



## Does the body give the brain an attentional boost? Examining the relationship between attentional and cardiac gating

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### ABSTRACT

Studies on mind-body interactions have largely focused on how mental states modulate bodily physiological responses. Increasing evidence suggests that bodily states also modulate mental states. Here we investigated how both may be integrated in the brain at the resolution of a heartbeat, examining how phasic fluctuations of peripheral blood pressure and central attentional resources combine to influence cognition. We examined the effects of cardiac phase on the performance of two simultaneous tasks: a go/no-go letter detection task where targets were concurrently presented on background faces and a short-term memory face discrimination task. Short-term memory for the background face was better when the initial face was encoded during the systole rather than diastole phase and when it was paired with a target rather than a distractor. There was no significant interaction between cardiac phase and letter detection. These data suggest that peripheral blood pressure and central attention independently regulate cognitive performance.

### 1. Introduction

The relationship between the mind and body is an age-old area of inquiry in philosophy and has been central to psychology (James, 1884). As originally theorized by W. James, fluctuations in peripheral physiological states, such as cardiac cycle, modulate the brain to affect cognitive performance (Duschek, Muckenthaler, Werner, & Reyes del Paso, 2009; Garfinkel et al., 2014). Conversely, a multitude of studies show that the manipulation of mental states can change physiological responses (Bates, Mächler, Bolker, & Walker, 2015; Cohen, Tyrrell, & Smith, 1991; Jacobs, 2001). Fluctuation of body states, controlled by the autonomic nervous system, reflect the regulation of limited peripheral bodily resources (Cannon, 1967; Critchley & Garfinkel, 2018; Critchley & Harrison, 2013). Similarly, attention has long been viewed as a fluctuating cognitive resource with limited capacity (Lavie, Hirst, De Fockert, & Viding, 2004; Tversky & Kahneman, 1973). There is increasing evidence that engagement of attention and its regulation of perceptual awareness is related to variation in noradrenaline in cortical areas (Todd et al., 2013, 2014, 2015). Because noradrenaline also plays a role in regulating input from peripheral baroreceptors to the brain (Aars, 1971), moment-by-moment fluctuations in attention may partially originate from autonomic peripheral regulation. To address the relationship between central and peripheral resources, here we examined how phasic fluctuations in attention and cardiac states combine

to regulate cognitive performance.

Recent studies have shown that attention to a behaviorally relevant event, such as a target in a detection task, can enhance the processing of unrelated background information. Attending to a briefly presented target in a continuous detection task “boosts” adaptation to visual stimuli (Pascucci & Turatto, 2013), and memory of coincident, unrelated background images or words (Lin, Pype, Murray, & Boynton, 2010; Makovski, Swallow, & Jiang, 2011; Spataro & Mulligan, 2013; Swallow & Jiang, 2014a, 2010). This ‘attentional boost effect’ is broad, influencing the processing of irrelevant stimuli in different sensory modalities (Mulligan, Spataro, & Picklesimer, 2014; Swallow & Jiang, 2010, 2014a), but transient, occurring only if the stimuli and the target are presented at the same time (Swallow & Jiang, 2011). This suggests that these fluctuations in attention are primarily over time rather than space (Makovski et al., 2011; Swallow & Jiang, 2010, 2012).

Like central attention, autonomic states regulate cognitive performance (Fiacconi, Owais, Peter, & Köhler, 2016; Garfinkel & Critchley, 2016; Thayer & Lane, 2000; Yasumasu, Reyes del Paso, Takahara, & Nakashima, 2006). A direct way to measure this relationship is to utilize the phasic nature of cardiac cycles, i.e., diastole when the ventricles are relaxed and systole when the ventricles contract to pump blood. Arterial baroreceptors fire strongly during the systole phase. These signals are transmitted to the brainstem, via the vagus and glossopharyngeal nerves (Mancia & Mark, 1983), and are then projected to

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forebrain regions (Dembowsky & Sellar, 1995; Garfinkel & Critchley, 2016), exerting influences on striatal and limbic function, which in turn affect cognition and emotion (Critchley & Harrison, 2013). By time-locking the stimulus presentation to either cardiac diastole or systole, it is possible to investigate how cardiac states affect cognitive functions. For instance, using cardiac cycle stimulus synchronization, studies have shown that decreased cortical arousal during systole, relative to diastole, is associated with decreased visual cortical evoked potential P1 magnitude reflecting early spatial attention (Walker & Sandman, 1982) and decreased effectiveness of a visual mask (Pramme, Larra, Schächinger, & Frings, 2014).

