Special issue: Review

The neural monitoring of visceral inputs, rather than attention, accounts for first-person perspective in conscious vision

Catherine Tallon-Baudry [a,], Florence Campana [a,b], Hyeong-Dong Park [a,c] and Mariana Babo-Rebelo [a]*

[a] *Laboratoire de Neurosciences Cognitives, Département d'études cognitives, Ecole Normale Supérieure (ENS), PSL Research University, INSERM, Paris, France*
[b] *The Dynamic Perception Lab, Department of Psychological & Brain Sciences, Johns Hopkins University, Baltimore, MD, USA*
[c] *Laboratory of Cognitive Neuroscience, Center for Neuroprosthetics and Brain Mind Institute, Ecole Polytechnique Fédérale de Lausanne (EPFL), Geneva, Switzerland*

ABSTRACT

Why should a scientist whose aim is to unravel the neural mechanisms of perception consider brain-body interactions seriously? Brain-body interactions have traditionally been associated with emotion, effort, or stress, but not with the "cold" processes of perception and attention. Here, we review recent experimental evidence suggesting a different picture: the neural monitoring of bodily state, and in particular the neural monitoring of the heart, affects visual perception. The impact of spontaneous fluctuations of neural responses to heartbeats on visual detection is as large as the impact of explicit manipulations of spatial attention in perceptual tasks. However, we propose that the neural monitoring of visceral inputs plays a specific role in conscious perception, distinct from the role of attention. The neural monitoring of organs such as the heart or the gut would generate a subject-centered reference frame, from which the first-person perspective inherent to conscious perception can develop. In this view, conscious perception results from the integration of visual content with first-person perspective.

Does it matter that the brain is embedded in a body to understand vision? Leaving the oculo-motor system aside, it is usually held that basic mechanisms of perception are independent from bodily influences except under special conditions of stress, arousal or emotion. We review here recent evidence suggesting a quite different picture, and explain how the neural monitoring of bodily signals could fill an important gap in our understanding of conscious vision. In the first part of the article, we argue that to understand how a conscious percept is formed, it is not sufficient to consider perceptual

mechanisms and higher cognitive functions such as attention and memory. A simple but core component of conscious perception, first-person perspective, has to be accounted for. In the second part, we present the hypothesis that first-person perspective derives from a subject-centered reference frame. This egocentric reference frame would be created by the neural monitoring of visceral organs. We review the recent experimental evidence supporting the hypothesis that to account for the statement "I have seen the stimulus", a neural model should not only describe mechanisms related to perceptual detection and decision making, but also propose a mechanism to explain where the "I" is coming from.

1. Perceptual consciousness: neither attention nor high-level cognition

Consciousness has long been conceived as an overarching cognitive function associated with high-level, finely tuned behavior. In an influential pioneering model (Baars, 1997), Baars defined consciousness as the spotlight of attention shining on the stage of working memory. In the following 20 years, a large number of experimental studies investigated the links between perceptual consciousness and attention and, to a lesser extent, working memory. In the section below, we review the arguments showing that those two high-level cognitive functions cannot explain perceptual consciousness. We argue that it is time to concentrate on another, core aspect of consciousness: first-person perspective.

1.1. Attention is distinct from consciousness

The idea that attention drives consciousness is appealing (Dehaene & Naccache, 2001; Dennett, 1991) and fits with numerous behavioral observations. For instance, attention facilitates detection (Solomon, 2004) and enhances perceived contrast (Carrasco, Ling, & Read, 2004). Conversely, in the absence of attention, salient stimuli may not be reported, as in inattentional blindness (Mack & Rock, 1998), change blindness (Simons & Levin, 1997), or during the attentional blink (Shapiro, Raymond, & Arnell, 1997). It thus seems that both attention and consciousness correspond to "perceiving better".

However, the fact that attention facilitates the report "I have seen the stimulus" that is the hallmark of visual consciousness does not imply that attention and consciousness are the same. Rather, attention and consciousness correspond to distinct neural mechanisms, that can both independently contribute to the final decision of reporting the presence or absence of the stimulus (Tallon-Baudry, 2012). This view is anchored in a growing number of experimental findings teasing apart the neural correlates of attention and consciousness and their behavioral consequences. In the past 10 years, the neural correlates of attention and consciousness could be repeatedly dissociated, either partly (Koivisto, Revonsuo, & Lehtonen, 2006; Watanabe et al., 2011; Webb, Igelström, Schurger, & Graziano, 2017) or fully (Schurger, Cowey, Cohen, Treisman, & Tallon-Baudry, 2008; Wyart & Tallon-Baudry, 2008; Wyart, Dehaene, & Tallon-Baudry, 2012). In parallel, a growing number of behavioral experiments

showed that attention can be triggered by unconscious cues or affect unconsciously processed targets (see e.g., Kentridge, Heywood, & Weiskrantz, 1999, 2004; Norman, Heywood, & Kentridge, 2013).

While the idea that attention and consciousness should not be conflated gained strength, it is still sometimes argued that attention is a gate for consciousness. If this were the case, attention should *always* facilitate consciousness, which is contradicted by three lines of findings. Firstly, the neural correlates of consciousness do not necessarily depend on attention (Koivisto et al., 2006; Wyart & Tallon-Baudry, 2008; Wyart et al., 2012). Secondly, attention and consciousness can have opposite behavioral consequences (van Boxtel, Tsuchiya, & Koch, 2010). Lastly, the conscious or unconscious status of the stimulus can determine the type of attention deployed, reversing the link of causality between attention and consciousness (Hsu, George, Wyart, & Tallon-Baudry, 2011).

1.2. The depth of unconscious processing

Other cognitive functions thought to be tightly associated with consciousness have seen their status revised. Neural markers of semantic information processing can be measured in response to unseen words (Luck, Vogel, & Shapiro, 1996). Unperceived stimuli can be maintained in short-term memory (King, Pescetelli, & Dehaene, 2016; Sergent et al., 2013; Soto, Mantyla, & Silvanto, 2011). Unconscious errors are detected by the anterior cingulate cortex (Hester, Foxe, Molholm, Shpaner, & Garavan, 2005). The frontal activations that were once thought to be markers of consciousness can contribute to unconscious and involuntary control (Lau & Passingham, 2007; Sumner et al., 2007; van Gaal, Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008) and are associated with behavioral report, rather than with conscious perception *per se* (Frässle, Sommer, Jansen, Naber, & Einhäuser, 2014).

Attention, memory, control, and semantic processing can thus operate on unconscious stimuli, and might be influenced by consciousness rather than driving it. It follows that i) unconscious processing is not limited to perceptual stages but can include high-level cognitive processing and ii) cognitive functions such as attention, memory and control, cannot explain conscious perception. It is thus time to reconsider the nature of perceptual consciousness.

1.3. First-person perspective as a core component of conscious experience

Experimentally, the hallmark of conscious vision is the report "I have seen the stimulus": it implies the existence of a subject, with his or her own first-person perspective. The point we want to make in this article is that to account for the statement "I have seen the stimulus", a neural model should not only describe mechanisms related to perceptual detection and decision making, but also propose a mechanism to explain where first-person perspective is coming from (Park & Tallon-Baudry, 2014).

