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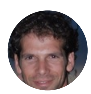

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REVIEW

Visual consciousness and bodily self-consciousness

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Purpose of review
In recent years, consciousness has become a central topic in cognitive neuroscience. This review focuses on the relation between bodily self-consciousness – the feeling of being a subject in a body – and visual consciousness – the subjective experience associated with the perception of visual signals.

Recent findings
Findings from clinical and experimental work have shown that bodily self-consciousness depends on specific brain networks and is related to the integration of signals from multiple sensory modalities including vision. In addition, recent experiments have shown that visual consciousness is shaped by the body, including vestibular, tactile, proprioceptive, and motor signals.

Summary
Several lines of evidence suggest reciprocal relationships between vision and bodily signals, indicating that a comprehensive understanding of visual and bodily self-consciousness requires studying them in unison.

Keywords
bodily illusions, bodily self-consciousness, body ownership, embodiment, visual consciousness

INTRODUCTION

Brain activity causes subjective experience. It 'feels like something' to see a rose, and this feeling is qualitatively different from touching or smelling it and seeing an orchid [2]. For the past 20 years, there have been considerable efforts to describe the so-called 'neural correlates of consciousness' (NCC), which is the minimal set of neuronal events and mechanisms sufficient for a specific conscious percept [3]. The NCC have traditionally been sketched using a contrastive approach, whereby neural and cognitive responses elicited by perceived vs. unperceived stimuli are compared [4]. Theories that emerged from this approach state that consciousness requires, for example, information integration throughout the brain, involving mechanisms such as short-range [5] or long-range [6] feedback connections, or neural synchrony [7]. Most data and greatest detail regarding the neural correlates of perceptual consciousness arguably comes from visual psychophysics and brain imaging, where an arsenal of techniques allows the display of subliminal, invisible images in various manners [8▪,9]. Although these studies led to a better understanding of visual consciousness, the interaction of conscious and unconscious vision with other senses remains to be explored, which is crucial considering the multisensory nature of perception [10▪]. One can note that the sense of touch constitutes a promising model to study perceptual consciousness, considering its rather 'primitive' attributes, with both phylogenetic and ontogenetic roots preceding those of vision [1]. Accordingly, its functional organization and the computational steps underlying tactile consciousness are likely to be simpler compared to vision, and therefore more accessible to empirical investigations and theoretical interpretations.

Moreover, subjective aspects of perceptual consciousness (or qualia) have remained elusive in models of visual consciousness or continue to be associated with most disagreement among consciousness researchers and philosophers (for a recent example, see [11] and the related commentary [12]). Notably, there is no consensus as to whether a theory of visual consciousness should explain how phenomenal experience arises from physical events in the brain (the hard problem or

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KEY POINTS

- BSC stems from the integration of visual, tactile, proprioceptive, and vestibular signals.
- Visual perception reflects the product of integration with other sensory signals, including bodily signals.
- Multisensory integration occurs unconsciously, prior to conscious access, potentially resulting in phenomenal unity.

phenomenal consciousness) or rather characterize the mechanisms supporting cognitive access to consciousness (the easy problem or access consciousness) [13,14].

Furthermore, the observer who is the subject of conscious experience is generally not accounted for by these models of visual consciousness. Yet, a fundamental property of consciousness is its link with the self: the subject of conscious experience. The 'rose' that is seen, felt, or smelled is bounded to the 'I' of subjective experience, is felt by somebody, the self or subject of experience. This sense of self and its close link to neural body representation has been termed bodily self-consciousness (BSC) and has been a target of recent research [15]. BSC is commonly thought to involve self-identification (the experience of owning 'my' body), self-location (the experience of where 'I' am in space), and first-person perspective (the experience from where 'I' perceive the world) [16]. The scientific study of BSC has expanded over the last years, benefiting from the examination of neurological patients with altered states of BSC and virtual reality coupled with robotics to induce well controlled states in the research laboratory. For instance, altered states of BSC of neurological origin may be experienced from a location and perspective that are not centered on the physical body of the observer, but are nevertheless characterized by an experience of the visual world that is complete, differentiated, and integrated. In these so-called out-of-body experiences, the subject or center of consciousness is experienced as being displaced to an elevated and down-looking first-person perspective and location [17]. The 'rose' on a table in the field of view of the observer would thus still be perceived consciously during an out-of-body experience, but seen from a distanced and elevated location and first-person perspective (see below for recent studies in healthy subjects on BSC).

