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

Roy Salomon

Melanie Lim

Bruno Herbelin

Guido Hesselmann

Olaf Blanke

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, prrereflexive 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; Tsa-kiris, 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; Ehrson, 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;
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 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
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 SDs from the mean (less than 3% of trials) were removed from the analysis. RTs were submitted to a 2 x 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, η² = 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, η² = 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 x 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, η² = 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 x 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 naive 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
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 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
consciousness arises from focal activity in specialized brain parts; responds to motor actions, and is involved in bodily self-consciousness, it is a possible candidate for modifying visual consciousness based on proprioceptive information. The EBA is also activated by unseen motor actions (Astafiev, Stanley, Shulman, & Corbetta, 2004) 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 peripersonal space (David et al., 2001). 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 role of proprioceptive information in the perception of the self in the current results is supported by previous studies (Graziano & Cooke, 2001) in which the EBA was observed to be activated by unseen motor actions. The EBA was also demonstrated to be activated by unseen motor actions in a study by Astafiev, Stanley, Shulman, & Corbetta (2004), suggesting that the EBA is involved in the perception of the self in the current results.

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.

Keywords: consciousness, proprioception, bodily consciousness, continuous flash suppression

Acknowledgments

G. H. was supported by the German Research Foundation (grant HE 6244/1-). O. B. is supported by the Bertarelli Foundation, the Swiss National Science Foundation, and the European Science Foundation. R. S. was supported by the National Center of Competence in Research (NCCR) “SYNAPSY—The Synaptic Bases of Mental Diseases” financed by the Swiss National Science Foundation (no. 51AU40_125759). B. H. was supported by VERE project grant FP7-ICT-2009-5 - Project 257695.

Commercial relationships: none.
Corresponding author: Roy Salomon.
Email: roy.salomon@epfl.ch.
Address: Laboratory of Cognitive Neuroscience, Ecole Polytechnique Fédérale de Lausanne (EPFL), Lausanne, Switzerland.

References


Blanke, O. (2012). Multisensory brain mechanisms of
sequences of one’s own and others’ behavior. Neuroimage, 36, 1004–1014.
sciousness, 135–146.
Neuron, 70, 200–227.
Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual
Fisch, L., Privman, E., Ramot, M., Harel, M., Nir, Y., Kipervasser, S., et al. (2009). Neural “ignition”: Enhanced activation linked to perceptual aware-
tive Sciences, 9, 381–388.
Moutoussis, K., & Zeki, S. (2002). The relationship between cortical activation and perception investi-
gated with invisible stimuli. Proceedings of the National Academy of Sciences, USA, 99, 9527.
doi.org/10.1016/j.cub.2008.05.048.
Rees, G. (2007). Neural correlates of the contents of visual awareness in humans. Philosophical Trans-
actions of the Royal Society B: Biological Sciences, 362, 877–886.
Seiss, E., Hesse, C. W., Drane, S., Oostenveld, R., Wing, A. M., & Praamstra, P. (2002). Propriocep-
tion-related evoked potentials: Origin and sensitiv-