Although many studies have investigated the separate effects of attention and cardiac states on cognitive performance, much less is known about their interaction. Investigation of this relationship will not only help examine how bodily and mental resources jointly regulate cognitive performance, but also shed light on the underlying mechanisms. One proposed common pathway of both effects is through the locus coeruleus (LC). The LC is a nucleus in the pons that is responsible for noradrenaline (NA) synthesis (Aston-jones & Cohen, 2005). Systole baroreceptor firing inhibits NA neurons in the LC (Morilak, Fornal, & Jacobs, 1986) and decreases cortical noradrenaline turnover (Persson & Svensson, 1981), which should inhibit cortical activity (Lipnicki, 2009; Rau, Pauli, Brody, & Elbert, 1993). Consistent with this inhibitory effect, sensorimotor control and task performance during systole are impaired in single-target paradigms (McIntyre, Ring, Edwards, & Carroll, 2008; Sandman, McCanne, Kaiser, & Diamond, 1977).

However, in more complex paradigms involving the regulation of interference, the results are mixed. It has been shown that the presentation of a high-contrast mask during systole rather than diastole is associated with better detection of a low-contrast target that appeared 100 ms later (Pramme et al., 2014). Though these data may indicate that cortical inhibition during systole reduces the effectiveness of the mask, other tasks with sequential stimulus presentations report no effect or an opposite effect of cardiac phase on stimulus processing. For example, fearful stimuli were better detected during systole than diastole with no significant effect on target detection using the attentional-blink paradigm, which combines attention and masking (Garfinkel et al., 2013, 2014). Thus, it is not entirely clear what functions cardiac systole impacts in paradigms that involve the presentation of multiple stimuli.

One possibility is that decreased LC activity and NA release to cortical areas during systole could result in smaller increases in spiking activity following targets, as in vigilance tasks (Delagrang, Canu, Rougeul, Buser, & Bouyer, 1993; Oken, Salinsky, & Elsas, 2006; Rajkowski, Kubiak, Ivanova, & Aston-Jones, 1997). In addition, reduced LC activity during systole might impair early memory consolidation (Garfinkel et al., 2013; Sara, 2009). Another possibility is that reduced cortical activity during systole, including smaller early visual cortical responses (Walker & Sandman, 1982), influences the degree to which competing stimuli interfere with each other. Because NA improves the signal to noise ratio, inhibition of LC and NA release during systole may allow task-irrelevant stimuli to influence processing for longer periods of time.

By contrast, in the attentional boost effect, detecting a target may not only boost processing of background information that coincides with a target across modalities and spatial locations, despite competition for attention (Swallow & Jiang, 2013), but it may also increase LC neuromodulatory influences throughout the cortex. Because both target detection and cardiac phase modulate the release of norepinephrine from LC neurons, their effects on cognition may have a common neurocognitive origin. To shed light on potential mechanisms of how bodily and attentional resources jointly contribute to cognitive performance and further clarify the role of cardiac gating in selective attention, we examined the attentional boost effect at distinct cardiac phases. At the beginning of each trial, a letter was presented in the center of a face (encoding display) and participants were required to respond with a

button press as quickly as possible to a predefined target letter, and made no response for other letters for the *detection* task. Then a second face appeared, 1500 ms after the encoding display, and participants performed a *face discrimination* task to measure short-term memory. Presentation of the encoding display was time locked to either cardiac systole or diastole using real time electrocardiography (ECG).

Consistent with attentional boost effect, we expected accuracy on the face discrimination task to be greater when the initial face was paired with a target rather than a distractor. If cardiac systole impairs attention and short-term memory, face discrimination should be worse for encoding displays presented during systole than during diastole. If systole inhibits interference, we would see better performance when the initial face is synced to systole. Finally, since attention and cardiac cycle both seem to involve the LC, we expected the effect of target detection on face discrimination performance to be greater during diastole than during systole, resulting in an interaction.

## 2. Methods

### 2.1. Participants

Power analysis was conducted using GPower 3.0.10 (Erdfelder, Faul, & Buchner, 1996), *a priori*, to determine the sample size. A sample size of 27 was expected to achieve 85% power based on three previous studies on attentional boost which have an average effect size,  $f$ , of 0.61 (Makovski et al., 2011; Swallow & Jiang, 2010, 2014b, range from 0.40 to 0.80). Similarly, to achieve 85% power on the cardiac effect on memory, a sample size of 17 would be required based on one study that has an effect size,  $f$ , of 0.78 (Garfinkel et al., 2013).

