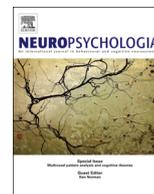




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# An invisible touch: Body-related multisensory conflicts modulate visual consciousness

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## ABSTRACT

The majority of scientific studies on consciousness have focused on vision, exploring the cognitive and neural mechanisms of conscious access to visual stimuli. In parallel, studies on bodily consciousness have revealed that bodily (i.e. tactile, proprioceptive, visceral, vestibular) signals are the basis for the sense of self. However, the role of bodily signals in the formation of visual consciousness is not well understood. Here we investigated how body-related visuo-tactile stimulation modulates conscious access to visual stimuli. We used a robotic platform to apply controlled tactile stimulation to the participants' back while they viewed a dot moving either in synchrony or asynchrony with the touch on their back. Critically, the dot was rendered invisible through continuous flash suppression. Manipulating the visual context by presenting the dot moving on either a body form, or a non-bodily object we show that: (i) conflict induced by synchronous visuo-tactile stimulation in a body context is associated with a delayed conscious access compared to asynchronous visuo-tactile stimulation, (ii) this effect occurs only in the context of a visual body form, and (iii) is not due to detection or response biases. The results indicate that body-related visuo-tactile conflicts impact visual consciousness by facilitating access of non-conflicting visual information to awareness, and that these are sensitive to the visual context in which they are presented, highlighting the interplay between bodily signals and visual experience.

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## 1. Introduction

Empirical investigations of consciousness have become a focus of study in cognitive neuroscience. Two important subfields of research have recently evolved: the study of bodily self-consciousness, investigating how the feeling of the self as a unified entity in the body arises from the integration of multisensory bodily signals (Blanke, 2012; Blanke et al., 2014; Ehrsson, 2007) and perceptual consciousness, focusing on the neural correlates of perceptual experiences (Dehaene et al., 2006; Rees, 2007).

The large majority of investigations in perceptual consciousness to date have focused on the visual modality and benefited from a large number of psychophysical methods to render stimuli invisible (Dehaene and Changeux, 2011; Dubois and Faivre, 2014; Kim and Blake, 2005). Paradigms making visual stimuli

unconscious have been used to understand the modulators of conscious access, as well as the extent of unconscious processing (Kouider and Dehaene, 2007; Mudrik et al., 2014; van Gaal and Lamme, 2012). However, following early suggestions of encapsulation and modularity of visual processing (Fodor, 1983; Zeki and Bartels, 1998) there have been few attempts to study how bodily signals affect visual awareness (Faivre et al., 2015). Yet, the fact that we experience a multisensory world around us, and not distinct unimodal worlds serves as a premise for a multimodal character of sensory processing and perceptual consciousness (Bayne, 2002; Deroy et al., 2014; Driver and Noesselt, 2008). While early theories of consciousness have proposed that multisensory integration cannot be achieved without awareness of the stimuli (Baars, 2002), several studies have now revealed multisensory integration in the absence of awareness. This has been shown in the olfactory (Arzi et al., 2012; Zhou et al., 2010), tactile (Lunghi and Alais, 2013; Lunghi et al., 2010; 2014), auditory (Alsius and Munhall, 2013; Conrad et al., 2010; Faivre et al., 2014), vestibular (Salomon et al., 2015) and proprioceptive (Salomon et al., 2013a) domains, suggesting that different multisensory signals below

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perceptual thresholds are integrated.

Such unconscious interactions between multimodal signals are of special interest as they are thought to underlie bodily self-consciousness (Blanke, 2012). Indeed, the experimental manipulation of bodily self-consciousness in healthy subjects typically involves multisensory conflicts notably by matching tactile stimulations on one's real body with synchronous visual stimulations seen on an avatar's body or rubber hand (Botvinick and Cohen, 1998; Ehrsson et al., 2004; Lenggenhager et al., 2007; Salomon et al., 2013b). For example, in the full-body illusion (FBI), participants feel a tactile stimulation on their body, while seeing it on a virtual body located 2 m away, which results in a spatial conflict between the avatar and the participant's physical body. When the viewed and felt visuo-tactile stimulation are synchronous, the multisensory conflict is enhanced, as participants feel the touch on their backs but see it at another spatial location (*I feel touch on my body and see synchronous touch on the avatar's body*). Such changes do not occur when the visuo-tactile stimulation is asynchronous (*I feel touch on my body and see unrelated touch on the avatar's body*). Importantly, these altered states of bodily self-consciousness are further modulated by the presence of a bodily form, as changes in bodily self-consciousness are smaller or absent if the viewed touch is presented on an object (*I feel touch on my body and see related or unrelated movement on an object*) (Aspell et al., 2009; Evans and Blanke, 2012; Lenggenhager et al., 2007; Tsakiris et al., 2010; Tsakiris and Haggard, 2005). Here we refer to the conflict arising from synchronous visuo-tactile stroking presented on a body (related to the RHI and FBI) as a body-related multisensory conflict. The presence of a bodily form has also been shown to impact cross-modal congruency effects (Aspell et al., 2013, 2009; Pavani et al., 2000; Salomon et al., 2012), as well as tactile acuity in the visual enhancement of touch (Kennett et al., 2001; Taylor-Clarke et al., 2002), suggesting a role for the visual body context in visuo-tactile interactions. Yet, while many studies have investigated the role of such bodily visuo-tactile conflicts on bodily self-consciousness there has been no attempt to investigate how such conflicts affect visual consciousness.

