

Cardiac afferent signals can facilitate visual dominance in binocular rivalry

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Reviewed Preprint

Published from the original preprint after peer review and assessment by eLife.

About eLife's process

Reviewed preprint version 1

April 11, 2024 (this version)

Sent for peer review

January 17, 2024

Posted to preprint server

December 16, 2023

 https://en.wikipedia.org/wiki/Open_access Copyright information

Abstract

Sensory signals from the body's visceral organs (e.g. the heart) can robustly influence the perception of exteroceptive sensations. This interoceptive-exteroceptive interaction has been argued to underlie self-awareness by situating one's perceptual awareness of exteroceptive stimuli in the context of one's internal state, but studies probing cardiac influences on visual awareness have yielded conflicting findings. In this study, we presented separate grating stimuli to each of subjects' eyes as in a classic binocular rivalry paradigm – measuring the duration for which each stimulus dominates in perception. However, we caused the gratings to “pulse” at specific times relative to subjects' real-time electrocardiogram, manipulating whether pulses occurred during cardiac systole, when baroreceptors signal to the brain that the heart has contracted, or in diastole when baroreceptors are silent. The influential “Baroreceptor Hypothesis” predicts the effect of baroreceptive input on visual perception should be uniformly suppressive. In contrast, we observed that dominance durations increased for systole-entrained stimuli, inconsistent with the Baroreceptor Hypothesis. Further, we show that this cardiac-dependent rivalry effect is preserved in subjects who are at-chance discriminating between systole-entrained and diastole-presented stimuli in a separate interoceptive awareness task, suggesting that our results are not dependent on conscious access to heartbeat sensations.

eLife assessment

This is a binocular rivalry study that uses ECG to present visual stimuli pulsing in line with cardiac events, to examine whether systole-entrained stimuli (i.e. presented during the period where the heart has contracted) are suppressed within visual awareness. Arguably out of line with this idea, the dominance durations were increased for systole-entrained stimuli. The manuscript addresses an **important**, precisely defined, and theoretically well-motivated question using sophisticated experimental and statistical methods. The interpretation of these results is not straightforward, however, such that they currently only provide **incomplete** support for the claims.

1. Introduction

Interoceptive sensory input ascending from visceral organs – such as the heart, lungs, and gut – impacts both spontaneous brain activity and that evoked by external stimuli (Azzalini et al., 2019; Critchley & Harrison, 2013). Cardiac effects on exteroceptive perception have recently become a subject of intense interest, due in no small part to recent theories that interoception plays an integral role in generating the subjective experience of self (Park & Tallon-Baudry, 2014; Seth & Tsakiris, 2018). Early work in this area resulted in the Baroreceptor Hypothesis (Lacey & Lacey, 1978), which states that baroreceptors located in the arterial walls respond to the increase in blood pressure following cardiac contraction, and the ascending input from these baroreceptors broadly suppress sensorimotor activity in the central nervous system. While recent reviews have noted the Baroreceptor Hypothesis still motivates much work in the study of interoceptive-exteroceptive integration (Park & Tallon-Baudry, 2014), more recent studies have indicated, in contrast, that visual skills such as discrimination (Pramme et al., 2014) and search (Pramme et al., 2016) are *facilitated* when stimuli are presented during cardiac systole. Work focused specifically on basic visual awareness rather than visual skills, however, has indeed continued to support the view that conscious access to a visual stimulus is suppressed during systole, and that this suppression is mediated by the insula, which is the primary thalamocortical recipient of baroreceptive input (Salomon et al., 2016, 2018). This discrepancy may be taken to suggest that cardiac inputs to the CNS are initially suppressive for the earliest stages of visual processing, consistent with the Baroreceptor Hypothesis, but have more heterogeneous effects downstream, enabling more complex “cardiac gating” effects such as systolic facilitation of threat (Garfinkel et al., 2014) and disgust responses (Gray et al., 2012) to visual stimuli. If so, however, the level of processing at which cardiac effects on visual perception may shift from suppressive to facilitatory remains unclear.

Resolving this ambiguity seems essential for understanding the proposed link between interoceptive-exteroceptive integration and self-awareness (Park & Tallon-Baudry, 2014; Seth & Tsakiris, 2018). Synchronizing visual stimuli to the heartbeat seems to affect the subjective experience of body ownership, indicating an important role of bodily sensations in carving out which parts of the exteroceptive sensory space belong to oneself – one in which interoceptive sensations provide a “ground truth” point of reference that must originate from one’s own body. For example, causing the color of a virtual body to pulse during cardiac systole facilitates the subjective embodiment of a virtual hand (Suzuki et al., 2013), a full virtual body (Aspell et al., 2013; Heydrich et al., 2018), and of a face image (Sel et al., 2017). In turn, changes in perceived embodiment are reflected in the magnitude of the central neural response to heartbeats (Park et al., 2016). Similar effects on embodiment can be seen for breathing (Monti et al., 2020) and gastric sensations (Monti et al., 2022). Since, simplistically, the two main ingredients of self-awareness would seem to be *self* and *awareness*, uniform suppression of sensations synchronized to interoceptive stimuli – those that are embodied as *self* – would arguably hinder an organism’s ability to become self-aware. However, whatever adaptive benefits of self-awareness may exist, they must be balanced against the imperative to suppress distracting sensory information from awareness, just as the cortical response to one’s heartbeat sounds appears to be suppressed (van Elk et al., 2014). Indeed, bodily sensations generally tend to fade from awareness as one goes about their day unless attention is drawn to them, which itself seems to be a core phenomenological characteristic of bodily self-awareness (Allen & Tsakiris, 2018). However, it is worth noting that volitional conscious access to one’s heartbeat sensations, while rare in the general population, is associated with improved emotional regulation and mental well-being, indicating that the ability to hold the direct sensory consequences of bodily events into consciousness can serve an adaptive function (Füstös et al., 2013; Tsakiris & Critchley, 2016).

In light of these considerations, we posit that the earliest level of sensory processing at which cardiac systole may become, in some contexts, facilitatory should be close enough to the level at which suppression has previously been observed to counter suppressive effects as needed.

