Posing for awareness: Proprioception modulates access to visual consciousness in a continuous flash suppression task

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The rules governing the selection of which sensory information reaches consciousness are yet unknown. Of our senses, vision is often considered to be the dominant sense, and the effects of bodily senses, such as proprioception, on visual consciousness are frequently overlooked. Here, we demonstrate that the position of the body influences visual consciousness. We induced perceptual suppression by using continuous flash suppression. Participants had to judge the orientation a target stimulus embedded in a task-irrelevant picture of a hand. The picture of the hand could either be congruent or incongruent with the participants' actual hand position. When the viewed and the real hand positions were congruent, perceptual suppression was broken more rapidly than during incongruent trials. Our findings provide the first evidence of a proprioceptive bias in visual consciousness, suggesting that proprioception not only influences the perception of one's own body and self-consciousness, but also visual consciousness.

Introduction

The sources and modulators of conscious experience have long been a matter of debate in psychology,

philosophy, and neuroscience (de Gardelle & Kouider, 2009; Pacherie, Green, & Bayne, 2006). Traditionally, the scientific study of consciousness has been divided along two lines. Thus, conscious perception has been studied extensively, mostly in the visual domain (Dehaene & Changeux, 2011; Dehaene & Naccache, 2001), whereas a different line of research investigated bodily self-consciousness and multimodal integration of bodily signals (Jeannerod, 2003). Both fields have typically been studied separately, thereby neglecting possible modulatory effects between bodily information and visual awareness.

Bodily self-consciousness refers to the integrated, prereflexive experience of being a self in a body and has been related to multimodal bodily information from tactile (Salomon, van Elk, Aspell, & Blanke, 2012), vestibular (Blanke, 2012), and proprioceptive (Costantini & Haggard, 2007) as well as visual and action information (Salomon, Malach, & Lamy, 2009; Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005). Clinical data from epilepsy and stroke patients are associated with disturbances in multisensory integration caused by damage to the temporoparietal cortex (Blanke, Landis, Spinelli, & Seeck, 2004), corroborating earlier findings on body schema disturbances in patients with visuospatial neglect following damage to similar regions.

Visual awareness has been investigated in a large variety of behavioral and neuroimaging experiments (Kim & Blake, 2005; Rees, 2007). In binocular rivalry paradigms, each eye is presented with a different image, and perception typically alternates between the two images (Tong, Nakayama, Vaughan, & Kanwisher, 1998). This allows for a controlled study of visual awareness as the same images are constantly present on the retina and only conscious perception alternates. Recently, a novel paradigm called the breaking continuous flash suppression (b-CFS) paradigm has been introduced as a particularly sensitive measure of invisible stimulus processing (Jiang, Costello, & He, 2007; Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006). This paradigm uses rapid presentation of high-contrast images to one eye to suppress visual target stimuli presented to the other eye, with the time that it takes targets to overcome interocular suppression being the dependent variable.

Previous studies have shown that parameters such as attentional load (Bahrami, Lavie, & Rees, 2007), inverted faces (Jiang et al., 2007), and natural scene content (Mudrik, Breska, Lamy, & Deouell, 2011) modulate suppression times in b-CFS. To what degree visual awareness may be modulated by nonvisual signals, in particular proprioceptive signals (which are a major determinant of bodily self-consciousness; Ehrsson, Spence, & Passingham, 2004), has so far not been investigated. In the present study, we used the b-CFS paradigm to test if changes in participants' hand position affect the duration of suppression when task-irrelevant images of hands in congruent and incongruent positions are co-presented with standard b-CFS stimuli. Previous studies using active tactile exploration (Lunghi, Binda, & Morrone, 2010) and olfaction have shown that congruent multisensory information causes shorter suppression times (Zhou, Jiang, He, & Chen, 2010) in interocular competition. We hypothesized that trials with congruent visual and proprioceptive information would have shorter suppression times than incongruent trials when suppressed by CFS but would show no difference when not visually suppressed.

Methods

Participants

Participants in the main experiment were 21 right-handed healthy volunteers (five women) from the student population at Ecole Polytechnique Fédérale de Lausanne (EPFL; age 19–30 years, $M = 23.6$ years). The control experiment included 19 right-handed participants (seven women; age 20–24 years, $M = 21.8$ years). All participants had normal or corrected-to-normal sight and no psychiatric or neurological history. They participated in the study for payment (about 15 CHF). All participants gave informed consent, and the study was approved by the ethics committee of EPFL. One participant was removed from the analysis because of reaction times longer than 2.5 SDs above the mean. Another participant could not finish the experiment as he did not break the perceptual suppression.

