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The heart of cognitive control: Cardiac phase modulates processing speed and inhibition

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Abstract

Bodily states are heavily intertwined with cognitive processes. A prominent communication channel between bodily signals and brain structures is provided by baroreceptors. Their phasic activity associated with the cardiac phase has been shown to modulate cognitive control in socio-emotional contexts. However, whether this effect is specific to the affective dimension or impacts general cognitive control processes remains controversial. The aim of the present study is to investigate the effect of cardiac phase on different facets of cognitive control. We built a nonemotional cognitive control task to delineate mechanisms such as processing speed, response selection, response inhibition, and conflict monitoring. We showed that the systole (after the blood is ejected from the heart), compared to the diastole, was related to faster responses. Moreover, the cardiac phase dynamics also impacted response inhibition, with an increased probability of failure toward the middle of the course of systole. Although the reported effects were small in terms of magnitude, they highlight the influence of bodily states on abstract cognitive processes.

KEYWORDS

cardiac phase, cognitive control, inhibition, interoception, systole

1 | INTRODUCTION

There is compelling evidence that the continuous dynamic brain representation of internal bodily signals sets the foundations for a sense of self as the basis for phenomenal states (Craig, 2009; Park, Correia, Ducorps, & Tallon-Baudry, 2014; Park & Tallon-Baudry, 2014). The body-brain interaction plays a causal role in driving spontaneous large-scale cortical activity (Park et al., 2014) that is known to shape the neural response (Greicius & Menon, 2004; He, 2013) and the subjective conscious experience (Boly et al., 2007; Sadaghiani, Hesselmann, & Kleinschmidt, 2009; Vinnik, Itskov, & Balaban, 2012) of physical stimuli. One prominent channel of brain and body communication is that conveyed by baroreceptors (i.e., the pressure and stretch-sensitive receptors within the heart and surrounding arteries) that inform the brain of the dynamic state of the heart and impact ascending neuromodulator systems involved in motivational behavior (Garfinkel & Critchley, 2016). Arterial baroreceptors have, for their part, a phasic activity associated with the pulse pressure wave of the cardiac phase. They fire maximally when the blood is ejected from the heart, i.e., after cardiac systole and minimally between heart beats, i.e., during cardiac diastole (Gray, Rylander, Harrison, Wallin, & Critchley, 2009). The activity of the baroreceptors has been shown to modulate the perception of bodily states, such as nociception (Edwards, Ring, McIntyre, & Carroll, 2001; Martins, Ring, McIntyre, Edwards, & Martin, 2009) or emotional arousal (Garfinkel et al., 2014; Gray et al., 2012).

However, the cardiac phase seems to also impact higher-level cognitive functions, such as stereotypes expression. Indeed, Azevedo, Garfinkel, Critchley, and Tsakiris (2017)

recently reported changes related to afferent cardiac activity in the appraisal of complex social stimuli (pictures of people) and associated behavioral consequences, such as racial bias. In particular, they found that, during systole as compared to diastole, participants better identified weapons primed by black faces and tools primed by white faces. In a second experiment employing a first-person shooter task (FPST; Correll, Park, Judd, & Wittenbrink, 2002), the authors showed that the likelihood of errors (i.e., of "shooting") unarmed Black targets compared to White targets was increased during systole. They suggest that, in the context of alertness to threat-signaling stimuli, increased brain representation of cardiac activity enhances the salience of social cues and promotes the expression of negative racial stereotypes. Arterial baroreceptors signals reach, through cranial nerves X and XI, the nucleus of the solitary tract, which has proximate connections with the thalamus and the amygdala, a region possibly involved in mechanisms underpinning the observed exaggeration of racial biases (Adolphs, 2010; Anderson & Phelps, 2001; Olsson & Phelps, 2007). Indeed, this center was shown to be involved in the baroreceptor effect influencing the processing of salient stimuli (Gray et al., 2009). Thus, Azevedo, Garfinkel, et al. (2017) suggested that their findings on the expression of racial stereotypes could be explained by the amygdala response, whose activity would be modulated by the properties of cardiac signals.

