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Afferent cardiac signals modulate attentional engagement to low spatial frequency fearful faces

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ABSTRACT

Despite the growing consensus that the continuous dynamic cortical representations of internal bodily states shape the subjective experience of emotions, physiological arousal is typically considered only a consequence and rarely a determinant of the emotional experience. Recent experimental approaches study how afferent autonomic signals from the heart modulate the processing of sensory information by focussing on the phasic properties of arterial baroreceptor firing that is active during cardiac systole and quiescent during cardiac diastole. For example, baroreceptor activation has been shown to enhance the processing of threat-signalling stimuli. Here, we investigate the role of cardiac afferent signals in the rapid engagement and disengagement of attention to fear stimuli. In an adapted version of the emotional attentional cueing paradigm, we timed the presentation of cues, either fearful or neutral faces, to coincide with the different phases of the cardiac cycle. Moreover, we presented cues with different spatial frequency ranges to investigate how these interoceptive signals influence the processing of visual information. Results revealed a selective enhancement of attentional engagement to low spatial frequency fearful faces presented during cardiac systole relative to diastole. No cardiac cycle effects were observed to high spatial frequency nor broad spatial frequency cues. These findings expand our mechanistic understanding of how body—brain interactions may impact the visual processing of fearful stimuli and contribute to the increased attentional capture of threat signals.

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1. Introduction

Despite the well documented autonomic components of emotion processing, physiological arousal is typically regarded only as a consequence (i.e., efferent responses) of subjective emotional states and rarely as a determinant of the emotional experience. Indeed, the contribution of central representations of bodily arousal to emotion and cognition

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has been largely overlooked in experimental research (Ainley, Apps, Fotopoulou, & Tsakiris, 2016; Allen et al., 2016; Babo-Rebelo, Richter, & Tallon-Baudry, 2016; Critchley & Harrison, 2013). An emerging line of research has set to address this issue by looking at how afferent signals originating in the phasic discharge of arterial baroreceptors set the physiological context through which body-to-brain effects influence the processing of sensory information (Critchley & Harrison, 2013). Arterial baroreceptors are pressure and stretch sensors located in the aortic arch and carotid sinus that detect changes in blood pressure and communicate to the brain the current state of cardiovascular arousal at each heartbeat. Recent experimental approaches capitalize on the phasic properties of baroreceptor firing, i.e., active during cardiac systole and quiescent during cardiac diastole, to study how afferent signals shape the processing of sensory (Edwards, McIntyre, Carroll, Ring & Martin, 2001; Edwards, Ring, McIntyre, Winer & Martin, 2009; Martins, Ring, McIntyre, Edwards, & Martin, 2009; Schulz et al., 2009), cognitive (Fiacconi, Peter, Owais, & Köhler, 2016) and emotional (Azevedo, Garfinkel, Critchley, & Tsakiris, 2017; Garfinkel et al., 2014; Gray et al., 2012) stimuli. Specifically, it has been shown that when certain categories of stimuli are presented during cardiac systole or diastole, stimulus processing is enhanced or attenuated. These cardiac cycle effects seem to be particularly evident in the enhancement of threat signals (Garfinkel and Critchley, 2016). Using an attentional blink paradigm, Garfinkel et al. (2014) found that systole facilitates the breakthrough of fearful stimuli into perceptual awareness. In a separate study, the authors also showed that fearful faces are rated as more intense when presented at systole as compared to diastole. This effect was associated with changes in activity in the amygdala (Garfinkel et al., 2014; see also; Gray, Rylander, Harrison, Wallin, & Critchley, 2009), a key region implicated in fear processing and autonomic regulation (Phelps & LeDoux, 2005). More recently, Azevedo et al. (2017) extended these findings to the social domain by showing enhanced activation of racial threat signals, and subsequent racially biased behaviour, at systole relative to diastole. Together, these studies suggest afferent baroreceptor information as an important mechanism of body-to-brain influences in the processing of fear stimuli.