Stimuli and procedure

Stimuli consisted of high-contrast dynamic noise patches suppressors ("Mondrians"; Hesselmann & Malach, 2011) and target stimuli. The target pictures were two pictures of hands (one dorsal up and one palm up, visual angle H:16° V:18°; Ionta & Blanke, 2009) in which we embedded the target region in a small white square (visual angle H:2° V:2°) with horizontal or vertical lines (Figure 1). Although stimuli were quite similar in their low-level features, as can be seen in the spectral power analysis in Supplementary Figure S1, our 2 × 2 full factorial design ensured that the low-level features of the images were controlled with respect to the experimental design. Stimuli were presented using ExpyVR, a custom-built multimedia stimuli presentation software developed with Python 2.6 and the Open Graphics Library v.2.2. The stimuli were viewed via a head-mounted display (HMD;
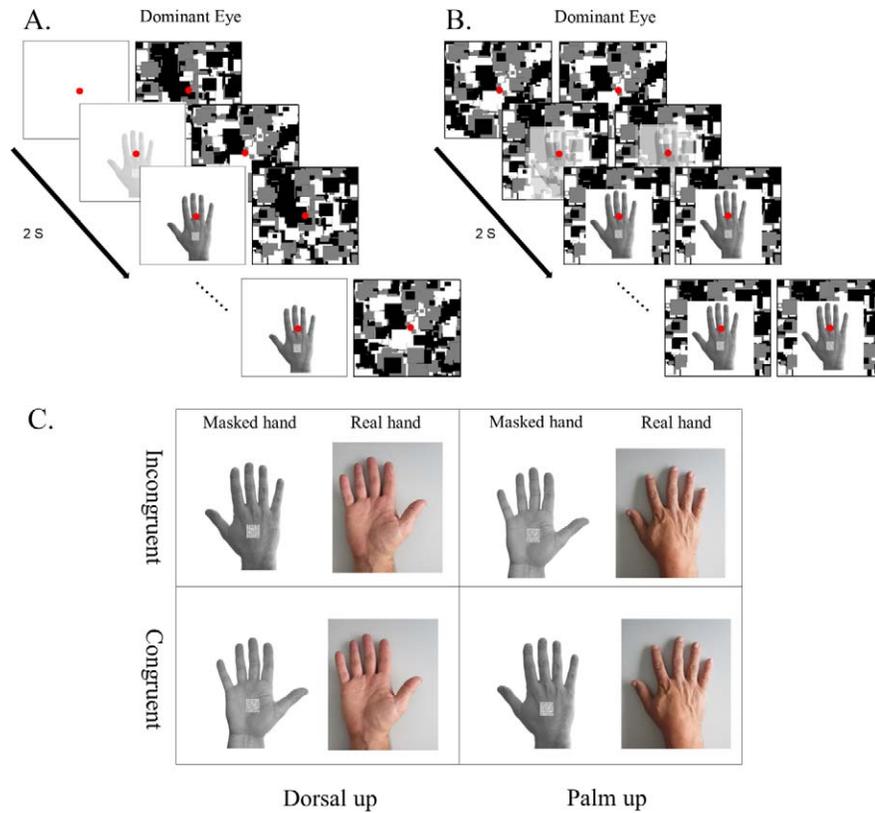
Figure 1. Experimental design. (A) CFS experiment, Mondrian masks were presented to the dominant eye. The target image presented to other eye was either congruent or incongruent with the participant's hand position. (B) Control experiment. Similar stimuli were presented to both eyes; hence, no binocular suppression. (C) A 2 × 2 full factorial design. Gray-scale hands are the task-irrelevant visual stimuli presented to the nondominant eye. Color hands represent the nonvisible hand position of the participant. Participants were required to indicate the orientation of lines in the square of the visually presented hand stimuli.

VR1280 Immersion Inc., SXGA, 60°, diagonal field of view, refresh rate 60 Hz). Mondrians were rapidly (10 Hz) flashed to the participants' dominant eye (visual angle H:48° V:36°), and the target was presented simultaneously to the other eye. A red fixation spot (visual angle H:3° V:3°) was presented to both eyes.

Participants were first tested for ocular dominance using the Miles test (Miles, 1930). They were then instructed to indicate the orientation of the lines inside the white box (horizontal or vertical) and to respond as quickly as possible. Participants were fitted with the HMD, which allowed them to view only the experimental display and not their hands or surroundings. The experimenter then placed their left hand on the response joystick, which was placed in front of them. Participants were required to hold the joystick in their left hand in a manner that compelled them to hold their hand perpendicular to the table, thus making the left hand position orthogonal to that used in the experimental conditions. The participant's right hand was comfortably placed on the table in front of their body with the palm up or the palm down (see Figure 1B).

