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Being in the dark about your hand: Resolution of visuo-proprioceptive conflict by disowning visible limbs

Hinze Hogendoorn[a,b,*,1], Marjolein P.M. Kammers[a,1], Thomas A. Carlson[a,b,c], Frans A.J. Verstraten[a]

[a] Helmholtz Institute, Experimental Psychology Division, Utrecht University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands
[b] Vision Sciences Laboratory, Harvard University, 33 Kirkland Street, Cambridge, MA 02138, USA
[c] Cognitive and Neural Systems, Department of Psychology, University of Maryland, College Park, MD 20742,USA

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ABSTRACT

Conflict between sensory modalities can be resolved by one modality overwriting another. For example, movement of a limb that is visible in a stationary visual afterimage results in selective fading of that limb in the afterimage. We investigated the interaction of these two sensory modalities by inducing a mismatch between visual and proprioceptive hand location. Whereas this discrepancy did not affect the initial appearance of the hand in the afterimage, it did prevent subsequent motion with the hand from affecting the hand's appearance. Location mismatch disconnected the visual and proprioceptive experiences of the hand, "protecting" the visual afterimage from interaction with proprioception. Investigation of subjective higher order bodily experiences showed a strong negative correlation between afterimage disruption and the subjective feeling of ownership, suggesting that the brain can resolve multimodal location mismatch by 'disowning' a visible limb, and that the interaction between proprioception and vision is mediated by higher order bodily experiences.

1. Introduction

Multimodal integration serves not only the ability to localize our body in space (Ernst & Banks, 2002; Graziano, 1999), but also various higher order subjective experiences of our own body, i.e., feeling of embodiment (Costantini & Haggard, 2007; Haggard & Wolpert, 2005; Longo, Schuur, Kammers, Tsakiris, & Haggard, 2008; Tsakiris & Haggard, 2005a). One approach to studying multimodal integration is by means of visual afterimages (Taylor, 1941). When a visual scene is briefly illuminated with a very bright flash after adapting to darkness, a positive visual afterimage can be observed. Because the afterimage is caused by a single bright flash and subsequently viewed in darkness, no new information enters the visual system, and the scene usually appears stationary for about 10 s before it fades. However, even in the absence of new visual input, it is possible to induce selective changes in the afterimage by giving proprioceptive feedback that a body part that is visible in the afterimage is moving. The visual image of that body part then appears to fade or "crumble" in the afterimage (Davies, 1973a; Gregory, Wallace, & Campbell, 1959). Proprioception overwriting visual information is remarkable, since vision is commonly the dominant modality, as demonstrated by compelling illusions such as the rubber hand illusion (Botvinick & Cohen, 1998; Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Tsakiris & Haggard, 2005b).

In the present experiment we investigate this multimodal interaction, while taking into account possible top-down modulation by feeling of agency over a movement, or feeling of ownership over the limb in the afterimage. Participants sat in a dark room and looked at their forearms, after which a bright flash briefly illuminated the visual scene. First, the relative contributions of afferent proprioceptive signals and centrally generated efference copy were investigated by contrasting active and passive movements. If efferent motor signals play a role in the interaction, we would expect greater disruption of the afterimage during active limb movement than during passive limb movement. In a second manipulation, a mismatch between the proprioceptive and visual position of the participant's hand was introduced, by either actively or passively relocating the hand during the brief blind period between the flash and formation of the afterimage. We hypothesized that introducing a mismatch by physical relocation of the limb (altering the proprioceptive input) might make the discrepancy between vision and proprioception sufficiently salient to modulate their interaction. In this case, moving the limb in its original location would cause maximal disruption of the afterimage, whilst relocating the limb would reduce the effect of subsequent movement on the afterimage.

* Corresponding author at: Helmholtz Institute, Experimental Psychology Division, Utrecht University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands. Tel.: +31 30 253 4023; fax: +31 30 253 4511.
E-mail address: j.h.a.hogendoorn@uu.nl (H. Hogendoorn).
[1] These authors contributed equally.

