

Wrinkles in subsecond time perception are synchronized to the heart

Saeedeh Sadeghi
Department of Psychology, Cornell University
Ithaca, USA
Email: ss3767@cornell.edu

Marc Wittmann
Institute for Frontier Areas of Psychology and Mental Health
Freiburg, Germany
Email: wittmann@igpp.de

Eve De Rosa
Department of Psychology, Cornell University
Ithaca, USA
Email: eve.derosa@cornell.edu

Adam K. Anderson
Department of Psychology, Cornell University,
Ithaca, USA
Email: anderson@cornell.edu

Abstract

The role of the heart in the experience of time has been long theorized but empirical evidence is scarce. Here we examined the interaction between fine-grained cardiac dynamics and the momentary experience of subsecond intervals. Participants performed a temporal bisection task for brief tones (80-188 ms) synchronized with the heart. We developed a cardiac Drift-Diffusion Model (cDDM) that embedded contemporaneous heart rate dynamics into the temporal decision model. Results revealed the existence of temporal wrinkles — dilation or contraction of short intervals — in synchrony with cardiac dynamics. A lower pre-stimulus heart rate was associated with an initial bias in encoding the millisecond-level stimulus duration as longer, consistent with facilitation of sensory intake. Concurrently, a higher pre-stimulus heart rate aided more consistent and faster temporal judgments through more efficient evidence accumulation. Additionally, a higher speed of post-stimulus cardiac deceleration, a bodily marker of attention, was associated with a greater accumulation of sensory temporal evidence in the cDDM. These findings suggest a unique role of cardiac dynamics in the momentary experience of time. Our cDDM framework opens a new methodological avenue for investigating the role of the heart in time perception and perceptual judgment.

Introduction

Time is a foundational resource (Post, 2019). Under time restriction, we need to prioritize sensory inputs (attention), evaluate them, and act. Perception of time is critical for budgeting it as a resource and catching up with the dynamic environment. However, subjective time is malleable. Rather than being a uniform dimension, perceived duration has "wrinkles", with certain intervals appearing to dilate or contract relative to objective time. Time malleability, although sometimes referred to as "distortion" (e.g. Eagleman, 2008), might be adaptive based

on bodily or cognitive demands as it potentially links time perception with the interactions between the brain and the body via the Autonomic Nervous System. The heart's interaction with the brain is specifically critical given that it serves to adjust energetic resources of the body based on peripheral and central cognitive-affective demands (Critchley & Garfinkel, 2018; Tsakiris & De Preester, 2018).

Involvement of the body in perceiving time was proposed nearly a century ago (François, 1927; Gardner, 1935; Hoagland, 1935; Schaefer & Gilliland, 1938). The influential pacemaker-accumulator models have theorized that time is perceived by an internal clock whose functioning is governed by central (attention) and (bodily) arousal (Treisman, 1963; Zakay & Block, 1997). The moment by moment experience of time may involve the brain's continually updating of the interoceptive representation of the body in the anterior insular cortex (Craig, 2009; Wittmann, 2013). While most bodily processes are on a slower time scale (Cannon, 1927), the brain is receiving cardiac afferents at every moment (Critchley & Garfinkel, 2018). Faster cyclical rhythms of the heart may therefore afford a higher resolution time keeping compared to other bodily signals. Heart rate is a peripheral indicator of metabolic needs and bodily arousal as well as an important interoceptive afferent source (Tsakiris & De Preester, 2018). The heart has long been a focus for its potential contribution to temporal perception (e.g. Meissner & Wittmann, 2011; Ochberg et al., 1964; Pollatos et al., 2014; Schwarz et al., 2013; Surwillo, 1982), due to its dual role as both a pacemaker and a moment-by-moment regulator of physiological energetics. While prior studies typically tend to examine cardiac measures averaged across multiple seconds to minutes (e.g. Ogden et al., 2022), here we provide a new perspective on the role of fine-grained interbeat heart dynamics in the temporal decision process for perception of very brief intervals in the order of tens of milliseconds.

Heart rate modulation by the brain has been theorized to have various adaptive functions. We used these functions as a guide to investigate the heart-time perception relationship. The heart receives input from both sympathetic and parasympathetic divisions of

the nervous system. When the environment is assessed as demanding, the sympathetic nervous system increases the heart rate. Such heart rate acceleration is part of an adaptive defense response (Vila et al., 2007). A parasympathetically-driven decrease in heart rate, on the other hand, occurs during the Orienting Response (OR) to novel or relevant stimuli (Berntson et al., 1997; Graham & Clifton, 1966; Sokolov, 1963). Cardiac OR (COR) is hence a phasic cardiac deceleration response accompanied by a central attentional orienting response.

The orienting-related deceleration versus defense acceleration have been theorized to have afferent adaptive utilities from perceptual and motivational perspectives (Vila et al., 2007). Based on the perceptual or cognitive view (Graham, 1979; Graham & Clifton, 1966; Lacey & Lacey, 1974), a lower heart rate facilitates sensory intake; it calms down the noise of internal cardiac cortical stimulation (interoception) to ease the processing of exteroceptive signals. In contrast, a higher heart rate marks a sensory rejection, thereby attenuating exteroception. The motivational view (Cannon, 1929; Obrist, 2012) explains the adaptive utility of heart rate changes based on the internal metabolism level and energetics needed for the bodily movement interaction with the external environment. A higher heart rate, in this view, influences the brain and behavior, thus helping to increase the central and bodily metabolism and preparedness for motor action (fight or flight); a lower heart rate is appropriate when it is needed to stand still and passively observe (Lacey & Lacey, 1974; Obrist, 2012; Vila et al., 2007). Here, we hypothesize how these adaptive influences of heart rate on perception and action could explain the relationship between beat-by-beat ups and downs of the heart rate and time perception.

Previous studies on the role of the heart on time perception have largely focused on estimating the average cardiac measures on longer time-scales (seconds to minutes). For instance, a number of studies investigated the relationship between average heart rate and perceived duration of an interval, with inconclusive results (Bell & Provins, 1963a; Osato et al., 1995; Schwarz et al., 2013). Few studies used other cardiac markers, such as the slope of change in heart rate during an interval (Angrilli et al., 1997; Meissner & Wittmann, 2011), the

amplitude of heartbeat-evoked potentials in the brain (Richter & Ibáñez, 2021), or the overall heart rate variability (HRV; Cellini et al., 2015; Fung et al., 2017; Ogden et al., 2019, 2022). Whereas these studies typically estimated average cardiac measures for longer intervals, here, we employed a different approach. We investigated the beat-by-beat fluctuations of the heart period on the experience of brief moments in time.

Compared to longer time scales, subsecond temporal perception has different underlying mechanisms, corresponding more closely to the direct and automatic perception and the direct experience of time (Eagleman, 2008; Lewis & Miall, 2003; Rammsayer, 1999). Brief intervals also require more precise computational analyzes to measure their real-time relationship with cardiac dynamics. A subsecond stimulus can be a small fraction of a single heartbeat. Such stimuli are so brief that they resemble spikes causing perturbations in the heart-period sequence, thus altering the subsequent cardiac contractions. Estimates such as average heart rate, average slope of heart rate change, or HRV measures calculated during longer intervals in previous studies are not applicable for the duration of subsecond intervals.

We examined how trial-by-trial cardiac dynamics track the subjective waxing and waning of subjective duration in a temporal bisection task with 88-188 ms durations. We analyzed the temporal perception process using the Drift-Diffusion Modeling (DDM) (Ratcliff & McKoon, 2008). DDM has been previously used in several tasks and contexts to illustrate the role of central measures of neural activity (e.g. Nunez et al., 2017; Turner et al., 2015; van Vugt et al., 2012) or peripheral physiological measures such as pupil dilation during the decision process (e.g. Cavanagh et al., 2014; Schriver et al., 2020). We propose that the bidirectional and multi-dimensional role of the heart rate during the temporal decision process makes DDM a suitable framework for understanding the heart-time perception interaction. In our DDM framework, the Decision Variable (DV) represents the amount of evidence in favor of a longer perceived duration (Balci & Simen, 2014). DV has initially a value reflecting the initial bias towards either response. The evidence is further accumulated in DV over time through a random walk with a

constant average pace, i.e., the *drift rate*. When the DV hits either *short* or *long* decision *thresholds*, the response is determined. The duration of the evidence accumulation process is the decision-time; while a *non-decision time* represents the duration needed to encode the stimulus, before the accumulation process, and the skeletomotor response after the decision is determined. Here, for the first time, we propose to utilize a cardiac DDM (cDDM), embedding the trial-by-trial cardiac measures in the DDM model parameters, including the initial bias, drift rate, and the non-decision time.