What do we mean by subjective experience? It refers to the fact that a consciously experienced stimulus "*feels like something*" for the *subject* (Block, 2007; Chalmers, 1995; Nagel, 1974; Searle, 2000; Zahavi, 2003). A conscious visual experience is

thus defined by a content, the *something*, that is experienced from the *subject* first person-perspective. We propose that the combination of first-person perspective with visual content defines subjective experience (Fig. 1). It could be tempting to think that content alone can be sufficient to account for consciousness. For instance, an elaborated and meaningful sensory content combined with cognitive processing would by nature be conscious. However, as reviewed above, unconscious processing might give rise to an elaborated content, but this content is not consciously experienced. Hence, content alone does not trigger conscious experience. We thus propose that the core, central property of conscious experience pertains to the link between content and first-person perspective. It could be further argued that there is no need for a *specific* mechanism to account for first-person perspective, since *any* neural process taking place inside the brain could be labeled as belonging to the organism, as being expressed from the first-person perspective of this particular subject. However, high-level visual or cognitive processing can take place unconsciously, i.e., without first-person perspective. Hence, neural processes are not equipped by default with the first-person perspective necessary for conscious experience.

The necessity to consider subjective experience as resulting from the combination of two separate entities, content and first-person perspective, is not intuitive because in our own conscious experience, they all come together. Dissociations can only be revealed by clever experimental manipulations (Lau & Passingham, 2006) or in specific patients (Schurger et al., 2008), where subjective experience can be either present or absent, while content, as assessed by measures of objective performance, remains identical. Before

proposing a mechanism to implement first-person perspective, we will now examine the notion of subjective experience, since the existence of subjective experience has been questioned.

1.4. Subjective experience is not an illusion

The very existence of subjective experience has been denied (Dennett, 1991; O'Regan & Noe, 2001): subjective experience would be a post-hoc cognitive reconstruction rather than an immediate experience (Cohen & Dennett, 2011; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). Indeed, spontaneous subjective reports do not always survive scientific scrutiny. In change blindness studies for instance (Rensink, 2002; Simons & Levin, 1997), two images of the same visual scene differing by one item are presented in rapid succession, separated by a blank screen. Although the change can be massive, it often remains unnoticed. In other words, subjects have the feeling they see the entire visual scene — a rich subjective experience — but when probed they are unable to report accurately the details of the visual scene. We have previously (Campana & Tallon-Baudry, 2013) pointed out that while the experimental manipulation used in change blindness paradigm does indeed prevent the conscious perception of details, the subject may nevertheless truly perceive consciously the gist of a visual scene. In this view presented in the left part of Fig. 1 and based on the influential reverse hierarchy theory (Hochstein & Ahissar, 2002), local details would first be processed unconsciously in early visual areas and rapidly combined, in a feed-forward and automatic manner, into a global scene in higher-order visual areas. The result of
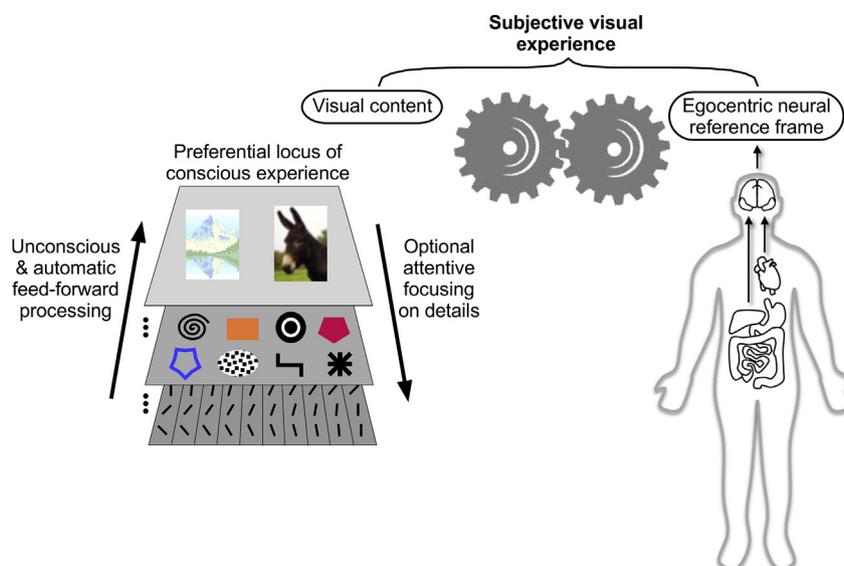

Fig. 1 — **Subjective visual experience arises from the integration of visual content with an egocentric reference frame based on the neural monitoring of visceral inputs. Left, schematic representation of information flow in the visual hierarchy. Visual processing begins with an unconscious and automatic wave of feed-forward processing, generating an integrated visual scene representation in higher-order visual areas. Conscious percepts are preferentially formed at this level. The conscious retrieval of details would require an additional and optional descending processing. Modified from Campana and Tallon-Baudry (2013). Right, the neural monitoring of ascending visceral inputs creates an egocentric reference frame, from which first-person perspective can develop. Modified from Park and Tallon-Baudry (2014). The integration of visual content and the egocentric reference frame gives rise to subjective visual experience.**

this first wave of computation is the gist of the scene and can be perceived consciously. The conscious perception of local details would require an additional and optional processing step proceeding from higher-order to lower-order areas.

The reverse hierarchy theory (Hochstein & Ahissar, 2002) was initially proposed to account for findings in perceptual learning but fits with experimental findings in the domain of perception and attention, such as the fact that attention proceeds from higher-order to lower-order visual areas (Buffalo, Fries, Landman, Liang, & Desimone, 2010; Luck, Chelazzi, Hillyard, & Desimone, 1997; Mehta, Ulbert, & Schroeder, 2000). However, the crucial prediction that conscious percepts are preferentially formed at a global level remained to be validated. To test this prediction, we designed new stimuli that are truly hierarchical, as opposed to the classic Navon's letters (Kimchi, 1992; Navon, 1977). Stimuli were composed of local and global information that could be varied independently, but where global information existed only by virtue of local information (Campana, Rebollo, Urai, Wyart, & Tallon-Baudry, 2016). We verified three key predictions. Firstly, participants respond faster when instructed to respond on global features than when instructed to respond on local features, showing that global information is easier to access than local details. Secondly, global information is computed by the brain irrespective of task demands, in line with the hypothesis that global information is automatically computed during the fast feed-forward sweep. Lastly, spontaneous reports were dominated by global information, in line with the hypothesis that conscious percepts are preferentially formed at a global level.

Conscious percepts are thus formed preferentially at the global level, and the conscious identification of local details is optional and time consuming, as could be predicted by the reverse hierarchy theory (Campana & Tallon-Baudry, 2013; Hochstein & Ahissar, 2002). It follows that this model offers an alternative and parsimonious explanation of the experimental findings in the change blindness paradigm: participants truly experience the gist of the scene but are prevented to further analyze local details because of time pressure and masking effects. Subjective experience is thus not an illusion, its properties derive from the architecture of the visual system. However, the architecture of the visual system by itself does not account for subjective experience. How is subjective experience implemented?

2.   Accounting for the "I" in the report "I have seen the stimulus"

2.1.   A subject-centered reference frame based on visceral inputs to account for first-person perspective

We have argued that subjective experience arises from the combination of content and first-person perspective. What type of signals could be good candidates for establishing first-person perspective? Signals originating in the body and relayed up to the brain could be self-specifying, since they could provide the brain with a definition of the organism. Bodily signals have been proposed to play a role in the emergence of subjectivity (Craig, 2009; Damasio, 2010; Gallagher, 2000; Zahavi, 2003). Experimental studies on agency (David,

Newen, & Vogeley, 2008) or bodily awareness (Blanke, 2012; Ferre, Lopez, & Haggard, 2014; Petkova et al., 2011) underline the role of sensory signals from the skin, limbs, joints or vestibular system. However, this type of bodily afferences cannot be sufficient. Locked-in patients, who are fully paralyzed and whose brain does not receive any feedback on bodily movement or action performance, are nevertheless conscious (Tononi & Koch, 2008).