Recent work demonstrating suppressive effects of cardiac input on visual awareness has used continuous flash suppression (CFS), a special case of binocular rivalry (Salomon et al., 2016 [↗](#), 2018 [↗](#)), and visual crowding (Salomon et al., 2016 [↗](#)) paradigms to mask stimuli from consciousness, and showed that the threshold for breaking through into awareness is higher in both cases when masked stimuli are entrained to cardiac systole. A commonality between both paradigms is that, at the beginning of each trial, the masked stimulus is just that – masked – and the trial ends when it breaks into awareness. However, theories of consciousness, particularly but not limited to the popular global neuronal workspace theory (Mashour et al., 2020 [↗](#)), tend to emphasize not just a stimulus' ability to initially break into consciousness but its ability to suppress competing stimuli so as to remain in consciousness. This sort of visual competition is exemplified by the classic binocular rivalry paradigm, in which incongruent stimuli are presented to subjects' two different eyes, and the brain resolves the conflict by switching back-and-forth between the two competing images rather than merging them (Carmel et al., 2010 [↗](#)). While reflecting the same mechanism of interocular suppression as the previously used CFS paradigms, the durations of dominance and suppression for the rival stimuli are the cumulative product of the feedforward drive ascending from the optic nerve, lateral inhibition between eyes, and feedback from higher-level visual or cross-modal areas such as in directed attention (Zhang et al., 2011 [↗](#)). In contrast, CFS breakthrough times are theoretically influenced primarily by modulation of the feedforward drive, rather than by lateral inhibition or consciously directed attention.

Thus, we designed an experiment in which we entrained dynamically “pulsing” rivalrous stimuli to systolic and diastolic cardiac phases, cueing pulses based on subjects' electrocardiogram (ECG) in real-time. The Baroreceptor Hypothesis would predict that the stimulus entrained to systole would spend more time suppressed and, conversely, less time dominant, as cortical activity would be suppressed each time that stimulus pulses. Indeed, such a finding would be consistent with the previously demonstrated (Salomon et al., 2016 [↗](#)) and replicated (Salomon et al., 2018 [↗](#)) suppression of stimuli entrained to cardiac systole in the CFS paradigm; this would suggest systolic modulatory effects do not become facilitative until a higher level of processing. An effect in the opposite direction – as we actually observe – would indicate that, at this early stage of visual processing, lateral inhibitory or top-down feedback mechanisms are sufficient to overcome the suppression effect observed in CFS. To differentiate between these two mechanisms, we then assess whether our main finding persists in those subjects who are at-chance at a heartbeat discrimination task.

2. Methods

2.1. Recruitment and Ethics Statement

We recruited 58 subjects (see *Sample Size Determination*) with self-reported normal color vision from our Psychology Department's subject pool, which consists of undergraduate students. Two subjects were dropped due to a technical error during data collection, and two subjects were dropped for failing to comply with task instructions, resulting in a final sample size of $n = 54$ subjects (15 biological males, 39 females, ages 20.4 ± 1.1 SD). Study procedures were approved by the Social and Behavioral Sciences Institutional Review Board (IRB23-1353) at the University of Chicago.

2.2. ECG Acquisition and Real-Time Processing

Electrocardiogram (ECG) was acquired at a 100 Hz sampling rate using a TMSi SAGA amplifier (TMSi, Netherlands) and a bipolar montage, with one electrode placed under the right clavicle, one at the bottom of the left ribcage, and ground under the left clavicle. Real-time analysis of the ECG data was implemented in Python (see *Data and Code Availability*) using Lab Streaming Layer (LSL, labstreaminglayer.org) and LabGraph (github.com/facebookresearch/labgraph). After digitizing, ECG data were bandpass filtered to 5-15 Hz, and R-peaks were detected using the Pan-Thompkins algorithm (Pan & Tompkins, 1985), modified from an existing implementation for LabGraph compatibility (Sznajder & Łukowska, 2017).

From the estimated R-peak times, we generated stimulus time courses on-the-fly as follows (in both the binocular rivalry task and the cardiac discrimination task). Since our ECG amplifier has a known analog-to-digital conversion latency of roughly 35 ms when acquiring data over LSL, we aimed for pulses of the in-phase/systole stimulus to peak at 175 ms, such that it would actually peak at 210 after each R-peak, following previous work on cardiac synchrony effects on embodiment (Suzuki et al., 2013). This timing coincides with peak systolic blood pressure, when the aortic baroreceptors are most active, and when heartbeats tend to be perceived in interoceptive sensitivity tasks (Brener et al., 1993; Wiens & Palmer, 2001). The anti-phase/diastole stimulus was delayed relative to the in-phase stimulus by half of the previous R-R interval. Since this delay was variable between heartbeats – thus distinct from a constant phase delay but, on average, still anti-phase. This avoided the impression that one stimulus was leading or lagging, but as a result, the precise cardiac phase (i.e. within diastole) that the anti-phase stimulus peaked varied across subjects, but it nonetheless peaked during diastole for all subjects (see *ECG Offline Processing and Analysis*). Stimulus “pulses” had the shape of a Gaussian bell curve with a scale (i.e. “standard deviation”) of 1/16 of a second (see **Fig. 1**). The target stimulus size was updated each time a new ECG sample was acquired (100 Hz), and total processing time to compute the intended stimulus time series was roughly a millisecond. On each screen refresh (60 Hz), the actual stimuli were updated to match their current target size.

2.3. Cardiac Binocular Rivalry Task

Subjects wore red-blue anaglyph glasses, such that a red image could be presented exclusively to the left eye and a blue image could be presented only to the right eye. The task consisted of two 10-minute blocks, in which incongruent gratings (256 x 256 pixels on a 1920 x 1080, 22” monitor, which subjects viewed from 2 feet away) were presented to opposite eyes, which is well known to result in the centrally perceived image alternating between the two gratings – rather than, say, merging them (Carmel et al., 2010). As in a typical binocular rivalry paradigm, the subjects indicated with a button press each time the dominant stimulus switched. One grating would “pulse” – the bars in the grating would briefly increase in width before returning to baseline, see **Figure 1** – during cardiac systole and one would pulse anti-phase to the systole pulse, during cardiac diastole (see *ECG Acquisition and Real-Time Processing*). In one 10-minute block, the red/left grating would be the systole/in-phase stimulus and the blue/right grating would be the diastole/anti-phase stimulus, and in the other block it would be reversed; block order was randomized. The durations during which each grating was dominant were recorded for analysis (see *Behavioral Data Analysis*). Subjects were not told that the movement of the stimuli was related to their heartbeat until after this block had ended, and the heartbeat discrimination task had begun.