We investigated a set of hypotheses regarding the role of heart rate features in modulating cDDM parameters. Cardiac markers associated with sensory intake (larger COR or lower heart rate upon stimulus onset) are anticipated to have the same effect on time perception as if the stimulus was sensorily stronger or more attended. These factors have been robustly associated with a dilation bias of perceived stimulus duration (reviewed in Matthews & Meck, 2016), and expected to reflect longer subjective duration. In contrast, according to the motivational perspective, a higher heart rate indicates central vigilance levels and preparedness for action (Borghini et al., 2014; Lohani et al., 2019; Olbrich et al., 2011). From this perspective, with a transition from a lower heart rate to a higher heart rate, one would expect faster and more efficient temporal judgements (**Figure 1**).

We first investigated the relation between cardiac features to an individual's internal consistency in time perception, their tendency to have temporal distortions (dilations vs contractions), and response time to making temporal judgments. We then dived deeper into the mechanistic modeling, testing whether adding cardiac dynamics to a temporal decision model provides a better account of the observed time perception behavior. Finally, we investigated whether the heart period and time perception interactions depend on individual differences in interoceptive awareness of cardiac afferents in a heartbeat counting task. The interoceptive sensitivity has been shown to be related to the “feeling” of time (Craig, 2009) in supra-second time scales (Meissner & Wittmann, 2011; Pollatos et al., 2014; Richter & Ibáñez, 2021; Teghil et

al., 2020). We examined whether individual differences in interoceptive awareness of heartbeats applies to subsecond intervals (Cellini et al., 2015). In combination, these investigations aim to shed light on the multidimensional role of the heart rate in high resolution temporal perception and the bioenergetic embodiment of the temporal decision process.

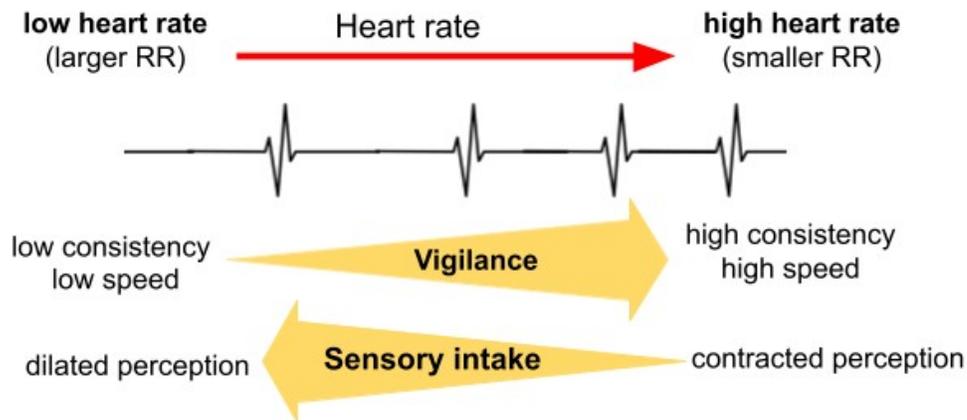


Figure 1. Two views on the impact of heart rate on the brain and behavior

Materials and Methods

Participants

A total of N=45 individuals (29 female) participated in the study. Participants were undergraduate students at Cornell University aged between 18 and 21 years. They received extra course credit as compensation for their time. All participants had normal or corrected to normal auditory acuity and had no history of heart disease. The study procedure was approved by the Cornell Institutional Review Board, and all participants provided their written informed consent for participation.

Procedure

Participants filled out the informed consent form after arriving at the lab, and the electrodes were attached for cardiac recording. They then performed a temporal bisection task followed by a heartbeat-counting task. The resting ECG signal was also recorded for an additional 3 minutes after the tasks during which participants were asked to relax and do nothing while they were sitting behind the computer. All experimental procedures were in accordance with the Declaration of Helsinki and received ethical approval from the Cornell University Institutional Review Board.

Temporal bisection task

Stimuli for the temporal bisection task were randomly generated white-noise tones with a sampling frequency of 441 Hz. Tones had seven duration levels varying by 18 ms, between 80 ms (short) and 188 ms (long) linearly spaced in 18 ms increments (80, 98, 116, 134, 152, 170, and 188 ms). The volume of the tones was adjusted to a comfortable level by the participant at the beginning of the procedure. A tone was played in each trial of the temporal bisection task, and the participant had to categorize it as either short or long. Participants first practiced to learn the reference tone durations before starting the main task.

In the training phase, participants heard the short (80 ms) and long (188 ms) reference tones as many times as they wanted by pressing the 'S' and 'L' labeled keys on the keyboard. Then either the short or long reference tone was played in each practice trial, and the participant responded whether it was short or long using S or L keys, respectively. Each response was followed by visual feedback indicating whether it was 'correct' or 'incorrect'. Practice was performed for a minimum of eight trials and proceeded until the experimenter and the participant believed that the discrimination had been learned.

After the practice session, the main test consisting 210 trials (15 blocks of 14 trials each) began. Each of the seven stimulus durations were played in two trials, ordered randomly in a

given block. A trial started with a fixation point at the center of a black screen with a randomly jittered duration (mean=500 ms, S.D.=280 ms), followed by playing the tone through headphones. To ensure control of the effect of cardiac phase at the tone onset time, all tones in each block were randomly assigned to be synchronized either with the systolic (50%) or with the diastolic (50%) phase of the cardiac cycle. The participant then gave a self-paced response to whether the tone duration was closer to the short or the long standard tones, by pressing the 'S' or 'L' key, respectively. A response was followed by an inter-trial-interval of 3500 ms, after which the next trial started. The task was developed in Python using the psychopy package. The 'S' and 'L' labels were located on the 'V' and 'B' keys on a standard US keyboard, counterbalanced across participants.

Heartbeat-counting task

We measured heartbeat-counting in three intervals following a protocol similar to Schandry (1981; see also Chick et al., 2020), to assess interoceptive awareness. The intervals were 25, 35, and 45 seconds unbeknownst to the participant and separated by 30-second rest periods. Participants were instructed not to touch their pulse and just to count their heartbeats by tuning into their bodily sensations. Each interval started with the words *Start counting* at the center of the screen and ended with the word *Stop*. Participants were then asked to enter their number of counted heartbeats on the keyboard.

Physiological recording

We recorded the ECG signal during the task with the Biopac M150 device. Two electrodes were placed over the approximate location of the corrugator supercilii with a third electrode on the participant's right cheekbone serving as the ground. To systematically control the phase between stimulus presentation and cardiac cycle, we performed real-time peak detection using the *rtpeaks* package in python (<https://github.com/rmarkello/rtpeaks>). We

counterbalanced the stimulus onset in the temporal bisection task according to the phase of the cardiac cycle. Half of the tones were played during the systole (starting at the R-peak+300ms) and the other half during diastole (starting at the R-peak).

Analysis

Psychometric analysis of temporal discrimination

Subjective point of equality, referred to as the bisection point in the temporal bisection task, was defined as the tone duration at which a person is equally likely to choose a short or a long response. Response time (RT) was estimated for each trial as the time from the end of the tone until the response button was pressed. Psychometric fitting was performed using the Palamedes toolbox in Matlab (Prins & Kingdon, 2009). We used the maximum-likelihood estimation to fit a logistic function to each individual's data. The guessing rate (γ) was set to 0 assuming no prior bias towards short versus long choices, and the lapse rate (λ) was fixed at 0.02 to allow for occasional random responses. Two measures of the bisection point and sensitivity (slope of the logistic model) were free parameters of the model estimated for each participant.

RR time series extraction

We estimated R-peaks in the ECG signal and accordingly, the RR intervals between consecutive peaks using the Peakdet toolbox in python (<https://github.com/physiopy/peakdet>). This resulted in a sequence of RR's indicating duration of interbeat intervals over time, where the value at each point (R-peak) was the duration of the preceding cardiac cycle. We interpolated the RR sequence into a continuous series with a constant resolution, to obtain the value of RR over time with a constant resolution (Allen et al., 2007; Paulus et al., 2016). This interpolation assumed that RR at any given time is a weighted average of the previous and

current interbeat intervals, weighted proportional to the relative distance from the previous and to the next beats. Here we refer to the resampled RR signal with the resolution of 100 ms as the *RR time series*.

Data pre-processing

The first three trials of the temporal bisection task were excluded from the analysis due to potential novelty effects on cardiac orienting. The last trial of each block ended with a message appearing on the computer screen immediately after the response, indicating the end of the block. This trial was also excluded from the cardiac data analysis due to the possible impact of the end-of-block message on the heartbeat intervals following the stimulus.