The brain has other major sources of bodily information: the viscera, that include organs such as the heart and the gut, constitute another excellent but overlooked candidate. Both the gut and the heart are pacemakers, in the sense that they generate their own electrical activity. While the pacemaker activity of heart is well known, the discovery that the digestive tract is lined with a specific cell type that intrinsically and continuously generates a slow electrical rhythm is more recent (Furness, 2006; Kelly & Code, 1971; Sanders, Koh, & Ward, 2006).

The potential role of this *ascending* information, from viscera to the neocortex, has been little explored so far (Critchley & Harrison, 2013; Park & Tallon-Baudry, 2014; Richter, Babo-Rebelo, Schwartz, & Tallon-Baudry, 2017). Rather, most neuroimaging studies focused on *descending* commands from the central nervous system that regulate cardiac function (Beissner, Meissner, Bar, & Napadow, 2013; Thayer, Ahs, Fredrikson, Sollers, & Wager, 2012; Wong, Masse, Kimmerly, Menon, & Shoemaker, 2007), and control autonomic outputs such as skin conductance level (Fan et al., 2012; Nagai, Critchley, Featherstone, Trimble, & Dolan, 2004) or pupil diameter (Murphy, O'Connell, O'Sullivan, Robertson, & Balsters, 2014).

We propose to view both the gut and heart as ticking clocks that constantly send intrinsically-generated ascending information up to the central nervous system. They could thus provide a stable source of signals defining the organism as an entity at the neural level. The monitoring of those signals by the brain would thereby create an ego-centric, self-centered neural reference frame (Fig. 1, right) from which first-person perspective can develop (Park & Tallon-Baudry, 2014).

Note that in this mechanistic framework, ascending signals from visceral organ do not have to be consciously perceived. The role of visceral afferents is here purely mechanistic: visceral organs feed the brain with signals that become self-specifying when reaching the brain, and lay the basis for a self-centered referential that is not experienced as such. Importantly, visceral signals do not have to necessarily indicate a change in bodily state to contribute to conscious perception, as opposed to their proposed role in influential theories on the self (Craig, 2002; Damasio, 2010) or on emotion, such as the James-Lange theory or the somatic marker hypothesis (Damasio, 1996).

2.2.   Neural responses to heartbeats

Cognitive neuroscience is fortunately equipped with a powerful tool to study the neural monitoring of the heart: heartbeat-evoked responses (Schandry & Montoya, 1996). Heartbeat evoked responses are obtained by averaging electrophysiological data time-locked to heartbeats (Schandry, Sparrer, & Weitkunat, 1986). They can thus be considered as

equivalent to classical evoked responses obtained by time-locking data to the presentation of a visual or auditory stimulus, but in this instance, the stimulus is internal. It is also important to bear in mind the presence of an associated cardiac artefact, because sensors on the head pick up not only the neural response to heartbeats, but also the electro-cardiogram (Dirlich, Vogl, Plaschke, & Strian, 1997).

Heartbeat evoked responses share a number of properties similar to classical sensory responses. Heartbeat evoked responses are modulated by attention, e.g., when participants have to count the occurrence of their own heartbeats, and the amplitude of the heartbeat evoked response relates to accuracy at the heartbeat counting task (Canales-Johnson et al., 2015; Montoya, Schandry, & Muller, 1993; Pollatos & Schandry, 2004; Schandry et al., 1986). The amplitude of the heartbeat evoked response depends on participant's state as measured by alpha power (Luft & Bhattacharya, 2015) or by sleep stages (Lechinger, Heib, Gruber, Schabus, & Klimesch, 2015). Heartbeat evoked responses are also modulated by emotion (Couto et al., 2015; Fukushima, Terasawa, & Umeda, 2011).

A possible origin of neural responses to heartbeats is the neural discharge of the mechano-receptors in the heart wall, aortic arch, carotid sinus and cardiopulmonary veins (Armour & Ardell, 2004; Shepherd, 1985). Those mechanoreceptors discharge at each cardiac cycle in response to the mechanical distortions of the cardiac, aortic and carotid walls. This information is relayed, through the vagal and glosso-pharyngeal nerves, to the nucleus tractus solitarius, the parabrachial nucleus and to the thalamus. Those nuclei in turn target a number of structures: the amygdala, the cerebellum, hypothalamus, locus coeruleus and nucleus accumbens, but also cortical structures such as the primary and secondary somatosensory cortices, the insula or the ventral anterior cingulate/ventro-medial prefrontal cortex (vACC-vmPFC) (Critchley & Harrison, 2013; Henry, 2002; Pritchard, Hamilton, & Norgren, 2000; Van der Werf, Witter, & Groenewegen, 2002; Vogt, Pandya, & Rosene, 1987). In addition, a direct spinal projection could recently be traced up not only to insular and secondary somatosensory cortex, but also to cingulate motor areas in monkeys (Dum, Levinthal, & Strick, 2009). It is worth mentioning that the mechanisms and pathways underlying neural responses to heartbeats are so far poorly characterized. The mechano-receptor hypothesis is compatible with known physiology and anatomy, but it has not been investigated directly by recording, for instance, neural discharges in response to heartbeats in nucleus tractus solitarius and cortical target sites. Recent findings suggest that other mechanisms might also play a role. For instance, somatosensory signals from the skin in the heart region might also contribute (Khalsa, Rudrauf, Feinstein, & Tranel, 2009). It has also recently been discovered that local changes in blood pressure provoke changes in spontaneous neural firing in rodent slices (Kim, Ramiro Diaz, Iddings, & Filosa, 2016), suggesting that vascular events can directly affect local neural activity, at least *in vitro*.

While the insula has often been presented as the primary visceral area, anatomy suggests a much more distributed pattern, as described in the preceding paragraph. Functional results confirm a distribution of neural responses to heartbeats in several regions predicted by anatomical pathways. In human intra-cranial recordings, neural responses to heartbeats have been observed in the primary somatosensory cortex (Kern, Aertsen, Schulze-Bonhage, & Ball, 2013), the vACC-vmPFC and the insula (Babo-Rebelo, Wolpert, Adam, Hasboun, & Tallon-Baudry, 2016). Source reconstruction of magneto-encephalographic (MEG) and electro-encephalographic (EEG) data points to neural responses to heartbeats in vACC-vmPFC (Babo-Rebelo, Richter, & Tallon-Baudry, 2016; Park, Correia, Ducorps, & Tallon-Baudry, 2014) and mid-cingulate motor cortex (Park et al., 2016). Functional responses have also been observed in other regions not directly predicted by anatomical pathways, such as the right angular gyrus (Park et al., 2014) and posterior cingulate cortex (Babo-Rebelo, Richter et al., 2016; Babo-Rebelo, Wolpert et al., 2016).

2.3. Heartbeat-evoked response and perception of gratings at threshold

Neural responses to heartbeats before stimulus onset predict whether a faint stimulus at detection threshold will be perceived or missed. We (Park et al., 2014) presented participants with gratings at threshold for detection (Fig. 2A). At each trial, when participants fixated properly, the fixation mark turned red to indicate the beginning of the trial. After a variable delay, a grating could appear or not. Participants were simply required to indicate at the end of the trial whether they thought a stimulus had been presented or not. This classic paradigm typically requires a subjective judgment, referring to a visual experience that cannot be verified objectively by the experimenter: stimulus contrast was maintained constant, but participants saw the stimulus in some trials, and did not see it in others. To verify the reliability of participants' reports, catch trials, that did not contain any stimulus, were intermixed with stimulus-present trials. False alarms, i.e., reporting seeing a stimulus when nothing was presented, were rare (2.6% of stimulus-absent trials), indicating that participants did not answer randomly.