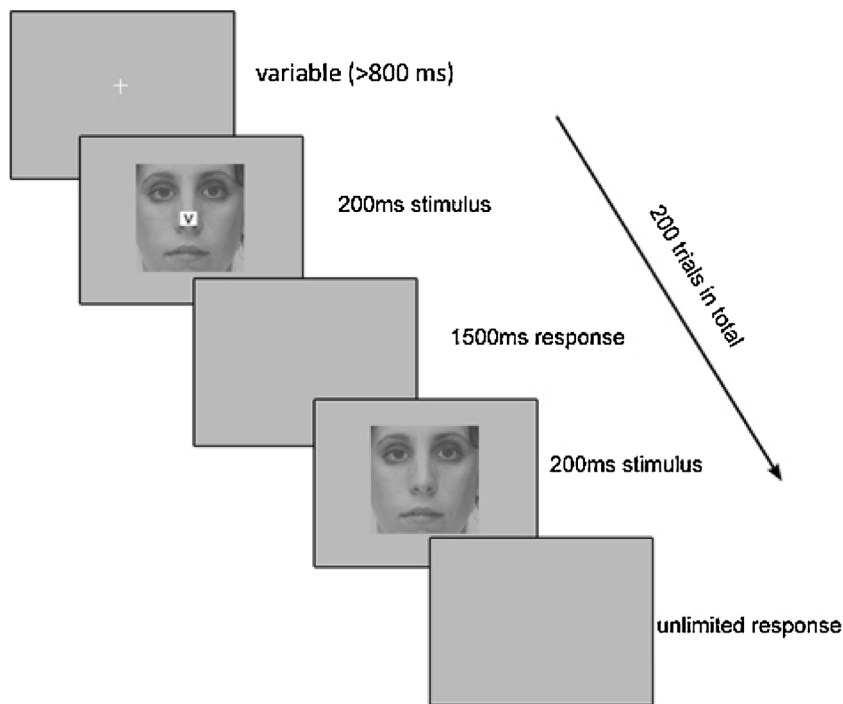
Twenty-nine participants were recruited via a Cornell University online system for course credit. All gave written consent. Two participants were excluded due to a programming error, one was excluded for low heart phase data quality, and another was excluded due to low detection task accuracy (accuracy = 50%, which was no better than chance level 50%,  $t = 0$ ,  $df = 199$ ,  $p = 1$  in a binomial test). This results in a final sample of  $N = 25$  for further analysis.

### 2.2. Stimuli

Stimuli were 330 Caucasian female faces with neutral expression. All stimuli were converted to gray-scale and normalized to the same contrast. They were then cropped to remove hair and chins to retain mostly internal facial features. Finally, they were aligned by eyes and resized or further cut to  $300 \times 300$  pixels.

### 2.3. Task and procedure

The task was programed by python 2.7 (<http://www.python.org>) using Pygame library 1.9.1 (<http://www.pygame.org>). Each trial consisted of a white fixation cross (800 ms + peak detection algorithm and cardiac phase lag), a combination stimulus consisting of a face with a letter in its center (200 ms), a blank interval (1500 ms), a second face (200 ms), and a final response period that lasted until a response was recorded (Fig. 1). Faces were presented briefly to limit the role of eye movements in the task. Participants performed two tasks on each trial. For the *detection task* participants were told to press the space bar as quickly as possible whenever a pre-defined target letter appeared in the center of the first face. For each participant, one of five letters, "T", "H", "X", "L", "V", was randomly assigned to be the *target* letter. This target letter appeared on half the trials and the four remaining *distractor* letters were evenly distributed across the other half. Responses to targets occurred during the 1500 ms blank interval between faces. For the *face discrimination task*, participants indicated whether the second face was identical to the first face in a trial by pressing 's' (for same) or 'd' (for different) during the final response interval. A same or different face was equally likely to follow the presentation of a target or

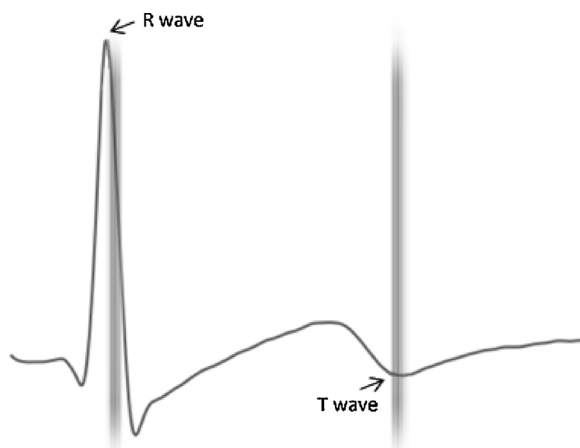


**Fig. 1. A sample trial of the behavioral task.** Each trial consisted of a white fixation cross (800 ms + peak detection algorithm and cardiac phase lag), a face with a letter in its center (200 ms), a blank interval (1500 ms), a second face (200 ms), and a final response period that lasted until a response was recorded. The stimuli and the superimposed letter are bigger than in the real task for display purposes. Participants pressed spacebar to target letters and then indicated same different face identity after the second face is presented.

distractor.