2.4. Heartbeat Discrimination Task

Our modified heartbeat discrimination task was designed to assess whether subjects would be able to discriminate which of the two stimuli in the rivalry task was entrained to systole versus to diastole, rather than to assess more general interoceptive ability. Thus, we ignored some of the

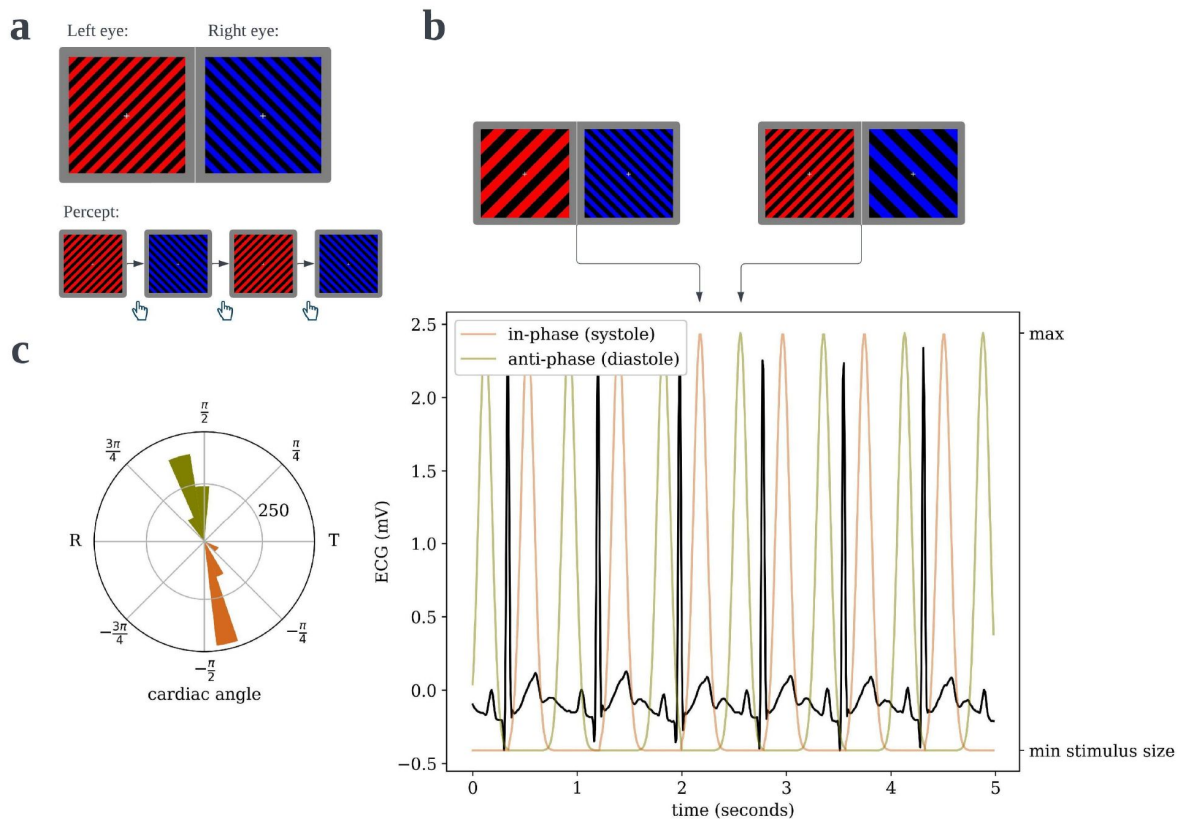


Figure 1

Cardiac Binocular Rivalry Task.

(a) As in a typical binocular rivalry paradigm, incongruent gratings were presented to the left and right eyes, causing the subjects' percept to alternate between the competing images. Each time the perceptually dominant image switched, subjects indicated so with a button press, and the durations of dominance were recorded. (b) The width of the bars in the grating would "pulse," one in-phase and one anti-phase to the period of maximal blood pressure and thus maximal aortic baroreceptor activity following ejection of blood from the heart. (c) An example circular histogram of the cardiac phases/angles at which grating pulses peak over a full 10-minute block, as recorded from an actual subject. Angles are scaled such that the R-peak is always at π radians and the offset of the T-wave is at 0 radians, thus the lower half of the circle is cardiac systole and the upper half is diastole.

recent developments in improving the validity of heartbeat discrimination tasks for assessing the latter (Brener & Ring, 2016 [↗](#)), and we used a bespoke task in which the manipulation closely matched that in our rivalry task. In particular, subjects saw two circles side-by-side on their screen, and the circles “pulsed” (i.e. transiently increased in radius from 60 to 120 pixels) following the same time course as the gratings in the rivalry task – that is, one during systole and one during diastole (see *ECG Acquisition and Real-Time Processing* and **Fig. 1** [↗](#)). On each of 120 10-second trials, the side of the systole stimulus and that of the diastole stimulus was randomized, and subjects were asked to report which circle was pulsing in synchrony with their heart. The accuracy of each response was recorded for analysis (see *Behavioral Data Analysis*).

2.5. Behavioral Data Analysis

For visualization and estimation of paired differences, the dominance durations for the systole-entrained and diastole-entrained gratings were averaged across all trials and block within each subject. Those measurements, and the bootstrap confidence intervals (10,000 samples) of their paired differences were plotted using the *DABEST* Python package for robust estimation statistics (Ho et al., 2019 [↗](#)). We additionally visualize these measurements broken up by whether the grating was presented to the left or the right eye, in case of baseline ocular dominance confounds.

For statistical inference on dominance durations, we apply a Gamma-family Generalized Linear Model (GLM) with a dummy predictor for cardiac systole to the trial-level data (i.e. each interval, unaveraged), fit using Generalized Estimating Equations in the *statsmodels* package to account for subject-level random effects (Rotnitzky & Jewell, 1990 [↗](#); Seabold & Perktold, 2010 [↗](#)). This approach appropriately deals with the approximate gamma distribution that dominance durations in binocular rivalry are known to follow, while remaining robust to violations of parametric assumptions (Carmel et al., 2010 [↗](#)).

We then re-ran the above GLM analysis on only those subjects who were at-chance at the heartbeat discrimination task, so we could assess whether the result from the first GLM would hold for only subjects who could not consciously distinguish which stimulus was in-phase with cardiac systole – and thus whether our results depend on conscious awareness of heartbeat sensations. Since identification of “at-chance” subjects would require interpretation of a null result in a frequentist setting (so we cannot just use a Binomial test), we estimate the probability each subject is at- or above-chance using a Bayesian mixture model, and then we call subjects “at-chance” if there is at least a 95% posterior probability they are indeed drawn from the at-chance distribution (see below).

In the mixture model, each subject i ’s number of correct trials k_i is modeled as coming from either an at-chance distribution $k_i | \text{at-chance} \sim \text{Binomial}(n_{\text{trials}}, 0.5)$ or an above-chance distribution $k_i | \text{above-chance} \sim \text{Binomial}(n_{\text{trials}}, p_i)$ where $p_i \sim 0.5 + \text{Beta}(\alpha, \beta)/2$, which spans the range [0.5, 1.0]. We pick priors for parameters $\alpha \sim \text{Exponential}(1.0)$ and $\beta \sim \text{Exponential}(0.5)$, which slightly favors distributions where accuracy p_i is more likely to be close to 0.5 than to 1.0, and we put a Uniform(0, 1) prior on the population prevalence of above-chance perceivers. Given posteriors for these parameters, each subject’s probability of coming from one distribution or another given their observed performance k_i is simply given by Bayes’ rule. Posterior distributions were approximated with 10,000 posterior samples in *PyMC* (Patil et al., 2010 [↗](#)).