A classical approach to such an experiment would be to focus on perceptual processing and decision making. Here, we adopted a different perspective. Our hypothesis was that part of the fluctuations between the report 'I have seen the stimulus' (hits) and the report 'I have not seen anything' (misses) is related to fluctuations of the 'I' and would be indexed by fluctuations in neural responses to heartbeats. Note that participants did not express their response in those terms: they had to choose between "stimulus present" and "stimulus absent". Those reports are intrinsically subjective and refer to the participant's experience from his or her own perspective. We thus analyzed heartbeat evoked responses, measured with magneto-encephalography, before stimulus onset, during the warning interval (Fig. 2B). Heartbeat evoked responses were larger in hits than in misses or correct rejections. Differential heartbeat evoked responses originated from the ventral anterior cingulate cortex/ventro-medial prefrontal cortex region (vACC-vmPFC) as well as from the right inferior parietal lobule (rIPL). The difference between heartbeat evoked responses in hits and misses remained below statistical threshold in the right insula. The difference in neural
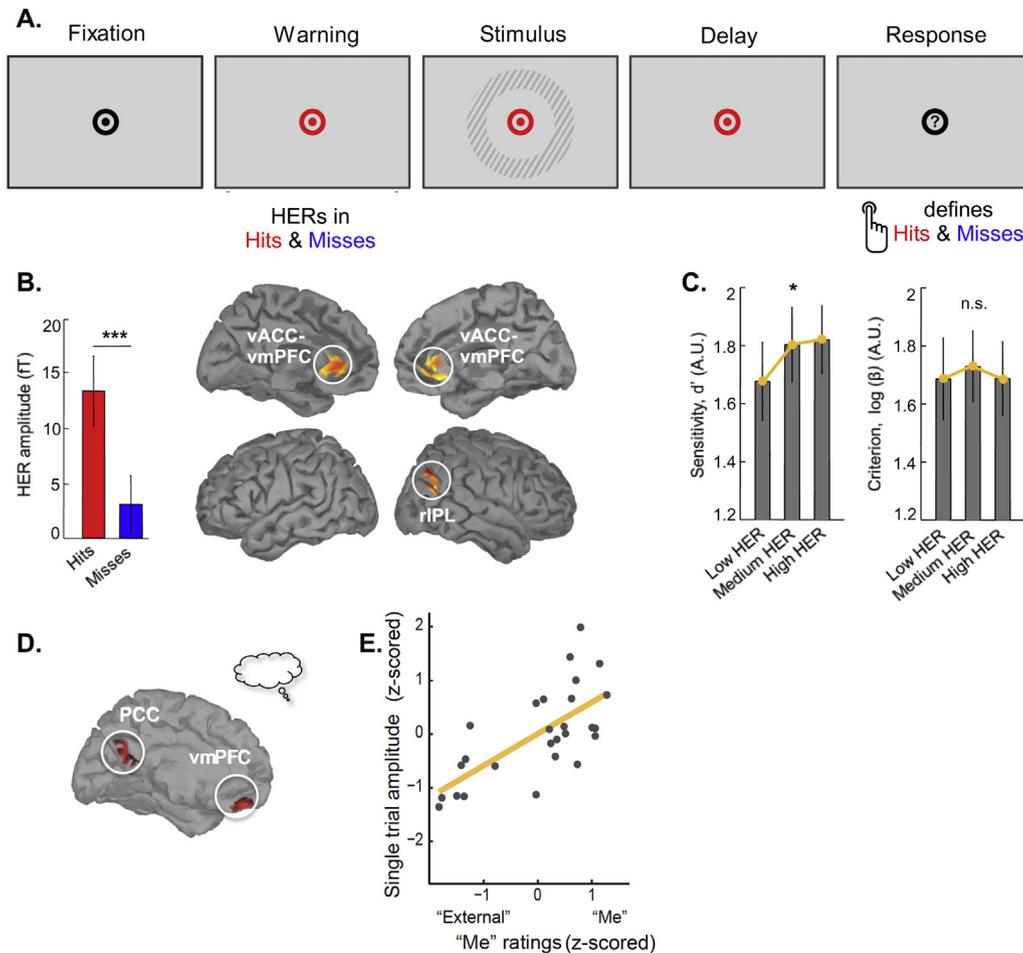
Fig. 2 — Neural responses to heartbeats and subjective experience. (A) Paradigm: participants fixate a central bull's eye that turns red to indicate the beginning of a trial. After a variable delay, a faint stimulus may or may not appear. After another variable delay, participants are prompted to report whether they have seen a stimulus or not. Participants' responses determine hits and misses. Heartbeat-evoked responses (HER) are computed as evoked responses to the heartbeats occurring in the warning interval. (B) HER amplitude in hits is larger than in misses, in vACC-vmPFC and rIPL. (C) HER amplitude increase corresponds to a significant increase in perceptual sensitivity (left), while decision criterion does not vary with HER amplitude (right). (D) Neural responses to heartbeats during spontaneous thoughts co-vary with the self-relatedness of the thought, in the midline nodes of the default network. (E) Correlation between single thought rating (thought oriented toward an external object or toward oneself) and the amplitude of neural response to heartbeats recorded intracranially from the vmPFC of an epileptic patient. Panels A—C modified from Park et al. (2014), panel D from Babo-Rebelo, Richter et al. (2016) and panel E from Babo-Rebelo, Wolpert et al. (2016). vACC: ventral anterior cingulate cortex; vmPFC: ventro-medial prefrontal cortex; rIPL: right inferior parietal lobule; PCC: posterior cingulate cortex.

responses to heartbeats occurred at a moment when there was no difference between hits and misses in none of the cardio-respiratory parameters we measured (electrocardiogram, heart rate, blood pressure, respiration rate and phase).

2.4. The heartbeat evoked response co-varies with perceptual sensitivity, not decision criterion nor arousal

The amplitude of heartbeat evoked responses before stimulus onset accounts for a modulation of the hit rate. But what does this modulation reflect? We first checked that the results did not reflect a global, non-specific difference in arousal state between hits and misses. There was no evidence that arousal differed between hits and misses before stimulus onset:

neither alpha power, nor pupil diameter, nor any of the measured cardio-respiratory parameters revealed any difference. In addition, the visual response to the warning stimulus was identical in hits and misses, suggesting that the larger responses to heartbeats in hits were not the result of a general, non-specific increase in cortical reactivity.

We then tested whether neural responses to heartbeats co-varied with sensitivity or criterion, and found clear-cut evidence that neural responses to heartbeats co-vary with perceptual sensitivity, not with decision criterion (Fig. 2C). In addition, the size of the effects of neural responses to heartbeats on sensitivity and hit rate were similar to the effects of spatial attention that we observed in previous experiments. We found that the amplitude of the neural response to

heartbeats accounts for 5 to 10 points of hit rate and for an 8% increase in sensitivity. Using similar gratings at threshold and manipulating spatial attention, we found in previous experiments that endogenous spatial attention modulates hit rate by 9 points (Wyart & Tallon-Baudry, 2008), and that exogenous spatial attention modulates sensitivity by 6% (Sergent et al., 2013). To summarize, neural activity obtained in response to heartbeats is used as sensory evidence in the final decision, and has as much influence on perceptual behavior as spatial attention would. But is it attention, or a neural marker of the "I"?