To investigate potential cardiac modulation of attention, the letter and face display of each trial was presented during different phases of the cardiac rhythm. ECG activity was recorded using BioPac MP150 device (<https://www.biopac.com/>). The letter/face stimulus on each trial was time-locked to the ECG: on half trials it was time-locked to the R wave (during the end of cardiac diastole) and the other half to the T wave (during cardiac systole). R waves (Fig. 2) were defined as the first peak in ECG activity after fixation that was detected by a custom real-time peak detection algorithm in Python library rpeaks (<https://github.com/rmarkello/rpeaks>). T waves were defined as the time point 300 ms after the preceding R wave (Edwards, Ring, McIntyre, Carroll, & Martin, 2007; Edwards, Ring, McIntyre, Winer, & Martin, 2009; Gray, Rylander, Harrison, Wallin, & Critchley, 2009).

Participants completed a total of 200 trials. These were evenly divided among the eight trial types that were created by crossing three



**Fig. 2. Stimulus presentation – heart phase alignment for trials included in further analysis.** The labels depict R wave (cardiac diastole) and T wave (cardiac systole). The time delay between the two is 300 ms. For each trial across all participants, a vertical bar indicates when the face/letter stimulus was presented. Because most onsets were within 50 ms of the preceding dot, the lines are tightly clustered.

factors (target/distractor letter, same/different face, and systole/diastole time-locking), resulting in 25 trials per condition. Trial order was randomized for each participant. Trials were divided into five blocks and separated by self-paced breaks. Each face was randomly assigned to conditions across participants. Each participant completed a practice block of 20 trials before the main task.

#### 2.4. Data analysis

Data analysis was done in Python 3.4 and R 3.3.1 (<https://www.r-project.org/>). Real-time heart phase detection results were plotted along with the ECG amplitude and visually inspected. One subject was excluded as the plotted detected peaks were apparently off. The remaining heart phase detection data were further examined by a post-hoc peak detection algorithm. Trials where the time discrepancy between the actual and expected times of the letter and face display were larger than 50 ms were excluded (65 trials, or 1.3% of the total).

To better model within and across subject variability, we fit a multi-level logistic regression model using the glmer function of the R package lme4 (Bates et al., 2015). The model used a centered-dummy coding scheme. Face discrimination task accuracy was entered as the dependent variable. Cardiac phase (systole/diastole), letter condition (target/distractor), and their interactions were entered as fixed effects, second face status (same/different) was entered as a covariate, trial number and block number were also entered as covariates to control for potential fatigue; subject ID and stimulus ID were entered as random effects. The status of the second face as same or different was included because cardiac phase influences the likelihood that one believes a novel face was recently encoded, though these effects were observed for cardiac phase gating during retrieval (Fiacconi et al., 2016). Post-hoc comparisons were performed using lsmeans package (<https://github.com/rvleneth/lsmeans>). To test for speed-accuracy trade-offs in face discrimination task performance, response times for correct same/different responses were fit in a multi-level regression model with the same independent variables as those used to model task accuracy.

Because performance on the memory task was relatively high, potential ceiling effects were examined. A random effects model with random slopes of letter and heart condition for each individual was performed, and coefficients of cardiac and target effect were extracted.

Correlations were performed between the two coefficients and individual memory task accuracy. If a ceiling effect does take place, we should expect diminished magnitude in the absolute value of the coefficients.

### 3. Results

#### 3.1. Heart phase detection

Stimuli were generally well aligned to heart phase. Sixty-five trials (1.30%) with heart-phase-stimuli time discrepancy larger than 50 ms were excluded for further analysis across all participants. Fig. 2 shows the alignment for the trials included in the analysis.

#### 3.2. Letter detection task accuracy

Accuracy across the 25 participants that met inclusion criteria was  $97.64\% \pm 0.37\%$  ( $n = 25$ , standard error). Neither letter detection accuracy nor reaction time (RT) significantly differed across systole and diastole trials (Welch two sample t-test, accuracy: systole  $97.86\% \pm 0.42\%$ , diastole  $97.42\% \pm 0.43\%$ ,  $t = 1.02$ ,  $df = 4922.7$ ,  $p = 0.31$ ; RT: systole  $446 \pm 19$  ms, diastole  $449 \pm 19$  ms,  $t = 0.42$ ,  $df = 2517.9$ ,  $p = 0.68$ ), indicating fixation duration does not appear to affect task performance in this study.