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Participants' main task was to rate the relative clarity of their two hands in the afterimage. Additionally, subjective experiences were assessed by means of a questionnaire, based on the commonly used traditional rubber hand illusion questionnaire (Botvinick & Cohen, 1998; Longo et al., 2008). We manipulated a sense of agency by comparing passive versus active movements, while feeling of ownership was manipulated by relocation movements before the appearance of the afterimage.

2. Methods

2.1. Participants

Nine participants took part in the experiment, of which five were male (age 22–34). All participants had normal or corrected-to-normal visual acuity; eight reported being right-handed and one reported being left handed. Participants were naïve to the rationale of the experiment. All participants reported observing stable afterimages on all trials.

2.2. Apparatus

Participants were seated at a table which was equipped with two movable mechanical arms, which were attached to the table edge at the hinge such that participants could comfortably rest their elbows on the hinges and grasp handles at the end of the two arms. The mechanical arms were designed such that participants could freely move their forearms in both horizontal and vertical planes. All trials started with the participants' hands close to the body midline. Participants' bare forearms were loosely fastened to the mechanical arms (Fig. 1).

The testing room was kept in complete darkness, and the entire apparatus as well as the portion of the room in the participants' visual field was black and non-reflective to ensure that participants' forearms were highly salient in the afterimage. A Speedotron 4803cx (Speedotron, Chicago, IL) flashbulb capable of delivering 2400 J within 1 ms was mounted directly behind the participant, oriented toward the white ceiling such that illumination was diffuse. One experimenter accompanied the participant, making sure that the participant's hands were in the correct configuration at the start of each trial and moving the participant's hands in trials with passive movement (see below). A second experimenter recorded responses and gave instructions about upcoming trials.

2.3. Design

Participants looked in the direction of their hands in total darkness. A brief flash of bright light was then used to induce a positive visual afterimage of the participants' own two hands. The flash was followed by a 1–2 s blind period, after which the afterimage developed, lasting about 6–10 s before fading. The subjective experience of such an afterimage is comparable to looking directly at one's own two hands in a dimly illuminated room. The experimental manipulation was to relocate and subsequently move one of the two hands in one of four combinations of possible hand motion. All motion in a given trial was carried out with one hand (the target hand), and the other hand (the reference hand) remained stationary. Target and reference hand identity was counterbalanced across trials. No direct contact between the experimenter and the participant occurred in any of the conditions.

Relocations were single motions made during the brief blind period after the flash (but before formation of the afterimage), where the participant moved the target hand outwards in the horizontal plane, away from the body midline. Relocation on a given trial could be either active (participants moved their hand away from their body midline themselves), passive (participants relaxed their limb and the experimenter moved their hand away), or absent (leaving both the participant's hands close to the body midline). Since the locations of the hands in the visual afterimage were identical in all conditions, relocating the target hand introduced a discrepancy between proprioceptive and visual information about its location.

Once the afterimage developed, participants repeatedly raised and lowered their target hand until the end of the trial. This *vertical hand movement* could also be made either actively, such that the participant raised and lowered their hand themselves, or passively, such that they relaxed their limb and the experimenter raised and lowered their hand. Although the motion of the hand (and thus the afferent proprioceptive signal about the motion) was therefore highly similar in the two conditions, additional efferent information about the motion was available in the active condition.

Participants carried out trials in the following four combinations of motions: no horizontal relocation followed by active vertical movement (1), no horizontal relocation followed by passive vertical movement (2), passive horizontal relocation followed by active vertical movement (3), and active horizontal relocation followed by active vertical movement (4). Condition 1 served as a critical condition to which condition 2 could be compared to address a possible additional effect of efferent information about limb movement, and to which conditions 3 and 4 could be compared to address visuo-proprioceptive location mismatch.