2.6. ECG Offline Processing and Analysis

While characteristics of the ECG data were not of particular interest in the present study outside of our online manipulation of stimulus timing (see *ECG Acquisition and Real-Time Analysis*), we did estimate the cardiac phase at which entrained stimuli actually peaked in the rivalry task as an offline manipulation check. (For instance, if the anti-phase stimulus did not peak during diastole, which could occur for a subject with a very fast heart rate, it might be prudent to exclude that subject from analysis – though this did not end up occurring, see *Results*.)

To this end, we applied the standardized NeuroKit pipeline, as implemented in version 0.2.7 of the *neurokit2* Python package, to delineate cardiac events in the ECG data from both blocks of the rivalry task (Makowski et al., 2021 [DOI](#)). In brief, this applies a 0.5 Hz high pass filter to the data, detects QRS complexes based on the steepness of the absolute derivative of the signal, then R-peaks (i.e. the start of systole) as the local maxima in the QRS complexes, and finally the offset of the T-wave (i.e. end of ventricular systole and the start of diastole) using the discrete wavelet method (Martínez et al., 2004 [DOI](#)). We then compute the “cardiac angle” at each peak of the entrained stimuli using the same physiologically motivated scaling implemented in the Cardiac Timing Toolbox (Sherman et al., 2022 [DOI](#)); phases of the cardiac cycle are expressed as an angle where π radians is always the R-peak and 0 radians is the offset of the T-wave, such that “negative” angles in the range $[-\pi, 0]$ occur during systole and “positive” angles in the range $[0, \pi]$ occur during diastole.

We then obtain (circular) means for the cardiac angle the synchronous and asynchronous stimuli peak for each subject by bootstrap with 10,000 samples. These are used for a manipulation check to confirm that the mean angle for the systole stimulus is negative for all subjects, and the mean angle for the diastole stimulus is positive for all subjects. We then estimate the group-level mean cardiac angles for both stimuli using a random-effects bootstrap scheme, which accounts for both the population sampling distribution and the within-subject sampling distribution (Chambers & Chandra, 2013 [DOI](#)). Group-level bootstrap means and confidence intervals are reported in results.

2.7. Sample Size Determination

Our sample size was initially determined arbitrarily (by time constraints on data collection). However, we did conduct a power calculation to assess whether this convenience sample was sufficiently large to detect a typical cardio-visual effect. To this end, we used the smallest standardized effect size (paired Cohen’s $d = 0.38$) reported across the 7 cardio-visual experiments reported by Salomon and colleagues (Salomon et al., 2016 [DOI](#)). This calculation yielded a power of 0.81 at a significance level of 0.05 for our original $n = 58$ subjects and 0.78 for our final $n = 54$ subjects, which we deemed sufficient to stop data collection.

2.8. Data and Code Availability

The raw data, organized according to the standardized Brain Imaging Data Structure (BIDS), is available on the *Open Science Framework* (<https://doi.org/10.17605/OSF.IO/6ZMU8> [DOI](#)). The complete code for the experiment (<https://doi.org/10.5281/zenodo.10367327> [DOI](#)) and data analysis (<https://zenodo.org/doi/10.5281/zenodo.10367248> [DOI](#)) are permanently archived on *Zenodo*.

3. Results

3.1. Entrainment to cardiac systole facilitates visual dominance

In the rivalry task, subject-wise mean dominance durations were 0.108 seconds (95% CI: [0.030, 0.29]) longer for stimuli pulsing in-phase with cardiac systole than those anti-phase to systole (i.e. in diastole). These paired differences are visualized in **Figure 2** [DOI](#), and are also shown separately for stimuli presented to the left ($M = 0.078$, 95% CI: [-0.093, 0.395]) and the right ($M = 0.156$, 95% CI: [0.050, 0.268]) eyes, for readers who wish to assess for effects of baseline ocular dominance.

Our estimated gamma GLM had a positive coefficient for the effect of synchronizing to cardiac systole ($\beta = 0.026$, 95% CI: [0.002, 0.050]), which was statistically significant ($Z = 2.157$, $p = 0.031$). The value of this coefficient can be interpreted to mean that we estimate a 2.64% increase (95% CI: 0.24, 5.09) in dominance duration for systole-entrained over diastole entrained stimuli, on average.

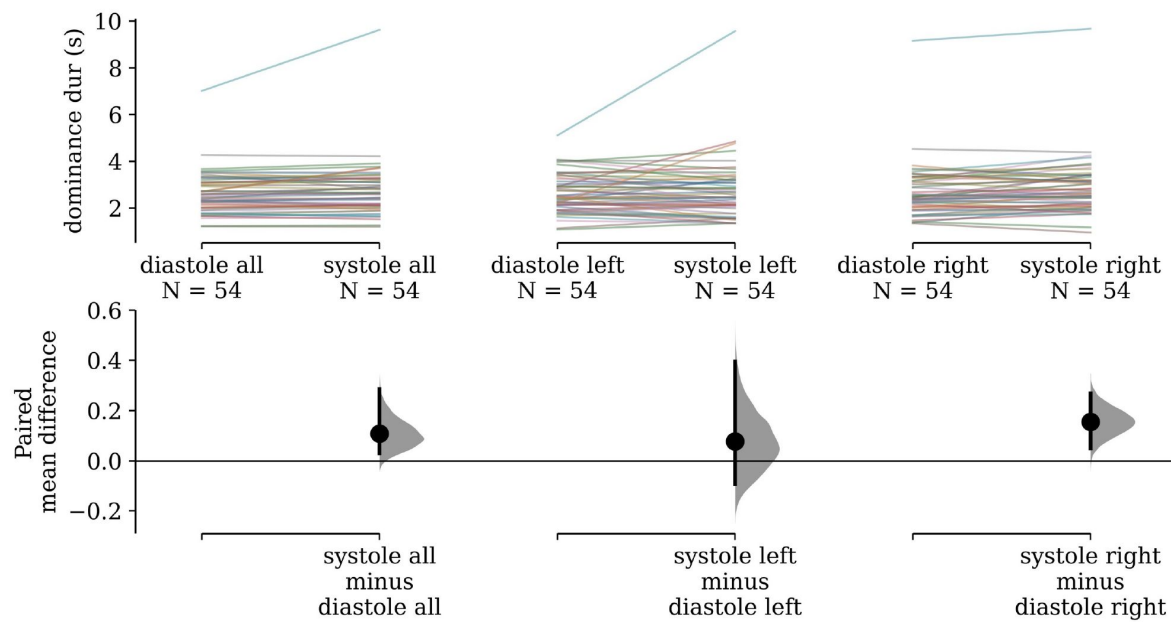


Figure 2

Paired differences in subjects' mean dominance durations.

(left) Subjects' mean dominance durations for grating stimuli that pulse in-phase with cardiac systole compared to those that pulse in diastole are shown on top. The colored lines denote individual subjects and connect their condition means. Bootstrap distributions and 95% confidence intervals of the paired differences between conditions are shown below. (middle) The same visualization is shown for only stimuli presented to the left eye, (right) and only to the right eye.