However, a second nonexclusive hypothesis is invoked by the authors, related to the inhibitory effect of cardiovascular baroreceptor firing on the dorsolateral prefrontal cortex (Pramme, Schaechinger, & Frings, 2015). The phasic deactivation of these regions could hinder the ability to inhibit the prepotent response. This would, in turn, increase the expression of racial stereotypes by decreasing control over undesirable automatic responses. However, the authors judge this explanation less likely to explain their pattern of results. Indeed, using a performance dissociation procedure (Ferreira, Garcia-Marques, Sherman, & Sherman, 2006), they showed that the cardiac phase impacted preferably automatic processes and threat-related stimuli rather than controlled processes and nonthreat-related stimuli (in their case, positive Black athletic stereotypes). Nevertheless, the FPST task can be seen as an "ecological," contextually rooted version of the go/no-go task, in which a participant must inhibit their response according to a specific condition. The investigation of the cardiac phase effect on a nonemotional version of the task could bring answers on the role of interoceptive signals on high-level cognition and its behavioral consequences. It is interesting to note that inhibition is related with heart rate activity. For example, Jennings, der Molen, Brock, and Somsen (1992) showed that successful action inhibition delays the heart rate recovery acceleration. Moreover, they further showed that the cardiac deceleration related to preparatory inhibition was correlated with the activity of the subthalamic nuclei (Jennings, Van Der Molen, & Tanase, 2009), a major component of a significant inhibitory network (Aron, 2008; van den Wildenberg et al., 2006). However, although suggesting an intertwined and complex relationship between inhibition and cardiac activity, these two studies did not examine the effect of cardiac phase per se.

The relationship between heart activity and general cognitive processes caught the interest of physiologists early on. Unfortunately, the effect of the cardiac phase on reaction times yielded very conflicting results (Carroll & Anastasiades, 1978), resulting in the absence of a simple and straightforward story. Nevertheless, discrepancies in the procedure, operationalization, and cardiac index choice or calculation render comparison of these studies difficult. These inconsistent data suggest that the effect of the cardiac phase, if existing, is tiny and very sensitive to context (Thompson & Botwinick, 1970). Nonetheless, it also supports the necessity of a precise description as well as technical and statistical control of the parameters at stake. Lacey and Lacey (2017) suggested that one such important piece of information to take into account could be the point within the cardiac cycle at which a stimulus is presented, suggesting a complex interaction between cardiac phase dynamics and cognitive processing.

Cognitive control can be defined as the ability to coordinate thoughts or actions in relation to internal goals (Koechlin, Ody, & Kouneiher, 2003). The aim of the present study was to investigate the effect of cardiac phase on different facets of cognitive control, especially conflict monitoring and response inhibition, as these two aspects were shown to be supported by different neural pathways (MacDonald, Cohen, Stenger, & Carter, 2000; Siemann, Herrmann, & Galashan, 2016; Simmonds, Pekar, & Mostofsky, 2008; Van Veen & Carter, 2005): conflict monitoring performance was related to activity in the anterior cingulate cortex (Botvinick, Cohen, & Carter, 2004; Van Veen & Carter, 2002), while response inhibition would be supported by networks such as dorsolateral and inferior frontal areas or inferior parietal circuit (Aron, Robbins, & Poldrack, 2014; Criaud & Boulinguez, 2013; Simmonds et al., 2008) With this aim, we built a cognitive control task based on the gradual addition of control processes, easing their further delineation, and investigated the effect of the cardiac phase.

Based on previous results and neuroanatomical data, we expected stimuli presented during systole to yield quicker reaction times (due to a preactivation of salience processing related areas) and more frequent response inhibition failures (due to deactivation of dorsolateral prefrontal areas), compared to diastole. Curiously, a recent study reported the opposite pattern using a stop signal task (Rae et al., 2018). The authors suggest that the quicker detection of salient stimuli at systole would also lead to the better prioritization of adaptive behavior, whether aversive reaction

(explaining why fearful faces are perceived as more intense during systole; Garfinkel et al., 2014) or response inhibition. Replication and generalization to other cognitive control mechanisms might be a way to confront this general "all-time adaptive systole" hypothesis with the "gut reaction" (fast but with less control) hypothesis. Critically taking into account the cardiac phase dynamics might cast a new light on these data.

2 | METHODS

2.1 | Participants

The study presented in this article is based on two distinct samples (henceforth referred to as Sample 1 and Sample 2). For Sample 1, 35 healthy participants were recruited using Internet advertisement. Inclusion criteria were age between 18 and 29, right-hand laterality, native French language, and absence of neurological or psychiatric disorders. They were asked to provide informed and written consent and were given 25€ for their participation. One participant was excluded because of technical problems in physiological recording. The final Sample 1 was composed of 34 participants (age: 24.13 ± 2.63, 76.47% female, years of higher education: 3 ± 1.86). For Sample 2, 40 university students were initially recruited with similar inclusion criteria and compensated by academic credits. Seven participants were excluded due to technical issues in the setup of the triggers. The final sample was composed of 33 participants (age: 20.18 ± 2.49, 87.88% female, years of education: 1 ± 1.63). The overall sample size included 67 participants (age: 22.18 ± 3.23, 82.09% female, years of education: 2 ± 2.01). The study was approved by the local ethics committee.