#### 3.3. Face discrimination task accuracy

Mean face discrimination task accuracy across the 25 subjects that met inclusion criteria was  $92.52\% \pm 0.97\%$  ( $n = 25$ ). All participants performed better than chance.

#### 3.4. Regression model on letter detection and face discrimination tasks

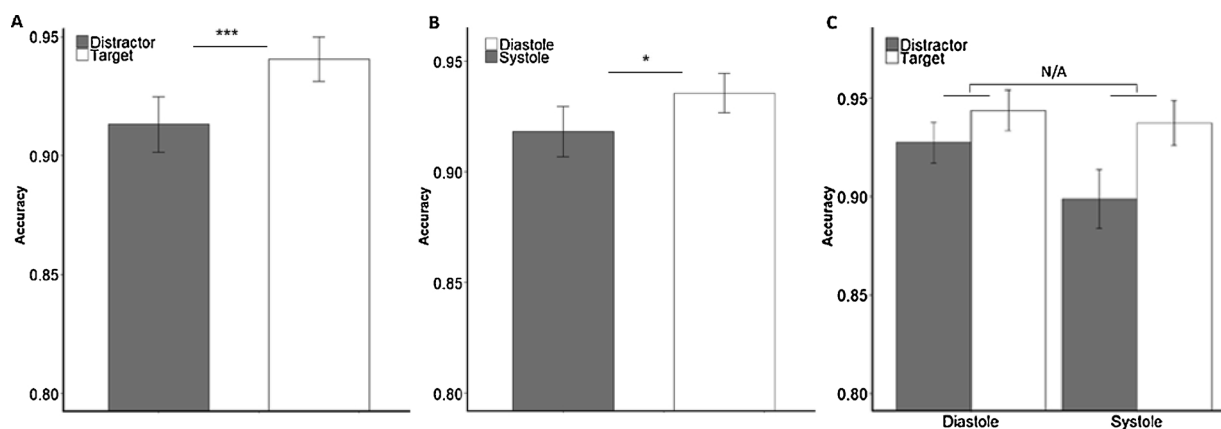
The main effects of letter condition and cardiac phase were examined. Positive beta weights were consistent with greater accuracy under target rather than distractor conditions, greater accuracy under systole than diastole cardiac phase conditions, and greater accuracy for different than same faces. The multi-level logistic regression on face discrimination task accuracy revealed a significant effect of letter condition ( $\beta = 0.39 \pm 0.11$ ,  $z = 3.54$ ,  $p = 4.00 \times 10^{-4}$ , Fig. 3A). Consistent with an attentional boost, face discrimination accuracy was greater when the first face was paired with the target letter rather than the distractor letter. A significant effect of heart condition ( $\beta = 0.22 \pm 0.11$ ,  $z = 1.98$ ,  $p = 0.048$ , Fig. 3B) indicated that face discrimination accuracy was better when the first face was displayed at systole compared to diastole. This suggests that cortical inhibition

during systole may suppress perceptual interference during a complex paradigm. No interaction between the two conditions was identified for face discrimination accuracy ( $\beta = -0.18 \pm 0.22$ ,  $z = -0.80$ ,  $p = 0.43$ , Fig. 3C), indicating letter condition and heart condition acted independently. Responses were reliably more accurate on ‘different’ trials than on ‘same’ trials ( $\beta = 0.27 \pm 0.11$ ,  $z = 2.48$ ,  $p = 0.013$ ), but this effect did not mask the effects of interest. Neither trial or block showed a significant effect ( $\beta_{\text{trial}} = -8.73 \times 10^{-3} \pm 4.74 \times 10^{-3}$ ,  $z = -1.84$ ,  $p = 0.065$ ,  $\beta_{\text{block}} = -0.036 \pm 0.038$ ,  $z = -1.83$ ,  $p = 0.35$ ).

To further investigate the potential relationship between the attentional boost effect and cardiac phase, the effect of letter condition within each phase was examined. These follow up contrasts revealed a significant effect of target letter in diastole ( $z = 3.19 \pm 0.15$ ,  $p = 1.40 \times 10^{-3}$ ), and a trending effect in systole ( $z = 1.87 \pm 0.16$ ,  $p = 0.06$ ). A second model that included random slopes for each individual further indicated a non-significant interaction: the correlation between the individual attentional boost effect (target-distractor) and the individual cardiac phase effect (systole-diastole) was not statistically significant ( $r = -0.18$ ,  $p = 0.40$ ).