3.2. Cardiac facilitation of dominance does not depend on awareness of heartbeat

Our mixture model, visualized in [Figure 3](#), estimated that 9.48% (95% HDI: [1.81, 18.4]) of the sampled population are above-chance cardiac perceivers, and that above-chance perceivers have a mean accuracy of 0.668 (95% HDI: [0.521, 0.847]). Note that, while the estimated 9.48% population prevalence closely agrees with the 9.26% of subjects who were significantly above-chance via a Binomial test in our sample, the mixture model still assigns substantial probability to an above-chance perceiver performing worse than that frequentist cutoff (see [Figure 3](#)), illustrating why interpreting a frequentist null result would be inappropriate in this case.

When we remove subjects with greater than a 0.05 probability of being an above-chance perceiver from our sample, 46 subjects (85.2%) remain. This amounted to an effective cutoff of 0.542 accuracy. When we repeat the GLM analysis from the above section on just these subjects that we are quite sure are at-chance, we still find an effect of entrainment to cardiac systole on dominance durations ($\beta = 0.028$, 95% CI: [0.001, 0.055], $Z = 2.021$, $p = 0.043$). The fact that the rivalry result can be found in a group of only cardiac non-perceivers indicates that the effect does not depend on subjects' conscious access to their heartbeat sensations, and thus also not on some conscious inference subjects may have made about which stimulus they are meant to attend to.

3.3. Manipulation check

For all subjects, bootstrap mean cardiac angles of the stimulus “pulse” times were negative (i.e. peaking in systole) for the in-phase stimulus and positive (i.e. in diastole) for the anti-phase stimulus, indicating our manipulation of cardiac phase was successful. The group mean cardiac angles for the systole-entrained pulses was -1.04 (95% CI: [-1.10, -0.99]) and for anti-phase pulses was 1.93 (95% CI: [1.88, 1.98]).

4. Discussion

In light of previous work demonstrating that visual stimuli presented during cardiac systole are less likely to break through interocular suppression initially ([Salomon et al., 2016](#), [2018](#)), presumably reflecting suppression of the feedforward drive ascending from the optic nerve through low-level visual areas, we suggest the facilitatory effect of systolic entrainment on interocular dominance observed in our rivalry paradigm is likely accounted for primarily by lateral inhibition between neurons responsive to each eye. In such an interpretation, this lateral inhibition is what would be potentiated by baroreceptive input in our rivalry task. Interestingly, this could occur merely as a function of lateral inhibition occurring simultaneously to the broad cortical suppression conjectured in the original version of the Baroreceptor Hypothesis, increasing the total amount of inhibitory neurotransmitter in the post-synaptic cleft ([Lacey & Lacey, 1978](#)). Thus, the same broad cortical suppression could have a suppressive or facilitatory effect on any given stimulus *depending on context*.

However, this explanation – while intriguing – raises the very issue that prevents us from making such an inference by comparison to past cardio-visual studies that used CFS. In the CFS paradigm used in previous work ([Salomon et al., 2016](#), [2018](#)), the mask stimulus is updated at a rate of 10 Hz to maintain suppression over time, and so new mask stimuli do appear several times each systolic phase. If lateral inhibition is indeed potentiated during systole as we suggest, and the mask stimulus is always dominant at trial start (which it is), then previous CFS findings could be re-interpreted as reflecting facilitation of the mask stimulus via lateral inhibition rather than direct suppression of the systole-entrained target stimulus via insula-to-visual projections. While this possibility seems to be made less likely by the fact that similar suppression of the systole-entrained

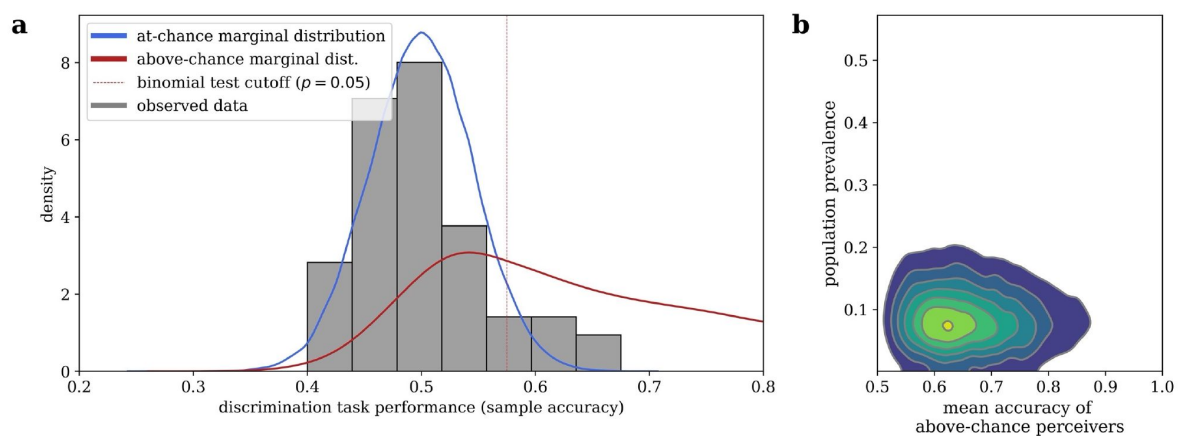


Figure 3

Bayesian Mixture Model of Interoceptive Accuracy.

(a) Observed accuracies on the heartbeat discrimination task are modeled as a mixture between an at-chance Binomial distribution and an above-chance Beta-Binomial distribution, the marginal posterior predictive likelihoods of which are shown. (b) Marginal likelihoods can be combined with the estimated population prevalence of above-chance performers to assign of posterior probability of belonging to each distribution to any given subject.

stimulus is also observed in visual crowding (Salomon et al., 2016 [↗](#)), the point remains the same as above: the same neural mechanism *could* result in either facilitation or suppression of a given sensory stimulus, depending on context. Indeed, such context-dependency could potentially explain the seemingly conflicting reports from previous studies on cardio-visual interaction (Critchley & Harrison, 2013 [↗](#)). It may be fruitful for future work to compare cardiac effects across CFS and traditional rivalry paradigms with accompanying neural recordings.

Interestingly, the facilitatory effect we see on visual dominance does not appear to depend on conscious access to one's heartbeat sensations, as removing subjects who are above-chance at discriminating which stimulus is synchronized to their heartbeat from our sample does not eliminate the effect. Many effects of cardiac timing on perception and cognition *are* modulated by conscious interoceptive accuracy or awareness (Koreki et al., 2022 [↗](#); Sel et al., 2017 [↗](#)), so it would be interesting to test whether interoceptive awareness potentiates the effect further. However, since we only had a handful of subjects in our sample that we could confidently conclude were above-chance heartbeat perceivers, this study cannot answer such a question with any statistical certainty.