RR intervals that were more than four standard deviations far from the mean were considered outliers (0.47% of all RR's), and were discarded and replaced by interpolated values in the RR series. Trials with RTs longer than 3000 ms were also considered as outliers and excluded from the RT analysis (2.0% of trials). The cardiac signal of three participants during the heartbeat-counting task was not saved due to a technical issue; they were therefore excluded from the heartbeat-counting task analysis.

Trial-by-trial cardiac feature extraction

RR-time series were calculated as the resampled RR signal (beat-to-beat interval) with the resolution of 100 ms following the above procedure for the cardiac data during the bisection task. Several measures were then defined to characterize the shape of the cardiac response in each trial to dissociate the phasic changes from the tonic state (**Figure 2** and **table 1**).

Pre-stimulus RR (preRR) indicates the baseline heart rate prior to the onset of the stimulus or fixation in each trial independent of the stimulus. RR time series on average started to increase at 1300 ms before the stimulus onset. Accordingly, preRR was defined as the

interbeat interval at $t=-1300$ ms. This time is approximately 800 ms prior to the onset of the fixation point and is unaffected by the orienting to the tone stimulus or the preparatory fixation.

Following the fixation and stimulus onset, there was an average increase in RR indicating a COR until it reached a maximum and returned to baseline before the next trial. The average RR time series resembled a bell-shaped curve with a maximum peak. To characterize this COR to stimulus we defined two measures of *COR magnitude*, that is the amount of increase in RR, and *COR peak latency* (in ms) from stimulus onset until the curve's peak. The maximum RR averaged across all subjects was 1400 ms after the stimulus onset (rounded to the 100 ms signal resolution). Specifically, COR peak latency was estimated for each single trial and for each individual as the time point in a 1000 ms time window around this mean (between $t=900$ and $t=1900$ ms) at which RR had its maximum value. This time window was chosen to allow flexibility for individual and trial-specific latencies of the COR peak around the average latency. COR magnitude in each trial was estimated as the value of RR at the peak, i.e. at $t=\text{COR peak latency}$ minus preRR. Hence, COR magnitude reflects the maximum amount of change in RR following the stimulus and COR peak latency indicates the duration that RR continues to increase following the stimulus. We would expect the peak latency to be correlated with preRR such that a higher heart rate before a trial leads to a shorter duration of and faster cardiac orienting due to higher preparedness (Sjöberg, 1975).

Post-orienting RR was also estimated as a measure of RR after the transient cardiac changes. Average trial RR time series was at its minimum following the stimulus at $t=3500$ ms. Post-orienting RR was therefore defined as the minimum RR value following the orienting response in a 1000 ms time window around this time (between $t=3000$ and $t=4000$ ms).

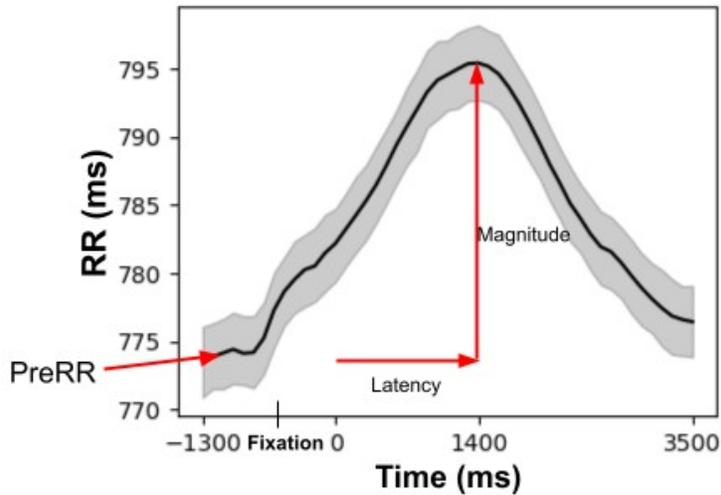


Figure 2. Average Cardiac Orienting Response (COR). The gray shade represents the 95% confidence interval. A fixation cue with jittered duration was presented with an average of 500 ms before the tone onset. COR peak latency represents latency to reach the maximum RR (R wave to R wave, representing the heart period) following the stimulus; COR magnitude represents the amount of increase in RR reflecting cardiac deceleration.

Table 1. Summary of main extracted trial-by-trial cardiac variables

	Description	Mean (sd)
PreRR	RR prior to stimulus onset	774 (56) ms
COR peak latency	The latency that RR reaches its peak following the stimulus	1396 (421) ms
COR	Overall change in RR following the stimulus, i.e., value of RR at peak minus preRR	39 (62) ms
COR slope	Instantaneous change in RR per unit of time following the stimulus, i.e., COR magnitude (RR at peak minus preRR) divided by COR peak latency	0.03 (0.05)

Heartbeat-counting task performance

We recorded the number of actual R-peaks in each interval of the heartbeat-counting task. Error rate in each interval was estimated by the following formula:

$$\left| \frac{\text{actual beats} - \text{counted beats}}{\text{actual beats}} \right|.$$

Error rates of the three intervals were then averaged, and task performance was estimated as $\ln(1 - \text{average error})$. The natural logarithm operation was applied in this formula to satisfy assumptions of the normality of the distribution across subjects.

Resting heart rate variability (HRV)

Peaks in the ECG signal were detected for the 3-minute resting state recording following the temporal decision task. The HRV analysis was performed using the RHRV package in R (Martínez et al., 2017). In the frequency domain analysis, the HF band was defined between 0.15 and 0.4 Hz as an index of vagal control (Berntson et al., 1997). Root Mean Square of Successive Differences in RR's (rMSSD) was also estimated as another measure of vagally induced HRV in the time domain.

DDM model description

We proposed a cardiac DDM (cDDM) that embeds the cardiac dynamics in the temporal decision process (**Figure 3**). In our temporal DDM model (**Figure 3-top**), Decision Variable (DV) at any point in time encodes the relative cumulative evidence for choosing the long vs the short response. This definition of DV has been shown to successfully fit the temporal judgment behavior in bisection tasks in previous studies (Balci & Simen, 2014; Tipples, 2015; De Kock et al., 2021). Given the short duration of the stimuli relative to the RT, we assumed that the random drift and diffusion process occurs after the stimulus offset in a single stage (in contrast to the two-stage DDM that has been proposed for longer durations; Balci & Simen, 2014).

Accordingly, the stimulus time window (88-188 ms) was modeled as one integrated percept prior to temporal evidence accumulation (Herzog et al. 2020). The decision process starts at $t=0$ with $DV=z$, which reflects the prior bias towards either short ($z<0$) or long ($z>0$), based on the initial encoding of the stimulus.

Following the stimulus encoding, temporal evidence accumulation occurs by referring to the echoic sensory memory (Sams et al. 1993). DV changes through a random walk process with an average rate of v (drift rate) until it hits a decision boundary (a for long and $-a$ for short). If $v>0$, then the DV is more likely to hit the upper threshold ($+a$) leading to the long response and if $v<0$ it is more likely to hit the lower threshold ($-a$), leading to short response. Decision threshold is a single free parameter capturing the distance between the short and long decision boundaries. Hence, it cannot be used to model any biased inclination towards one response over another. However, in general, a more positive v is associated with greater evidence accumulation; therefore, the longer a tone is, the greater is the drift rate, increasing the intake of temporal evidence per unit of time during the decision process (Balci & Simen, 2014). This can be modeled by setting the drift rate as a linear function of the stimulus duration. The model also includes a delay of T_{er} (non-decision time) which is added to the duration of the decision process demonstrating the sensory encoding of the stimulus and the motor execution (either before or after the drift and diffusion process). Given that the decision process was modeled with a single stage, differences in stimulus duration were considered by T_{er} , accounting for the delay for initial stimulus encoding. Sensory encoding of a longer stimulus takes a longer time, and hence leads to a larger T_{er} . Accordingly, in the basic DDM, v and T_{er} were modeled as:

$$\begin{aligned}
 v &= \beta_0 + \beta_1 * duration \\
 T_{er} &= \beta_2 + \beta_3 * duration \\
 z &= \beta_4 \\
 \alpha &= \beta_5
 \end{aligned}
 \tag{Eq. (1)}$$

where $\beta_0, \beta_1, \beta_2, \beta_3, \beta_4, \beta_5$ are free parameters that fit to the data, whereas β_1 and β_3 are expected to be positive. Note that z (initial DV) and α (threshold) are assumed constant across trials within each participant and are fitted to the data (β_4, β_5). We compared this base behavioral model with a cardiac model, i.e. cDDM, embedding the trial-by-trial cardiac measures of *preRR* and *COR* into the model parameters to test our hypotheses about the role of the heart.