Do visual consciousness and BSC relate to each other? It has been argued that (visual) perception is by essence embodied within an egocentric, body-centered framework ([18,19]; but see [20] for a critical discussion about embodiment and consciousness). Much less is known about whether and how bodily processing impacts visual consciousness and how visual processing relates to BSC, as each aspect of consciousness has mostly been studied in relative separation. However, consciousness at the phenomenal level is an integrated and unitary experience: integrated as multiple sensory streams are seamlessly joined, and unitary as consciousness is experienced by a singular self [21]. Interestingly, integrated visual consciousness may break down in neurological patients with simultagnosia reporting the inability to perceive more than one object at once [22], while unitary consciousness may break down in neurological patients with heautoscopy reporting two simultaneous, but distinct, centers of consciousness [23▪]. Here, we review empirical results documenting the interplay between visual consciousness and BSC, pointing toward the importance of their combined investigation for a fuller understanding of consciousness.

INFLUENCES OF VISION ON BODILY SELF-CONSCIOUSNESS

There is now compelling evidence that BSC involves the cortical integration of different signals from the external environment (exteroception: visual, auditory, and tactile senses, see [24] for a review) and the body (vestibular and proprioceptive senses; interoceptive cardiac and respiratory signals, see [25]). Data from neurological patients with altered states of BSC were associated with deficits in multisensory integration and involved the right temporoparietal cortex with abnormal self-location and first-person perspective, but unitary consciousness [26], and the left insula with abnormal self-location, first-person perspective, and the loss of unitary consciousness [23▪]. Recent experimental paradigms in healthy participants employed multisensory conflicts, reporting modulations of the three aforementioned main aspects of BSC. For example, in the well known rubber-hand illusion, participants viewing an artificial hand being stroked in synchrony with their own occluded hand (placed at a different position) experience that the artificial hand belongs to their own body, and perceive their hand as shifted toward the artificial hand's position [27]. This illusion is thought to stem from visual capture of the multisensory conflict between visual, proprioceptive, and tactile stimuli that are temporally synchronous (visual, tactile) but spatially incongruent (visual, proprioceptive): what is seen (an artificial hand being stroked) does not match with what is felt (one's hand being stroked). With temporal delay between the visual and tactile stimulation, the illusion and shift in perceived hand position vanish (but see [28]). In recent years, the development of video, virtual reality, and robotic devices have allowed researchers to extend the study of limb ownership to full-body ownership and other aspects of BSC [15]. In the so-called full-body (or 'out-of-body') illusion (FBI), multisensory conflicts modulate not only limb ownership but also ownership/self-identification as well as self-location for the full body, mimicking neurological conditions such as out-of-body experiences, heautoscopy, and related altered states of BSC [29,30]. Typically, participants view their filmed own body (a 'virtual body') from a posterior third-person perspective while perceiving repeated tactile stimulations on their back or chest. As in the rubber-hand illusion, conflicting multisensory stimulation exists between what is seen (the avatar being stroked) and what is felt (the participant's back being stroked). Compared to asynchronous visuotactile stroking, participants in synchronous visuotactile stroking self-identify more with the seen virtual body, judge their positions as closer to it, and mislocalize the tactile stimulus to the virtual body. Additional studies have shown autonomic bodily responses, such as skin cooling stemming from such bodily illusions [31,32▪]. Brain imaging studies using the FBI have revealed that the premotor cortex, intraparietal sulcus, and extrastriate visual regions are involved in the sense of body ownership, whereas the temporoparietal cortex and insula are involved in the sense of self-location and first-person perspective [26,33▪,34].