Lastly, this finding may have implications for how we interpret the relationship between visual awareness and bodily self-awareness. A growing body of evidence suggests that visual self-recognition can occur in the absence of conscious awareness, as self-selective neural and behavioral responses can be observed for stimuli presented subliminally (Bola et al., 2021 [↗](#); Doradzińska et al., 2020 [↗](#); Geng et al., 2012 [↗](#); Ota & Nakano, 2021 [↗](#); Pfister et al., 2012 [↗](#); Shafto & Pitts, 2015 [↗](#)) or too early after a stimulus event for subjects to have yet become consciously aware (Veillette et al., 2023 [↗](#)). If so, self-awareness may result from a first-order awareness of self-referential cognitive processes (*some* of which need not depend on conscious awareness to function), as previously suggested as a possibility by some researchers (Dehaene, 2014 [↗](#)), rather than a higher-level sort of “awareness of being aware” as it may be understood by some cognitive scientists or in popular culture. In such a view – which, to be clear, may be incorrect – then any common factor which facilitates both awareness and perceived embodiment, even if by separate pathways, could be a contributing mechanism that facilitates self-awareness. Considering the present results in light of previous work on embodiment (Aspell et al., 2013 [↗](#); Heydrich et al., 2018 [↗](#); Sel et al., 2017 [↗](#)), interoceptive-exteroceptive synchrony seems as if it might meet both those criteria.

References

- Allen M., Tsakiris M. (2018) **The body as first prior: Interoceptive predictive processing and the primacy** *The Interoceptive Mind: From Homeostasis to Awareness* 27
- Aspell J. E., Heydrich L., Marillier G., Lavanchy T., Herbelin B., Blanke O. (2013) **Turning Body and Self Inside Out: Visualized Heartbeats Alter Bodily Self-Consciousness and Tactile Perception** *Psychological Science* 24:2445–2453 <https://doi.org/10.1177/0956797613498395>
- Azzalini D., Rebollo I., Tallon-Baudry C. (2019) **Visceral Signals Shape Brain Dynamics and Cognition** *Trends in Cognitive Sciences* 23:488–509 <https://doi.org/10.1016/j.tics.2019.03.007>
- Bola M., Paž M., Doradzińska Ł., Nowicka A. (2021) **The self-face captures attention without consciousness: Evidence from the N2pc ERP component analysis** *Psychophysiology* 58 <https://doi.org/10.1111/psyp.13759>

- Brener J., Liu X., Ring C. (1993) **A method of constant stimuli for examining heartbeat detection: Comparison with the Brener-Klavitse and Whitehead methods** *Psychophysiology* **30**:657–665
- Brener J., Ring C. (2016) **Towards a psychophysics of interoceptive processes: The measurement of heartbeat detection** *Philosophical Transactions of the Royal Society B: Biological Sciences* **371** <https://doi.org/10.1098/rstb.2016.0015>
- Carmel D., Arcaro M., Kastner S., Hasson U. (2010) **How to Create and Use Binocular Rivalry** *JoVE (Journal of Visualized Experiments)* **45** <https://doi.org/10.3791/2030>
- Chambers R., Chandra H. (2013) **A random effect block bootstrap for clustered data** *Journal of Computational and Graphical Statistics* **22**:452–470
- Critchley H. D., Harrison N. A. (2013) **Visceral Influences on Brain and Behavior** *Neuron* **77**:624–638 <https://doi.org/10.1016/j.neuron.2013.02.008>
- Dehaene S. (2014) **Consciousness and the brain: Deciphering how the brain codes our thoughts**
- Doradzińska Ł., Wójcik M. J., Paż M., Nowicka M. M., Nowicka A., Bola M. (2020) **Unconscious perception of one's own name modulates amplitude of the P3B ERP component** *Neuropsychologia* **147** <https://doi.org/10.1016/j.neuropsychologia.2020.107564>
- Füstös J., Gramann K., Herbert B. M., Pollatos O. (2013) **On the embodiment of emotion regulation: Interoceptive awareness facilitates reappraisal** *Social Cognitive and Affective Neuroscience* **8**:911–917 <https://doi.org/10.1093/scan/nss089>
- Garfinkel S. N., Minati L., Gray M. A., Seth A. K., Dolan R. J., Critchley H. D. (2014) **Fear from the Heart: Sensitivity to Fear Stimuli Depends on Individual Heartbeats** *Journal of Neuroscience* **34**:6573–6582 <https://doi.org/10.1523/JNEUROSCI.3507-13.2014>
- Geng H., Zhang S., Li Q., Tao R., Xu S. (2012) **Dissociations of subliminal and supraliminal self-face from other-face processing: Behavioral and ERP evidence** *Neuropsychologia* **50**:2933–2942 <https://doi.org/10.1016/j.neuropsychologia.2012.07.040>
- Gray M. A., Beacher F. D., Minati L., Nagai Y., Kemp A. H., Harrison N. A., Critchley H. D. (2012) **Emotional appraisal is influenced by cardiac afferent information** *Emotion* **12**
- Heydrich L., Aspell J. E., Marillier G., Lavanchy T., Herbelin B., Blanke O. (2018) **Cardio-visual full body illusion alters bodily self-consciousness and tactile processing in somatosensory cortex** *Scientific Reports* **8** <https://doi.org/10.1038/s41598-018-27698-2>
- Ho J., Tumkaya T., Aryal S., Choi H., Claridge-Chang A. (2019) **Moving beyond P values: Data analysis with estimation graphics** *Nature Methods* **16** <https://doi.org/10.1038/s41592-019-0470-3>
- Koreki A., Goeta D., Ricciardi L., Eilon T., Chen J., Critchley H. D., Garfinkel S. N., Edwards M., Yogarajah M. (2022) **The relationship between interoception and agency and its modulation by heartbeats: An exploratory study** *Scientific Reports* **12** <https://doi.org/10.1038/s41598-022-16569-6>