The present study aims to look further into the mechanisms underlying the cardiac cycle enhancement of fear processing by investigating its impact on attentional capture processes. The orienting component of attention, or the aligning of attention with a source of sensory input (Posner, Rothbart, Thomas-Thrapp, & Gerardi, 1998, pp. 269–289) is believed to encompass at least three distinct processes, i.e., shift, engagement and disengagement. These can be recruited by two either endogenous or exogenous cues, subserved by interacting, yet distinguishable, neural networks (Posner & Rothbart, 2007). Specifically, attention needs to be: 1) *shifted* from the current object of focus to the new cue; 2) *engaged* with this incoming information; and finally 3) *disengaged* from it. "Exogenous" attentional processes are stimulus-driven, depend on reflexive and bottom-up mechanisms and are sustained by a posterior attention network, encompassing the superior parietal cortex, pulvinar and superior colliculus. Conversely, "endogenous" attentional processes rely on reflective and top-down mechanisms, underpinned by an anterior attention network including the anterior cingulate and prefrontal cortex. These processes can be experimentally assessed using a spatial cueing paradigm (Posner, 1980). In this task, participants are requested to fixate a central point in a computer screen and to detect as fast as possible the location of a target appearing on left or on the right hand side of the screen. Crucially, previous to target presentation, participants' attention is directed to the left or right of the central fixation point via the brief presentation of a task-irrelevant cue. The cue and the target can be presented either on the same (valid trials) or on the opposite (invalid trials) location of the screen. A faster detection of the target is typically observed for valid trials and slower detection on invalid trials. Moreover, the time between the onset of the cue and that of the target, i.e., the stimulus onset asynchrony (SOA), can be shorter (i.e., >150 msec) or longer (i.e., >300 msec) to engage the exogenous or endogenous attentional processes, respectively (Posner & Cohen, 1984). Finally, one version of this task includes both emotional, particularly threat-related, and non-emotional stimuli as cues (Armory & Dolan, 2002; Stormark, Hugdahl, & Posner, 1999). An increased cueing effect when the cue is emotional reflects a bottom-up influence exerted by the affective content of the cue on visual attention. Faster response times (RTs) on valid trials indicate facilitated attentional engagement to the emotional content. Conversely, slower target detection following the presentation of invalid fear cues reflects delayed attentional disengagement from the emotional content.

In the current study, we adapted an emotional spatial cueing task to investigate the role of cardiac afferent signals in the rapid engagement and disengagement of attention to fear stimuli. Specifically, we timed the presentation of cues, either fearful or neutral faces, to coincide with the different phases of the cardiac cycle. Moreover, to investigate how these interoceptive signals interact with visual processing we presented cues at different spatial frequency ranges. We capitalized on the fact that analysis of visual input takes place in distinct neural pathways selectively sensitive to different ranges of spatial frequency information (Garrido et al., 2012; Mendez-Bertolo et al., 2016; Vuilleumier, Armony, Driver, & Dolan, 2003). Broad spatial frequencies (BSF) pictures encompass all the spatial frequency ranges and can be filtered to include only either low spatial frequencies (LSF) or high spatial frequencies (HSF). LSF carry coarse visual information, such as motion and rough configurational cues, and HSF carry fine-grain information, such as colour, texture and contrast. Importantly, research suggests that LSF fearful faces are rapidly processed and conveyed by the magnocellular pathway, through the superior colliculus and the pulvinar to the amygdala (Bar, Neta, & Linz, 2006; Mendez-Bertolo et al., 2016; Vuilleumier et al., 2003; but for a discussion see also: Pessoa & Adolphs, 2010). Conversely, through the parvocellular pathway, engaging ventral visual cortical areas such as the fusiform and inferior temporal-occipital cortex (Vuilleumier et al., 2003). Thus, testing for distinct cardiac cycle effects in emotional attentional capture as a function of stimuli spatial frequency can expand our understanding of how body–brain interactions impact the neural processing of visual fear signals.

In line with reported baroreceptor effects in the detection of threat signals (Garfinkel et al., 2014) and subsequent behavioural modulation (Azevedo et al., 2017) we predicted increased engagement and decreased disengagement to fear cues presented during cardiac systole relative to diastole. We also predicted that such cardiac cycle effects would be observed to LSF and BSF cues but not to HSF faces. These predictions were based on previous research showing the importance of the amygdala both in the modulation of threat processing by baroreceptor activity (Garfinkel et al., 2014; Gray et al., 2009) and in the processing of BSF and LSF, but not HSF, fearful faces (Vuilleumier et al., 2003). Finally, heart rate variability (HRV), an index of the functional state of the parasympathetic nervous system (Friedman, 2007; Thayer, Ahs, Fredrikson, Sollers Iii, & Wager, 2012), has been shown to be relevant to several dimensions of emotional processing (e.g., Kemp & Quintana, 2013; Pappens et al., 2014; Sütterlin et al., 2011) including enhanced emotional attentional capture as a function of stimulus' spatial frequencies (Park, Van Bavel, Vasey, & Thayer, 2012a; 2013). In particular, low vagally mediated HRV is believed to be associated with poor inhibition and emotional regulation abilities and is often regarded as a marker of sensitivity to stress (Friedman, 2007; Kemp & Quintana, 2013; Thayer et al., 2012). Thus, we estimated participants' HRV at rest to explore if individual differences in this index are related to the cardiac cycle modulation of attention to emotional stimuli. Because vagally mediated HRV is believed to be closely associated to parasympathetic activation via baroreceptor firing we hypothesized that individuals with high HRV at rest would show stronger cardiac cycle effects.