These results support the idea that BSC stems from the integration of visual, tactile, proprioceptive [35], and vestibular [36] signals. Both in the rubber-hand and the FBIs, subjective changes in BSC are held to arise from a resolution of multisensory conflicts by means of minimization of error signals [37▪▪,38▪▪]. Visual dominance is prevalent in that respect, as it dominates proprioceptive inputs [39] when the apparent seen location of a body part does not match its actual location. Such visual modulation of bodily signals is also reflected in the tactile domain, as seeing one's hand improves tactile acuity on the hand, compared to seeing a nonhand object (visual enhancement of touch [40]). This latter effect is further boosted by hand ownership manipulations [41], as revealed by the crossmodal congruency effect for hands [42] and avatars [43]. Taken together, these results highlight the role of visual signals in experimentally and neurologically induced altered states of BSC. In the next section, we evaluate the complementary idea by assessing whether vision is affected by bodily signals.

INFLUENCES OF BODILY SIGNALS ON VISION

On a continuous basis, coalitions of interoceptive and exteroceptive sensors convey information about various aspects of the body and the environment. Despite this tremendous amount of information, percepts are not experienced as sums of independent features, but as integrated multimodal scenes [21]. That is, colors, smells, and textures are all experienced as integrated into a common perceptual object. The same holds for bodily experience, as subjects typically experience themselves as a unified whole (but see heautoscopy; [16,23▪]). As argued above, consciousness is a unified and essentially multisensory experience, rather than a sum of unimodal features [10▪]. Multisensory integration – the function whereby information from different sensory modalities is combined together – is thus central to both visual consciousness and BSC. Building upon the notion of phenomenal unity (i.e., the perception of multiple sensory streams as a multimodal), most theories of visual consciousness postulate strong interdependencies between multisensory integration and consciousness (see [44▪▪] for a review). Yet, these interdependencies are unlikely to imply necessity, as sensory signals from different modalities are integrated at early stages or processing already in subcortical structures, arguably unconsciously [45]. In addition, there is also compelling evidence for unconscious multisensory integration of more complex stimuli, as the perception of invisible images can be modulated by the simultaneous presence of another supraliminal stimulus presented in the auditory [46▪,47▪], tactile [48,49▪], or proprioceptive modalities [50▪]. Beyond the integration of a supraliminal and a subliminal stimulus, a recent study showed that an invisible stimulus can also be integrated with an inaudible one (up to semantic levels), therefore arguing for high-level multisensory integration in the complete absence of perceptual consciousness [51▪]. Taken together, these results suggest that multisensory integration that is of relevance for visual consciousness and BSC most likely is an automatic brain process, governed by bottom-up mechanisms that precede conscious access.

If perception and visual consciousness are embodied, changes in visual consciousness depending on bodily signals are expected. Yet, the mere idea of all-or-none modulations of visual perception depending on BSC seems hardly testable empirically, as bodily signals of interoceptive, vestibular, or proprioceptive origin are never completely disrupted, even in the most severe neurological conditions (e.g., locked-in syndrome, deafferentation, and tetraplegia) or experimental manipulations (e.g., sensory deprivation).

However, several studies have investigated directly the impact of bodily signals on thresholds for visual consciousness. One focused on proprioception and showed that images of hands emerged faster into visual consciousness when their orientation was congruent with the actual position of the participants' hands when seeing the display (palm up vs. palm down) [50▪]. This suggests that proprioceptive signals can modulate the threshold for visual consciousness for an object in a quantitative manner. Another study applied a similar experimental logic to touch–vision interactions showing facilitatory effects of congruent tactile stimuli on visual consciousness [52▪]. More recently, it was also shown that neural events locked to heartbeats correlated with the detection of a faint visual grating, revealing the impact of interoceptive bodily cues (cardiac signal) on visual consciousness [53▪] as also revealed for BSC [25,54▪]. Taken together these studies suggest that visual consciousness is facilitated when visual signals are congruent with bodily signals at the spatial or temporal level, and inhibited in the presence of multimodal conflicts. Further studies are required to investigate these effects and the possible influences of other sensory modalities such as vestibular signals on visual consciousness, and the involved neural mechanism responsible for such multisensory effects.