2.5. Neural responses to heartbeats index self-relatedness

Let us consider an attentional interpretation. It is known that when participants pay attention to their heartbeats, the amplitude of the heartbeat-evoked response increases (Schandry & Montoya, 1996). It seems unlikely that participants were counting or explicitly paying attention to their heartbeats while attempting at detecting a grating at threshold. Besides, interoceptive attention modulates activity in the insula (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004), whereas we found the largest differential responses to heartbeats in vACC-vmPFC and rIPL. However, it might be that participants' attention sometimes wandered away from the task and the screen, and turned inwards, to internal, task-unrelated thoughts. Such an "attention inward" situation would lead to both larger responses to heartbeats and a greater probability of missing the stimulus displayed on screen. This interpretation does not fit with the observed data: larger responses to heartbeats were associated with an increase in hit rate, not with an increase in miss rate as predicted by the "attention inward" interpretation.

If neural responses to heartbeats are not related to an attentional effect, how can they behave as sensory evidence? Neural responses to heartbeats co-vary with visual sensitivity but are neither directly related to visual processing, since it occurs in response to heartbeats outside the visual system, nor directly related to the attentional modulation of visual processing. To interpret this intriguing finding, it is useful to explicitly formulate the statement that corresponds to hits and misses. In response to the same physical stimulus, participants report "I have seen the grating" in hits, and "I have not seen anything in misses". The classical approach to determine the neural mechanisms leading to such a statement focuses on perceptual and decisional processes. We suggest here that neural responses to heartbeats might have something to do with the "I" part of the sentence, with the fact that this statement comes from a subject having an experience: saying "I have seen the stimulus" implies the existence of the first-person perspective of the experiencing subject (Park & Tallon-Baudry, 2014).

This interpretation is strengthened by a series of recent experiments pointing toward a direct link between cardiac inputs and the self. We ran an interrupted thought experiment, where participants could let their mind wander freely but were interrupted from time to time and asked to rate the self-relevance of the current thought. In two separate experiments using either MEG in healthy participants (Babo-Rebelo, Richter et al., 2016) or intracranial EEG in epileptic patients (Babo-Rebelo, Wolpert et al., 2016), we found that neural responses to heartbeats indexed self-relevance (Fig. 2D). Self-relevance was defined as thinking about oneself, such as in "I am thirsty", or as being the subject experiencing or acting in the thought, such as "I will go to the supermarket this evening". Participants were first trained to rate the self-relevance of written sentences, corresponding to thoughts reported verbally by a pilot group of participants. In a second step, participants were tested on a new set of written sentences. Inter-participant agreement on the ratings was high, showing that participants had understood how to use the self-relevance scales. We then proceeded with the recordings, while participants rated their own spontaneous thoughts.

Neural responses to heartbeats in vmPFC varied depending on whether the participant was thinking about himself/herself, or about an external object or event. This effect could be reproduced in intracranial recordings in vmPFC, with a significant correlation between the content of a single thought and the amplitude of neural responses to heartbeats in vmPFC during that thought (Fig. 2E). Neural responses in the posterior cingulate cortex co-varied with more experiential or agentive aspects of the self. This aspect of the self is pre-reflective, in the sense that one usually thinks about going to the supermarket without reflecting on oneself, but rather concentrating on the list of groceries. This form of pre-reflective self is always present in conscious mental life, but can be more (as in "I will call the travel agency") or less pronounced (as in "It's raining"). Note that in this interrupted thought paradigm, participants also rated their thoughts according to their emotional content. Neural responses to heartbeats did not vary with the emotional rating.

Neural responses to heartbeats do thus vary with self-relevance. In addition, in both the interrupted thought experiment and in the perception at threshold experiment, neural responses to heartbeats took place in the midline nodes of the default-network, that have been repeatedly associated with the self in fMRI (Qin & Northoff, 2011). Note that in those experiments (Babo-Rebelo, Richter et al., 2016; Babo-Rebelo, Wolpert et al., 2016; Park et al., 2014), the involvement of the insula was limited, remaining below statistical threshold. It might be that the insula is more involved in explicit interoception tasks, such as when participants are instructed to detect their heartbeats, and less so in the more automatic, unconscious monitoring process we targeted.

Another line of evidence for a link between neural responses to heartbeats and self-relatedness comes from studies on the bodily self. The experience of body ownership can be modulated by manipulating the synchrony between visual and tactile inputs. When those external stimuli are synchronized with the timing of heartbeats, illusions are enhanced (Aspell et al., 2013; Sel, Azevedo, & Tsakiris, in press; Suzuki, Garfinkel, Critchley, & Seth, 2013), and neural responses to heartbeats co-vary with illusion strength (Park et al., 2016; Sel et al., in press). The modulation of heartbeat-evoked responses related to the bodily self takes place in midline motor and premotor regions (cingulate motor areas, supplementary motor area) (Park et al., 2016).

3. Conclusion, limitations and future directions

We have shown on the one hand that the sensory representations most likely to give rise to a conscious percept have a global, integrated content, corresponding to high-level visual areas. On the other hand we have provided evidence that neural responses to heartbeats predict conscious perception by signaling a simple form of self, in particular in the default network. We propose that subjective experience results from the integration of visual content with the self-relatedness provided by neural responses to heartbeats (Fig. 1). Note that other signals might contribute to this egocentric reference frame, for instance the stomach that intrinsically generates an electrical rhythm that impacts brain dynamics (Richter et al., 2017), as well as proprioceptive and vestibular inputs (Blanke, 2012). Besides, while we focused here on perception, our proposal can in principle extend to any cognitive process that includes a subjective aspect, for instance subjective value in value-based decision-making, or emotional appraisal.

3.1. From correlation to causation

The evidence presented in this article is correlational: neural responses to heartbeats before stimulus onset correlate with visual sensitivity, neural responses to heartbeats correlate with self-relevance. These correlation could stem from a third factor influencing both heartbeat related neural processing, and visual subjective experience or self-relevance. Typical third-factor candidates are attention and arousal. We have argued above that attention to the external environment versus attention to the body is unlikely, and we could not detect changes in arousal state as measured with heart rate, pupil diameter or cortical alpha rhythm. Still, other factors may vary, notably neuromodulatory, hormonal or even immune factors. While there are interactions between heartbeat-evoked responses and cortisol for instance (Schulz et al., 2013), it remains to be determined whether such factors could vary fast enough to account for changes in perception from one trial to the next, when trials are separated by only a few seconds as in the experiment on perception at threshold.

Moving from correlation to causation is an important but notoriously difficult step. Two approaches can be considered: altering viscera-to-brain communication, or establishing a mechanistic model of integration of visceral and cognitive information to generate new predictions that can be tested experimentally.

It would be tempting to think that altering cardiac activity would be sufficient to test our hypothesis. However, in our experiments, cardiac parameters did not vary; rather, neural responses to heartbeats varied in the absence of measured changes in cardio-respiratory parameters. While fluctuations in some cardiac parameters may not have been adequately measured, this suggests that neural variability, rather than cardiac variability, is crucial. To probe whether the neural monitoring of visceral signals plays causal role, the critical targets are thus the viscera-to-brain pathways and the central monitoring of visceral signals. Ascending pathways, from viscera to brain, can follow several routes (vagal and glossopharyngeal, spinal), that are unlikely to be all severed in patients. In addition, all pathways convey information in both directions, from viscera to brain and from brain to viscera. It follows that neither vagus nerve stimulation nor vagotomy specifically target ascending pathways. Besides, those interventions leave both the spinal and glossopharyngeal pathways intact. Still, it is worth mentioning that bariatric surgery, that usually implies vagotomy, increases the risk of self-harm behavior (Bhatti et al., 2016; Tindle et al., 2010), which may point to an underlying disturbance of the self.