- Lacey B. C., Lacey J. I. (1978) **Two-way communication between the heart and the brain: Significance of time within the cardiac cycle** *American Psychologist* **33**:99–113 <https://doi.org/10.1037/0003-066X.33.2.99>
- Makowski D., Pham T., Lau Z. J., Brammer J. C., Lespinasse F., Pham H., Schölzel C., Chen S. A. (2021) **NeuroKit2: A Python toolbox for neurophysiological signal processing** *Behavior Research Methods* :1–8
- Martínez J. P., Almeida R., Olmos S., Rocha A. P., Laguna P. (2004) **A wavelet-based ECG delineator: Evaluation on standard databases** *IEEE Transactions on Biomedical Engineering* **51**:570–581
- Mashour G. A., Roelfsema P., Changeux J.-P., Dehaene S. (2020) **Conscious processing and the global neuronal workspace hypothesis** *Neuron* **105**:776–798
- Monti A., Porciello G., Panasiti M. S., Aglioti S. M. (2022) **Gut markers of bodily self-consciousness in men** *iScience* **25** <https://doi.org/10.1016/j.isci.2022.105061>
- Monti A., Porciello G., Tieri G., Aglioti S. M. (2020) **The “embreathment” illusion highlights the role of breathing in corporeal awareness** *Journal of Neurophysiology*
- Ota C., Nakano T. (2021) **Self-Face Activates the Dopamine Reward Pathway without Awareness** *Cerebral Cortex* **31**:4420–4426 <https://doi.org/10.1093/cercor/bhab096>
- Pan J., Tompkins W. J. (1985) **A real-time QRS detection algorithm** *IEEE Transactions on Biomedical Engineering* **3**:230–236
- Park H.-D., Bernasconi F., Bello-Ruiz J., Pfeiffer C., Salomon R., Blanke O. (2016) **Transient Modulations of Neural Responses to Heartbeats Covary with Bodily Self-Consciousness** *Journal of Neuroscience* **36**:8453–8460 <https://doi.org/10.1523/JNEUROSCI.0311-16.2016>
- Park H.-D., Tallon-Baudry C. (2014) **The neural subjective frame: From bodily signals to perceptual consciousness** *Philosophical Transactions of the Royal Society B: Biological Sciences* **369** <https://doi.org/10.1098/rstb.2013.0208>
- Patil A., Huard D., Fonnesbeck C. J. (2010) **PyMC: Bayesian Stochastic Modelling in Python** *Journal of Statistical Software* **35**:1–81
- Pfister R., Pohl C., Kiesel A., Kunde W. (2012) **Your Unconscious Knows Your Name** *PLOS ONE* **7** <https://doi.org/10.1371/journal.pone.0032402>
- Pramme L., Larra M. F., Schächinger H., Frings C. (2014) **Cardiac cycle time effects on mask inhibition** *Biological Psychology* **100**:115–121 <https://doi.org/10.1016/j.biopsycho.2014.05.008>
- Pramme L., Larra M. F., Schächinger H., Frings C. (2016) **Cardiac cycle time effects on selection efficiency in vision** *Psychophysiology* **53**:1702–1711
- Rotnitzky A., Jewell N. P. (1990) **Hypothesis testing of regression parameters in semiparametric generalized linear models for cluster correlated data** *Biometrika* **77**:485–497
- Salomon R., Ronchi R., Dönz J., Bello-Ruiz J., Herbelin B., Faivre N., Schaller K., Blanke O. (2018) **Insula mediates heartbeat related effects on visual consciousness** *Cortex* **101**:87–95 <https://doi.org/10.1016/j.cortex.2018.01.005>

- Salomon R., Ronchi R., Dönz J., Bello-Ruiz J., Herbelin B., Martet R., Faivre N., Schaller K., Blanke O. (2016) **The Insula Mediates Access to Awareness of Visual Stimuli Presented Synchronously to the Heartbeat** *Journal of Neuroscience* **36**:5115–5127 <https://doi.org/10.1523/JNEUROSCI.4262-15.2016>
- Seabold S., Perktold J. (2010) **Statsmodels: Econometric and Statistical Modeling with Python** *Proceedings of the 9th Python in Science Conference* :92–96 <https://doi.org/10.25080/Majora-92bf1922-011>
- Sel A., Azevedo R. T., Tsakiris M. (2017) **Heartfelt Self: Cardio-Visual Integration Affects Self-Face Recognition and Interoceptive Cortical Processing** *Cerebral Cortex* **27**:5144–5155 <https://doi.org/10.1093/cercor/bhw296>
- Seth A. K., Tsakiris M. (2018) **Being a Beast Machine: The Somatic Basis of Selfhood** *Trends in Cognitive Sciences* **22**:969–981 <https://doi.org/10.1016/j.tics.2018.08.008>
- Shafte J. P., Pitts M. A. (2015) **Neural Signatures of Conscious Face Perception in an Inattentive Blindness Paradigm** *Journal of Neuroscience* **35**:10940–10948 <https://doi.org/10.1523/JNEUROSCI.0145-15.2015>
- Sherman M. T., Wang H.-T., Garfinkel S. N., Critchley H. D. (2022) **The Cardiac Timing Toolbox (CaTT): Testing for physiologically plausible effects of cardiac timing on behaviour** *Biological Psychology* **170** <https://doi.org/10.1016/j.biopsycho.2022.108291>
- Suzuki K., Garfinkel S. N., Critchley H. D., Seth A. K. (2013) **Multisensory integration across exteroceptive and interoceptive domains modulates self-experience in the rubberhand illusion** *Neuropsychologia* **51**:2909–2917 <https://doi.org/10.1016/j.neuropsychologia.2013.08.014>
- Sznajder M., Łukowska M. (2017) **Python Online and Offline ECG QRS Detector based on the Pan-Tomkins algorithm (v1.0.0) [Computer software]** <https://doi.org/10.5281/zenodo.583770>
- Tsakiris M., Critchley H. (2016) **Interoception beyond homeostasis: Affect, cognition and mental health** *Philosophical Transactions of the Royal Society B: Biological Sciences* **371** <https://doi.org/10.1098/rstb.2016.0002>
- van Elk M., Lenggenhager B., Heydrich L., Blanke O. (2014) **Suppression of the auditory N1-component for heartbeat-related sounds reflects interoceptive predictive coding** *Biological Psychology* **99**:172–182 <https://doi.org/10.1016/j.biopsycho.2014.03.004>
- Veillette J. P., Lopes P., Nusbaum H. C. (2023) **Temporal Dynamics of Brain Activity Predicting Sense of Agency over Muscle Movements** *Journal of Neuroscience* **43**:7842–7852 <https://doi.org/10.1523/JNEUROSCI.1116-23.2023>
- Wiens S., Palmer S. N. (2001) **Quadratic trend analysis and heartbeat detection** *Biological Psychology* **58**:159–175
- Zhang P., Jamison K., Engel S., He B., He S. (2011) **Binocular rivalry requires visual attention** *Neuron* **71**:362–369

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Reviewer #1 (Public Review):

Summary:

The aim of the study described in this paper was to test whether visual stimuli that pulse synchronously with the systole phase of the cardiac cycle are suppressed compared with stimuli that pulse in the diastole phase. To this end, the authors employed a binocular rivalry task and used the duration of the perceived image as the metric of interest. The authors predicted that if there was global suppression of the visual stimulus during systole then the durations of the stimulus that were pulsing synchronously with systole should be of shorter duration than those pulsing in diastole. However, the results observed were the opposite of those predicted. The authors speculate on what this facilitation effect might mean for the baroreceptor suppression hypothesis.

Strengths:

This is an interesting and timely study that uses a clever paradigm to test the baroreceptor suppression hypothesis in vision. This is a refreshingly focussed paper with interesting and seemingly counterintuitive results.