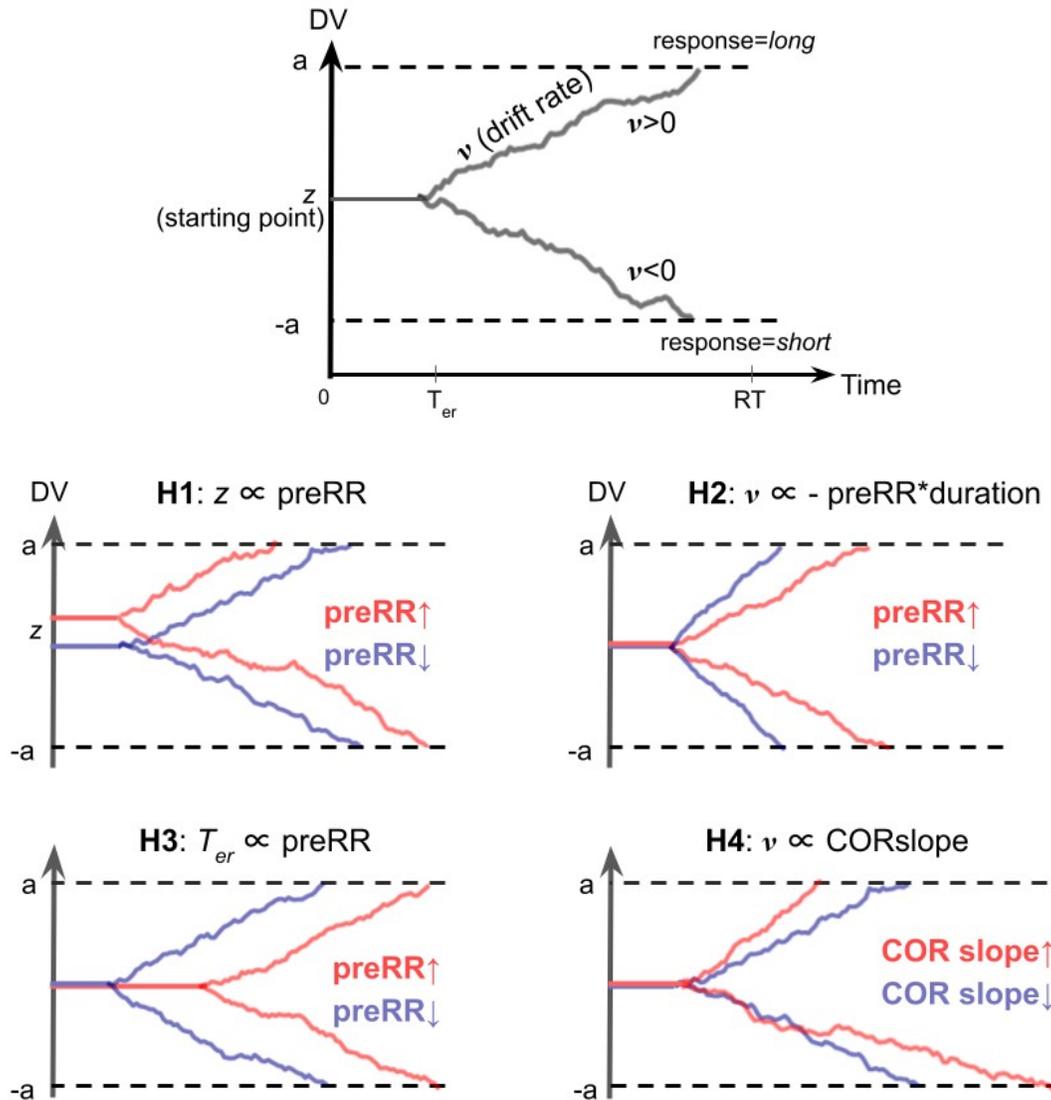


Figure 3. Top: Schematic of the DDM used for modeling temporal responses (short-long) and Response Time (RT). DV=decision variable; T_{er} = non-decision time; RT = response time; a = decision threshold; Bottom: visual representation of the four hypotheses in the cDDM. Each plot demonstrates the effect of higher versus lower *preRR* or *COR* on DV over time if the corresponding hypothesis holds. Parameter magnitudes are only for illustration purposes.

Table 2. Summary of hypotheses

	Hypothesis	cDDM denotation	choice outcome	RT outcome
H1	A larger preRR facilitates sensory encoding, towards longer.	$z \sim \text{preRR}$	bias \sim preRR	RT \sim -preRR*duration
H2	A smaller preRR leads to more efficient temporal evidence accumulation.	$v \sim -\text{duration}*\text{preRR}$	consistency \sim preRR	RT \sim preRR
H3	A smaller preRR aids faster skeletomotor response execution.	$T_{er} \sim \text{preRR}$	-	RT \sim preRR
H4	COR reflects attentional orienting, increasing temporal drift rate.	$v \sim \text{CORslope}$	bias \sim COR	RT \sim -COR*duration

~ symbol indicates that the left term is a linear function of the right term.

Hypotheses

In a set of hypotheses, we associated RR dynamics during a trial with the trial-by-trial variation in DDM parameters. We hypothesized two roles for preRR (**Figure 1**), one associating a larger preRR with sensory facilitation biasing time towards *long* (H1), and the other, relating a smaller preRR with more vigilance and action preparedness leading to more consistent and faster temporal perceptions (H2, H3). We also hypothesized a post stimulus role of COR, the cardiac marker of central phasic attention, in biasing time perception towards the *long* response (H4). Below we elaborate H1-4 in the context of DDM (also see **table 2** and **Figure 3**).

H1) We hypothesized that the sensory facilitatory effect of a lower heart rate is reflected in the initial bias for encoding the tone stimulus as more intense (larger initial DV). Note that the stimulus duration was considered as part of the initial encoding of the stimulus, reflected in the non-decision time (T_{er}), prior to the onset of evidence accumulation for the temporal decision. Therefore, a more intensely perceived stimulus should have its influence on subjective time in

the initial encoding phase, rather than the drift-diffusion phase during which the stimulus is no longer present. Formally, we hypothesized that a larger preRR facilitates initial sensory encoding of the brief stimulus ($z \propto preRR$), moving the starting point z closer to the upper “long” decision threshold a . The consequence of this effect on temporal choice is that a larger preRR would increase the response bias towards *long*. Furthermore, this hypothesis entails that a larger preRR decreases RT when the stimulus is long and increases RT when it is short, implicating an interaction between preRR and stimulus duration in explaining RT (see the H1 plot in **Figure 3**).

H2) To account for the effect of preRR on accuracy and speed, we hypothesized that it modulates the drift rate for the temporal decision. The temporal decision would be more consistent and faster if the absolute magnitude of drift rate is accelerated. In other words, a faster and more accurate decision occurs if drift rate is more positive when the stimulus is long, and more negative when the stimulus is short. Therefore, in H2 we hypothesized that when stimulus duration is longer, a higher preRR (lower heart rate) negatively biases the drift rate towards smaller values (more negative) and when duration is shorter, it positively biases it towards larger values (more positive). This can be formulated by assuming an interaction between stimulus duration and preRR in modulating the drift rate ($v \propto -duration * preRR$; a smaller preRR increases v when objective duration is long and decreases v when duration is short). Note that including preRR in drift rate simultaneously modulates both accuracy and speed, aligned with our hypothesis about the role of vigilance and preparedness. That is, when drift rate is more efficient (with smaller preRR), DV hits the consistent decision threshold faster, leading to a shorter RT (H2 plot in **Figure 3**).

H3) Another possible source of preRR influencing the speed (but not consistency) of temporal response in cDDM is by modulating the non-decision component of response time. The non-

decision time (T_{er}) includes the latency of the motor action since the response is determined until the response key is pressed. A larger preRR (lower heart rate) can lead to a slower skeletomotor response execution due to decreased bodily metabolism. Therefore, H4 hypothesizes that $T_{er} \propto preRR$.

H4) Unlike preRR, which had two possible roles, on bias due to sensory facilitation (H1), and on consistency and speed (H2-3), we hypothesized only one potential role for COR. The increase in RR following the stimulus (i.e. COR) is a specific marker of phasic allocation of attentional resources towards the stimulus following its onset. With more attention, we would expect more temporal bias towards *long*, based on the expected effect of attention on dilating subjective time. COR occurs following the stimulus with a peak near or even after the decision is made (**Figure 2**), making it associable to the evidence accumulation process rather than initial encoding. We would therefore anticipate a role of COR in biasing the drift rate towards the *long* response. In the cDDM, drift rate demonstrates the average amount of evidence per each small-time step, which is added (accumulated) to all of the evidence in previous time steps, until a decision is made. COR in the context of DDM was defined as change per unit of time, in accordance with the cumulative nature of the model over time. We hypothesized that the drift rate is modulated by the slope of COR, that is, the average rate of instantaneous change in RR at any small time step. Thus, H4 stated that a larger slope of COR leads to a larger drift rate ($v \propto CORslope$). In the context of behavioral regression analysis, we used the overall COR (rather than slope) since the instantaneous within-trial dynamics was not modeled. COR in that context can be viewed as the accumulated COR (slope) per each time step making up the overall magnitude.