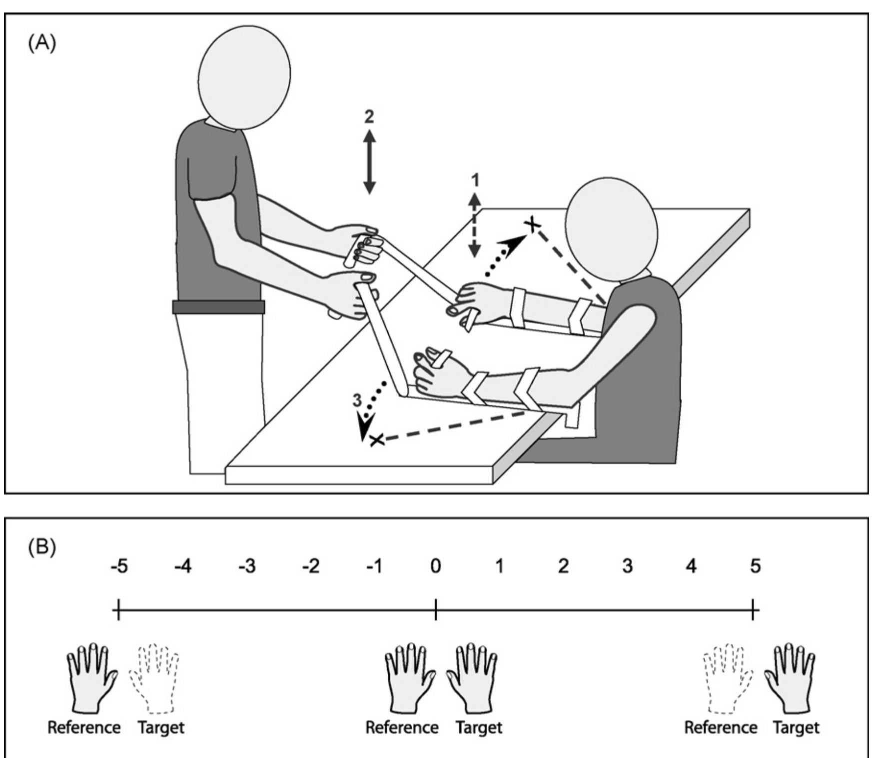

Fig. 1. (A) Experimental setup. The participant sat at a table with his or her forearms strapped to mechanical arms which were hinged at the elbow and could move freely in both vertical and horizontal directions. Vertical hand movements were made either actively (1) or passively (2). To investigate visuo-proprioceptive mismatch, we compared conditions in which the participant's arm either remained in its original position or was passively or actively relocated horizontally (3). (B) Participants rated the relative clarity of their target hand with respect to their reference hand in the afterimage on an 11-point scale.

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Table 1
Questionnaire statements. Participants rated their agreement on a scale from −3 (strongly disagree) to +3 (strongly agree).

During the movement it seemed like
I couldn't really feel where my hand was.
I felt my hand disappear.
I saw my hand disappear.
I was in control of the visible-hand.
I was looking directly at my own hand, rather than at an after image.
I was unable to move my felt-hand.
my felt-hand was numb.
my felt-hand was out of my control.
my hand felt in the location where I saw my hand.
the visible-hand belonged to me.

2.4. Dependent measures

Participants' primary task was to report the relative clarity of the target hand relative to the reference hand in the afterimage at two points in each trial: once directly after the formation of the afterimage and once during the vertical movement of the target hand. The difference between these two reports was taken as a measure of disruption caused by the vertical hand movement. Participants were instructed to incorporate any perceived change in luminance, stability, crispness, intensity, or vividness in their judgment, which was given on an 11-point scale ranging from −5 (the reference hand was much clearer than the target hand) to +5 (the target hand was much clearer than the reference hand).

This relative, within-trial quantification of the qualitative change in afterimage clarity addresses an important problem in the literature. Because participants rated the impression of the moving hand relative to their other, stationary hand, rather than on an absolute scale, each observation had its own baseline. This makes ratings robust to trial-by-trial variations in participants' adaptation state. Progressive dark adaptation over the course of the experiment, in particular, can cause such variation, and many afterimage studies take measures to prevent this (Bross, 2000; Davies, 1973a, 1973b; Gregory et al., 1959).

For each of the four conditions, participants completed a questionnaire consisting of 10 statements about their visual and proprioceptive experience of the target hand. Participants rated their agreement with each statement on a 7-point scale from −3 (strongly disagree) to +3 (strongly agree). The 10 statements were loosely based on a standard rubber hand illusion questionnaire (Botvinick & Cohen, 1998), but carefully worded to specifically probe either the visual or proprioceptive experience. The questionnaire was presented in a random, different order after each block and for each participant (Table 1).