2. Methods

2.1. Participants

37 students (10 males) at Royal Holloway University of London volunteered for this study. The data of 3 participants were excluded because of movement artefacts ($n = 1$) or high percentage of errors during the task ($n = 2$; see "Results" section). Of the remaining 34 (10 males), mean age was 22.6 (SD = 3.7). The final sample size was selected based on previous studies using similar methodologies (Azevedo et al., 2017; Park, Van Bavel, Vasey, & Thayer, 2013). Subjects received a financial compensation for their participation (10 GBP/hour).

2.2. Ethics statement

The study was approved by the Department of Psychology Ethics Committee at Royal Holloway University of London. All participants gave written informed consent and were free to withdraw at will.

2.2.1. Procedure
All participants were tested individually. After the presentation of the study, participants were asked to attach three disposable ECG electrodes in a modified lead II chest configuration: two electrodes were positioned underneath the left and right collarbone and another on the participant's lower back on the left side. The signal was recorded with a Powerlab 8/35 and a Bio Amp 132 (Powerlab, ADInstruments, http://www.adinstruments.com/) using LAbchart 8 Pro software. The sampling rate was 1000 Hz and a hardware band-pass filter between .3 and 1000 Hz was applied. A hardware-based function (Fast output response) in Powerlab was used to detect heartbeats online with delays <1 msec. Customised software, implemented in Matlab (The Mathworks, Natick, MA), was used to time cue onset to coincide with the systolic (~300 msec after the R-wave) or diastolic (~500 msec after the R-wave) phases of the cardiac cycle (Azevedo et al., 2017; Gray et al., 2009; Garfinkel et al., 2014). After placement of the electrodes, participants were instructed to seat comfortably in an armchair and rest for 5 min. Their ECG was recorded during this period to allow the estimation of rest HRV. Then, participants executed an adapted version of the emotional spatial cueing task (Park et al., 2013; Stormark et al., 1999). At the end of the experimental session, subjects were debriefed for their participation and received their financial compensation.

2.2.2. Heart rate variability (HRV)
ECG data recorded during the 5-min rest period was used to estimate participants' rest HRV. The root mean square of successive differences of RR intervals (RMSSD) was derived from the time series of interbeat intervals and estimated using the HRV function implemented in Labchart (v 8.1; ADInstruments). This index is believed to reflect the strength of parasympathetic influence (Thayer et al., 2012). Higher values indicate higher HRV. Data was visually inspected to detect artefacts and misidentified R-waves. Manually correction was performed where appropriate.

2.2.3. Emotional engagement and disengagement attentional processes
Attention orienting processes to emotional and non-emotional exogenous stimuli were measured with an adaptation of the emotional spatial cueing paradigm. In this task, the participant was requested to detect the position of a target (i.e., a black dot) while fixating a white cross in the centre of the screen. Two gray boxes, of 6° horizontally and 6° vertically at a viewing distance of 60 cm, were displayed on the left and right hand side of the screen; targets appeared at the centre of on one of these boxes (located at a distance of 6° from the fixation point). Participants were instructed to indicate by pressing "E" when a target was presented on the left box or "I" when a target was shown on the right, as quickly and accurately as possible. The target that participants had to detect was a black dot, subtending a visual angle of .6° across the diameter.

The targets were cued by fearful and neutral faces with different spatial frequencies (BSF, LSF, HSF), presented in one of the two gray boxes against a black background (see Fig. 1). Participants were told they should ignore the faces and keep their eyes focused on the fixation point on the centre of the screen. They were informed that the cues did not predict where the target would appear. Stimuli [i.e., 60 different pictures of faces for each Emotion (fear, neutral) × Spatial Frequency (BSF, LSF, HSF) condition] were taken from Park et al. (2013) and have been kindly shared by Gewhni Park (for an exhaustive description of the stimuli, please refer to Park et al., 2013).
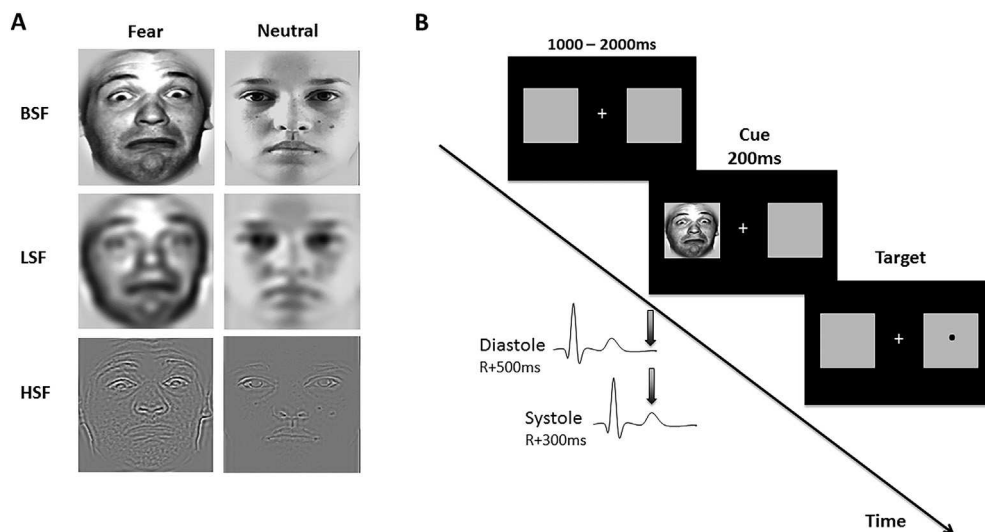
Fig. 1 − **(A) Examples of stimuli used and (B) and graphic description of the experimental procedure. Cue onset was synchronized with the different phases of the cardiac cycle—systole or diastole—to study the influence of cardiac afferent signals on attentional capture of fearful faces.**