The behavioral consequence of H4 is that a larger COR magnitude increases the chance of choosing the *long* response, which in turn leads to a larger response bias (more dilation of time). As shown in **Figure 3-H4 plot**, this hypothesis entails an interaction between

stimulus duration and COR in predicting RT, such that a larger COR increases RT more when the stimulus is short rather than long: $RT \propto -COR * duration$

Table 2 presents a summary of all hypotheses along with their predicted impact on choice (consistency or bias) as well as RT. The parameters of the cDDM model, when embedding all H1-4 into the model are as follows:

$$\begin{aligned}
 v &= \beta_0 + \beta_1 * duration + a_2 * duration * preRR + a_4 * COR * slope \\
 T_{er} &= \beta_2 + \beta_3 * duration + a_3 * preRR \\
 z &= \beta_4 + a_1 * preRR \\
 a &= \beta_5
 \end{aligned}
 \tag{Eq. (2)}$$

Here a_1, a_2, a_3 and a_4 are free parameters (coefficients of cardiac terms) that are fitted to the data in the proposed cDDM, in addition to the base parameters $(\beta_0, \beta_1, \beta_2, \beta_3, \beta_4, \beta_5)$. The four hypothesis predict significance of a_1, a_2, a_3 and a_4 in the following directions: H1) $a_1 > 0$; H2) $a_2 < 0$; H3) $a_3 > 0$; H4) $a_4 > 0$.

In cDDM, we have both preRR and COR as variables that independently modulate different components of the decision process. Because of the correlation between these measures, preRR was regressed out of COR before fitting the models to data. This helped to correct for collinearity, obtaining a measure of instantaneous change in RR independent of the magnitude of RR prior to the orienting response.

DDM Model fitting

We used hierarchical Bayesian modeling to fit the base DDM and the cDDM model to the data. This was implemented by the *hddm* library in python (Wiecki et al., 2013). In this method, parameters are treated as random effects that are specific for each individual but are constrained by the group distribution. Each model parameter is assumed to have a normal distribution across individuals with the mean centered at the group mean. The Markov Chain

Monte-Carlo (MCMC) method was used to generate the posterior probability distribution of parameters through a random walk with N=2000 samples (The first 1000 samples in the chain were discarded as burn-in). Deviance Information Criterion (DIC) was used to measure goodness of model fit and compare the base DDM with the different cardiac DDM's. DIC is a measure for model comparison in Hierarchical Bayesian modeling that takes into account the likelihood while also penalizing the number of model parameters (smaller DIC indicates better fit).

Cardiac measures were standardized to have a standard deviation of 1 before fitting the models. Also, for easier interpretability, the bisection point duration was subtracted from the stimulus duration, such that a positive duration indicated that the stimulus was long, and a negative duration indicated that it was short.

Regression analysis

We intended to examine whether heart rate variation could be associated with distortions in perceived time across different trials within individuals. For this purpose, we defined trial-by-trial measures of temporal *bias*, and temporal *consistency*. Temporal bias in a given trial was based on perceived duration of the tone relative to the middle duration level (134 ms): bias=+1 (dilation) indicates that the tone was shorter than 134 ms and perceived long; bias=-1 (contraction) indicates that the tone was longer than 134 ms and perceived short; and bias=0 neither dilation or contraction.

To define temporal consistency, we assumed that the *consistent response* (response of a hypothetical person with perfect temporal consistency) is *long* when the stimulus duration is above the subjective bisection point, and *short* below the bisection point. Temporal perception in a trial was considered to be consistent (consistency=1), if the participant's response matched the consistent response, and inconsistent (consistency=0), if it did not. Tones with a duration

closest to the bisection point (1/7 of trials) were excluded from the analysis of consistency; because even the most consistent hypothetical perceiver could respond randomly close to the transition between short and long. It is worth noting that consistency is closely related to the absolute value of bias, i.e. inconsistency is either contraction or dilation (although, bias was defined based on the objective middle duration to reflect bias from an objective reality; while consistency was defined based on the subjective bisection point to reflect internal consistency).

All intra-individual statistical tests examining the relationships between trial variables in the temporal bisection task were based on linear or logistic mixed-effects regression models unless otherwise stated (lmer and glmer packages in R). Logistic regression was used when there was a binary dependent variable such as a short/long response, and linear regression for a continuous dependent variable such as COR. Mixed effect models enabled us to obtain intra-individual effects, taking into account the inter-individual variations of the intercept by defining a participant-specific random intercept. Coefficients of explanatory variables were set as fixed effects unless otherwise stated. For each mixed-effect logistic regression model, we reported the coefficient (beta) of the fixed-effect explanatory variables of interest (on a logit scale), z-statistic and p-value representing the coefficients' significance. We reported t-statistics, degrees of freedom for linear regressions instead of the z-statistics. RR or RR change, RT, or stimulus duration were all measured on a millisecond time scale.

Results

Temporal bisection performance

Participants performed a binary temporal dissection task of presented tones. **Figure 4** shows the average psychometric function across all participants. The mean bisection point was 133 ms (Median=132 ms, SD=11 ms, min=114 ms, max=156 ms), which very closely approximated the middle duration level between short and long durations (134 ms). There was

no significant average bias towards short or long responses (one-sample t-test comparing bisection point with 134, $t(44)=-0.52$, $p=0.60$) and both the longest and shortest durations were discriminated with near perfect accuracy (number of responding *long* for the shortest or *short* for the longest tones < 2%). The average RT was 729 ms (median=750 ms, SD=370 ms). Stimulus duration did not predict RT ($\beta=0.04$, $t(8135)=0.36$, $p=0.72$). The slope of the psychometric function, which indicates the sensitivity of an individual in perception of duration, had a mean of 0.107 1/ms (median=0.106, SD=0.027). An increase from 25% to 75% in perception of long duration was on average associated with 30 ms difference in tone duration.

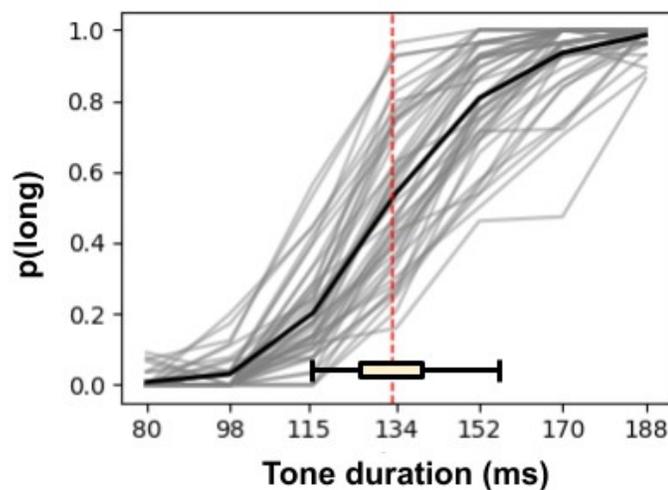


Figure 4. Psychometric function of temporal bisection. The proportion of times a tone was perceived as long is plotted for the different objective tone durations, for individual participants (gray) and average of all participants (black). The vertical dotted line represents the average subjective bisection point (duration=133 ms). The boxplot representing quantiles of the bisection point distribution across participants is shown at the bottom. N.B.: the duration of subject equivalence is near the objective midpoint at 134 ms.

Average trial cardiac dynamics

We obtained the RR time series during each trial, aligning the tone onset time to $t=0$. Participants exhibited an increased heart period (increased RR interval) after tone onset which

returned to baseline before the next trial, following an average canonical bell shape (**Figure 2**). **Table 1** shows the summary of the main cardiac measures extracted from each trial. The peak of the RR time series (peak latency) averaged across all trials and participants was at $t=1396$ ms (range across participants = 1186 to 1552 ms) after the tone onset. Heart period began to lengthen before tone presentation, indicating orienting following visual fixation (average at $t = -500$ ms). The preRR subtracted from the RR at $t=1400$ ms was significantly above zero (estimate=21.59 ms, $t(43.9)=12.5$, $p<0.0001$), indicating a highly reliable lengthening of heart periods following the tone onset, which is consistent with a cardiac orienting response (COR) in relation to the temporal task. In addition, a lower pre-stimulus RR, i.e. higher heart rate preceding the stimulus onset, predicted a larger COR magnitude indicating increased cardiac deceleration (beta=-0.52, $t(7497)=47.1$, $p<0.001$). That is, a higher heart rate before the task was followed by a larger COR in response to stimulus, consistent with a state of motivational vigilance antecedent to the temporal task, was associated with a larger orienting toward the presented tone.