Two of the questionnaire items were of particular interest. The statement "*during the movement, it seemed like my felt-hand was out of my control*" was included to evaluate participants' subjective experience of agency over their hand's movement. The statement "*during the movement, it seemed like the visible hand belonged to me*" was included to evaluate participants' feeling of ownership over the hand in the afterimage. This is in line with the results of Longo et al. (2008), who identified agency and ownership as dissociable aspects of the subjective experience of embodiment.

2.5. Procedure

Before being adapted to total darkness for 10 min, participants received instruction and demonstration of the different motion conditions that would be tested during the experiment. After this initial adaptation period, the experiment began. Aside from the 1 ms flash at the start of each trial, the testing room was kept in total darkness for the duration of the experiment. Conditions were blocked such that participants were tested in four blocks, each consisting of four trials, the order of which was counterbalanced across participants. Target hand identity was pseudo-randomized within blocks. At the end of each block, a questionnaire was conducted verbally and participants rated their agreement with 10 statements concerning their subjective experiences during that block.

Before each trial, participants were instructed which hand was the target hand on that trial, and reminded of the combination of hand motions that was being tested in the block. Participants fixated an imaginary spot in the darkness, approximately between their two hands. A countdown then preceded the flash. On trials with horizontal relocation movement, this movement was made immediately following the flash, in the 1–2 second blind period before formation of the afterimage. Once the afterimage had formed, participants moved their hand *vertically*, and continued moving until the afterimage faded entirely. They then reported their ratings of the relative clarity of the target hand compared to the reference hand *before* the vertical movement and *during* the vertical movement. See Fig. 2 for a sample trial timeline. All experimental manipulations and hand motions were made *after* the flash, and the starting position of participants' hands was the same in all conditions. The visual scene was therefore identical in all trials in all conditions across the entire experiment. Trials were separated by 3 min of top-up adaptation, during which participants were encouraged to verbally describe any additional qualitative observations. The entire experiment took about 90 min per participant.

3. Results

3.1. Active and passive movement – clarity ratings

To address the influence of efference copy on multimodal integration, we compared the two experimental conditions in which no relocation took place, such that participants' two hands remained in their original position. The two conditions differed in whether the subsequent vertical hand movement *during* the afterimage was made passively or actively (Fig. 3A). Differences in relative clarity before and during movement of the target hand were compared using *t*-tests. Movement of the target hand significantly disrupted the visual sensation of that hand in the afterimage, both when the movement was made passively ($t = -5.7$, df = 8, $p < 0.001$) and when it was made actively ($t = -7.8$, df = 8, $p < 0.001$). Importantly, there was no difference between passive and active movement (paired samples *t*-test: $t = -1.7$, df = 8, $p > 0.12$).

Our findings replicate previous findings that moving a limb that is visible in an afterimage selectively disrupts the visual afterimage of that limb (Davies, 1973a), and that afferent proprioceptive information alone is sufficient to induce changes in the visual afterimage (Bross, 2000; Carey & Allan, 1996). The fact that disruption of the afterimage following passive and active movement did not differ suggests that efferent information about the movement of the limb has little or no contribution to the interaction between vision and proprioception, indicating that the effect of movement on a visual afterimage might be driven primarily by the interaction between afferent proprioception and vision.

3.2. Active and passive movement – subjective experiences

A multivariate analysis of variance showed a significant difference between the two passive and active movement conditions on one of the ten questionnaire items: "*during the movement, it seemed like my felt-hand was out of my control*" ($F = 8.233$, df = 1, $p < 0.011$). This statement probed the subjective experience of agency over the limb's movement. When participants actively moved their hand, they disagreed strongly with this statement (mean ± SEM, -2.78 ± 0.14). This disagreement disappeared when participants' hands were moved by the experimenter (-0.22 ± 0.88). No differences were observed on the other nine questions (all $p > 0.135$). The fact that we find a strong difference in the subjective experience of agency in the absence of a comparable difference in afterimage disruption suggests that sense of agency does not play a critical role in the multimodal interaction that we probe in this paradigm.