According to our hypothesis, focal lesions affecting neural relays of visceral information should affect first-person perspective. A key relay structure in the pons, the nucleus tractus solitarius can sometimes be lesioned bilaterally, with the patient undergoing not only marked fluctuations in blood pressure, but also an "impaired mental status", with "episodes of disorientation" (Biaggioni, Whetsell, Jobe, & Nadeau, 1994). However, the lesion included other structures, such as the substantia nigra for instance, and it seems unlikely that a pure bilateral lesion of the nucleus tractus solitarius can occur in humans. Besides, as mentioned earlier, other pathways have to be considered, that bypass the nucleus tractus solitarius: direct spinal projections to the insula, secondary somatosensory cortex, and cingulate motor areas (Dum et al., 2009), somatosensory information from the skin on the chest (Khalsa et al., 2009), putative direct vascular influence on local neural activity within the central nervous system (Kim et al., 2016). The multiplicity of heart-to-brain pathways underlines the importance of those pathways for life-supporting physiological interactions, and maybe also first-person experience, but implies that the suppression of all afferent cardiovascular information is probably difficult to achieve in humans, where subjective reports can best be probed.

Another promising option is to establish a mechanism of integration of visual information and visceral information, and then selectively perturb it. One needs to identify when and how sensory evidence in the visual system is combined with the self-related information carried by neural responses to heartbeats in the default network. This question taps onto the general issue of large-scale information integration in the brain, that is far from being solved. Still, if a specific integration mechanism, be it convergence in a given area or oscillatory synchrony at a given frequency between two areas, were identified, this mechanism could be selectively disrupted using transcranial magnetic stimulation for instance.

3.2. Links with other experimental findings

We have reviewed evidence relating neural responses to heartbeats to the signaling of self-relatedness. Other types of cardiac-related effects have been described, called cardiac cycle effects or cardiac synchrony effects. Cardiac activity occurs in cycles of contraction and relaxation of the atria and ventricles, as reflected by the peaks of the electrocardiogram (ECG). Between the R and T peaks of the ECG, blood pressure is maximal (systole), as opposed to later in the cardiac cycle where blood pressure decreases (diastole). Supra-threshold stimuli presented during systole versus diastole [for review, (Park & Tallon-Baudry, 2014); see also (Salomon et al., 2016)]

are detected at different speeds in simple reaction time tasks and generate sensory evoked responses of different sizes. Oculo-motor behavior also depends on the cardiac cycle, with an excess of micro-saccades and fixational drifts at short latencies after the R peak, during systole (Ohl, Wohltat, Kliegl, Pollatos, & Engbert, 2016). However, peri-threshold stimuli tell a different story. The detection of neither visual (Elliott & Graf, 1972) nor auditory (Delfini & Campos, 1972; Velden & Juris, 1975) stimuli at threshold depend on the timing of the stimulus with respect to the cardiac cycle. In line with those findings, in our experiment on vision at threshold (Park et al., 2014), the perceived or unperceived fate of the stimulus did not depend on its position in the cardiac cycle. It remains to be determined whether the self-relatedness expressed by neural responses to heartbeats and the cardiac-cycle effects can be reconciled in the same framework.

4. Conclusion

We propose here that conscious visual experience results from the integration of visual content with an egocentric, self-related reference frame based on the neural monitoring of visceral organs (Fig. 1). This proposal accounts for both the "I-related" and vision-related aspects of the report "I have seen the stimulus" that is the hallmark of visual consciousness. While recent experimental evidence support our proposal, the mechanism integrating visual information and neural responses to heartbeats, that are encoded in distinct brain areas, remains to determined. In this framework, attention is not the selection process that brings some items to the conscious mind, but rather a prioritization computational process that can operate on, or be triggered by, either consciously perceived or unconsciously processed stimuli. It follows from our proposal that even for a "cold" process such as vision at threshold, the fact that the brain is embedded into a body matters.

Acknowledgements

REFERENCES

Armour, J. A., & Ardell, J. L. (2004). Basic and clinical neurocardiology. Oxford University Press.

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.

Baars, B. J. (1997). In the theatre of consciousness: Global workspace theory, a rigorous scientific theory of consciousness. Journal of Consciousness Studies, 4, 292−309.

Babo-Rebelo, M., Richter, C. G., & Tallon-Baudry, C. (2016a). Neural responses to heartbeats in the default network encode the self in spontaneous thoughts. Journal of Neuroscience, 36, 5200−5216.

Babo-Rebelo, M., Wolpert, N., Adam, C., Hasboun, D., & Tallon-Baudry, C. (2016b). Is the cardiac monitoring function related to the self in both the default network and right anterior insula? Philosophical Transactions of the Royal Society B, 371.

Beissner, F., Meissner, K., Bar, K. J., & Napadow, V. (2013). The autonomic brain: An activation likelihood estimation meta-analysis for central processing of autonomic function. The Journal of Neuroscience, 33, 10503−10511.

Bhatti, J. A., Nathens, A. B., Thiruchelvam, D., Grantcharov, T., Goldstein, B. I., & Redelmeier, D. A. (2016). Self-harm emergencies after bariatric surgery: A population-based cohort study. JAMA Surgery, 151, 226−232.

Biaggioni, I., Whetsell, W. O., Jobe, J., & Nadeau, J. H. (1994). Baroreflex failure in a patient with central nervous system lesions involving the nucleus tractus solitarii. Hypertension, 23, 491−495.

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. Nature Reviews. Neuroscience, 13, 556−571.

Block, N. (2007). Consciousness, accessibility, and the mesh between psychology and neuroscience. The Behavioral and Brain Sciences, 30, 481−499. discussion 499−548.

van Boxtel, J. J., Tsuchiya, N., & Koch, C. (2010). Opposing effects of attention and consciousness on afterimages. Proceedings of the National Academy of Sciences of the United States of America, 107, 8883−8888.

Buffalo, E. A., Fries, P., Landman, R., Liang, H., & Desimone, R. (2010). A backward progression of attentional effects in the ventral stream. Proceedings of the National Academy of Sciences of the United States of America, 107, 361−365.

Campana, F., Rebollo, I., Urai, A., Wyart, V., & Tallon-Baudry, C. (2016). Conscious vision proceeds from global to local content in goal-directed tasks and spontaneous vision. The Journal of Neuroscience, 36, 5200−5213.

Campana, F., & Tallon-Baudry, C. (2013). Anchoring visual subjective experience in a neural model: The coarse vividness hypothesis. Neuropsychologia, 51, 1050−1060.

Canales-Johnson, A., Silva, C., Huepe, D., Rivera-Rei, A., Noreika, V., Garcia Mdel, C., et al. (2015). Auditory feedback differentially modulates behavioral and neural markers of objective and subjective performance when tapping to your heartbeat. Cerebral Cortex, 25, 4490−4503.

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. Nature Neuroscience, 7, 308−313.

Chalmers, D. J. (1995). Facing up to the problem of consciousness. Journal of Consciousness Studies, 2, 200−219.

Cohen, M. A., & Dennett, D. C. (2011). Consciousness cannot be separated from function. Trends in Cognitive Sciences, 15, 358−364.

Couto, B., Adolfi, F., Velasquez, M., Mesow, M., Feinstein, J., Canales-Johnson, A., et al. (2015). Heart evoked potential triggers brain responses to natural affective scenes: A preliminary study. Autonomic Neuroscience: Basic & Clinical, 193, 132−137.

Craig, A. D. (2002). How do you feel? Interoception: the sense of the physiological condition of the body. Nature Reviews. Neuroscience, 3, 655−666.

Craig, A. D. (2009). How do you feel-now? The anterior insula and human awareness. Nature Reviews. Neuroscience, 10, 59−70.

Critchley, H. D., & Harrison, N. A. (2013). Visceral influences on brain and behavior. Neuron, 77, 624−638.

Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. Nature Neuroscience, 7, 189−195.