Here we sought to determine whether body-related visuo-tactile conflicts and the presence of a body form would modulate access to visual consciousness. We used the continuous flash suppression (CFS) paradigm, in which highly salient stimuli presented to one eye prevent the visibility of a target stimulus presented to the other eye for extended periods of time (Tsuchiya and Koch, 2005). After some time the target stimulus "breaks through" the interocular suppression and becomes visible. The time required to break suppression can be used as a dependent measure indicating unconscious processing (Gayet et al., 2014; Jiang et al., 2007; Mudrik et al., 2011; Salomon et al., 2013a; Stein and Sterzer, 2014; Stein et al., 2012). We employed virtual reality with a robotic haptic stimulation platform to stroke the participants' back (Duenas et al., 2011; Pfeiffer et al., 2013) while masking the visual stroking with continuous flash suppression. Participants were asked to indicate the color of a moving dot as soon as it broke suppression and thus became visible. Critically, as in the full body illusion, the dot could be moving synchronously or asynchronously with the tactile stroking on the back. In three experiments we investigated (i) if body-related visuo-tactile conflict affected the time required to break suppression (exp.1), (ii) if this effect was modulated by the presence of a body form vs. an object (exp.3), (iii) if the results could be due to detection or response biases (exp.2). Additionally, we replicated our results in a fourth experiment, using a within-subject design, controlling more rigorously for low-level visual differences between the object and body stimuli, and assessing the specificity of multisensory stimulation vs. unimodal visual stimulation. In line with previous results on integration of bodily and visual signals in the absence of

consciousness (Lunghi et al., 2010; Salomon et al., 2013a; Salomon et al., 2015) we predicted that CFS would be broken faster in the absence of body-related visuo-tactile conflict (i.e. asynchronous stroking compared to synchronous stroking) but only in the presence of a visual body form.

## 2. Methods

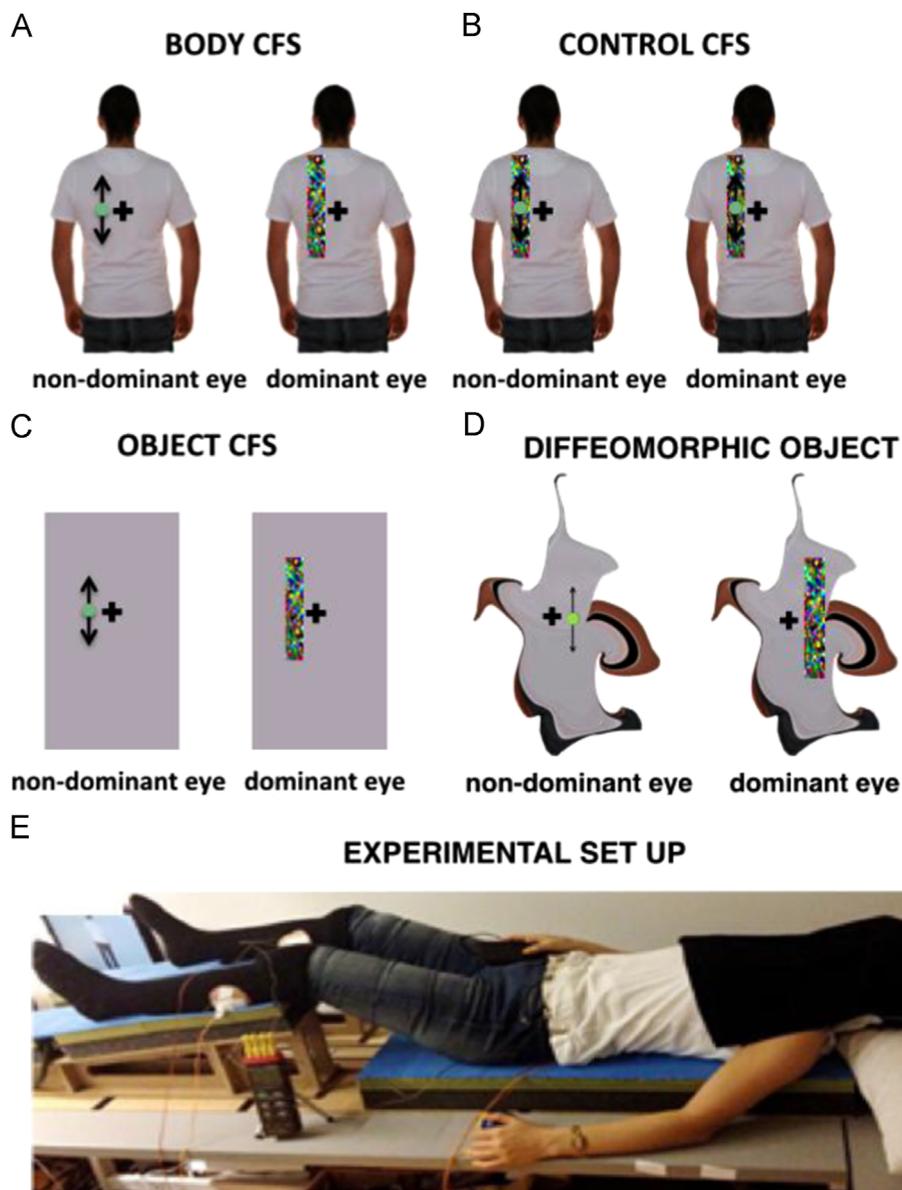
### 2.1. Participants

Seventeen healthy subjects (8 males, mean age 22.9 years, SD=3.5 years, range 18–29) from the student population at Ecole Polytechnique Fédérale de Lausanne (EPFL) took part in the body CFS experiment and another 15 participants (9 males, mean age 28.5, SD=1.7 years, range 25–31) participated in the control experiment. The third experiment included other 18 participants (13 males, mean age 22 years, SD=3.2 years, range 18–29). The fourth experiment included 19 participants (10 males, mean age 22.1 years, SD=2.6 years, range 18–26). All participants were right-handed, had normal or corrected-to normal sight and no psychiatric or neurological history. They were paid 20–25 CHF. All participants gave informed consent; the study was approved by the ethics committee of EPFL and was performed in accordance with the Declaration of Helsinki. Overall, one participant was removed from the analysis because of chance level performance in some conditions, one participant was removed due to haptic robot failure and three other participants were excluded as they could not complete the experiment (i.e. did not break suppression at all).