3.3. Relocation – clarity ratings

Relocation of the target hand during the blind period immediately following the flash, just before formation of the afterimage, was administered to investigate how visuo-proprioceptive mismatch about the location of the hand affected the degree to which subsequent hand movements disrupt the afterimage. To this end, we compared conditions in which the participant's hand was either not relocated, passively relocated, or actively relocated. Subsequent vertical hand movements were active in all three conditions.

Relocation of the target hand had no effect on the initial appearance of the afterimage. There was no difference between the initial appearance of target and reference hands in any of the conditions (paired samples *t*-tests: all *p*-values > 0.07), and no difference between the conditions (one-way analysis of variance: $F = 2.73$, df = 2, $p > 0.08$). In other words, the initial appearance of the two hands in each afterimage was identical in all relocation conditions.

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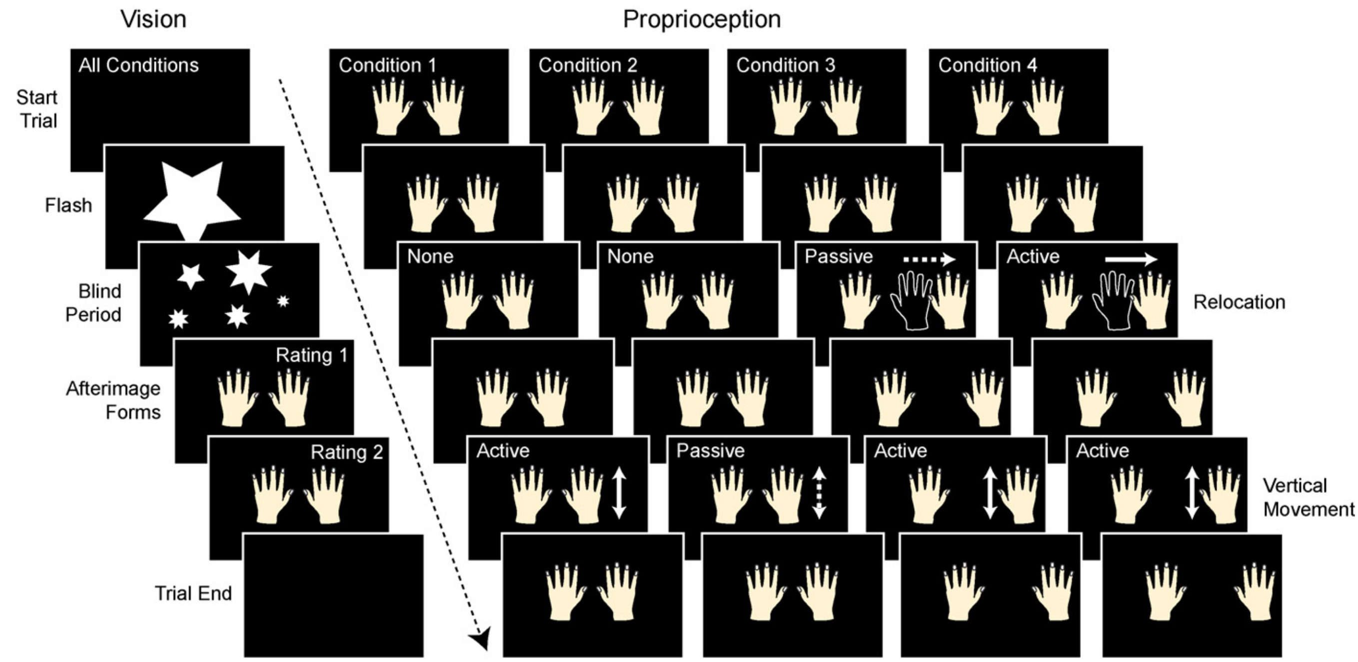

Fig. 2. Timeline of experimental procedure. Trials in all four experimental conditions were visually identical, differing only in the combination of hand movements made after the flash.