2.2 | Procedure

Experimental sessions started at 1:30 p.m. in a sound-attenuated, dimly lit room. The task discussed in the present article took place in a broader protocol including questionnaires and neuropsychological tests. Tasks not relevant for the current study will not be discussed.

2.2.1 | Procedure

The cognitive control test (CoCon) was developed to assess, in a relatively short time (8.56 ± 0.48 min with setup and instructions), several processes related to cognitive control: simple reaction time, choice reaction time, inhibition, and conflict resolution. In order to isolate and delineate them, the task was composed of four distinct parts. The number and characteristics of the stimuli present in each part is described in Table 1. In all parts, the stimuli appeared on a neutral gray screen (128, 128, 128 in RGB mode) and lasted until the participant responded, followed by a randomly jittered intertrial interval (ITI), uniformly ranging from 33 (i.e., one frame on a 60 Hz monitor) to 2,000 ms. Stimuli consisted of a local shape (a triangle) displayed on a global shape (a circle or triangle, depending on the conflict condition). Shapes could be of four colors (yellow, blue, orange, white) and pointing in four directions (left, right, top, bottom). Examples of stimuli are presented in Figure 1. The task, programmed on Python 3.6 with the Neuropsydia module (Makowski & Dutriaux, 2017), is freely available in open access at <https://github.com/DominiqueMakowski/CoCon.py>.

The experiment was divided in four parts. In Part 1, participants were instructed to press (with the index of their dominant hand), as quickly as they can, one key (the down arrow), as soon as a stimulus appeared on screen. Part 2 added the response selection condition: participants had to indicate the direction of the local triangle by pressing the corresponding keyboard arrows (left, down, right) with their index, middle, or ring finger, respectively. When the local triangle was pointing to the top, they were instructed not to respond. The no-response trials are designed to test the correct noninitiation of response related to response unavailability. Part 3 added the contextual no-go condition: when the global (i.e., the background) circle was white, participants were instructed not to respond. Finally, Part 4 added the conflict condition, inspired by the flanker task (Eriksen & Eriksen, 1974; Van't Ent, 2002). The trials were either congruent—the global (background) triangle pointing in the same direction as the local (small) triangle—or incongruent—with the background triangle pointing in the opposite direction of the triangle indicating the required response. Trials ended if no button was pressed after 2,000 ms. The number of trials for Sample 1 (see Table 1) was selected after a pretest by looking at the point of stabilization of the cumulative average (the number of trials beyond that additional trials do not critically impact the average). For Sample 2, we doubled the number of trials. To minimize the contamination of our data by the reversed relationship, that is, the cardiac reactivity to cognitive control (Jennings et al., 1992) or error processing (Łukowska, Sznajder, & Wierzchoń, 2018), we started by removing trials with ITI < 300 ms (~15%). Outlying RTs (±2 *SD*) were removed separately for each part (5.58%, 5.41%, and 4.59% in Parts 1, 2, and 4, respectively). Error rates in the four parts were, respectively, 0.04%, 4.30%, 9.47%, and 3.59%, and the ratio of no-response trials in Parts 2, 3, and 4 was 9%, 11%, and 11%, respectively.

2.2.2 | Measures

Simple reaction time, choice reaction time, and conflict resolution were operationalized as the duration between the stimulus appearance and the response in Parts 1, 2, and 4, respectively. Response inhibition was operationalized as the

TABLE 1 CoCon stimuli list

Part	*n* stimuli	Global shape	Global color	Local shape	Local color	Response
1	30	Circle	Blue, orange, yellow, white	Triangle (left, right, top, bottom)	Blue, orange, yellow, white	Down
2	30	Circle	Blue, orange, yellow, white	Triangle (left, right, bottom)	Blue, orange, yellow, white	Left, right, down
	3	Circle	Blue, orange, yellow, white	Triangle (top)	Blue, orange, yellow, white	None
3	40	Circle	Blue, orange, yellow	Triangle (left, right, bottom)	Blue, orange, yellow	Left, right, down
	3	Circle	Blue, orange, yellow	Triangle (top)	Blue, orange, yellow	None
	6	Circle	White	Triangle (left, right, bottom)	Blue, orange, yellow	None
	3	Circle	White	Triangle (top)	Blue, orange, yellow	None
4	40	Triangle (incongruent)	Blue, orange, yellow	Triangle (left, right, bottom)	Blue, orange, yellow	Left, right, down
	3	Triangle (incongruent)	Blue, orange, yellow	Triangle (top)	Blue, orange, yellow	None
	6	Triangle (incongruent)	White	Triangle (left, right, bottom)	Blue, orange, yellow	None
	3	Triangle (incongruent)	White	Triangle (top)	Blue, orange, yellow	None
	40	Triangle (congruent)	Blue, orange, yellow	Triangle (left, right, bottom)	Blue, orange, yellow	Left, right, down
	3	Triangle (congruent)	Blue, orange, yellow	Triangle (top)	Blue, orange, yellow	None
	6	Triangle (congruent)	White	Triangle (left, right, bottom)	Blue, orange, yellow	None
	3	Triangle (congruent)	White	Triangle (top)	Blue, orange, yellow	None