### 2.2. Experiment 1: body CFS

#### 2.2.1. Continuous flash suppression task

Tactile stimulation was delivered by a custom-built haptic robot system (Duenas et al., 2011; Salomon et al., 2013b). The tactile stimulation used several pre-set motion profiles with variable velocity ranging from 0 to 67 cm/sec ( $M=4.69$  cm/sec,  $SD=1.41$  cm/sec). These were coupled with visual motion profiles of a moving dot at the corresponding location scaled for the visual display (in the synchronous condition), or at a non-corresponding location (in the asynchronous condition). In the body continuous flash suppression experiment (body CFS), visual stimuli consisted of high-contrast dynamic noise patches suppressors ("Mondrians", as described in Hesselmann and Malach, 2011; Salomon et al., 2013a) and a target stimulus. The background picture was a picture of a man wearing a white t-shirt seen from the back (size H: 20.5°, W: 11.3°) (Ionta et al., 2011), on top of which we displayed either the Mondrians or the target stimulus – a small dot moving up and down along the left side of the man's back. The dot could be either green or blue with equal luminance (size: H: 0.7°, W: 0.7°, blue: R 134 G 133 B 255, green: R 110 G 173 B 118). Stimuli were presented using ExpyVR, an in-house multimedia stimuli presentation software developed with Python 2.6 and the Open Graphics Library v.2.2 (available at <http://lnco.epfl.ch/>). The stimuli were projected onto a head-mounted display (HMD; VR1280 Immersion Inc., SXGA, 1280 × 1024 pxl, 60° diagonal field of view, refresh rate 60 Hz). Mondrians were rapidly (10 Hz) flashed to the participants' dominant eye (visual angle H: 8.9°, W: 1°), and the dot was presented concurrently to the other eye. There were four types of trials depending on the synchrony between the tactile and visual stroking (synchronous/asynchronous), and the color of the dot (blue/green). Each type of trial was repeated 40 times in a randomized order. In total, the 160 trials were grouped in 4 blocks of 7 min each. Each trial began with the simultaneous presentation of the Mondrians and the dot to separate eyes (see Fig. 1). The contrast of the dot was ramped up from zero to full contrast over



**Fig. 1.** Visual stimuli in the three experiments (body CFS, control CFS, object CFS) and set up. (A) Body CFS: the body form and Mondrians were displayed to the dominant eye, while the moving dot was projected to the non-dominant eye; (B) control CFS: the body form, Mondrians and moving dot were displayed to both eyes at the same time so that no interocular suppression occurred; (C) object CFS: the object form and Mondrians were displayed to the dominant eye, while the moving dot was projected to the non-dominant eye. The black arrows indicate schematically the movement of the dot and were not present during the experiment. (D) Diffeomorphic object: the object used in experiment 4 was a diffeomorphic transformation of the body image, possessing similar low-level features. (E) Schematic representation of the experimental set up. Participants were fitted with the HMD and asked to lie down supine on the stroking robot.

7 s, so that it became fully visible without CFS after about 1 s. Participants were asked to press a key on a numeric keypad to indicate their response (blue or green) as soon as they saw the dot. Regardless of when the response was provided, the stroking continued for 10 s to allow the robot to return to its baseline location.

### 2.2.2. Procedure

At the beginning of the experiment, participants were briefed about the stimuli they were going to experience and instructed about the task they were asked to perform. To increase visual similarity with the virtual body all participants wore a white t-shirt. Then, demographic data were collected and participants were tested for ocular dominance using the Miles test (Miles, 1930). Afterwards, they were fitted with the HMD and asked to lie down supine on the stroking robot. The experimenter laid their right

hand on the response keypad, which was placed next to them. The participant's left hand was comfortably placed on the table matching the posture of the body image. Experimenter instructed participants to indicate the color of the moving dot by pressing one of two buttons and to respond as quickly as possible with the index or middle finger. During the experiment white noise was played through the headphones in order to mask the sound of the robot. A short resting period was allowed between each block. No feedback was provided during the experiment. All subjects completed a short training session prior to the experimental blocks. Finally, we interviewed participants about their sensations during the experiment, i.e. difficulty of the task, awareness of the study purpose, and differences in perceptual experience between synchronous and asynchronous conditions. The total duration of the experiment was about 1 h.

### 2.3. Experiment 2: control

We designed a control experiment (control continuous flash suppression) to check for potential differences in detection time due to biases in response or detection criteria (e.g. shorter reaction times, see Salomon et al., 2013a; Stein et al., 2011). The control experiment was identical to the main experiment except that the target images were blended into the Mondrians and presented to both eyes. Hence, in the control experiment, there was no interocular suppression: we projected both the Mondrian and the dot at the same time to both eyes together. Crucially, comparison of the results from the control CFS and body CFS experiments allowed one to test if the results in the body CFS experiment were exclusive to the visual suppression condition or reflected a more general bias (Stein and Sterzer, 2014; Stein et al., 2012).