The task included 480 trials, 20 of each condition: Cardiac Cycle (Systole, Diastole) × Emotion (Fear, Neutral) × Cue Validity (valid, invalid) × Spatial Frequency (BSF, LSF, HSF). Trial presentation was organized in 6 blocks, 2 for each spatial frequency, presented randomly. Within-blocks, conditions were presented in fully randomized order. Participants were requested to rest for at least 1 min between blocks. Each trial started with the initial fixation cross, followed by a face cue at the left or right hand side of the screen for 200 msec. The target was presented at the centre of either the left-or the right-side boxes immediately after cue offset and remained visible until the participants provided a response (for a maximum of 1000 msec). Cue onset was synchronized to coincide with either the participants' cardiac systole or cardiac diastole. The duration of the intertrial interval varied between 1000 and 2000 msec (see Fig. 1). These presentation timings, i.e., SOA of 200 msec, were adopted to be consistent with previous research showing effects of cardiac signals in enhancing threat representations using a similar cue/prime presentation followed by a quick response to a target (Azevedo et al., 2017). Target and cue presentation sides were randomized such that each combination occurred an equal number of times, i.e., valid and invalid trials were equally like to occur. For each participant, stimuli were randomly assigned to the systole and diastole conditions.

3.   Results

RTs of correct trials were analysed (see Table 1). RTs faster than 150 msec or exceeding 1000 msec were considered anticipatory and delayed responses, respectively, and were therefore discarded. Participants ($n = 2$) with erroneous responses in more than 15% of trials were excluded from analyses (cf. Park et al., 2013). The average percentage of errors of

the remaining was 4.7% (SD = 3.8) and the average RMSDD HRV (mean = 48.4, SD = 35) was comparable to values previously reported in the literature (mean = 42, SD = 15; Nunan, Sandercock, & Brodie, 2010). Data normality was tested with Shapiro−Wilk test. Only HRV RMSSD indices were found to violate normality assumptions ($p < .001$, all other $ps > .22$). HRV data was normalized via log-transformation and participants divided into high and low HRV based on a median-split.

Log-transformed RTs were submitted to a 3 Spatial Frequency (BSF/LSF/HSF) × 2 Emotion (Fear/Neutral) × 2 Validity (Valid/Invalid) × 2 Cardiac Cycle (Systole/Diastole) repeated-measures ANOVA with HRV (High/Low) as between-participants factor. The 5-way interaction was not significant $F_{(2,64)} = 1.41$, $p = .25$, partial $\eta^2 = .042$. However, the crucial interaction Spatial Frequency × Emotion × Validity × Cardiac Cycle was significant, $F_{(2,64)} = 3.58$, $p = .034$, partial $\eta^2 = .10$, confirming that cardiac cycle modulated emotional attention processes as a function stimuli spatial frequency. The Validity main effect ($F_{(1,32)} = 4.37$, $p = .045$, partial $\eta^2 = .12$), the Spatial Frequency × Validity interaction ($F_{(2,64)} = 22.28$, $p < .001$, partial $\eta^2 = .41$), and the Validity × HRV interaction ($F_{(1,32)} = 9.14$, $p = .005$, partial $\eta^2 = .22$) were also significant.[2] No other main effect or interaction was significant ($ps > .05$).