Note: Number and characteristics of the stimuli present in the four parts for Sample 1. For Sample 2, the number of each trial by conditions was double.

errors in the no-go trials in Part 3. Errors in the no-go trials in Part 4 were used to observe the effect of conflict on inhibition.

2.2.3 | Electrocardiogram

Cardiac activity (electrocardiogram [ECG]) was recorded using BioPac MP150 system (BioPac Systems Inc., USA) and the AcqKnowledge Software 4.3 with a sampling frequency of 1,000 Hz. To maximize the QRS signal, ECG electrodes were placed according to a modified Lead II configuration (Takuma et al., 1995) on the right and left subclavicular spaces (the deltopectoral fossae) and on the left lower rib. About 5 min of activity were recorded before starting the experiment to allow participants to adapt to the recording equipment. Event timings were recorded with BioPac alongside the bodily signals by a photosensor attached to a corner of the screen, on top of a small rectangle that turned to black whenever the stimulus actually appeared on the screen.

Using Python and the NeuroKit package (Makowski, 2017), the ECG signal was FIR band-pass filtered (3–45 Hz, 3rd order), and the QRS complexes were segmented using Hamilton's (2002) method. As previous literature showed that cardiac phase timings were highly dependent on the heart rate (Boudoulas, Geleris, Lewis, & Rittgers, 1981; Chung, Karamanoglu, & Kovács, 2004; Husmann et al., 2007) and thus different across participants and trials, we defined the cardiac phase based on physiological features rather than on R peak distance-based heuristics. After segmentation of the cardiac complex, we designated the interval between the R peak and the end of the following T wave as the systole, and the remaining interval as the diastole. Finally, we extracted the ongoing cardiac phase at each stimulus display as well as the time point in the cycle corresponding to the percentage of current phase completion.

2.3 | Data analysis

We performed the analysis under the Bayesian framework (which demonstrated better reliability in noisy data and better estimation for small samples; Andrews & Baguley, 2013; Etz & Vandekerckhove, 2016; Kruschke, 2010; Kruschke,