Regression analysis across trials

Figure 5 shows the average RR time series during the time course of a trial for different levels of objective and subjective temporal perceptions. The objective stimulus duration (seven possible values) linearly predicted neither the cardiac orienting measures of COR magnitude (beta=-0.026, $t(7613)=-1.3$, $p=0.18$) nor the COR peak latency (beta=-0.077, $t(7624)=-0.33$, $p=0.74$; **Figure 5.A**). Thus, we did not observe a significant modulation of the cardiac signal or latency to the behavioral response based on the objective duration of the stimulus. There were, however, reliable differences in heart-rate dynamics and variability in subjective temporal judgments. We next examine the behavioral consequence of each of our hypotheses.

H1: effect of heart rate on response Bias and RT

Direction of temporal bias (-1, 0, +1) was not explained by preRR (beta=-6.4e-5, t(4587)=-1.28, p=0.22) or post-orienting RR (t(6515)=0.79, p=0.43). Therefore, our hypothesis about the effect of lower heart rate on temporal dilation (**H1**) was not confirmed in the regression analysis. However, we observed a significant interaction effect between preRR and stimulus duration on explaining RT (t(8073)=-3.1, p<0.01), confirming the RT-related consequence of H1. Specifically, a larger preRR increased RT more when the stimulus was shorter rather than longer in accordance with H1.

H2 and H3: effect of heart rate on response consistency and speed

There were notable differences in heart-rate dynamics in consistent versus inconsistent temporal duration judgments aligned with **H2** (**Figure 5-B** and **Figure 6** middle column). Consistent trials had a shorter COR peak latency indicating an earlier COR peak (beta=-2.42, z=-3.53, p=0.0004) and a lower preRR (beta=-0.002, z=-2.9, p=0.004), in agreement with the choice outcome in **H2**. Additionally, consistency was predicted from RR at peak of the COR (beta=-0.001, z=-2.2, p=0.025), post-orienting RR (beta=-0.006, z=-2.63, p=0.009), and the average of the pre-stimulus and post-orienting RR (beta=-0.002, z=-2.7, p=0.007). As such, an overall drift shifting up the heart periods series during, before or after a trial was associated with inconsistency in temporal judgments.

The RT-related outcome of **H2** and **H3** was also confirmed, with a faster RT associated with a shorter preRR (beta=0.0.16, t(7416)=5.5, p<0.0001). Faster RT was also correlated with an earlier COR peak latency (beta=-0.77, t(218)=-6.9, p<0.0001; **Figure 6** right column). Additionally, RT and consistency were inter-related: Faster RT significantly predicted higher consistency (beta=-0.001, z=-16.78, p<0.0001). All in all, preRR, COR peak latency and RT were highly interrelated, and associated with variability in temporal judgment consistencies across trials. This is in agreement with **H2** that preRR modulates the drift rate, simultaneously

influencing both accuracy and speed. Further cDDM analysis (next section) could shed light on whether preRR also modulates RT through the non-decision time, as hypothesized in **H3**.

H4: effect of COR on response bias and RT

Temporal bias was linearly related to COR magnitude ($\beta=1.6e-4$, $t(6466)=2.88$, $p=0.004$). The greater the cardiac deceleration in anticipation of the tone, the greater the dilation of its subjective duration, aligned with **H4** (**Figure 5.C**, and **Figure 6** bias column). There was a significant main effect of COR on RT with slower responses corresponding with larger COR ($t(7332)=3.79$, $p<0.001$). This could originate from the participant's self-detection of unpreparedness upon the stimulus onset prior to response, leading to both a larger post-stimulus orienting and slowing (hence a correlation between the two). However, there was no significant interaction between COR and stimulus duration in explaining RT ($t(7334)=0.75$, $p=0.45$), not supporting the RT-related prediction of **H4**.

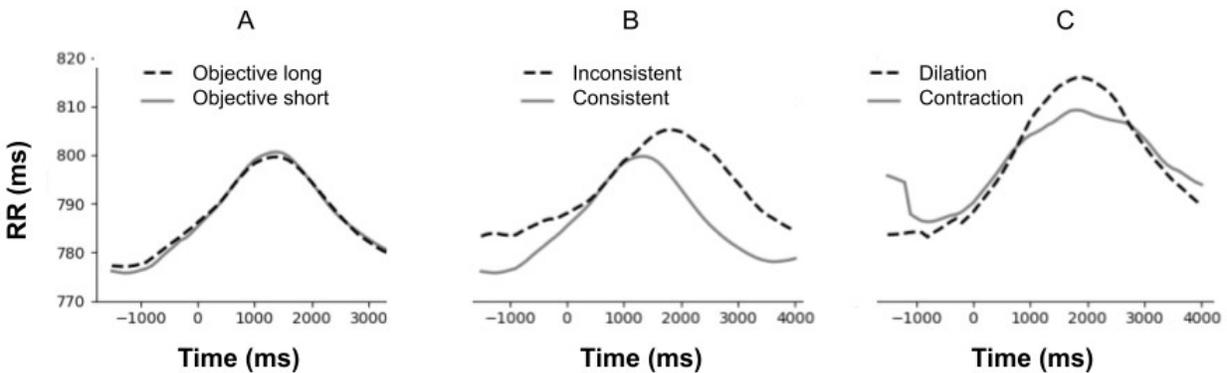


Figure 5. Average RR time series. A) objective short (duration<134 ms) versus the objective long (duration>134 ms). **B)** contraction versus dilation of subjective time, and **C)** consistent versus inconsistent temporal perception. Time=0 is the tone onset time.

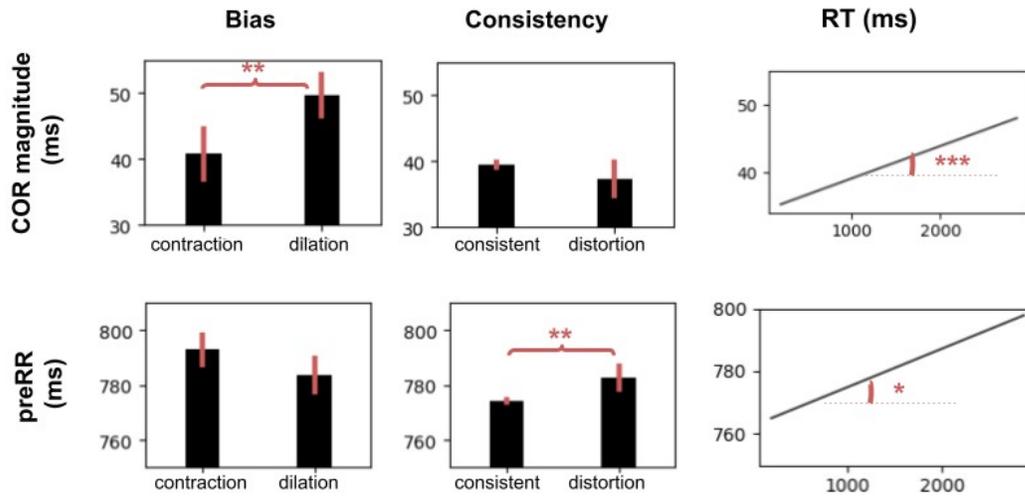


Figure 6. Relation between features of heart-rate dynamics (COR magnitude, and preRR) with behavioral markers of temporal perception (temporal bias, temporal consistency, and response time (RT)). Bar plots represent the means and standard errors of mean for different trial types (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

DDM

To characterize temporal decisions in a model-based framework we employed drift diffusion modeling (DDM). DDM affords a framework to model latent variables associated with evidence accumulation that explains observed temporal decisions. We proposed a variation of the framework for cardiac DDM (cDDM) that embeds cardiac dynamics in the temporal decision process (**Figure 3**, **table 2**, also compare **Eq. 1** and **Eq. 2**). Our four hypotheses associated cardiac dynamics to three variables related to the assessment of temporal intervals: initial DV (z , representing the initial bias towards *long* over *short*), non-decision time (T_{er} , representing delay of initial stimulus encoding or post-decision motor execution) and drift rate (v , representing the speed of evidence accumulation).

According to our basic assumptions (**Eq. 1**), duration of the initial encoding of the stimulus (captured by T_{er}) and the evidence accumulation rate (v) are a linear function of the objective stimulus duration in each trial. The Base model only included the non-cardiac terms aligned with the basic assumptions, whereas the cDDM embedded additional linear

relationships between DDM components and cardiac dynamics based on H1-H4 (see methods for details).