Weaknesses:

The paper could benefit from a clearer explanation of the predicted results. For those not experts in binocular rivalry, it would be useful to explain the predicted results. Does pulsing stimuli in this way change durations in such a task? If there is global suppression of visual stimuli why would this lead to shorter/longer durations in the systole compared to the diastole conditions? In addition, the duration lengths in both conditions seem to be longer than one cardiac cycle. If the cardiac cycle modulates duration it would be interesting to discuss why this occurs on some cycles but not on others. If there is a facilitation effect why does it only occur on some cycles?

<https://doi.org/10.7554/eLife.95599.1.sa2>

Reviewer #2 (Public Review):

Summary:

This is a binocular rivalry study that uses electrocardiogram events to modulate visual stimuli in real-time, relative to participants' heartbeats. The main finding is that modulations during the period around when the heart has contracted (systole) increase rivalry dominance durations. This is a really neat result, that demonstrates the link between interoception and vision. I thought the Bayesian mixture modelling was a really smart way to identify cardiac non-perceivers, and the finding that the main result is preserved in this group is compelling. Overall, the study has been conducted to a high standard, is appropriately powered, and reported clearly. I have one suggestion about interpretation, which concerns the explanation of increased dominance durations with reference to contemporary models of binocular rivalry, and a few minor queries. However, I think this paper is a worthwhile addition to the literature.

<https://doi.org/10.7554/eLife.95599.1.sa1>

Reviewer #3 (Public Review):

Summary:

The manuscript addresses a question inspired by the Baroreceptor Hypothesis and its links to visual awareness and interoception. Specifically, the reported study aimed to determine if the effects of cardiac contraction (systole) on binocular rivalry (BR) are facilitatory or suppressive. The main experiment - relying on a technically challenging procedure of presenting stimuli synchronised with the heartbeats of participants - has been conducted with great care, and numerous manipulation checks the authors report convincingly show that the methods they used work as intended. Moreover, the control experiment allows for excluding alternative explanations related to participants being aware of their heartbeats. Therefore, the study convincingly shows the effect of cardiac activity on BR - and this is an important finding. The results, however, do not allow for unambiguously determining if this effect is facilitatory or suppressive (see details below), which renders the study not as informative as it could be.

While the authors strongly focus on interoception and awareness, this study will be of interest to researchers studying BR as such. Moreover, the code and the data the authors share can facilitate the adoption of their methods in other labs.

Strengths:

(1) The study required a complex technical setup and the manuscript both describes it well and demonstrates that it was free from potential technical issues (e.g. in section 3.3. Manipulation check).

(2) The sophisticated statistical methods the authors used, at least for a non-statistician like me, appear to be well-suited for their purpose. For example, they take into account the characteristics of BR (gamma distributions of dominance durations). Moreover, the authors demonstrate that at least in one case their approach is more conservative than a more basic one (Binomial test) would be.

(3) Finally, the control experiment, and the analysis it enabled, allow for excluding a multitude of alternative explanations of the main results.

(4) The authors share all their data and materials, even the code for the experiment.

(5) The manuscript is well-written. In particular, it introduces the problem and methods in a way that should be easy to understand for readers coming from different research fields.

Weaknesses:

(1) The interpretation of the main result in the context of the Baroreceptor hypothesis is not clear. The manuscript states: The Baroreceptor Hypothesis would predict that the stimulus entrained to systole would spend more time suppressed and, conversely, less time dominant, as cortical activity would be suppressed each time that stimulus pulses. The manuscript does not specify why this should be the case, and the term 'entrained' is not too helpful here (does it refer to neural entrainment? or to 'being in phase with?'). The answer to this question is provided by the manuscript only implicitly, and, to explain my concern, I try to spell it out here in a slightly simplified form.

During systole (cardiac contraction), the visual system is less sensitive to external information, so it 'ignores' periods when the systole-synchronised stimulus is at the peak of its pulse. Conversely, the system is more sensitive during diastole, so the stimulus that is at the peak of its pulse then should dominate for longer, because its peaks are synchronised with the periods of the highest sensitivity of the visual system when the information used to resolve the rivalry is sampled from the environment. This idea, while indeed being a clever test of the hypothesis in question, rests on one critical assumption: that the peak of the stimulus pulse (as defined in the manuscript) is the time when the stimulus is the strongest for the visual system. The notion of 'stimulus strength' is widely used in the BR literature (see Brascamp et al., 2015 for a review). It refers to the stimulus property that, simply speaking, determines its tendency to dominate in the BR. The strength of a stimulus is underpinned by its low-level visual properties, such as contrast and spatial frequency content. Coming back to the manuscript, the pulsing of the stimuli affected at least spatial frequency (and likely other low-level properties), and it is unknown if it was in phase with the pulsing of the stimulus strength, or not. If my understanding of the premise of the study is correct, the conclusions drawn by the authors stand only if it was.

In other words, most likely the strength of one of the stimuli was pulsating in sync with the systole, but is it not clear which stimulus it was. It is possible that, for the visual system, the stimulus meant to pulse in sync with the systole was pulsing strength-wise in phase with the diastole (and the one intended to pulse with in sync with the diastole strength-wise pulsed with the systole). If this is the case, the predictions of the Baroreceptor Hypothesis hold, which would change the conclusion of the manuscript.

(2) Using anaglyph goggles necessitates presenting stimuli of a different colour to each eye. The way in which different colours are presented can impact stimulus strength (e.g. consider that different anaglyph foils can attenuate the light they let through to different degrees). To

deal with such effects, at least some studies on BR employed procedures of adjusting the colours for each participant individually (see Papathomas et al., 2004; Patel et al., 2015 and works cited there). While I think that counterbalancing applied in the study excludes the possibility that colour-related effects influenced the results, the effects of interest still could be stronger for one of the coloured foils.

(3) Several aspects of the methods (e.g. the stimuli), are not described at the level of detail some readers might be accustomed to. The most important issue here is the task the participants performed. The manuscript says that they pressed a button whenever they experienced a switch in perception, but it is only implied that there were different buttons for each stimulus.

Brascamp, J. W., Klink, P. C., & Levelt, W. J. M. (2015). The 'laws' of binocular rivalry: 50 years of Levelt's propositions. *Vision Research*, 109, 20-37. <https://doi.org/10.1016/j.visres.2015.02.019>

Papathomas, T. V., Kovács, I., & Conway, T. (2004). Interocular grouping in binocular rivalry: Basic attributes and combinations. In D. Alais & R. Blake (Eds.), *Binocular Rivalry* (pp. 155-168). MIT Press

Patel, V., Stuit, S., & Blake, R. (2015). Individual differences in the temporal dynamics of binocular rivalry and stimulus rivalry. *Psychonomic Bulletin and Review*, 22(2), 476-482. <https://doi.org/10.3758/s13423-014-0695-1>

<https://doi.org/10.7554/eLife.95599.1.sa0>