### 2.4. Experiment 3: object CFS

In Experiment 3 (object continuous flash suppression), participants performed a continuous flash suppression task as in Experiment 1. However, the background image on which the Mondrians and the dot were displayed was a body-sized object, instead of the virtual body. The object was a rectangle with the same color as the region on which the dot was presented in the body experiment (RGB: 187, 179, 179) and of the same size as the body template used in the previous experiments. All other parameters and procedures were identical to Experiment 1.

### 2.5. Experiment 4: within-subject body-diffeomorphic object-visual only CFS

In Experiment 4 (within-subject replication), participants performed a task as in the previous experiments, with one exception that the dot and Mondrians were presented on the right side of the avatar's body and stroking was delivered to the right side of participant's back instead of on the left side like in the experiments 1-3. This experiment included three conditions: the body condition was identical to that of Experiment 1. In the object condition, to avoid possible confounds relating to the low level features of the object stimulus, we employed a diffeomorphic transformation on the body image (see Fig. 1D) that preserves the basic perceptual properties of the image while removing its meaning (Stojanowski and Cusack, 2014). Finally, a unimodal visual condition was introduced. A new HMD device was employed in this experiment, as the previous HMD was inoperative. We used an Oculus Rift DK, <http://www.oculus.com/rift/> with resolution of the screen 1280 × 800 pxl, 110 diagonal field of view, and refresh rate of 60 Hz. Conditions (body, object, visual only) order was randomized for each subject.

### 2.6. Data analysis

In order to study the impact of visuo-tactile conflict on the content of visual consciousness we calculated mean reaction times (RTs) to report breaks in continuous flash suppression (i.e. the time required for the target to become visible (Jiang et al., 2007; Mudrik et al., 2011; Stein et al., 2012)). Trials with incorrect target discrimination (corresponding to 3.6% on average across experiments), and reaction times longer than 2.5 standard deviations from the individual's mean RT, or shorter than 750 ms (the minimal exposure time for a perceivable tactile stimulation) were excluded from further analyses (corresponding to 8.6% of correct trials on average across experiments). In order to reduce deviations from normality, we performed an inverse transformation of reaction times (Whelan, 2008). We performed mixed ANOVAs with experiment as between-subject factor (body CFS/control CFS/

object CFS) and synchrony (synchronous/asynchronous visuo-tactile stroking) as within-subject factor both for RTs and accuracy, followed by *t*-test planned contrasts. All statistical tests were two-sided unless otherwise stated. Data from Experiment 4 was analyzed using a 2 (body/diffeomorphic object) × 2 (synchronous/asynchronous visuo-tactile stroking) repeated measures ANOVA. The effects of multisensory vs. unisensory stimulation were analyzed using a one-way repeated measures ANOVA including RTs in all experimental conditions (synchronous body/asynchronous body/synchronous object/asynchronous object/visual only) both for RTs and accuracy, followed by *t* tests for planned contrasts. For a better estimation of effect sizes we re-inverted reaction times and reported effect sizes and 95% confidence intervals in milliseconds rather than the inverted unit. Statistical analyses were performed using R (R Foundation for Statistical Computing, Vienna, Austria).