Results of the base model (model that had no cardiac terms) and cDDM both confirmed the validity of the basic behavioral assumptions for the DDM. As expected, the effect of duration on drift rate (β_1 in **Eq. 1**) was significantly positive ($\beta_1 > 0$ in 100% of samples in both models; **Figure 7.a**), confirming that a longer objective stimulus duration was associated with more accumulation of evidence towards *long* rather than *short*, thus a higher chance of hitting the long response threshold. Similarly, the effect of duration on non-decision time (β_3 in **Eq. 1**) was positive in 100% of samples in both models ($\beta_3 > 0$; **Figure 7.b**) confirming that longer tones had a longer non-decision time for encoding the stimulus.

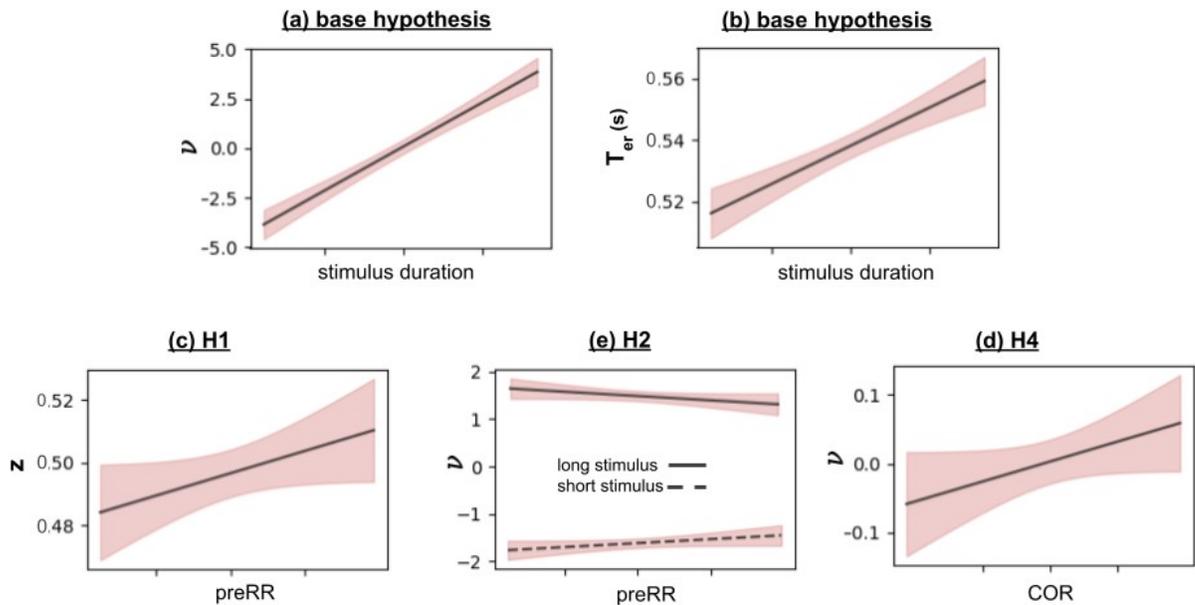


Figure 7. significant linear relationships of cDDM components with stimulus duration (**a, b**; confirming base assumptions), and with cardiac dynamics (**c, d, e**; confirming H1-H3). Each plot demonstrates the linear regression line according to the fitted coefficients in **Eq. (2)**. The three ticks on

each x-axis represent mean-sd, mean, and mean+sd. The pink shades represent 95% confidence intervals.

Model comparison results revealed that including the cardiac terms in cDDM improved the model relative to the base model (base DDM DIC= 4408.0; cDDM DIC=4401.0; difference=7.0). cDDM fitted the behavioral data better than the base behavioral model, aligned with the multi-dimensional influence of heart rate on the decision process and its capability to best explain behavioral data when these effects are taken into account. The fitted parameter values of cardiac terms in cDDM were all different from zero in a significant number of samples for H1, H2, H4 (a_1 , a_2 , a_4), but not for H3 (a_3). Results of these significant linear relationships are illustrated in **Figure 7.c-e** and elaborate below:

H1: effect of preRR on z

The coefficient of preRR in explaining the Initial bias (z), i.e. a_1 , was positive in a significant number of fitted samples ($a_1 > 0$ in 99% of samples, **Figure 7.c**). Therefore, a lower heart rate before the stimulus onset led to initial encoding of the stimulus as longer, in agreement with H1.

H2: effect of preRR on v

A larger preRR significantly deviated the drift rate (v) towards the inconsistent response such that the preRR negatively interacted with stimulus duration (**H2**; $a_2 < 0$ in 96.1% of samples). **Figure 7.c** illustrates this interaction, such that when the stimulus was objectively short, increase in preRR increased the drift rate, and when it was long, it decreased the drift rate. That is, in both cases the drift rate inclined towards the inconsistent choice. This effect can therefore not only explain the effect of preRR on consistency of response, but also its impact on the speed of response, as reported before in the behavioral regression analysis. When drift rate becomes less informed (by increase in preRR), it takes an average longer amount of time for the evidence to reach a decision threshold and therefore RT is increased.

H3: Effect of preRR on T_{er}

preRR did not have a significant direct impact on the non-decision component of the RT as hypothesized in **H3** ($a_3 > 0$ only in 9.8% of samples). This indicates that the effect of preRR on RT as seen in regression analysis mainly originates from the drift rate (H2), rather than the non-decision time (H2).

H4: Effect of COR on v

Drift rate was a function of COR with a positive coefficient ($a_4 > 0$ in 97.0% of samples, **Figure 7.d**) in agreement with **H4**. Therefore, a steeper deceleration of the heart rate following the stimulus inclined the evidence towards the *long* threshold.

Individual differences

While our analyses have focused on individual trial level temporal decisions, we lastly examined individual differences in heart dynamics and time perception. Variation in heart (HRV) is a reliable indicator of individual differences in ANS and specifically vagal activity and has been related to both cognitive and motivational factors (Kim et al. 2018; Forte et al. 2019). HRV is also partly regulated from baroreceptor sensing of pulse, which has potent influences on the brain and behavior (Critchley & Garfinkel, 2018; Azzalini et al. 2019). We found that there was a significant correlation between an individual's average COR magnitude and spectral and temporal indices of vagally mediated HRV during rest (HF: $r=0.44$, $p=0.004$; rMSSD: $r=0.56$, $p=0.0002$). Individuals with higher baseline vagal control demonstrated a greater COR in response to the temporal task, consistent with greater adaptability (Thayer et al., 2009). However, individuals with a greater vagally mediated HRV did not differ in temporal bias, i.e., a significantly longer temporal bisection point (HF: $r=0.14$, $p=0.41$; rMSSD: $r=-0.17$, $p=0.30$), or sensitivity, i.e, the slope of the psychometric function describing the function between tone duration and perceived duration (HF, $r=-0.02$, $p=0.88$; rMSSD: $r=0.16$, $p=0.32$).

With respect to individual differences in interoceptive awareness, participants had on average an absolute error of 46.8% (SD=43%) in counting their heartbeats, consistent with the low accuracy previously reported with this measure (Zamariola et al., 2018). Performance in the heartbeat-counting task was not significantly correlated with temporal perception sensitivity ($r = -0.15$, $p=0.32$), or bias across individuals ($r=0.15$, $p=0.32$). There was no significant correlation between heartbeat-counting performance and other heart period dynamics: average COR magnitude in the temporal task ($r=-0.2$, $p=0.16$), average preRR ($r= 0.24$, $p=0.12$), or COR peak latency ($r=-0.04$, $p=0.81$). As such, while cardiac dynamics influenced perceptions of very brief temporal durations, heartbeat awareness, i.e., counting heartbeats, is unlikely to have contributed to these beat-to-beat modulations of experienced time.

Conclusions

Results revealed the multi-faceted role of beat-by-beat cardiac period variation in the high-resolution experience of time. Auditory stimuli were shorter than a quarter of a single cardiac cycle, varying in duration in steps of 18ms. While heart-rate dynamics were not associated with objective durations, they were highly related to subjectively perceived durations. This was demonstrated by a regression analysis, as well as the cDDM fitting, mechanistically modeling the sources of cardiac involvement in different components of the perceptual decision-making process. Our novel cDDM framework demonstrated that the diffusion and drift decision model can be improved to better explain behavior, when we consider the modulation of model components by cardiac dynamics.

The regression analysis was mainly in agreement with our hypotheses about the role of the heartbeat in time perception, except for the response bias prediction in H1, and the RT prediction in H4, for which the regression result was not significant. While we only considered the trial-by-trial final responses (*short* or *long*) in our regression analysis, cDDM confirmed H1

as well as H2 and H4, when cardiac dynamics were jointly embedded in the hypothesized decision components to mechanistically explain both RT and response. These results confirm the multiple concurrent effects of the fine-grained heart rate dynamics on perception of brief temporal durations. In contrast to the relationship between the heart-rate dynamics and individual subjective temporal perceptions, there was no evident relationship with individual differences in interoceptive awareness (the heartbeat perception task) between participants. One may therefore conclude that the heart-brain interaction during high-resolution temporal perception of brief stimuli does not depend on conscious interoceptive heartbeat sensations (although the validity of the heart-beat counting task has been contested as we further discuss).