To follow-up on this we carried out 3 separate 2 Emotion (Fear/Neutral) × 2 Validity (Valid/Invalid) × 2 Cardiac Cycle

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[2] We re-ran the analyses using the high-frequency HRV index (HF HRV; ranges .15 Hz to .45 Hz) instead of the time domain RMSSD. As expected, RMSSD and HF HRV indices were strongly correlated ($r = .804$, $p < .001$). Analyses revealed equivalent results to those reported with the time domain index RMSSD. That is, HF HRV only interacted with Validity effect [$F_{(1,32)} = 7.43$, $p = .010$, partial $\eta^2 = .18$]. The critical interaction Spatial Frequency × Emotion × Validity × Cardiac Cycle was still significant, $F_{(2,64)} = 3.58$, $p = .032$, partial $\eta^2 = .10$.

Table 1 — Average (SEM) RTs for each condition.

	BSF				LSF				HSF			
	Fear		Neutral		Fear		Neutral		Fear		Neutral	
	Valid	Invalid	Valid	Invalid	Valid	Invalid	Valid	Invalid	Valid	Invalid	Valid	Invalid
Systole												
Mean	347.5	339.0	340.2	335.9	334.6	343.1	340.6	337.6	330.9	344.3	330.7	345.9
s.e.	6.9	7.5	6.7	7.2	6.8	8.1	6.7	7.9	7.1	8.3	7.9	8.3
Diastole												
Mean	344.9	340.8	338.1	340.4	342.9	339.0	338.8	342.0	327.1	347.9	327.7	345.4
s.e.	6.2	7.1	6.8	7.2	6.7	7.7	6.7	8.6	6.3	7.8	6.0	7.8

(Systole/Diastole) ANOVAs with HRV as between-participants factor for each spatial frequency. For the HSF analyses, cardiac cycle did not significantly interact with any factor ($Fs < 3.43$, $ps > .073$, partial $\eta s^2 < .10$). Only the main effect of Validity [$F(1,32) = 27.13$, $p < .001$, partial $\eta^2 = .46$] and the interaction Validity × HRV [$F(1,32) = 6.59$, $p = .015$, partial $\eta^2 = .17$] were significant. On the BSF analyses, the main effect of Emotion [$F(1,32) = 11.34$, $p = .002$, partial $\eta^2 = .26$] and the Validity × HRV interaction [$F(1,32) = 4.94$, $p = .033$, partial $\eta^2 = .13$] were found to be significant. The interactions Emotion ×Validity [$F(1,32) = 3.93$, $p = .056$, partial $\eta^2 = .11$] and the Emotion × Validity × Cardiac Cycle × HRV [$F(1,32) = 3.50$, $p = .071$, partial $\eta^2 = .10$] approached significance. However, contrary to our hypothesis, Cardiac Cycle did not interact significantly with any factor (all $ps > .070$). The LSF analysis showed that, in line with our primary hypothesis, cardiac cycle modulates attentional capture of LSF fearful faces as the 3-way Emotion × Validity × Cardiac Cycle interaction on the low spatial frequency cues was found to be significant, $F(1,32) = 6.74$, $p = .014$, partial $\eta^2 = .17$. With the exception of the Validity × HRV [$F(1,32) = 7.24$, $p = .011$, partial $\eta^2 = .18$], no other main effect or interaction was found, $Fs < .80$, $ps > .38$, partial $\eta s^2 < .025$. To decompose the significant interaction on LSF stimuli, attentional engagement ($RT_{neutral\ valid\ cues} - RT_{fearful\ valid\ cues}$) and attentional disengagement ($RT_{fearful\ invalid\ cues} - RT_{neutral\ invalid\ cues}$) scores were calculated (see Fig. 2; Koster, Crombez, Verschuere, Van Damme, & Wiersema, 2006; Park et al., 2013). In both cases, positive scores reflect increased attentional capture by fearful faces compared to neutral faces. Differences in attentional engagement and attentional disengagement to cues presented at systole versus diastole were tested with separate two-tailed pairwise t-tests. HRV was no longer included in the analyses because this factor did not interact with cardiac cycle effects (note: equivalent results are observed when HRV is included). A significant difference on attentional engagement scores, $t(1,33) = 2.47$, $p = .019$, Cohen's $d = .42$, revealed faster attentional engagement to fearful faces (vs neutral) when the cues were presented at systole than when presented at diastole. No difference was found for attentional disengagement scores, $t(1,30) = 1.57$, $p = .13$, Cohen's $d = .27$.