The b-CFS experiment included 320 trials divided into two blocks. The total duration of the experiment was about 1 hour. Each trial began with the simultaneous presentation of the Mondrians and target image to separate eyes (see Figure 1A). The contrast of the target image was ramped up from zero to full contrast over 2 s. The trial ended when participants pressed a key on a joystick to indicate their response. Target orientation was randomized, and the participants' right hand position was changed between blocks. Initial hand position and condition order were randomized between participants.

Following the experiment, participants filled in a questionnaire for demographic data and were asked to indicate the perceived content of the pictures they viewed, what they believed the objective of the experiment was, and whether they felt that their right hand position affected their performance on the task.

Following Jiang et al. (2007), we employed a control experiment to control for possible differences in detection time due to response or detection criteria. The control experiment was identical to the main experiment except that the target images were blended into the Mondrians (Figure 1B) and presented to both eyes. Hence, in the control experiment, there was no flash suppression. Therefore, comparison of the results from
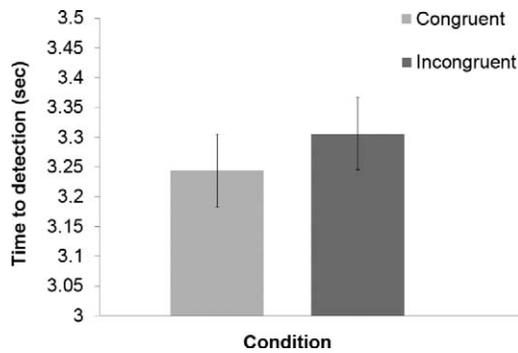
Figure 2. Mean detection time by congruency. Note significantly reduced suppression time when hand posture and task-irrelevant visual hand are congruent. Error bars are *SEM*.

the control and b-CFS experiments would allow one to test if the results in the b-CFS experiment are exclusive to the visual suppression condition or may reflect a more general bias (Mudrik et al., 2011).

Results

Reaction times

Response times (RTs) for erroneous trials and reaction times more than 2.5 *SD*s from the mean (less than 3% of trials) were removed from the analysis. RTs were submitted to a 2 × 2 repeated-measures ANOVA with viewed hand orientation (dorsal/palm) and hand position congruency (congruent/incongruent) as within-subject factors. The results showed (Figure 2) a main effect for congruency, $F(1, 18) = 4.52$, $p = 0.04$, $\eta^2 = 0.2$, with trials in which the viewed and real hand positions were congruent breaking suppression more rapidly ($M = 3.24$ s, $SE = 0.56$ s) than in the incongruent situation ($M = 3.30$ s, $SE = 0.58$ s). A main effect for viewed hand orientation was also found, $F(1, 18) = 5.8251$, $p = 0.026$, $\eta^2 = 0.24$, with responses on trials with a dorsal hand view ($M = 3.21$ s, $SE = 0.58$ s) being more rapid than in the palm-up condition ($M = 3.33$ s, $SE = 0.56$ s). No interaction between the factors was found ($F < 1$).

Control experiment RTs were submitted to an identical 2 × 2 analysis of variance (ANOVA). Unlike the CFS results, the control experiment results indicated neither any difference between the congruent ($M = 2.08$ s, $SE = 0.22$ s) and incongruent ($M = 2.06$ s, $SE = 0.21$ s) conditions, $F(1, 18) < 1$, nor for the viewed hand orientation, $F(1, 18) = 2.3$, $p = 0.15$, or interaction, $F(1, 18) < 1$. A joint analysis of the CFS and control experiments in a repeated-measures ANOVA with experiment as a between-subject factor revealed a significant interaction between experiment and congruency, $F(1, 36) = 4.43$, $p = 0.04$, $\eta^2 = 0.1$, with

a significantly larger difference between congruent and incongruent in the b-CFS experiment than in the control experiment in addition to main effects (Figure 3).

To further test the robustness of the congruency effect, we used a permutation test in which the congruency score (incongruent-congruent) of each participant was randomly divided into two groups. The difference in the congruency score between the two shuffled groups was computed. This was repeated 10,000 times to create a null distribution, and the true difference between the CFS and control scores was compared with the 95th percentile of the resulting distribution (Supplementary Figure S2). The true difference was larger than the 95th percentile ($p = 0.023$).