Our cDDM results confirmed that heart rate before the stimulus onset contributes to subjective temporal wrinkles, i.e. dilation or contraction of the following stimulus. A lower pre-stimulus heart rate increases the initial DV, biasing the response towards *long* in an additive fashion prior to the decision process (**H1**). It is possible that this effect is causal: lower heart rate aids to “open up” the sensory gates eliminating the afferent cardiac noises during the sensory processing (Lacey & Lacey, 1974; Obrist, 2012). Therefore, “more” of the external world is sensed, mimicking the effect of attention or stimulus intensity on lengthening perceived duration (Matthews & Meck, 2016). A strong support for this causal account comes from a recent study showing that duration of a brief neutral stimulus is perceived longer if presented on the cardiac diastole (compared to systole), when baroreceptors are less active (Arslanova & Tsakiris, 2022). Diastole becomes a more dominant cardiac phase as the duration between heartbeats (RR) gets longer, and therefore its impact is likely to resemble the effect of a lower heart rate.

Results did reveal that faster RT was associated with an earlier COR peak and thus shorter duration of cardiac deceleration. This may indicate a dissociation between how much and for how long attention is engaged. Latency in the context of COR has sometimes been defined as the time from stimulus onset until a specific amount of heart rate deceleration is reached (Kable et al., 2015; Mesa et al., 2017), indicating the delay in COR initiation. We

defined latency as the duration that the deceleration continued (time to peak), marking the time course of attention. Regression results showed a close association between COR peak latency, RT, temporal consistency, and overall trial heart rate (RR before or after the stimulus).

These observations systematically demonstrate that the cardiac dynamics, even within a few heartbeats, is related to the temporal decision-making process: Heart rate deceleration following the stimulus, likely marks attention during the evidence accumulation, until the decision is made, such that a shorter RT denotes a shorter latency of COR peak. A shorter RT is a natural outcome of a more efficient evidence accumulation in the DDM along with higher accuracy (Ratcliff & McKoon, 2008). The fact that a lower heart rate prior to the stimulus, a lower response consistency, and a slower RT, were all highly interrelated with each other, suggests that the effect of pre-stimulus heart rate on RT and consistency may originate from a shared source. These were all matching with **H2**, confirmed with cDDM analysis that a lower heart rate resulted in a less efficient evidence accumulation leading to both slower and less consistent responses. That is, lower heart rate biased the drift rate towards short when the stimulus was long, and biased it towards long when the stimulus was short. This effect of heart rate on temporal consistency is aligned with previous studies in the visual domain showing that higher subjective arousal levels at the time of stimulus onset enhanced perceptual sensitivity (Kim et al., 2017; Woods et al., 2013). The task here was not inherently arousing but did require fast and accurate responses. Hence, changes in heart rate were only detectable in lower, more parasympathetically controlled heart rate ranges. Whether these results can be generalized to perception of more arousing stimuli and higher heart rate ranges requires further investigation.

It has been theorized that heart rate acceleration in response to motivationally intense stimuli aids to increase metabolism to be more vigilant and act faster, while the heart rate deceleration in response to less intense but relevant stimuli facilitates sensory intake (Vila et al., 2007; Lacey & Lacey, 1974; Cannon, 1929). Even though such accelerations and decelerations occur for different reasons, the afferent influence of heart rate magnitude at any point in time

can be simultaneously associated with both of these effects (**Figure 1**). cDDM confirmed this dual role of heart rate on perception of time. While a lower heart rate increased initial bias (sensory intake), it also made the response less consistent and slower (decreased vigilance) by modulating the drift rate (H2). These results suggest that a lower heart rate may deviate the temporal response towards inconsistency, but more so towards the longer durations; and these effects occur concurrently when considered in the same cDDM.

cDDM analysis further revealed that heart rate prior to a trial did not have a direct influence on the motor response execution through the non-decision component of the RT, not supporting **H3**. One possible explanation could be that the range of heart rate changes in our task was too narrow to significantly impact muscle metabolism and motor speed. Therefore, the behavioral observation of heart rate predicting RT, originated only from its impact on drift rate and not the motor delay.

The deceleration of the heart rate coincident with the tone presentation, i.e. COR, is a classical marker of central attention (Sokolov, 1963) known to adaptively facilitate external sensory intake. In this way, the construct of central attention to increase signal and decrease noise (Posner & Petersen; 1990), may originate from and work in concert with evolutionarily more primitive systems of regulating cardiovascular dynamics. cDDM results confirmed that the speed of cardiac deceleration following the stimulus modulates the drift rate in rendering a temporal decision, functionally to greater accumulation of evidence towards *long* rather than *short* (H4). That is, the cardiac modulation of evidence accumulation is part of time perception itself, with greater evidence accumulation resulting in longer temporal perceptions. The causality of the effect of COR on dilating perceived duration, however, is uncertain. The heartbeat time series has a low temporal resolution (mean of RR: 785 ms) to capture the precise cardiac changes before, during or after the decision process. The average COR peak occurred 1400 ms after the stimulus onset, which is after the response (mean of RT: 729 ms). Nevertheless, the temporal precedence of COR relative to time perception is difficult to determine. It is possible

that at least part of the reason COR magnitude tracks temporal dilation originates from the central attentional orienting (increase in drift rate) that causes both the dilation of time and deceleration of the heart rate (Graham & Clifton, 1966; Sokolov, 1963).

One theory is that the heart influences perception of time through interoceptive afferents from the heart to the brain (Craig, 2009; Meissner & Wittmann, 2011). According to this theory, integration of bodily signals in the anterior insula contributes to perception of time, to experience the 'global emotional moment' (Craig, 2002, 2009). While interoceptive awareness of the heart is assessed across beats from baroreceptor sensing of blood volume changes, our examination was of the perception of durations a fraction of a heartbeat in length, that were synchronized to occur with a cardiac cycle. As such, it is not surprising that we found no correlation between cardiac or behavioral correlates of time perception and heartbeat counting. We used the heartbeat-counting task because it had previously been shown to relate to time perception accuracy in the multiple-seconds range (Meissner & Wittmann, 2011; see also Otten et al., 2015, for a failure to replicate). Reporting the number of times the heartbeat was felt during a specified time period is potentially influenced by knowledge of roughly how many heartbeats should occur during a subjectively estimated time span (Windmann et al., 1999; Murphy et al. 2018). It is possible that temporal perception on such a short time scale is faster than and thus unrelated to interoceptive conscious awareness (Cannon, 1927). Consistent with our results, Cellini et al. (2015) found no correlation between subsecond duration perception and heartbeat counting accuracy.

The resting HRV had a significant correlation with the individuals' average COR during the task. This is consistent with the view of HRV as an index of adaptability to environmental demands (Thayer et al., 2009), here decelerating the heart rate in face of central attentional demands following the stimulus onset. However, HRV did not explain individual differences in temporal perception. It is worth noting that the resting HRV was measured for each individual at the end of the experiment. As such, our HRV measure was not a trait, but a state measure

following a mental challenge. If the resting condition was prior to any mental task, we could reach more conclusive results about the relationship between trait HRV and time perception.

The close connection between time perception and the heart, a principal bodily metabolic regulator, advocates for possible roots of time perception in bioenergetics. The field of emotion has widely studied the adaptive utility of bodily changes associated with emotional stimuli (Keltner & Gross, 1999). Bodily adaptations not only influence feelings but also conscious sensory perception (Zadra & Clore, 2011; Critchley & Garfinkel, 2018). In a similar manner, temporal malleability might be another subjective facet of the body's adaptive changes. The shift from lower heart rate to higher heart rate alters one's subjective experience from centrality of the external world to the centrality of the body and our place in it (Vila et al., 2007), where the experience of time is weighted more toward external stimulus features (Coull et al., 2011) versus internal interoceptive cues.

Our cDDM not only does provide important insights about the role of heart rate in time perception, but it also more generally offers a new outlook on how the perceptual decision-making process is interwoven with the heart. Interbeart cardiac dynamics has a rich interaction with the decision-making process (Critchley & Garfinkel, 2018; Azzalini et al. 2019), which, to our knowledge, had not been modeled within the DDM framework. The current cDDM scheme can be applied to other modalities and decision-making contexts illustrating how the different components of the perceptual process are a function of cardiac dynamics. Future studies in this direction would shed new light on the cardiac involvement in the perceptual decision-making process and the underlying embodied mechanisms.

Competing interest

The authors declare that no competing interests exist.

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