Importantly, we were interested in the effect of the vertical hand movement on the visual afterimage, as a function of the preceding relocation movement. A one-way analysis of variance showed a significant effect of relocation on the difference in relative clarity before and during movement of the target hand ($F = 5.89$, df = 2, $p = 0.008$). Specifically, disruption of the afterimage by movement was maximal when the limb was not relocated, reduced when it was passively relocated, and eliminated when it was actively relocated (Fig. 3B; all post hoc comparisons significantly different, $p < 0.038$).

3.4. Relocation – subjective experiences

A multivariate analysis of variance on the 10 questions revealed a significant effect of relocation on one item: "*during the movement, it seemed like the visible hand belonged to me*" ($F = 4.80$, df = 2, $p < 0.018$). This item was included to evaluate the subjective experience of feeling of ownership over the visible target hand in the afterimage. When the target hand remained in its original location, participants indicated modest agreement with this statement (mean ± SEM, 0.77 ± 0.49). However, agreement dropped following passive relocation of the hand (−0.77 ± 0.61), and dropped yet further (to strong disagreement) when relocation was active (−1.77 ± 0.64) (Fig. 3C; all post hoc comparisons significantly different, $p < 0.042$). No differences were observed on the other 9 questions (all $p > 0.195$).

3.5. Relocation – free report

Participants were encouraged to freely describe what they experienced during the previous trial. A commonly reported observation was that moving the target hand up and down in its original location (either actively or passively) caused the target hand to appear to move or "jitter" in the afterimage. Some participants specifically reported that the jitter was in phase with the actual movement of the hand: "*I saw the motion of the target arm in the afterimage that seemed to go more in synchrony with the actual movement, definitely up and down*". Several participants commented on the dissociation between the proprioceptive and visual experience of the hand caused by relocation of the hand: "*The feeling of dissociation was strong; the visual image did not feel like it was attached to my body*

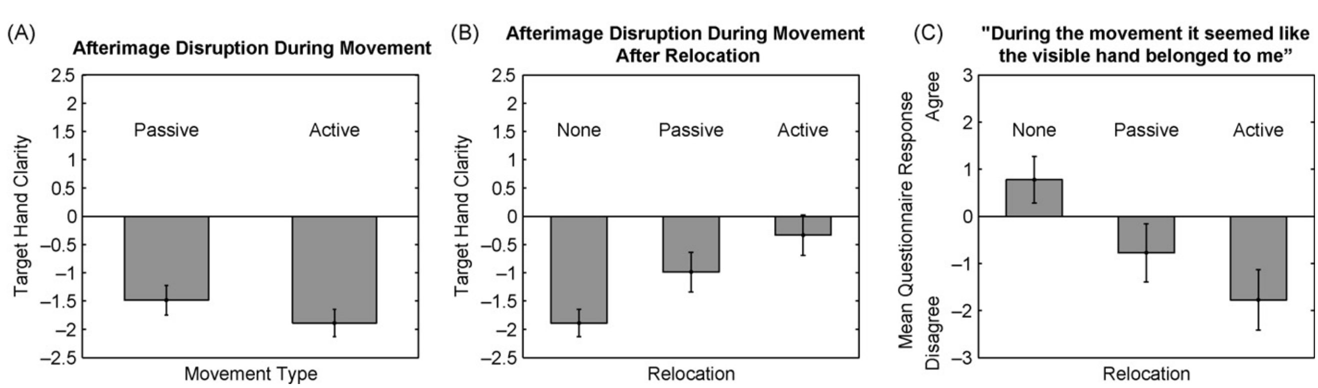

Fig. 3. Results: (A) Disruption of the hand in the afterimage as a result of passive and active movement with that hand. Error bars indicate standard errors of the mean. (B) Disruption of the hand in the afterimage as a result of active movement following either no relocation, passive relocation, or active relocation. Error bars indicate standard errors of the mean. (C) Subjective ratings of feeling of ownership over the hand in the afterimage following either no relocation, passive relocation, or active relocation. Error bars indicate standard errors of the mean.

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or as me". One reported that after relocation, "*the visual afterimage does not seem to be me anymore, because my hand is somewhere else*".