Finally, to test for possible effects of ocular dominance or block order, we employed an additional ANOVA with ocular dominance (left/right) and block order (dorsal first/palm first) as between-subject factors. No effects of these factors on RTs were found (all $p > 0.1$).

Accuracy

Overall accuracy in the b-CFS condition was 95.9%. A 2 × 2 repeated-measures ANOVA with viewed hand orientation (dorsal/palm) and hand position congruency (congruent/incongruent) as within-subject factors revealed no differences between conditions (all $p > 0.1$). In the control experiment, the overall accuracy was 97.2%. Results of an identical ANOVA showed no effect of the conditions on accuracy (all $p > 0.25$).

Questionnaire data

Of the 19 participants in the experiment, five (26%) were not aware of the presentation of both dorsal and palmar pictures of the hand. All participants remained naïve to the true aim of the experiment. Only one participant noticed the manipulation of hand position between blocks as relevant to the experiment. Finally, all participants claimed that their hand position had no effect on their task performance.

Discussion

Our results provide clear evidence that the congruency of our participants' limb position with the task-irrelevant co-presented hand affected visual consciousness in the absence of visual awareness. This is, to the best of our knowledge, the first demonstration of the
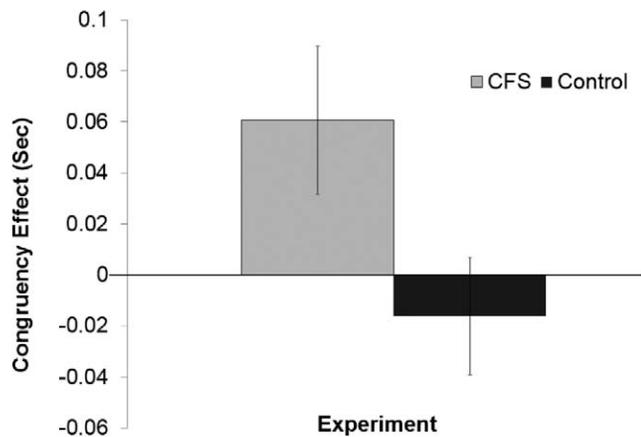
Figure 3. Congruency effect in the CFS and non-CFS experiments. The congruency effect (incongruent-congruent) in the CFS experiment was positive and significant. No such effect was found in the non-CFS control experiment. Error bars are *SEM*.

effects of proprioception on visual consciousness. Results from the control experiment allow us to rule out alternative explanations of these results such as partial awareness, detection, or response biases. Furthermore, the results show that the dorsal view of the hand gains access to consciousness more rapidly than the palm view regardless of the congruency with the participants' limb position. Importantly, our results were found for both hand orientations in a full factorial design, ensuring that they did not arise from the visual characteristics of the presented images but rather from the integration of visual-proprioceptive information.

Interestingly, several b-CFS studies have found that upright faces break suppression more rapidly than inverted faces (Jiang et al., 2007; Stein, Hebart, & Sterzer, 2011). Although these findings have been attributed to the visual familiarity of the upright images, the congruent proprioceptive information arising from the participants' posture during the experiment may have contributed to this effect as well. This interpretation is strengthened by the finding that visually inverted objects did not show longer suppression times than the same objects in their familiar upright positions (Stein, Sterzer, & Peelen, 2012).

The finding that visual stimuli that are congruent with the current body position gain more rapid access to visual consciousness extends the findings from previous studies of cross-modal effects on visual consciousness in other nonvisual modalities (Van Ee, van Boxtel, Parker, & Alais, 2009). For example, using a b-CFS paradigm, Zhou and colleagues (2010) found that olfactory stimuli that matched the visual image (e.g., a rose) had shorter suppression times than incongruent smells. Another study, using active exploration of tactile stimuli that were spatially congruent to one percept in a binocular rivalry paradigm, caused longer dominance times for the congruent visual stimuli

(Lunghi et al., 2010). However, an important difference between these studies and the current one is that in the current design, the hand position and the visual hand were task irrelevant, whereas in the tactile study, the active exploration of the tactile grating clearly made them explicitly relevant to the visually presented corresponding gratings. In addition, visual stimuli that were consistent with participants' voluntary movements were found to have longer dominance times and shorter suppression times than stimuli moving in an inconsistent manner (Maruya, Yang, & Blake, 2007). These findings suggest that cross-modal information biases visual consciousness toward the congruent resolution of the interocular visual conflict. More recently, it has been shown that for purely visual information, the inclusion of an incongruent object in a natural scene (e.g., a basketball player holding a watermelon) had shorter suppression times than identical ones with congruent objects (Mudrik et al., 2011). This may indicate a difference in unconscious integration of cross-modal information, for which congruent multisensory information shows shorter suppression times (Zhou et al., 2010). Conversely, in unimodal visual perceptual conflicts, incongruent information result in shorter suppression times (Mudrik et al., 2011).