4. Discussion

Recently developed experimental paradigms enabled us to explore how a fundamental communication pathway between the heart and brain that reflects bodily arousal influences cognition and emotional processing. Specifically, by timing the presentation of brief stimuli to the distinct phases of the cardiac cycle, i.e., systole or diastole, it is possible to study the influence of baroreceptor firing on brain—body interactions across a variety of psychological domains (Garfinkel and Critchley, 2016). Here, we have combined this experimental technique with a well validated emotional spatial cueing paradigm to expand our knowledge on the role of cardiac afferent signals on the attentional capture of threatening signals. Importantly, we presented stimuli at different spatial frequency ranges to capitalize on the fact that different neuronal pathways in the visual system are selectively sensitive to distinct ranges of spatial frequencies. First, results showed different effects of baroreceptor activity in attentional engagement and disengagement processes. Specifically, we found that the cardiac cycle selectively enhanced attentional engagement but not attentional disengagement to fearful stimuli. Second, these effects were only observed on LSF trials, and neither on high (HSF) nor on broad (BSF) spatial frequencies trials, which suggests that baroreceptor firing modulates the processing of fearful faces at specific stages of visual processing. Together, our findings enhance the understanding of how afferent bodily signals interact with the visual processing of threat-related stimuli and impact the allocation of attentional resources.

Orienting attention to new salient incoming sensory information, especially those that may indicate a potential threat in the individual's environment, is crucial for adaptive functioning. The paradigm adopted in this study was specifically designed to test the extent to which orienting attention is controlled by exogenous processes. Exogeneous attention refers to a bottom-up, stimulus-driven process, activated by external events in the environment (i.e., without volitional control over the attentional set, e.g., sudden onset of a stimulus in the visual field; Posner & Cohen, 1984). Emotional stimuli, such as those signalling threat, are particularly likely to elicit such recruitment of attentional resources in order to enable prompt responses to the stimulus. What we observed here is that the rapid allocation of attention to threat cues is modulated by ongoing representations of bodily signals. Specifically, fearful faces presented at systole, i.e., when the representation of cardiac signals in the brain is maximal, were more likely to capture attention and bias participants' behaviour than fearful faces presented at diastole, i.e., when the representation of cardiac signals in the brain is minimal. Moreover, the influence of these interoceptive signals seems to be particularly evident when the individual engages attention to the incoming
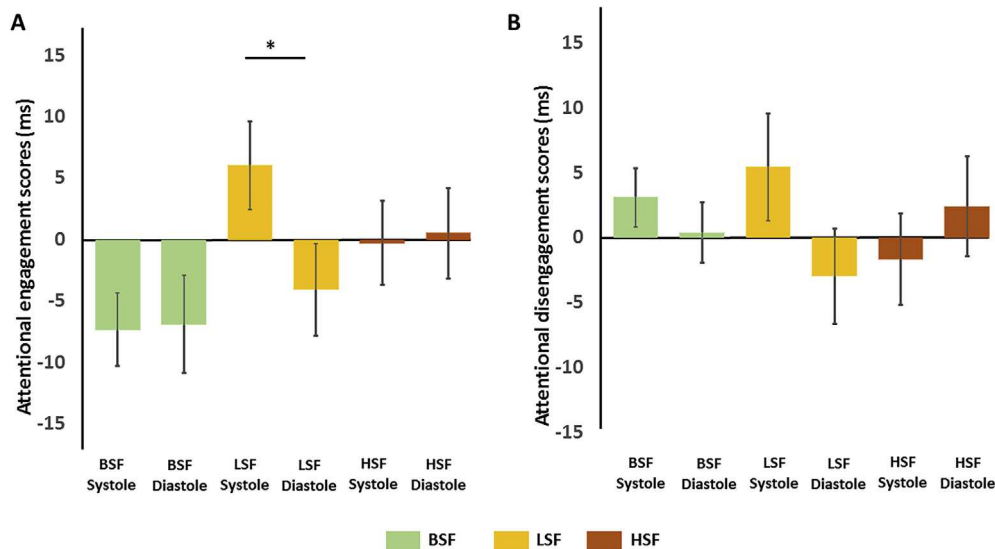
Fig. 2 − Average (SEM) attentional engagement (A) and attentional disengagement (B) scores as a function of cue spatial frequency and cardiac cycle conditions. *p < .05.

fearful faces, i.e., attentional engagement, and not when diverting the attention from them, i.e., attentional disengagement. These results highlight the role of cardiac afferent signals in heightened vigilance to threat stimuli and are consistent with evidence collected in previous studies (Azevedo et al., 2017; Garfinkel et al., 2014). In particular, a study conducted by Garfinkel et al. (2014), using an emotional blink paradigm, showed that fearful faces presented at systole are more likely to breakthrough to awareness than those presented at diastole. Another study looking at the effects of cardiac cycle in the processing of social threat signals suggested that the enhanced activation of threat representations at systole (vs diastole) reflects baroreceptor influence over automatic rather than controlled processes (Azevedo et al., 2017). Taken together, existing evidence converges to suggest that baroreceptor firing, conveying signals of cardiac arousal to the brain, enhance automatic bottom-up attentional capture of emotional cues.

