke & Metzinger, 2009; Ehrsson et al., 2004; Kalckert & Ehrsson, 2012; Serino et al. 2013; Tsakiris & Haggard, 2005). Relevant to the present study, the experience of body ownership is also modulated by interoceptive signals, as demonstrated by providing participants with visual information about their heartbeat. In particular, presenting a visual feedback in-sync with the heartbeat (nearly coincident with the systolic phase) led to an enhanced experience of ownership of a virtual hand, and a greater shift in self-location towards a virtual body, compared to the cardiac asynchronous visual feedback (Aspell et al. 2013; Heydrich et al. 2018; Suzuki et al., 2013). Moreover, Aspell et al. (2013) noted that the synchronous cardio-visual signals also altered the perception of tactile stimuli, so that touch was mislocalized towards the virtual body, further strengthening the link between somatosensory perception and cardiac cortical processing.

Someone could argue that there would be a systematic influence of fixed ITI on RTs, caused by shorter ITIs preceding systolic trials and longer ITIs before the diastolic ones. However, this relationship is not always straightforward (Vallesi, Lozano, & Correa, 2013) and the additional jitter provided by the variability in the inter-beat interval excluded this potential confound (see [Supplementary Materials](#)).

Although the results about perception and cardiac interoception agree with most previous studies, some limitations should be noted. The study employed a time-locked presentation of stimuli at 250 ms and 500 ms post R peak instead of uniformly sampling the cardiac cycle. Nevertheless, those fixed intervals allowed us to have a comparable

number of trials between conditions as required by the RMI analysis. Also, the use of an electrical pulse as a tactile stimulus can be considered a potential weakness. Indeed, the detection accuracy for tactile inputs was lower compared to other stimuli probably due to adaptation (Graczyk et al., 2018; Kaczmarek et al., 1991). However, the percentage of correctly detected trials was enough to perform RMI analysis.

In conclusion, the present study enriches current knowledge on the impact of the cardiac phase on sensory perception, including the multisensory domain. Our findings show that Audio-Tactile and Visuo-Tactile integration is reduced when stimuli are presented in-time with the cardiac systole. We interpret these results within the interoceptive predictive coding framework, according to which brain-body interactions shape the perception of the external environment. Future studies should consider the role of another fundamental body rhythm, such as respiratory activity, in modulating multisensory integration, given the tight coupling with cardiac activity and its well-described influence on brain activity and cognitive functions (Allen et al., 2022; Heck et al. 2022; Kluger et al., 2021; Kluger & Gross, 2021; Varga & Heck, 2017; Zaccaro et al., 2022). Moreover, the electrophysiological correlates of interoceptive influences on multisensory integration should be tested taking, for instance, the inter-trial coherence as an index of cardiac driven cross-sensory phase resetting.

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Declaration of Generative AI and AI-assisted technologies in the writing process

The authors did not use generative AI technologies for the preparation of this work.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.biopsycho.2023.108642](https://doi.org/10.1016/j.biopsycho.2023.108642).

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