Although performance on target trials did not depend on cardiac phase, this may have been partly influenced by a ceiling effect. If differences in accuracy across conditions were masked by high levels of task performance, then the magnitudes of the letter condition and cardiac effects should decrease as accuracy increases. For each individual, overall face discrimination task was correlated with the absolute values of their random slope coefficients for the effects of the letter condition and cardiac phase. Individual face discrimination accuracy did not significantly correlate with the effect of letter condition (target-distractor,  $r = -0.35$ ,  $p = .085$ ) or the effect of cardiac phase (systole-diastole,  $r = -0.18$ ,  $p = 0.387$ ). This indicates that high levels of accuracy did not mask differences between conditions.

Because discrimination task accuracy was very high, the effects of cardiac phase and letter detection on the memory task may be most apparent in response times. Consistent with the accuracy data, the reaction time model indicated that discrimination performance was faster on trials that included a target rather than a distractor letter ( $\beta = -0.11 \pm 0.015$ ,  $z = -6.92$ ,  $p = 5.04 \times 10^{-12}$ ). However, response times for the discrimination task did not significantly differ across cardiac phases ( $\beta = -7.59 \times 10^{-3} \pm 0.015$ ,  $z = -0.49$ ,  $p = 0.62$ ). The interaction term also was non-significant ( $\beta = -6.42 \times 10^{-3} \pm 3.09 \times 10^{-3}$ ,  $z = -0.21$ ,  $p = 0.84$ ). These findings indicate that the effects of cardiac phase and letter condition on discrimination task accuracy were not the result of a speed-accuracy trade-off. Furthermore, RT did not reveal an interaction between letter condition and cardiac phase.



**Fig. 3. Face discrimination task accuracy by conditions.** A. Participants performed better in the target letter condition than the distractor letter condition, and B. in the systole condition than the diastole condition. C. No interaction was identified between the letter condition and heart condition. (\*\*\*:  $p < 0.001$ , \*:  $p < 0.05$ , N/A: not significant).

#### 4. Discussion

We examined the role of bodily states and attentional resources in regulating short-term memory. We replicated previous findings showing that the behavioral relevance of targets boosts the encoding of and subsequent short-term memory of concurrently presented background information (Makovski et al., 2011; Swallow & Jiang, 2010). Similarly, cardiac cycle regulated the ability to simultaneously detect a target and encode a face, with short-term memory performance being better for stimuli presented during systole. Counter to our expectations, these two effects were largely complementary and independent. Instead, the data suggest that cardiac gating of cognition and the attentional boost effect may work through different underlying pathways.

One major source of information regarding body state to the brain is baroreceptor firing. When arterial blood pressure increases during systole, baroreceptors on the aortic arch and carotid bodies fire. This information is relayed through the vagus and glossopharyngeal nerve afferents to the nucleus of the solitary tract in the medulla (Mancia & Mark, 1983) and in turn affects cognition through subcortical and cortical regulatory influences (Critchley & Harrison, 2013). This vagal pathway is involved in regulating heart rate variability (HRV), which also modulates cognitive and affective processes, including executive function and inhibitory control (Thayer & Lane, 2000; Thayer, Hansen, Saus-Rose, & Johnsen, 2009). Phasic baroreceptor feedback has been proposed as one of the sources of high frequency HRV that are associated with greater cognitive control (Hansen, Johnsen, Sollers, Stenvik, & Thayer, 2004). Individuals with trait high frequency HRV, which is associated greater baroreceptor sensitivity (Pikkuja et al., 1998), can better ignore fearful faces (Park, Van Bavel, Vasey, & Thayer, 2013). This greater regulation of attention is thought to reflect enhanced vagal nerve activity, or vagal “tone”, which has been proposed to enhance inhibitory control (Daniela et al., 2015; Thayer, Åhs, Fredrikson, Sollers, & Wager, 2012). The regular, cyclic inhibition by baroreceptors of cortical activity has led to the suggestion that cardiovascular cycle may be another source of oscillatory regulation of neural processing and communication within the brain (Garfinkel & Critchley, 2016). Engaging in demanding cognitive tasks, such as the one used here, has been shown to reduce variability in heart rate and the influence of baroreceptor signaling on cardiac cycle regulation (Duschek et al., 2009), potentially increasing the importance of cardiac rhythms on cortical oscillatory activity at these times. However, these findings are related to chronic trait level adaptations that may be related baroreceptor sensitivity but are largely agnostic to within person state level fluctuations, let alone modulation within the cardiac cycle.