Interestingly, cardiac cycle modulation of behaviour was selective to LSF trials and did not have a significant effect on HSF nor BSF trials. These results provide the first evidence on how afferent bodily signals may interact with the visual processing of emotional information. A substantial body of research has shown that distinct spatial frequencies convey different information about the appearance and quality of a stimulus. While LSF carry coarse information such as rough configurational cues, HSF carry fine-grained visual information, such as texture and contrast. In the case of faces, LSF are believed to be particularly important in the swift detection of facial emotional expressions (Bar et al., 2006; Holmes, Green, & Vuilleumier, 2005; Mendez-Bertolo et al., 2016; Schyns & Oliva, 1999). Conversely, the processing of HSF is thought to be relatively slower and support more detailed feature processing of faces (Goffaux, Hault, Michel, Vuong, & Rossion, 2005). Moreover, research suggests that LSF and HSF are processed in distinct neural pathways. Specifically, on the one hand, LSF

processing may be primarily sustained by a subcortical pathway, comprising the superior colliculus and the pulvinar, to the amygdala (Mendez-Bertolo et al., 2016; Vuilleumier et al., 2003), structures well known for its role in fear detection and processing (Phelps & LeDoux, 2005). On the other hand, HSF may follow the parvocellular pathway to ventral visual cortical areas. Such data are typically interpreted as evidence for the role of LSF information on the amygdala-mediated valence evaluation of visual signals and fast detection of threat. There is, however, some discussion on the specificity of these pathways in the processing of threatening stimuli (Pessoa & Adolphs, 2010). This debate is supported by evidence showing: i) the involvement of other brain regions, such as the orbitofrontal cortex, in the fast discrimination of emotional stimuli (Kawasaki et al., 2001) and ii) the use of HSF in the identification of fearful expressions (Stein, Seymour, Hebart, & Sterzer, 2014). Nevertheless, converging evidence suggests that the processing of coarse LSF information relies on amygdala activity (Mendez-Bertolo et al., 2016; Vuilleumier et al., 2003) and mediates the fast extraction and attentional engagement to threat cues but is not important to more sustained attentional processing (Holmes et al., 2005; Lojowska et al., 2015; Park et al., 2013). Our results provide a significant advance to this literature by showing how the representation of ongoing bodily states influences visual threat processing. Specifically, they suggest that visual processing of LSF information and attentional capture of fear signals is modulated by afferent cardiac activity. While formal direct fMRI investigations are needed to establish the neural substrates of the observed effects, our findings are consistent with the known impact of baroreceptor firing in the modulation of activity in several subcortical structures, including the amygdala. Arterial baroreceptor signals are carried by the vagus nerve to the brainstem where they are relayed to the basal ganglia and amygdala, and onwards to higher order viscerosensory cortices via thalamocortical projections

(Garfinkel and Critchley, 2016). Importantly, neuroimaging studies have further indicated that baroreceptor modulation of salient and threat signals is associated with changes in amygdala activity (Garfinkel et al., 2014; Gray et al., 2009). Given such evidence it is reasonable to expect that the processing of (LSF) visual threat is influenced by concurrent modulation of amygdala activity by baroreceptor firing. We propose that the feedback of bodily states of arousal to the brain facilitate the processing of visual information in brain regions responsible for the fast detection of threat. Nonetheless, neuroimaging studies are needed to confirm the neural substrates of the observed body—brain interaction in attentional capture.

Contrary to our expectations, and in apparent contrast with previous research showing baroreceptor modulation on the appraisal of BSF fearful faces (Garfinkel et al., 2014), we did not observe cardiac cycle effects on BSF trials. It is worth noting that, using a similar paradigm, Park et al. (2013) found that individual differences in cardiac vagal tone are selectively associated with bottom-up attentional engagement to LSF fearful faces but not HSF nor BSF fearful faces. While the reasons for these seemingly surprising results remain unknown, it is possible that with the present paradigm cardiac cycle effects are stronger when only LSF is presented. Cardiac signals may be particularly effective in modulating attentional capture when visual processing is largely dependent on amygdala processing and less when it relies on additional processing at higher-order visual areas, such as to stimuli containing HSF. Moreover, while HSF contain fine-grained visual information used in the conscious discrimination of fearful expressions (Stein et al., 2014), the information conveyed by LSF is rather coarse and may be perceptually more ambiguous (Holmes et al., 2005; Park, Vasey, Kim, Hu, & Thayer, 2016; Vuilleumier et al., 2003). Such relative perceptual ambiguity in explicit appraisal may also contribute to enhance amygdala mediated stimulus processing (Adolphs, 2013).