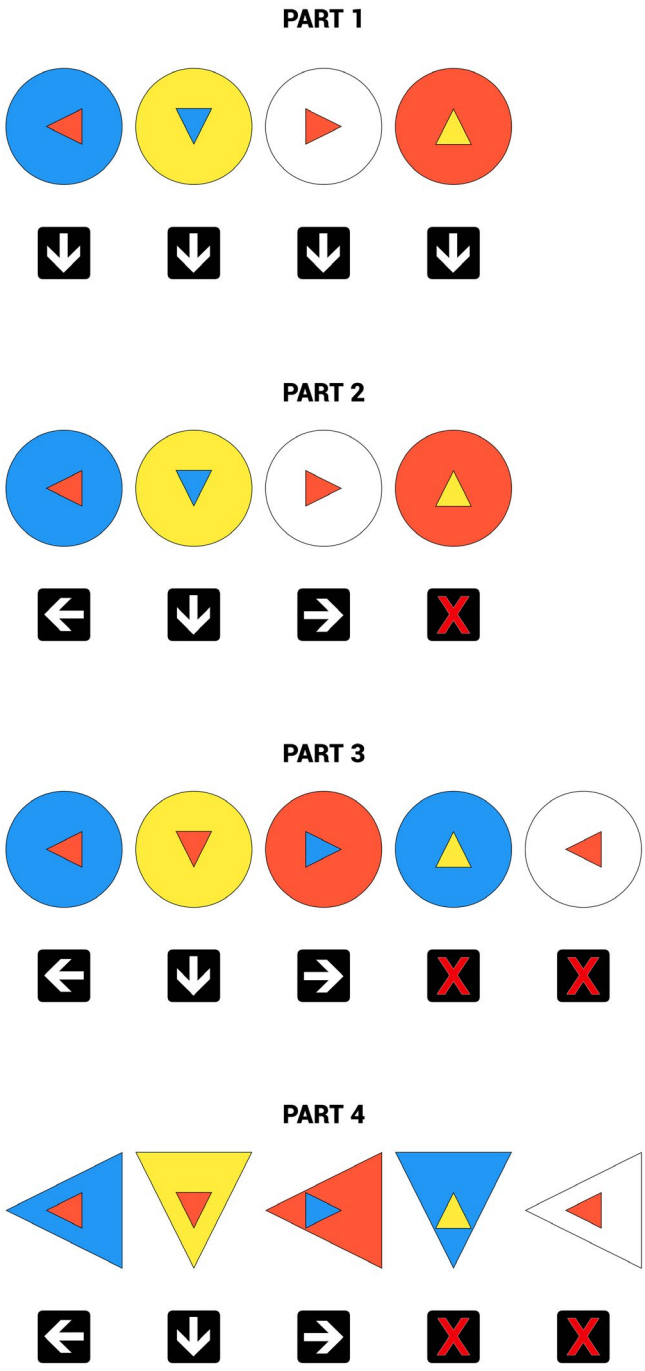

FIGURE 1 Task procedure. Examples of stimuli presented in each part and the associated correct response. Part 1 requires pressing the down arrow at presentation of any stimuli. Part 2 requires selecting between three answers depending on the stimulus (with one "unavailable response" stimulus type). Part 3 requires inhibiting the response when the background circle was white. Part 4 adds flanker style perceptual conflict

Aguinis, & Joo, 2012; Wagenmakers et al., 2018) in conjunction with mixed models, able to handle unbalanced data, nested designs, crossed random effects, and missing data (Kristensen & Hansen, 2004). The analysis relied on linear models to predict response times in Parts 1, 2, and 4 (together and separately) and logistic models to predict inhibition errors in Part 3. We started by fitting the simplest model (with the cardiac phase [systole/diastole] as the only predictor). In a second step, we added the percentage of cardiac phase completion (with its 2nd order polynomial degree to evaluate a nonlinear relationship) as predictor to account for the underlying dynamics of the cardiac phase. Moreover, this could potentially mitigate for the fact that time immediately after the R wave, although labeled as systole, precedes baroreceptors stimulation, which is the primary mechanism supporting the effect of the cardiac phase. Finally, in a third step, we added the ITI, also with its 2nd order polynomial degree, to test its interaction with the effect of cardiac phase.

In each model, we entered participants and stimuli features (color and orientation of the local triangle) as random factors to account for interindividual and item-related variability. We also added the sample (Sample 1, Sample 2), to account for differences between these two pools of participants. Priors were set as noninformative (normally centered around zero). Instead of a point estimate of each effect associated with a *p* value, we will report characteristics of the posterior distribution (the probabilities of different effects given the observed data), such as the median (comparable to the beta of frequentist regressions), 90% credible interval, and the probability of direction (*pd*; an index of effect existence corresponding to the probability that the effect is in the median's direction, i.e., positive or negative). We will consider effects as relevant if their *pd* (an index strongly correlated with the frequentist *p* value) is superior to 95% (Makowski, Ben-Shachar, Chen, & Lüdecke, 2019; Makowski, Ben-Shachar, & Lüdecke, 2019).

Statistics were performed using R 3.5 (R Development Core Team, 2008), the *rstanarm* package (Gabry & Goodrich, 2016), and the *easystats* (Lüdecke, Waggoner, & Makowski, 2019; Makowski, 2018) suite. For each model, we will describe only the noteworthy effects, the full analysis script and results description being available in online supporting information. Note that orthogonal polynomial coefficients have a meaningless value scale: their interpretation is best obtained from a graphic representation (presented in Figure 2).

3 | RESULTS

The proportion and average duration of systole and diastole trials were, respectively, 38% (300.84 ± 58.39 ms) and 62% (491.45 ± 90.75 ms).

3.1 | Reaction time—General

We selected all trials without conflict or inhibition. Note that a model comparing the two participant samples suggested that Sample 2 possibly had overall slower reaction times