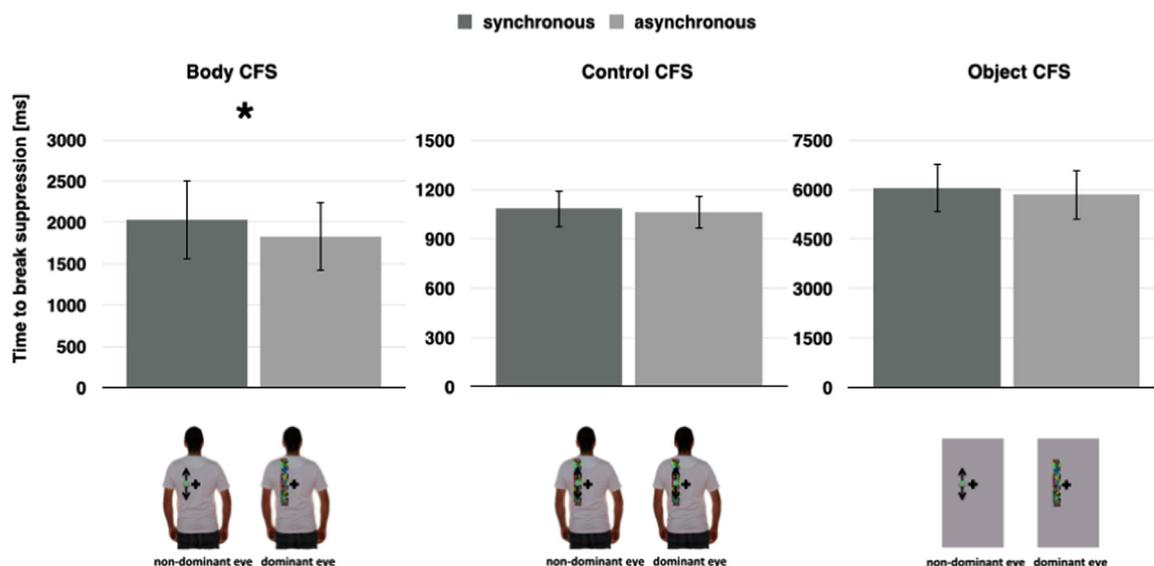
## 3. Results

### 3.1. Experiments 1-3

#### 3.1.1. RTs

After removing incorrect trials and outlier reaction times we conducted a mixed ANOVA to compare reaction times across conditions and experiments. We found a main effect of experiment ( $F_{(2,43)}=72.08$ ,  $p < 0.001$ , partial eta square  $\eta^2=0.77$ ), revealing that average reaction times (reflecting the time before conscious access) were overall longer in the object CFS condition ( $5951 \pm 519$  ms 95% confidence interval) compared to the body CFS condition ( $1930 \pm 313$  ms) and control condition ( $1070 \pm 74$  ms). We also found a main effect of condition ( $F_{(1,43)}=19.58$ ,  $p < 0.001$ ,  $\eta^2=0.31$ ), revealing that reaction times were shorter (i.e. suppression was broken faster) in the asynchronous visuo-tactile condition ( $2958 \pm 689$  ms) compared to the synchronous visuo-tactile condition ( $3105 \pm 706$  ms). Crucially, an interaction between synchrony and experiment ( $F_{(2,43)}=6.514$ ,  $p=0.003$ ,  $\eta^2=0.23$ ) suggested that the presence of a visuo-tactile conflict had a different incidence depending on the experiment type. To test what was driving this interaction, we computed a synchrony effect index (synchronous RT-asynchronous RT) for each subject in each experiment. We then explored this effect by running planned comparisons for the synchrony effect indexes in each experiment to directly compare the body CFS with the object CFS experiment, and the body CFS with the control CFS experiment. We found a significant difference depending on the synchrony of visuo-tactile stroking both between the body CFS and the object CFS ( $t_{(29)}=-3.30$ ,  $p=0.003$ ) and between the body CFS and the control CFS ( $t_{(28)}=-2.22$ ,  $p=0.03$ ); moreover the body experiment showed the greatest effect, with the largest RTs difference between the synchronous and asynchronous conditions.

We then examined if the RTs synchrony effects were significant within each experiment. As predicted, in the body experiment (body CFS) RTs in the asynchronous condition ( $1828 \pm 417$  ms) were significantly shorter than in the synchronous condition ( $2034 \pm 478$  ms 95% confidence interval;  $t_{(14)}=3.8$ ,  $p=0.002$ ). Accordingly, 87% of the participants (13/15) showed shorter times to break suppression when the masked visual stimuli and tactile stimulation were temporally asynchronous than synchronous, with a mean difference of 206 ms. The difference between the synchronous and asynchronous conditions was not significant in the control experiment (control CFS: synchronous:  $1081 \pm 110$  ms; asynchronous:  $1059 \pm 103$  ms;  $t_{(14)}=1.9$ ,  $p=0.08$ ) nor in the object experiment (object CFS: synchronous:  $6057 \pm 733$  ms; asynchronous:  $5845 \pm 754$  ms;  $t_{(15)}=1.2$ ,  $p=0.24$ ). For all mean RTs in synchronous and asynchronous conditions in all three experiments,



**Fig. 2.** Mean time to break suppression (RTs) in the three experiments (body CFS, control CFS, object CFS). Comparison of RTs (in ms) between synchronous and asynchronous conditions revealed that in the body CFS experiment RTs is longer under the synchronous visuo-tactile stimulation comparing to the asynchronous one. Significant differences were absent in the control and object CFS (\* $p < 0.05$ ; 95% Confidence Interval bars).

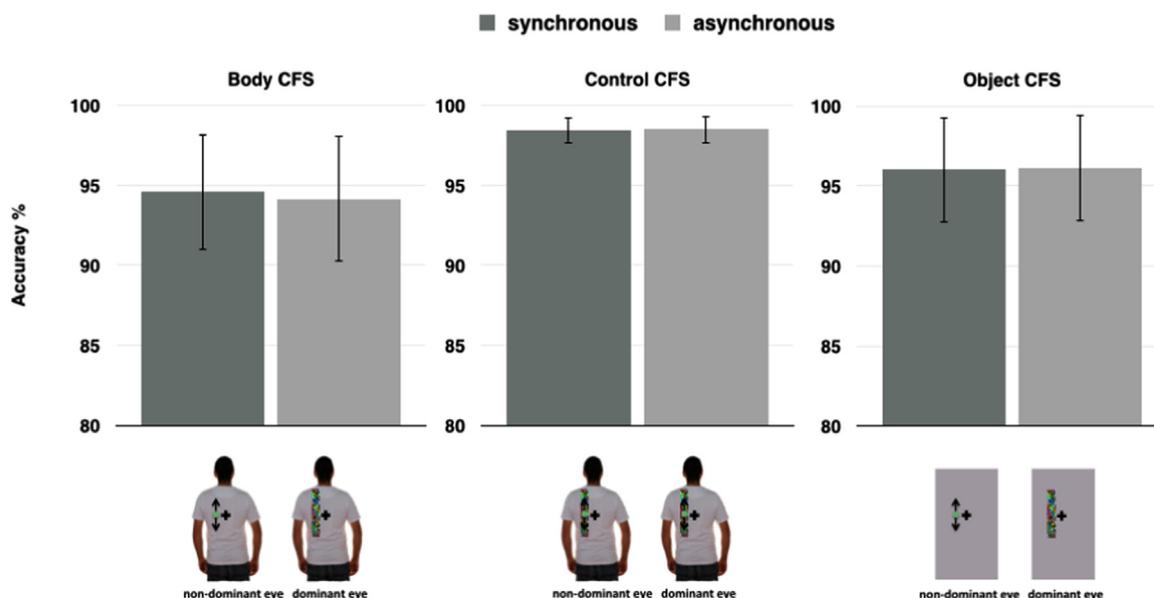
see Fig. 2. Further analyses using RTs normalization procedures yielded identical results (see [Supplementary materials](#) for details).