Beyond the threshold for visual consciousness, there is long-standing compelling evidence that bodily signals can alter the content of visual perception. Indeed, numerous studies reported changes in visual percepts depending on vestibular inputs (e.g., oculogravic illusion [55,56]; bistable perception [57▪]), proprioceptive inputs (e.g., Taylor illusion [58]; kinesthesic visual motion [59▪]), tactile inputs (e.g., bistable perception [52▪]), and motor inputs (e.g., biological motion [60–62]). An open question is also whether certain signals impacting BSC, play a particular role in shaping visual consciousness.

Taken together, the reviewed data suggest that the quality of visual perception is not a simple function of retinal input, but also the product of integration with other sensory signals, including bodily signals. This bidirectional interaction in which bodily and visual information modulate one another indicate that to comprehensively understand visual consciousness, or BSC, or both, they must be studied together, including their influence on self-consciousness.

OPEN QUESTIONS

We reviewed clinical and experimental evidence suggesting a bidirectional relationship between visual consciousness and BSC. Many questions remain regarding this relationship, with three intriguing examples below.

Does bodily self-consciousness require perceptual consciousness?

Is BSC based on the (perceptually) conscious brain or are unconscious multisensory processes sufficient to induce BSC? The latter seems likely considering that vestibular and proprioceptive signals are both primordial for BSC, while remaining most of the time outside the stream of perceptual consciousness under normal conditions. Progress on this issue would require assessment of whether changes of self-identification and self-location can be obtained in cases when multisensory conflicts are not detected explicitly (i.e., participants feel the visuotactile stimuli but cannot discriminate whether they are synchronous or asynchronous), or in case the visuotactile stimuli themselves remain under the threshold for perceptual consciousness (i.e., due to psychophysical manipulations or pathological conditions such as blindsight).

Does bodily self-consciousness involve attention?

Although the necessity and sufficiency of attention for visual consciousness is subject to a heated debate [63–65], it has only rarely been explicitly explored in the field of BSC, with the exception of neurological research revealing close links between attention and altered states of BSC (e.g., somatoparaphrenia). We recently showed in a visual search paradigm with self-motion and nonself-motion stimuli that self-movement 'pops-out', suggesting that visual attention is integrated with efferent information at early stages of processing [66▪]. Experiments manipulating attention and investigating its influence on BSC (and visual consciousness) would be important and may range from investigations of preattentive to explicit top–down aspects.

Does bodily self-consciousness influence cognitive processes beyond perception?

Recently, metacognitive vision, that is the second-order knowledge about a visual process, or 'knowing about seeing', has received much attention [67]. So far, studies about metacognition have focused on unisensory perception, and the role of multisensory processes in metacognitive processes remains unknown: is what we feel we know about a bimodal stimulus substantially better than what we know about a unimodal stimulus? Although, distinct from the notion of the minimal sense of self reviewed here (BSC), it seems interesting to investigate whether metacognition relates differentially to BSC ('knowing about feeling') vs. more classical cognitive aspects of the self (such as narrative, remembered, and conceptual aspects of the self) ('knowing about knowing').

CONCLUSION

Picturing the interplay between visual consciousness and BSC presents both methodological and theoretical challenges. We believe that deciphering the interactions between perception of the environment, perception of one's body, and their respective necessity and sufficiency for visual consciousness and BSC require an integrated, multisensory study of consciousness.

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Conflicts of interest

There are no conflicts of interest.

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