Damasio, A. R. (1996). The somatic marker hypothesis and the possible functions of the prefrontal cortex. Philosophical Transactions of the Royal Society B: Biological Sciences, 351, 1413−1420.

Damasio, A. (2010). *Self comes to mind: Constructing the conscious brain*. New York: Pantheon Books.

David, N., Newen, A., & Vogeley, K. (2008). The "sense of agency" and its underlying cognitive and neural mechanisms. *Consciousness and Cognition, 17*, 523–534.

Dehaene, S., Changeux, J. P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: A testable taxonomy. *Trends in Cognitive Sciences, 10*, 204–211.

Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition, 79*, 1–37.

Delfini, L. F., & Campos, J. J. (1972). Signal detection and the "cardiac arousal cycle". *Psychophysiology, 9*, 484–491.

Dennett, D. C. (1991). *Consciousness explained*. Boston, MA: Little, Brown & Co.

Dirlich, G., Vogl, L., Plaschke, M., & Strian, F. (1997). Cardiac field effects on the EEG. *Electroencephalography and Clinical Neurophysiology, 102*, 307–315.

Dum, R. P., Levinthal, D. J., & Strick, P. L. (2009). The spinothalamic system targets motor and sensory areas in the cerebral cortex of monkeys. *The Journal of Neuroscience, 29*, 14223–14235.

Elliott, R., & Graf, V. (1972). Visual sensitivity as a function of phase of cardiac cycle. *Psychophysiology, 9*, 357–361.

Fan, J., Xu, P., Van Dam, N. T., Eilam-Stock, T., Gu, X., Luo, Y. J., et al. (2012). Spontaneous brain activity relates to autonomic arousal. *The Journal of Neuroscience, 32*, 11176–11186.

Ferre, E. R., Lopez, C., & Haggard, P. (2014). Anchoring the self to the body: Vestibular contribution to the sense of self. *Psychological Science, 25*, 2106–2108.

Frässle, S., Sommer, J., Jansen, A., Naber, M., & Einhäuser, W. (2014). Binocular rivalry: Frontal activity relates to introspection and action but not to perception. *Journal of Neuroscience, 34*, 1738–1747.

Fukushima, H., Terasawa, Y., & Umeda, S. (2011). Association between interoception and empathy: Evidence from heart-beat evoked brain potential. *International Journal of Psychophysiology, 79*, 259–265.

Furness, J. B. (2006). *The enteric nervous system*. Blackwell Publishing.

van Gaal, S., Ridderinkhof, K. R., Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. (2008). Frontal cortex mediates unconsciously triggered inhibitory control. *The Journal of Neuroscience, 28*, 8053–8062.

Gallagher, S. (2000). Philosophical conceptions of the self: Implications for cognitive science. *Trends in Cognitive Sciences, 4*, 14–21.

Henry, T. R. (2002). Therapeutic mechanisms of vagus nerve stimulation. *Neurology, 59*, S3–S14.

Hester, R., Foxe, J. J., Molholm, S., Shpaner, M., & Garavan, H. (2005). Neural mechanisms involved in error processing: A comparison of errors made with and without awareness. *NeuroImage, 27*, 602–608.

Hochstein, S., & Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron, 36*, 791–804.

Hsu, S. M., George, N., Wyart, V., & Tallon-Baudry, C. (2011). Voluntary and involuntary spatial attentions interact differently with awareness. *Neuropsychologia, 49*, 2465–2474.

Kelly, K. A., & Code, C. F. (1971). Canine gastric pacemaker. *American Journal of Physiology, 220*, 112–118.

Kentridge, R. W., Heywood, C. A., & Weiskrantz, L. (1999). Attention without awareness in blindsight. *Proceedings of the Royal Society of London Series B: Biological Sciences, 266*, 1805–1811.

Kentridge, R. W., Heywood, C. A., & Weiskrantz, L. (2004). Spatial attention speeds discrimination without awareness in blindsight. *Neuropsychologia, 42*, 831–835.

Kern, M., Aertsen, A., Schulze-Bonhage, A., & Ball, T. (2013). Heart cycle-related effects on event-related potentials, spectral power changes, and connectivity patterns in the human ECoG. *NeuroImage, 81C*, 178–190.

Khalsa, S. S., Rudrauf, D., Feinstein, J. S., & Tranel, D. (2009). The pathways of interoceptive awareness. *Nature Neuroscience, 12*, 1494–1496.

Kimchi, R. (1992). Primacy of wholistic processing and global/local paradigm: A critical review. *Psychological Bulletin, 112*, 24–38.

Kim, K. J., Ramiro Diaz, J., Iddings, J. A., & Filosa, J. A. (2016). Vasculo-neuronal coupling: Retrograde vascular communication to brain neurons. *The Journal of Neuroscience, 36*, 12624–12639.

King, J. R., Pescetelli, N., & Dehaene, S. (2016). Brain mechanisms underlying the brief maintenance of seen and unseen sensory information. *Neuron, 92*, 1122–1134.

Koivisto, M., Revonsuo, A., & Lehtonen, M. (2006). Independence of visual awareness from the scope of attention: An electrophysiological study. *Cerebral Cortex, 16*, 415–424.

Lau, H. C., & Passingham, R. E. (2006). Relative blindsight in normal observers and the neural correlate of visual consciousness. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 18763–18768.

Lau, H. C., & Passingham, R. E. (2007). Unconscious activation of the cognitive control system in the human prefrontal cortex. *The Journal of Neuroscience, 27*, 5805–5811.

Lechinger, J., Heib, D. P., Gruber, W., Schabus, M., & Klimesch, W. (2015). Heartbeat-related EEG amplitude and phase modulations from wakefulness to deep sleep: Interactions with sleep spindles and slow oscillations. *Psychophysiology, 52*, 1441–1450.

Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology, 77*, 24–42.

Luck, S. J., Vogel, E. K., & Shapiro, K. L. (1996). Word meaning can be accessed but not reported during the attentional blink. *Nature, 383*, 616–618.

Luft, C. D., & Bhattacharya, J. (2015). Aroused with heart: Modulation of heartbeat evoked potential by arousal induction and its oscillatory correlates. *Scientific Reports, 5*, 15717.

Mack, A., & Rock, I. (1998). *Inattentional blindness*. Cambridge, Massachussets: MIT Press.

Mehta, S. D., Ulbert, I., & Schroeder, C. E. (2000). Intermodal selective attention in monkeys. I: Distribution and timing of effects across visual areas. *Cerebral Cortex, 10*, 343–358.

Montoya, P., Schandry, R., & Muller, A. (1993). Heartbeat evoked potentials (HEP): Topography and influence of cardiac awareness and focus of attention. *Electroencephalography and Clinical Neurophysiology, 88*, 163–172.

Murphy, P. R., O'Connell, R. G., O'Sullivan, M., Robertson, I. H., & Balsters, J. H. (2014). Pupil diameter covaries with BOLD activity in human locus coeruleus. *Human Brain Mapping, 35*, 4140–4154.

Nagai, Y., Critchley, H. D., Featherstone, E., Trimble, M. R., & Dolan, R. J. (2004). Activity in ventromedial prefrontal cortex covaries with sympathetic skin conductance level: A physiological account of a "default mode" of brain function. *NeuroImage, 22*, 243–251.

Nagel, T. (1974). What is it like to be a bat? *The Philosophical Review, 83*, 435–450.

Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology, 9*, 353–383.

Norman, L. J., Heywood, C. A., & Kentridge, R. W. (2013). Object-based attention without awareness. *Psychological Science, 24*, 836–843.

O'Regan, J. K., & Noe, A. (2001). A sensorimotor account of vision and visual consciousness. *The Behavioral and Brain Sciences, 24*, 939–973. discussion 973–1031.