### 3.2. Accuracy

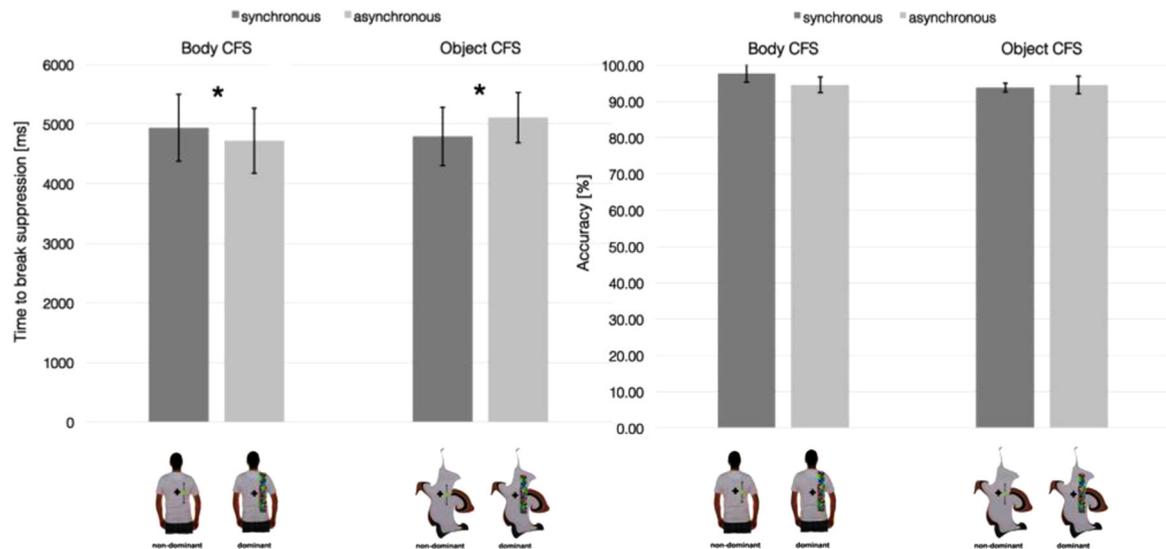
Overall accuracy in the three experiments was above 90% (body CFS =  $94.38\% \pm 2.63$ , control CFS =  $98.46\% \pm 0.59$ , object CFS =  $96.08\% \pm 2.3$ ). The mixed ANOVA revealed no significant main effect of experiment ( $F_{(2,43)} = 1.88$ ,  $p = 0.16$ ,  $\eta^2 = 0.08$ ); no significant main effect of synchrony ( $F_{(1,43)} = 0.038$ ,  $p = 0.84$ ,  $\eta^2 < 0.01$ ) nor interaction ( $F_{(2,43)} = 0.21$ ,  $p = 0.80$ ,  $\eta^2 = 0.01$ ). Fig. 3.

### 3.3. Experiment 4

As reaction times were much longer in the object condition compared to the body condition, we estimated that we insufficiently controlled for low-level perceptual differences between the object and body stimuli. Thus, we conducted an additional experiment using a within-subject design and a new object stimulus created by a diffeomorphic transformation of the body image (Stojanoski and Cusack, 2014). We also added a unimodal visual condition (i.e. without tactile stimulation) to check whether visuo-tactile stimulation changes sensory processing and affects access of visual stimuli to consciousness as compared to uni-sensory stimulation.



**Fig. 3.** Accuracy in the three experiments (body CFS, control CFS, object CFS). Comparison of accuracy (in percentage) between synchronous and asynchronous conditions did not reveal any significant difference in any of the three experiments (all  $p > 0.40$ ; 95% Confidence Interval bars).



**Fig. 4.** Reaction times and accuracy in experiment 4. Left, reaction times for synchronous and asynchronous conditions for the body and diffeomorphic visual contexts. Right, accuracy for synchronous and asynchronous conditions for the body and diffeomorphic visual contexts (\* $p < 0.05$ ; 95% Confidence Interval bars).

### 3.3.1. RTs

After removing incorrect trials (6.6% of trials) and outlier reaction times (1.75% of trials) we conducted a repeated-measures ANOVA to compare reaction times across conditions. The analysis showed no effect of synchrony ( $F_{(1,17)}=0.8$ ,  $p=0.38$ , n.s.) nor any main effect of visual context ( $F_{(1,17)}=1.11$ ,  $p=0.3$ , n.s.) revealing that the RTs for the new diffeomorphic object image were not longer than in the body CFS condition. Importantly, the interaction between synchrony and visual context was significant ( $F_{(1,17)}=5.49$ ,  $p=0.03$ ,  $\eta^2=0.24$ ) showing that synchrony had a different effect depending on the visual context (see: Fig. 4). We further explored this effect by running planned comparisons for each condition to directly compare the RTs in the body and diffeomorphic object conditions as a function of visuo-tactile synchrony. As predicted, in the body condition RTs in asynchronous condition ( $4719 \pm 1178$  ms) were significantly shorter than in the synchronous condition ( $4936 \pm 1217$  ms 95% confidence interval;  $t_{(17)}=1.89$ ,  $p=0.037$ , one-tailed). In the object condition a trend for the opposite result emerged ( $t_{(17)}=2.01$ ,  $p=0.06$  two-tailed) with shorter RTs in the synchronous condition ( $4793 \pm 1061$  ms) compared to the asynchronous condition ( $5105 \pm 906$  ms). Further analyses using RT normalization procedures yielded similar results (see [Supplementary materials](#) for details). For mean RTs and accuracy in synchronous and asynchronous conditions in body CFS and diffeomorphic object CFS, see Fig. 4. The one-way repeated measures ANOVA including RTs in all experimental conditions (synchronous body/asynchronous body/synchronous object/asynchronous object/visual only) revealed no differences in overall RTs between the multisensory and visual only conditions ( $F_{(4,68)}=0.92$ ,  $p=0.4$ , n.s.).