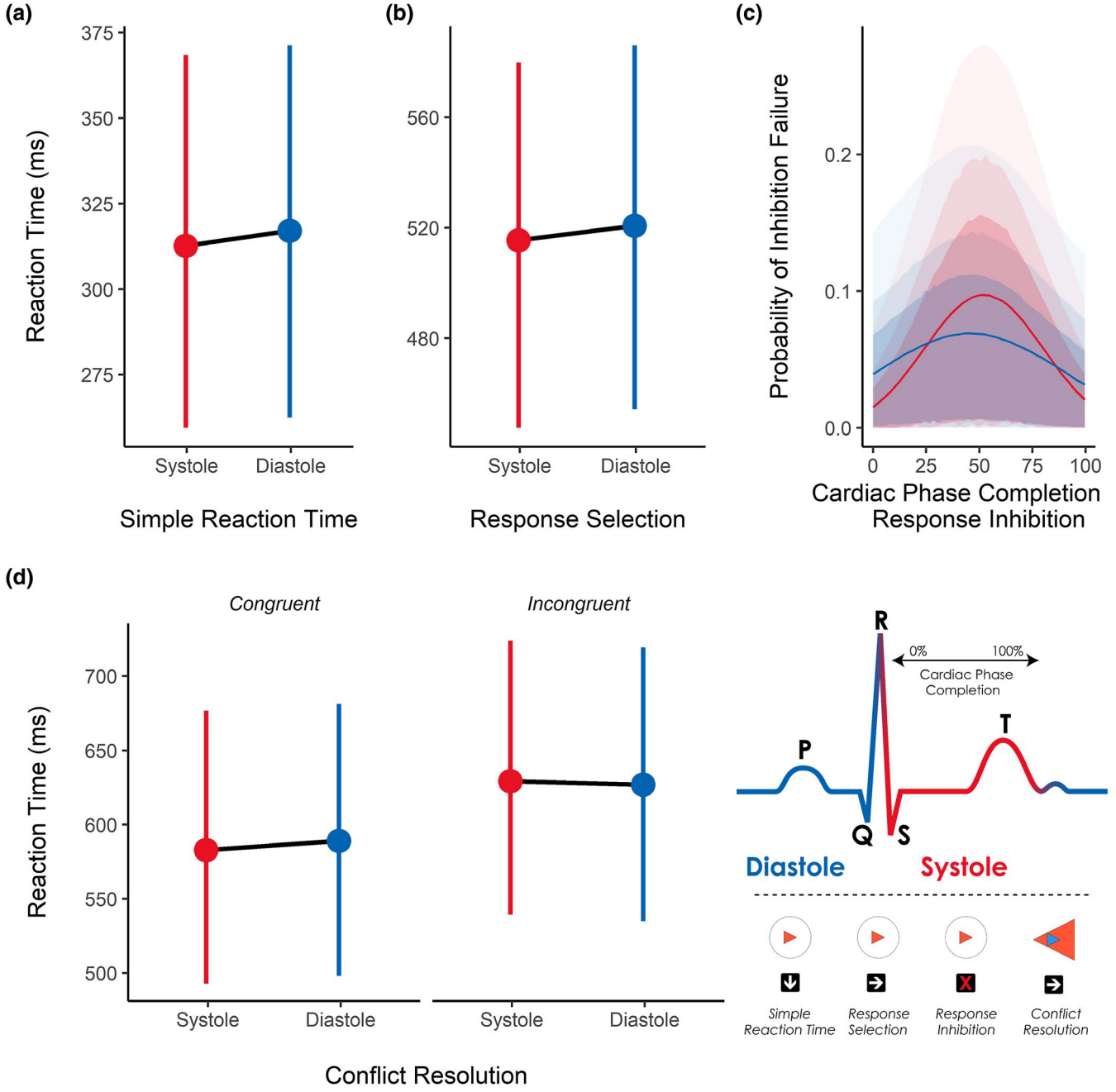

FIGURE 2 The effect of cardiac phase (systole in red, diastole in blue) for different facets of cognitive control: (a) simple reaction time in Part 1, (b) response selection in Part 2, (c) probability of response inhibition failure in Part 3, and (d) conflict resolution. For response inhibition (Part 3), the percentage of cardiac phase completion (*x* axis) shows that the probability of response inhibition failure is maximal during the middle of systole. Error bars represent the 90% credible interval of the estimated means in each condition and not the error related to the difference between diastole and systole. It shows the large variability in the RTs compared to the size of the difference between systole and diastole (with diastole related to slower RTs than systole), which seems to exist, in particular for simple reaction times (a). Bottom-right panel shows a canonical representation of the QRS complex (upper part) to illustrate the location of the cardiac phases as well as example of the stimuli and the required response (bottom part) corresponding to the four parts of the task

(the fact that the RT difference between Sample 2 and Sample 1 has a probability of 94.99% of being positive, with a median of 24.12, 90% CI [0.09, 46.92]), provides argument for adjusting the following models for the sample).

The simple model (R^2 median = .25; intercept median = 451.70) suggested that the difference of RT between diastole and systole (diastolic RT − systolic RT) had a probability of 98.50% of being positive (median = 5.77, 90% CI [1.46, 10.27]). The second model, including the cardiac phase completion (R^2 median = .25; intercept median = 452.61), showed no evidence for its interaction with the effect of diastole. The third model (R^2 median = .25;

intercept median = 453.12), by adding the ITI to the simple model, revealed a negative linear relationship between ITI and RT (median = −9.25, 90% CI [−14.32, −4.31], *pd* = 99.85%) and a possible interaction with the effect of the diastole: the higher the ITI, the smaller the effect of diastole (median = −4.54, 90% CI [−9.31, 0.27], *pd* = 94.38%).