The current results showed that dorsal hand images that are more familiar visually break suppression more rapidly than palm-up images. This finding extends previous findings from mental imagery showing more rapid processing of dorsal hand image rotation with respect to palm image rotations (Ionta & Blanke, 2009). Interestingly, a recent study using a novel version of the hand laterality task has suggested that proprioceptive information is used to match the representation of the viewed hand to one's own hand in order to decide about the laterality of the hand when this is ambiguous (Viswanathan, Fritz, & Grafton, 2012). The rapid breaking of suppression by the dorsal view suggests that during unconscious processing, visual consciousness is biased toward more familiar images. This is in line with findings from previous studies using b-CFS showing more rapid breaking of suppression for familiar words as well as upright faces (Jiang et al., 2007; Stein et al., 2011).

The mechanism by which proprioceptive information may bias visual consciousness is likely related to integration of bodily signals with visual information to create a coherent sense of bodily self-consciousness (Blanke, 2012). However, a previous study using binocular rivalry has shown that visual imagery can affect subsequent visual consciousness (Pearson, Clifford, & Tong, 2008), indicating the involvement of high-level cognitive processes such as mental imagery in binocular rivalry. However, several lines of evidence suggest that mental imagery of hand position was not

responsible for the results presented here. First, participants donned the HMD prior to the positioning of the hand on the table; hence, they had no perceptual image of their hand position on the table. In the article by Pearson and colleagues (2008), having a clear and specific percept (the image shown on a previous trial) was shown to be an important factor affecting rivalry. The authors suggest that the effect is a form of perceptual priming, whereby imagery of a previously displayed stimulus facilitates the perception of a similar stimuli (Pearson et al., 2008). Furthermore, Pearson and colleagues show evidence that viewing a competing stimulus during the imagery epochs caused the imagery to be ineffective in influencing rivalry. Because in our experiments, participants were not requested to attend to proprioceptive stimuli and were constantly bombarded with highly salient visual stimuli, it is highly unlikely that mental imagery had a significant influence on the results.

The neural mechanisms underlying visual consciousness have been the focus of many studies (Haynes & Rees, 2005; Rees, 2007). Specifically, binocular rivalry paradigms have shown that activity in the primary (Haynes & Rees, 2005) and extrastriate (Tong, 2003) visual cortex correlate with the dominant percept. Thus, it is widely accepted that the formation of visual consciousness in a rivalry situation involves interplay between low-level visual regions and higher-order areas located in the extrastriate regions (Sterzer, Kleinschmidt, & Rees, 2009). However, the current results show that proprioceptive signals known to be encoded in sensorimotor regions, such as postcentral gyrus areas 3a and 2 (Seiss et al., 2002) as well as area 5 (Graziano, Cooke, & Taylor, 2000) influence visual consciousness. A possible region that may play a role in the integration of such bodily and visual information is the extrastriate body area (EBA). The EBA was originally considered to be a visual region with a selective preference for body parts (Downing, Jiang, Shuman, & Kanwisher, 2001). However, later studies have shown that the EBA is also activated by unseen motor actions (Astafiev, Stanley, Shulman, & Corbetta, 2004) as well as incongruence between visual and executed movements (David et al., 2007). The EBA is also part of the network related to bodily self-consciousness (Ionta et al., 2011). Because the EBA is activated by viewed body parts, responds to motor actions, and is involved in bodily self-consciousness, it is a possible candidate for modifying visual consciousness based on proprioceptive signals. Further studies are needed to identify the neural underpinnings of this effect.

Finally, our findings are pertinent to a fundamental question relating to the neural correlates of consciousness. Several studies suggest that perceptual consciousness arises from focal activity in specialized brain regions (Fisch et al., 2009; Moutoussis & Zeki, 2002), whereas others propose that consciousness is related to widespread activity across multiple brain regions (Dehaene & Naccache, 2001). The current results suggest that perceptual consciousness results from integration of information from several cortical processing sites, as we show that proprioceptive information coded in sensorimotor regions affects visual consciousness.

To summarize, our results show that the congruence of real and viewed hand position influences the formation of visual consciousness even when it is task irrelevant. This is the first demonstration that proprioceptive information affects visual consciousness and suggests that body signals may actively influence consciousness.

Acknowledgments

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