### 3.4. Accuracy

Overall accuracy in the three conditions was above 90% (body= $94.15\% \pm 2.63$ , diffeomorphic object= $96.19\% \pm 0.59$ , visual only= $98.33\% \pm 2.48$ ). The repeated measure ANOVA revealed no significant main effect of synchrony ( $F_{(1,17)}=0.08$ ,  $p=0.76$ ,  $\eta^2=0.005$ ), no significant main effect of visual context ( $F_{(1,17)}=0.63$ ,  $p=0.43$ ,  $\eta^2=0.003$ ) nor interaction ( $F_{(1,17)}=3.5$ ,  $p=0.08$ ,  $\eta^2=0.17$ ).

## 4. Discussion

The present study investigated the effects of body-related visuo-tactile conflicts on visual consciousness. The results revealed three main findings: (i) body-related visuo-tactile conflicts modulated access to visual consciousness; (ii) this effect depended on the synchrony and the visual context of the stimulation; (iii) the modulation of visual consciousness occurred even when the tactile stimulation was passive and task irrelevant.

Our results indicate that the modulation of visual consciousness by passive visuo-tactile stimulation depends on the synchrony and the visual context. Longer times for conscious access were found when stimulation was synchronous versus asynchronous and presented in the context of a body, while no such suppression was found when the same tactile stimulation was depicted on an object. This suggests that this modulation is stroking-dependent and body-specific. Interestingly, the presence of a bodily context is important for the induction of changes in bodily self-consciousness in both the rubber-hand illusion (Botvinick and Cohen, 1998; Costantini and Haggard, 2007; Ehrsson et al., 2005; Tsakiris and Haggard, 2005) and in the full-body illusion (Aspell et al., 2009; Ehrsson, 2007; Lenggenhager et al., 2007; Petkova and Ehrsson, 2008), since these modulations of BSC are typically found only when the synchronous visuo-tactile stimuli are presented on an image of a body or limb but not a control object. Thus, our present findings extend this effect to visual consciousness, by showing that body-related conflicting visuo-tactile stimulation modulates conscious access to a visual stimulus according to the context in which it is presented. Previous work has already identified some influences of visual bodily information on tactile processing (Cardini et al., 2011; Salomon et al., 2012; Serino et al., 2008). The presentation of a body form is known to enhance the spatial acuity of touch (Cardini et al., 2011, 2013; Kennett et al., 2001) and to reduce the perceived intensity of acute pain (Longo et al., 2009; Mancini et al., 2011; Romano et al., 2014). Here, the visual context in which the visual target was presented (body vs. object) modulated the time to break suppression as a function of the visuo-tactile synchrony. Synchronous stroking (inducing a body-related multisensory conflict – *I feel touch on my back but see synchronous touch on the avatar's back*) compared to asynchronous stroking (without a body-related multisensory conflict) caused longer times to break suppression in the context of a body image. While synchronous stroking on a non-body image (hence without

a body-related multisensory conflict) did not cause an elongation of RTs.

These results show that multisensory perception, that has been proposed to be a key factor for the sense of the bodily self or BSC (Bermúdez et al., 1998; Blanke, 2012; Ehrsson, 2012; Gallagher and Meltzoff, 1996), also affects visual consciousness. Previous studies have shown that BSC arises through the continuous integration of multiple sensory stimuli leading to robust own body representations for BSC (Aspell et al., 2009; Ehrsson et al., 2005; Lopez et al., 2008; Pfeiffer et al., 2013; Suzuki et al., 2013; Tsakiris and Haggard, 2005). Accordingly, conflicting multisensory signals in a visual bodily context as used in the present study are not properly integrated within such body representations and are held to induce bodily illusions for hand, face, or full-body (Apps and Tsakiris, 2014; Costantini and Haggard, 2007; Seth et al., 2011; Tsakiris and Haggard, 2005). Here we show that, the same multisensory conflict producing bodily illusions, in particular those employed in full-body illusions (Ionta et al., 2011; Salomon et al., 2013b) causes visual stimuli to take longer to break into awareness, compared to non-conflicting signals. One interpretation is that there is preferential cortical processing for non-conflicting multisensory signals, even when these are not consciously perceived, which thus facilitates their entrance to awareness. This is in line with several studies showing dominance of such non-conflicting multisensory stimuli in visual awareness (Aller et al., 2015; Alsius and Munhall, 2013; Favre et al., 2015; Lunghi et al., 2010, 2014; Maruya et al., 2007; Salomon et al., 2015; Salomon et al., 2013a).

Contrary to early accounts of visual consciousness and visual information processing suggesting that the visual system is modular and encapsulated (Fodor, 1983; Zeki and Bartels, 1998) and that multisensory integration requires consciousness (Baars, 2002) our results support recent findings (Lunghi and Alais, 2013; Lunghi et al., 2010, 2014; van Ee et al., 2009) showing that tactile information is integrated with visual information and affects conscious access during binocular rivalry (for related work on auditory and olfactory effects on visual consciousness see Conrad et al., 2010; Favre et al., 2014; Zhou et al., 2010). As the visual information presented to the observer was identical in the synchronous and asynchronous conditions the difference in suppression cannot be due to any disparity in the visual stimuli per se, but must be related to visuo-tactile coupling. Previous investigations of visual biases depending on touch have shown that tactile information may play a role for disambiguating visual information (Blake et al., 2004; Butz et al., 2010). For example, Lunghi and colleagues have shown, using binocular rivalry, that active haptic exploration of a tactile stimulus congruent with a current visual stimulus prolonged the maintenance of the visual percept, while incongruent tactile information increased the probability of perceptual switches. Moreover, this effect was sensitive to the specific matching of spatial frequencies between the haptic and visual images (Lunghi et al., 2010). However, our results differ considerably from those of Lunghi and colleagues as we showed that even passive and task-irrelevant tactile stimulation on the back modulates the conscious access to continuously suppressed visual stimuli. Thus, multisensory information is shown to be integrated in the absence of perceptual awareness, often facilitating the experience of congruent crossmodal stimuli.