Ohl, S., Wohltat, C., Kliegl, R., Pollatos, O., & Engbert, R. (2016). Microsaccades are coupled to heartbeat. *The Journal of Neuroscience, 36*, 1237–1241.

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. *The Journal of Neuroscience, 36*, 8453—8460.

Park, H. D., Correia, S., Ducorps, A., & Tallon-Baudry, C. (2014). Spontaneous fluctuations in neural responses to heartbeats predict visual detection. *Nature Neuroscience, 17*, 612—618.

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*, 20130208.

Petkova, V. I., Bjornsdotter, M., Gentile, G., Jonsson, T., Li, T. Q., & Ehrsson, H. H. (2011). From part- to whole-body ownership in the multisensory brain. *Current Biology: CB, 21*, 1118—1122.

Pollatos, O., & Schandry, R. (2004). Accuracy of heartbeat perception is reflected in the amplitude of the heartbeat-evoked brain potential. *Psychophysiology, 41*, 476—482.

Pritchard, T. C., Hamilton, R. B., & Norgren, R. (2000). Projections of the parabrachial nucleus in the old world monkey. *Experimental Neurology, 165*, 101—117.

Qin, P., & Northoff, G. (2011). How is our self related to midline regions and the default-mode network? *NeuroImage, 57*, 1221—1233.

Rensink, R. A. (2002). Change detection. *Annual Review of Psychology, 53*, 245—277.

Richter, C. G., Babo-Rebelo, M., Schwartz, D., & Tallon-Baudry, C. (2017). Phase-amplitude coupling at the organism level: The amplitude of spontaneous alpha rhythm fluctuations varies with the phase of the infra-slow gastric basal rhythm. *NeuroImage, 146*, 951—958.

Salomon, R., Ronchi, R., Donz, J., Bello-Ruiz, J., Herbelin, B., Martet, R., et al. (2016). The insula mediates access to awareness of visual stimuli presented synchronously to the heartbeat. *The Journal of Neuroscience, 36*, 5115—5127.

Sanders, K. M., Koh, S. D., & Ward, S. M. (2006). Interstitial cells of Cajal as pacemakers in the gastrointestinal tract. *Annual Review of Physiology, 68*, 307—343.

Schandry, R., & Montoya, P. (1996). Event-related brain potentials and the processing of cardiac activity. *Biological Psychology, 42*, 75—85.

Schandry, R., Sparrer, B., & Weitkunat, R. (1986). From the heart to the brain: A study of heartbeat contingent scalp potentials. *International Journal of Neuroscience, 30*, 261—275.

Schulz, A., Strelzyk, F., Ferreira de Sa, D. S., Naumann, E., Vogele, C., & Schachinger, H. (2013). Cortisol rapidly affects amplitudes of heartbeat-evoked brain potentials—implications for the contribution of stress to an altered perception of physical sensations? *Psychoneuroendocrinology, 38*, 2686—2693.

Schurger, A., Cowey, A., Cohen, J. D., Treisman, A., & Tallon-Baudry, C. (2008). Distinct and independent correlates of attention and awareness in a hemianopic patient. *Neuropsychologia, 46*, 2189—2197.

Searle, J. R. (2000). Consciousness. *Annual Review of Neuroscience, 23*, 557—578.

Sel, A., Azevedo, R. T., & Tsakiris, M. (2017). Heartfelt self: Cardio-visual integration affects self-face recognition and interoceptive cortical processing. *Cerebral Cortex* (in press).

Sergent, C., Wyart, V., Babo-Rebelo, M., Cohen, L., Naccache, L., & Tallon-Baudry, C. (2013). Cueing attention after the stimulus is gone can retrospectively trigger conscious perception. *Current Biology: CB, 23*, 150—155.

Shapiro, K. L., Raymond, J. E., & Arnell, K. M. (1997). The attentional blink. *Trends in Cognitive Sciences, 1*, 291—296.

Shepherd, J. T. (1985). The heart as a sensory organ. *Journal of the American College of Cardiology, 5*, 83B—87B.

Simons, D. J., & Levin, D. T. (1997). Change blindness. *Trends in Cognitive Sciences, 1*, 261—267.

Solomon, J. A. (2004). The effect of spatial cues on visual sensitivity. *Vision Research, 44*, 1209—1216.

Soto, D., Mantyla, T., & Silvanto, J. (2011). Working memory without consciousness. *Current Biology: CB, 21*, R912—R913.

Sumner, P., Nachev, P., Morris, P., Peters, A. M., Jackson, S. R., Kennard, C., et al. (2007). Human medial frontal cortex mediates unconscious inhibition of voluntary action. *Neuron, 54*, 697—711.

Suzuki, K., Garfinkel, S. N., Critchley, H. D., & Seth, A. K. (2013). Multisensory integration across exteroceptive and interoceptive domains modulates self-experience in the rubber-hand illusion. *Neuropsychologia, 51*, 2909—2917.

Tallon-Baudry, C. (2012). On the neural mechanisms subserving consciousness and attention. *Frontiers in Psychology, 2*, 397.

Thayer, J. F., Ahs, F., Fredrikson, M., Sollers, J. J., 3rd, & Wager, T. D. (2012). A meta-analysis of heart rate variability and neuroimaging studies: Implications for heart rate variability as a marker of stress and health. *Neuroscience and Biobehavioral Reviews, 36*, 747—756.

Tindle, H. A., Omalu, B., Courcoulas, A., Marcus, M., Hammers, J., & Kuller, L. H. (2010). Risk of suicide after long-term follow-up from bariatric surgery. *The American Journal of Medicine, 123*, 1036—1042.

Tononi, G., & Koch, C. (2008). The neural correlates of consciousness — an update. *Annals of the New York Academy of Sciences, 1124*, 239—261.

Van der Werf, Y. D., Witter, M. P., & Groenewegen, H. J. (2002). The intralaminar and midline nuclei of the thalamus. Anatomical and functional evidence for participation in processes of arousal and awareness. *Brain Research Reviews, 39*, 107—140.

Velden, M., & Juris, M. (1975). Perceptual performance as a function of intra-cycle cardiac activity. *Psychophysiology, 12*, 685—692.

Vogt, B. A., Pandya, D. N., & Rosene, D. L. (1987). Cingulate cortex of the rhesus monkey: I. Cytoarchitecture and thalamic afferents. *The Journal of Comparative Neurology, 262*, 256—270.

Watanabe, M., Cheng, K., Murayama, Y., Ueno, K., Asamizuya, T., Tanaka, K., et al. (2011). Attention but not awareness modulates the BOLD signal in the human V1 during binocular suppression. *Science, 334*, 829—831.

Webb, T. W., Igelström, K. M., Schurger, A., & Graziano, M. (2017). Cortical networks involved in visual awareness independent of visual attention. *Proceedings of the National Academy of Sciences of the United States of America, 113*, 13923—13928.

Wong, S. W., Masse, N., Kimmerly, D. S., Menon, R. S., & Shoemaker, J. K. (2007). Ventral medial prefrontal cortex and cardiovagal control in conscious humans. *NeuroImage, 35*, 698—708.

Wyart, V., Dehaene, S., & Tallon-Baudry, C. (2012). Early dissociation between neural signatures of endogenous spatial attention and perceptual awareness during visual masking. *Frontiers in Human Neuroscience, 6*.

Wyart, V., & Tallon-Baudry, C. (2008). A neural dissociation between visual awareness and spatial attention. *The Journal of Neuroscience, 28*, 2667—2679.

Zahavi, D. (2003). *Husserl's phenomenology*. Stanford, California: Stanford University Press.