3.2 | Reaction time—Simple

In Part 1, after data exclusion, the average number of analyzed trials by participant after data exclusion was 23.38 ± 2.95 and 47.39 ± 4.94 in Sample 1 and 2, respectively. The simple model (R^2 median = .50; intercept median = 312.70) suggested that the difference of RT between diastole and systole had a probability of 95.40% of being positive (median = 4.25, 90% CI [0.12, 8.39]). The second model, including the cardiac phase completion (R^2 median = .25; intercept median = 317.22), showed no evidence for its interaction with the effect of diastole. The third model (R^2 median = .51; intercept median = 315.89), by adding the ITI to the simple model, revealed a negative linear relationship between ITI and RT (median = −14.29, 90% CI [−18.95, −9.40], *pd* = 100%), but no interaction with the effect of the diastole.

3.3 | Response selection

In Part 2, after data exclusion, the average number of analyzed trials by participant after data exclusion was 21.62 ± 4.18 and 44.88 ± 7.30 in Sample 1 and 2, respectively. The simple model (R^2 median = .34; intercept median = 515.48) suggested no consistent difference of RT between diastole and systole (median = 5.30, 90% CI [−0.84, 11.80], *pd* = 91.28%). The second model, including the cardiac phase completion (R^2 median = .34; intercept median = 519.54), showed no evidence for its interaction with the effect of diastole. The third model (R^2 median = .34; intercept median = 519.18), by adding the ITI to the simple model, revealed a negative linear relationship between ITI and RT (median = −9.72, 90% CI [−16.7, −3.01], *pd* = 98.98%) but no interaction with the effect of the diastole.

3.4 | Conflict resolution

In Part 4, after data exclusion, the average number of analyzed trials by participant after data exclusion was 59.26 ± 12.06 and 121.58 ± 17.22 in Sample 1 and 2, respectively. The models predicting RTs (for go trials only) included the conflict condition (congruent, incongruent) as additional predictor. The simple model (R^2 median = .34; intercept median = 582.73) suggested, for congruent trials, the difference of RT between diastole and systole a probability of 94.88% of being positive (median = 6.28, 90% CI [0.02, 12.96]). Incongruent trials (with perceptual conflict) were related to a slower RT with a probability of 100% (median = 47.11, 90% CI [39.25, 53.70]). Moreover, there was an interaction between incongruence and the effect of diastole, the latter being decreased in incongruent trials with a probability of 94.56% (median = −9.48, 90% CI [−18.11, 0.44]). The second model, including the cardiac phase completion (R^2 median = .34; intercept median = 581.66), showed no evidence for its interaction with the effect of diastole. The third model (R^2 median = .34; intercept median = 583.03), by adding the ITI to the simple model, revealed no consistent relationship between ITI and RT and no interaction with the effect of the diastole.

3.5 | Response inhibition

In Part 3, after data exclusion, the average number of analyzed trials by participant after data exclusion was 14.59 ± 1.88 and 28.85 ± 2.85 in Sample 1 and 2, respectively. The simple model (R^2 median = .06; intercept median = −2.69) predicting inhibition errors suggested no consistent difference of errors between diastole and systole (median = −0.08, 90% CI [−0.57, 0.42], *pd* = 61.65%). However, adding the cardiac phase completion in the model (R^2 median = .07; intercept median = −4.17) suggested a significant quadratic relationship (inverse U shape) between the probability of error and the cardiac phase completion only during systole (1st order polynomial: median = 0.07, 90% CI [0.02, 0.13], *pd* = 99.08%; 2nd order polynomial: median = −0.001, 90% CI [−0.002, −0.001], *pd* = 99.05%). Finally, adding the ITI to the previous model (R^2 median = .11; intercept median = −3.92) revealed no effect of ITI nor interaction with the cardiac phase effect or its completion state.

4 | DISCUSSION

We investigated the effect of the cardiac phase upon presentation of a stimulus in four conditions involving simple to complex aspects of cognitive control. We built a cognitive control task to measure processes such as simple reaction time, response selection, response inhibition, and conflict monitoring and, through the incremental structure of the task, to allow their delineation. We reported that reaction times were consistently faster during systole compared to diastole. The magnitude of this effect being, nevertheless, very small (less than 10 ms), this effect was stronger when other processes were not involved (such as response selection and conflict monitoring). Moreover, the time course of systole was related to a modulation of the probability of response inhibition failure that was higher at the middle of its time course.