Within the cardiac cycle, cardiac systole may induce general cortical inhibition (Lipnicki, 2009; Rau et al., 1993). One potential consequence of baroreceptor activity during systole is the inhibition of mechanisms that increase the signal to noise ratio in perceptual processing, such as NA release from the LC (Morilak et al., 1986). In this way, baroreceptor activity could degrade the quality of stimulus representations. Consistent with this possibility, in a low-contrast target discrimination task where the targets need to be selected against a preceding high contrast mask, target detection was better when the mask were presented during cardiac systole (Pramme et al., 2014). Noisier processing of stimuli presented during systole is also consistent with findings that suggest poorer performance on simple tasks when trials are presented at these times (McIntyre et al., 2008; Sandman et al., 1977). However, reductions in cortical activity due to baroreceptor firing may also interfere with selection mechanisms that help resolve interference. Consistent with this possibility, Walker and Sandman (1982) found that the visual cortical evoked potential P1, an EEG component that indexes visual attention, is reduced during systole relative to diastole. In addition, the effects of systole on cognitive processing are not limited to attention. When participants tried to remember briefly presented words after a one-hour delay, those words that were presented during systole were less likely to be remembered than those words that were presented

during diastole (Garfinkel et al., 2013).

In contrast to these earlier findings of impaired attention and memory during systole, in this experiment short-term memory for faces was enhanced when they were initially encoded during systole rather than during diastole. These data may reflect impaired attentional selection during systole. Impairments in selection typically result in poorer task performance. However, because participants were required to attend to both stimuli in this task, performance may have benefitted from the inhibition of selection mechanisms. Because the letter/face display was not masked, impaired attentional selection during systole could increase the likelihood that the face is still being processed when baroreceptors fall silent in subsequent phases of the cardiac cycle. It also is possible that discrepancies in the effects of cardiac phase and memory in these data and other studies reflect a fundamental difference between mechanisms that support representations for a couple seconds at a time (as in short-term memory tasks), and those that form longer lasting representations. If selection of the letter at the expense of the face in this task is inhibited during systole, then the face may be better maintained in memory for a brief period of time. In contrast, the suppression of LC activity during systole may interfere with encoding an item presented at those times into more stable forms of memory supported by the hippocampus (Garfinkel et al., 2013; Sara, 2009).

Though some types of cognitive tasks are inhibited during cardiac systole, exceptions occur when stimuli evoke limbic computations. For example, fearful, rather than neutral faces that are presented during cardiac systole are more likely to be detected during the attentional blink, when new stimuli are typically not consciously perceived (Garfinkel & Critchley, 2016). Similarly, categorization tasks that are sensitive to racial threat stereotypes evoke more biased behaviors when the stimuli are presented during cardiac systole rather than diastole (Garfinkel, Critchley, Tsakiris, & Azevedo, 2017). In these studies, a person is more likely to consciously perceive a fearful face or to be influenced by negative racial stereotypes when the information is encountered during the systole phase of the cardiac cycle. The effects of cardiac gating on task performance may therefore reflect a central role of forebrain structures involved in affective processing, such as the amygdala, in regulating cortical responses to behaviorally relevant stimuli (Garfinkel et al., 2014; Schmitz, Rosa, De, & Anderson, 2009; Todd, Talmi, Schmitz, Susskind, & Anderson, 2012). Under conditions of higher motivational significance, such as threat (Garfinkel & Critchley, 2016; Park et al., 2013), attention and cardiac gating may interact in regulating common afferent regions such as the amygdala that modulate subcortical and cortical arousal to influence attention, perception, and memory (Stoyanova, Pratt, & Anderson, 2007). Under low arousal conditions like those in our experiments, however, attentional and cardiac gating may represent complementary regulatory paths. Attention involves both boosting and suppressing sources of information. These gain/excitatory and tuning/inhibitory aspects of attention are dissociable (Schmitz, Dixon, Anderson, & De Rosa, 2014). The independence of cardiac gating and attentional boosting may reflect this dissociation. We show that short-term memory for the face behind the letter was increased during cardiac systole relative to diastole. Other studies examining the effect of baroreceptor firing on selective inhibition found that negative priming was abolished during baroreceptor loading related to head tilt (Pramme, Schächinger, & Frings, 2015), suggesting potential link between cardiac cycle an inhibitory control of attention. By contrast, attentional boosting has been shown to reflect enhancement rather than distractor suppression of irrelevant information (Swallow & Jiang, 2013, 2014b). Target stimuli enhanced long term memory for background faces simultaneously presented with targets, relative to faces either presented with distractors or alone (Swallow & Jiang, 2014b), consistent with increased gain. Thus, the attentional boost effect presumably reflects increased gain while cardiac modulation may regulate inhibitory control.