It should be noted that, even if cardiac cycle effects on attentional disengagement were not significant, the present study could not completely rule out the role of cardiac activity in top-down inhibition processes. It is known that procedural differences, such as SOAs duration and the probability of occurrence of each stimulus type, determine how much a task is able to tap into attentional disengagement processes (e.g., Koster et al., 2006; Vossel, Thiel, & Fink, 2006). Here, to study cardiac cycle modulation in both attentional engagement and disengagement processes, we adopted a fully balanced design, i.e., valid and invalid trials were equally like to occur (as in for example, Mogg & Bradley, 2002; Bradley, Mogg, Falla, & Hamilton, 1998) instead of the often used 75%-valid to 25%- invalid trial ratio. The approach adopted here has the advantage of reducing top-down influences in attentional processes related to expectations of target location (Vossel et al., 2006), but may lead to a somewhat weaker overall attentional capture. Moreover, to be consistent with previous research on cardiac cycle modulation of threat signals (Azevedo et al., 2017), we adopted a SOA of 200 msec. These presentation timings have been shown to elicit both bottom-up attentional engagement and disengagement to emotional cues (e.g., Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004; 2006) but are slightly longer than the optimal SOA commonly used to study exogenous attentional capture (Posner & Rothbart, 2007; Theeuwes, Atchley, & Kramer, 2000). Future experimental designs with higher percentage of valid trials and testing several SOAs will allow the study of the specific influence of interoceptive signals in both bottom-up and higher-order attentional mechanisms.

The spatial cueing paradigm has proved particularly useful in studying the relationship between attentional biases and anxiety disorders. It is mostly held that highly anxious people not only tend to easily engage their attention to threat-related cues as they also struggle to then disengage their focus of attention from these cues (Bradley et al., 1998; Fox, Russo, Bowles, & Dutton, 2001; Koster et al., 2006; Salemink, van den Hout, & Kindt, 2007). This can be observed in behaviours such as the hyper-vigilance to specific environmental information (e.g., a faster detection of spiders for individual with arachnophobia) and the subsequent difficulties to distract their attention from them. More recently, the efficiency of the attentional orienting system has been linked to crucial transdiagnostic processes. For instance, it has been shown to be predictive of the intensity of ruminative thinking (Pecher, Quaireau, Lemercier, & Cellier, 2011; Tortella-Feliu et al., 2014), an important maintenance factor in several psychopathologies (Mansell, Harvey, Watkins, & Shafran, 2009). However, in these studies, the contribution of bodily states to emotional experience was typically overlooked. More recently, Park et al. (2012b; 2013) observed that participants with low cardiac vagal tone exhibited enhanced neural reactivity and increased engagement to LSF fearful cues. Cardiac vagal tone is an index of the functional state of the parasympathetic nervous system that has been linked to emotional and attentional regulation abilities and suggested as a marker of sensitivity to stress (Friedman, 2007; Thayer et al., 2012). Importantly, the current study demonstrates within-participants interoceptive-driven modulations in attentional capture. We identified a neurophysiological mechanism through which ongoing bodily signals influence the flexible allocation of attentional resources to threat signals. However, despite the fact that baroreceptor signals have a substantial impact on parasympathetic activity and heart rate oscillations, contrary to our predictions, we did not observe any interactions between HRV and cardiac cycle effects. It may be that rest HRV, a trait index, is not a good predictor of the effects that our manipulation, i.e., presentation of threat cues concurrent with baroreceptor activation, has on cognition. It is known that a considerable portion of HRV variance is explained by state-specific factors (Bertsch, Hagemann, Naumann, Schächinger, & Schulz, 2012). Moreover, several other mechanisms not explored by our manipulation, such as respiratory activity (Eckberg, 2003; Schulz, Schilling, Vögele, Larra, & Schächinger, 2016), are also important contributors to beat-to-beat changes in heart rate. On the other hand, the lack of significant HRV effects may reflect type-II error inherent to single HRV measurements with relatively small sample size (Bertsch et al., 2012). This could potentially also explain the fact that we did not replicate Park et al. (2013) findings of a relationship between rest HRV and attention capture to emotional stimuli. We note however

that we did find a relationship between HRV and general attentional capture processes, i.e., irrespective of cue type. It is possible that the methodological differences discussed above, particularly the equal number of valid and invalid trials, may have also contributed to a lack of difference between individuals with high and low HRV in their tendency to engage and disengage to cues as a function of its emotional meaning. Nevertheless, our primary goal here was to investigate the main role of the mechanism of baroreceptor firing in emotional attention, over and above individual differences in HRV. Future research should build on these findings to better understand the relationship between interoceptive processing, autonomic regulation and anxiety (Garfinkel et al., 2014; Paulus & Stein, 2010; Terasawa, Shibata, Moriguchi, & Umeda, 2013) and investigate the interplay between bodily, attentional and psychopathological processes.

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