While the aim of this study was to investigate if multisensory conflicts shown to modulate BSC also affect visual awareness, we also examined if the multisensory conditions affected RTs in relation to unimodal (visual only) stimulation (Exp.4). Previous studies have shown enhanced awareness for congruent multisensory conditions compared to unimodal visual only stimulation (Lunghi and Alais, 2013). Comparing RTs in the multisensory conditions vs. unimodal visual condition in the present study revealed no significant differences, suggesting that the multisensory

stimulation did not enhance or suppress access to awareness per se (Stein, 2012; Wallace et al., 2004) but rather granted a faster conscious access to visuo-tactile signals when they were congruent, and presented in a bodily context. This might be due to the fact that in our design, the tactile stimulation was passively delivered by the robot and task irrelevant. This may reduce facilitation or inhibition related to multisensory processing of the visual and tactile stimuli compared to paradigms using active haptic exploration (e.g. Lunghi and Alais, 2013, 2015). Although congruency effects for passive visuo-tactile stimulation in binocular rivalry were recently reported (Lunghi and Morrone, 2013), the methods of this latter study were very different from the present study and included both passive and active conditions which may have caused residual attention to be allotted to the tactile stimuli even in the passive conditions. Furthermore, in the current study which was based on the FBI paradigm (Ionta et al., 2011; Salomon et al., 2013b) there was no spatial correspondence between visual stimuli (viewed in front of the subjects) and the tactile stimulation (felt on the back) which may have reduced multisensory facilitation and inhibition. Future studies should investigate this issue directly.

In the control experiment (Exp.2) in which the stimuli were displayed to both eyes (no inter-ocular suppression), no difference between the two visuo-tactile stimulation conditions was found. This suggests that the results in the body CFS experiment were not due to a response or detection bias (Jiang et al., 2007; Mudrik et al., 2011; Salomon et al., 2013a). Thus, the present modulation of visual consciousness by body-related visuo-tactile conflicts in the presence of a body form shows that the interactions between visual and tactile signals are important not only for bodily self-consciousness (Ehrsson, 2007; Lenggenhager et al., 2007), but also for the formation of visual consciousness (Blake et al., 2004; Lunghi et al., 2010).

The brain mechanisms by which body-related visuo-tactile stimulation modulates visual consciousness are unclear. Even though no imaging data has been collected in the present study, some speculation regarding the involved cortical mechanisms seems merited. It has been suggested that the integration of multisensory signals underlying bodily self-consciousness, such as body-related visuo-tactile stimuli shown here, are driven by bimodal neurons (i.e. responsive to both tactile and visual stimulation) in premotor, parietal, and posterior temporal regions (Blanke, 2012; Ehrsson et al., 2004; Makin et al., 2007). Such bimodal visuo-tactile neurons have been reported in non-human primates and have been linked to representation of space near the body (Bremmer et al., 2002; Duhamel et al., 1998; Graziano et al., 1997). Neuroimaging in human subjects have shown several brain regions in frontal, parietal, and temporo-occipital cortices, which respond to both tactile and visual stimulation (Calvert, 2001; Cardini et al., 2011; Gentile et al., 2011; Makin et al., 2007). Two candidate regions for such integration of tactile and visual signals are the extrastriate body area (EBA) and parietal regions such as the temporo-parietal junction. The EBA responds to visual images of the body and body parts (Downing et al., 2001) and is, along with the TPJ, part of the network important for bodily self-consciousness (Arzy et al., 2006; Ionta et al., 2011, 2014). This region is also sensitive to the synchrony of visuo-tactile stimulation (Ionta et al., 2011) and sensorimotor conflicts (Astafiev et al., 2004) when projected on a body. Considering that CFS has been shown to impact visual representations at early stages (i.e. primary visual cortex (Yuval-Greenberg and Heeger, 2013)) one could speculate that the bimodal regions described above may play a modulating role on visual consciousness through feedback connections with visual cortex selectively strengthening neural representations of target stimuli and fastening its access to consciousness. However, further studies are needed to determine the neural mechanisms of

tactile modulation of visual consciousness.

## 5. Concluding remarks

Visual consciousness and bodily self-consciousness have been studied in relative isolation with few attempts to test the effect of bodily signals on visual consciousness. Previous work has found that proprioceptive information modulates suppression time in a continuous flash suppression task (Salomon et al., 2013a). Others have shown that in binocular rivalry, tactile stimuli congruent with a current visual percept (Lunghi et al., 2010) as well as voluntarily actions causing changes in visual stimuli (Maruya et al., 2007) prolonged maintaining the percept, while incongruent increased the probability of switching it. Taken together, these studies suggest that bodily and unconsciously processed visual signals can be integrated into multimodal representations, and that signal's congruency facilitates conscious access. Here we extend this by showing that the visual context affects whether a given visuo-tactile stimulation is congruent or conflicting. A body-related visuo-tactile conflict, defined by tactile signals synchronous to an unseen visual stimulus displayed on a visible body image, elicits longer suppression times than the same stimuli presented with no visuo-tactile synchrony. Our results link visuo-tactile stimulation, when presented in the context of a body, to modulation of visual perceptual consciousness, indicating that similar factors affect both visual and bodily self-consciousness and opening the possibility that similar mechanisms underlie both of these effects.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2015.10.034>.

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