Empirical findings suggesting the mind and body have potent interactions (Garfinkel & Critchley, 2016; Jacobs, 2001; Thayer & Lane,

2000). By contrast, our finding suggests that cardiac and attentional gating act independently, at least in this paradigm. However, current accounts of both cardiac gating and attentional boost effects at least partially implicate the LC (Rau et al., 1993; Swallow & Jiang, 2013). Baroreceptor suppression of noradrenergic neurons in the LC during systole may be the source of general cortical inhibition (Lipnicki, 2009; Morilak et al., 1986; Murase, Inui, & Nosakat, 1994; Rau et al., 1993). Though the neural mechanism that produces the attentional boost effect is less clear, it has been proposed that enhanced gain and widespread cortical responses to targets during a detection task could originate from the LC (Swallow & Jiang, 2013), which projects to regions throughout the brain (with a few exceptions; Schwarz et al., 2015). Consistent with this possibility, larger pupillary responses (associated with increased LC activity) to targets in a detection task are associated with enhanced memory for concurrent images (Hoffing & Seitz, 2015).

However, because the interaction between the attentional boost effect and cardiac phase in the current paradigm was not significant, these effects may rely on separate, co-localized mechanisms. Moreover, anatomical tracing and neurophysiological methods suggest that subsets of neurons within the LC project to different cortical areas and are associated with different computations during learning (Berridge & Waterhouse, 2003; Kitabatake et al., 1983; Schwarz et al., 2015; Seo & Bruchas, 2017). The rostral ventrolateral medulla, involved in cardiovascular regulation, projects to the ventral and dorsolateral regions of LC, while prefrontal cortex sends inputs to pericoerulear regions to potentially regulate attentional functions (Berridge & Waterhouse, 2003; Samuels & Szabadi, 2008). In addition, although LC neurons integrate information from a large variety of regions, the relative contributions of each of these regions differs across different populations of LC neurons, allowing these neurons to display heterogeneous functional properties (Schwarz et al., 2015). This heterogeneity in function may be specific to low arousal, neutral states that are likely during the task used here. When aversive stimuli are encountered, the LC may adopt a more global response mode that affects processing throughout the brain (Kitabatake et al., 1983; Seo & Bruchas, 2017). It is therefore possible that the same LC subpopulations are recruited when processing high arousal stimuli, enhancing their significance; however, in current paradigm with low arousal stimuli, cardiac gating and the attentional boost effect may reflect differential engagement of LC subpopulations, different response modes, or both.

Differences in LC dynamics during high and low arousal states highlight the need for additional research that characterizes the effects of target detection and cardiac phase on attention across a variety of paradigms and situations. The magnitude of the effects for both manipulations were small in the current study, but may have an impact on how well participants are able to process, respond to, and remember briefly presented or near threshold visual information. However, situations that strengthen the relationship between cardiac phase, attention and memory may reveal larger and potentially interactive effects. For example, the attentional boost effect is larger when processing of the face is temporally restricted and long-term memory is tested (e.g., Swallow & Jiang, 2014a, 2014b).

The independence of cardiac gating and attentional boost effects in the current study could also reflect the temporal dynamics of the LC. Because the LC interacts reciprocally with cortical regions (Aston-jones, Rajkowski, & Cohen, 2000), and has response properties that are dependent on task difficulty (Rajkowski, Majczynski, Clayton, & Aston-Jones, 2004), any effect that the LC has on cortical processing in response to targets may occur at a slightly different time scale than within cycle cardiac modulations. Although phasic LC responses to targets occurs relatively quickly for simple detection tasks (~100 ms; Aston-jones & Cohen, 2005), this response is delayed when targets must be discriminated from distractors (~150 ms), is even later when targets and distractors are perceptually similar (~175 ms), and increases with increased behavioral response times (Rajkowski et al., 2004). In contrast, baroreceptor inputs to the brainstem and LC may take around

300 ms to arrive after the R wave peak. Importantly, however most of this work has been performed on different species performing simpler tasks, making it difficult to draw clear conclusions about the temporal dynamics of LC in this experiment.

Attentional and cardiovascular gating may be co-localized, but over evolutionary time, LC nuclei may have differentiated away from bodily regulatory functions to reflect more top down cortical control. These regulatory influences may no longer be tightly coupled at the level of moment-to-moment dynamics. Together, our conjoint examination of phasic fluctuations in attentional gating and cardiac cycle reveal independent contributions to cognitive performance. These findings have theoretical implications for understanding of how bodily and mental resources are integrated in the brain at the resolution of a heartbeat. In terms of practical significance, cardiac gating and attention can be viewed as complementary, with maximal short-term memory performance achieved when systole and attentional selection align.

#### Declaration of conflicting interests

The author(s) declared that there were no conflicts of interest with respect to the authorship or the publication of this article.

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