Simple reaction time, a measure of processing speed (and a general index of "fluid" intelligence; Jakobsen, Sorensen,

Rask, Jensen, & Kondrup, 2011; Sheppard & Vernon, 2008; Woods, Wyma, Yund, Herron, & Reed, 2015), can be considered as part of cognitive control (Koechlin et al., 2003). This result could be related to findings reporting a facilitated processing of visual stimuli during systole (Pramme, Larra, Schächinger, & Frings, 2016), such as low-frequency fearful faces (Azevedo, Badoud, & Tsakiris, 2017). Taken together, these results tend to be coherent with the underlying neuroanatomical pathways of baroreceptor signal central integration. In particular, the priming of the amygdala and the associated saliency network during systole might, in our case, ease the stimulus processing and accelerate the action command, resulting in quicker reaction times. Interestingly, while previous research investigating the impact of cardiac phase on low-level processes reports results in line with our findings (Stewart, France, & Suhr, 2006), other studies did not report any influence of the cardiac phase on RT (Birren, 1965; Edwards, Ring, McIntyre, Carroll, & Martin, 2007; Rae et al., 2018; Thompson & Botwinick, 1970). Moreover, McIntyre, Ring, Hamer, and Carroll (2007) found an opposite pattern (with slower RTs early in the cardiac phase), but the conjunction of postural changes (legs up/down) and preparation effect (the participants had to press a button on a preparation signal and release their finger as quickly as possible on another signal, always triggered within 5 s after the preparation signal) might be important keys to explain this pattern. Nevertheless, these inconsistencies suggest that the effect is rather small and easily overshadowed in the presence of other processes. Moreover, some of these studies reported simple RTs generally lower than ours with the use of different protocols or response-collecting devices. These discrepancies could contribute to the inconsistencies in the findings reported by the literature, to which the present results might not be generalizable.

Interestingly, we reported a facilitating effect mainly on reaction times in the simplest condition (where the participant had to press the same key at the appearance of any stimuli). This effect was dampened when other processes, such as response selection or conflict monitoring, were at stake. This pattern change under cognitive load might explain findings showing an absence of cardiac phase effect on RT in decision-making tasks (Jennings & Wood, 1977).

Critical to the currently investigated issue, the reported increase of no-go errors during the middle of systole might be related to the phasic deactivation of dorsolateral prefrontal regions, known to be engaged in cognitive control tasks (Niendam et al., 2012; Simmonds et al., 2008). This suggests that the effect reported by Azevedo, Garfinkel, et al. (2017), that is, the increased likelihood of errors in a FPST during systole, might be linked to failures of inhibition rooted at an abstract level rather than being solely related to social material. Interestingly, a recent study investigating a similar question did not report that result on response inhibition (Rae et al., 2018). The authors used the stop signal task, in which the inhibition is directed at the motor (or premotor) command (the stop signal appearing after the go signal). In our case (where the go and no-go signal are concurrent), the inhibition might happen before or at action initiation. While this subtle difference might contribute to the discrepancies in results, it also underlines the need for further exploration.

5 | LIMITATIONS AND FUTURE DIRECTIONS

Although revealing a coherent pattern of results suggesting that the systole phase is related to a faster and less controlled response, this study presents some substantive limitations. Importantly, the high variability of RTs in regard to the effects investigated led to a high uncertainty (large credible intervals) in the parameter estimation. Although the selected and discussed effects have an acceptable probability (around 95%) of existing (i.e., being different from zero), their actual size appears as very small, and their precise estimation is subject to caution. A second concern might be made based on the variability induced by a random ITI, leading to a variable influence of previous trials upon the physiological reactivity and cognitive processing of new trials. Although this randomness provides some amount of control (as the possible reminiscent effects should flat down) when the number of trials is high, and that we did not report any interaction with the effect of cardiac phase, it remains a question that should be addressed by future studies. Importantly, discrepancies with studies investigating cognitive control (and inhibition) could also be related to the subprocesses at stake (for instance, the target and timing of response inhibition), underlining the complexity of the presently investigated issue.

In summary, this exploratory study shows that the cardiac phase and its dynamics modulate our efficiency in non-emotional (i.e., does not include affective stimuli) cognitive control tasks. We showed that cardiac systole, that is, upon activation of arterial baroreceptors, was related to shorter simple reaction times and modulated the probability of response inhibition failures. These results advocate for the role of interoceptive pathways and brain-body communication on higher-order cognitive processes, such as cognitive control. Taken together, that data could be of importance for interventions with interoceptive processes as mechanism or target, such as biofeedback or mindfulness meditation (Farb, Segal, & Anderson, 2012; Lehrer & Gevirtz, 2014).

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