4. Discussion

In the present experiment we investigated multimodal integration of proprioception and vision by means of visual afterimages, taking into account higher order bodily experiences. More specifically, we manipulated (i) active versus passive hand movement to investigate the contribution of efferent signals, and (ii) introduced a discrepancy between the visual and proprioceptive positions of the limb to investigate the effect of position mismatch. Previous studies using similar paradigms have demonstrated that proprioceptive information about the movement of a limb that is visible in the afterimage can affect the appearance of that limb in the afterimage, despite the absence of new visual information, even after inducing a location mismatch between the visual and "proprioceptive" hand (Davies, 1973a, 1973b; Ramsay, Carey, & Jackson, 2007). However, studies using visual afterimages have rarely considered the possible involvement of top-down influences of higher order subjective experiences. Because such influences have frequently been implicated in various bodily illusions in which multimodal integration plays a key role (such as the rubber hand illusion), we probed participants' subjective bodily experiences by means of a questionnaire to explore whether such experiences might mediate the integration of proprioception and vision in the afterimage paradigm.

Disruption of the afterimage as a result of self-motion was similar whether the movement was made actively or passively, suggesting that afferent proprioceptive signals, rather than centrally generated efferent signals, interact with the visual experience. Additionally, questionnaire responses indicated that participants experienced a decreased sense of agency over the limb's movement when it moved passively as compared to when they moved it actively. Since the effect on the visual experience was nonetheless comparable in the two conditions, this result demonstrates that the higher order experience of agency is not necessary for new proprioceptive information to affect the visual afterimage. This is striking, since efferent signals have been shown to be important for several psychological self-concepts, such as self-recognition, movement recognition and feeling of authorship over an action (Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2006; Tsakiris & Haggard, 2005a).

Critically, relocating the limb during the brief blind period immediately following the flash, thereby introducing a mismatch between the proprioceptive and visual location of the hand, weakened subsequent interaction between the two modalities. Whereas movement of the limb in its visual position resulted in strong disruption of its visual appearance in the afterimage, this disruption was much reduced when the limb was passively relocated, and completely eliminated when the limb was actively relocated. This novel result stands in stark contrast to the findings of Ramsay et al. (2007), who introduced position mismatch by means of prism glasses and found the effect of proprioception on the visual afterimage undiminished. However, when using prism glasses the entire visual afterimage is relocated, and the authors report that participants were not able to detect the effect of the prism lenses, indicating that no higher order bodily experiences were affected by the manipulation. Conversely, the relocation manipulation we report is specific to only one hand and did affect the feeling of embodiment: subjective ratings showed that relocating the hand prior to the formation of the afterimage resulted in a decrease in the subjective feeling of ownership over the hand that was visible in the original position in the afterimage.

Together, these findings suggest that it is not visuo-proprioceptive position mismatch *per se* that prevents the two modalities from interacting, but that disruption of the afterimage might be mediated by the higher order experience of feeling of ownership over the visual limb. When the participant's hand is not relocated, such that the participant feels a sense of ownership over the visual hand, a conflict develops as soon as the participant starts moving his or her hand. This conflict between proprioception ("my hand is moving") and vision ("my hand is stationary") is resolved by eliminating the visual representation of the stationary hand. Conversely, relocation of the hand results in an initial location conflict that appears to be resolved by disowning the visual hand. This loss of ownership prevents subsequent movement with the hand from affecting the afterimage, because proprioception ("my hand is moving") and vision ("there is a stationary hand, but it's not mine") are no longer inconsistent.

Additionally, we demonstrated that the degree of disruption of the visual afterimage is dependent on the type of relocation movement. The fact that disruption is significantly weaker following active relocation than following passive relocation suggests that the more reliable the proprioceptive information of the relocation is (i.e., when efferent, as well as afferent, information is available), the less the hand that is visible in the afterimage feels like part of one's own body, and the stronger the disconnection between the two senses. This interpretation is supported by the results from the questionnaire probing participants' subjective experiences: feeling of ownership over the hand that was visible in the afterimage was indeed significantly reduced following active relocation as compared to passive relocation. This correlation between the reduction in feeling of ownership and the reduction of afterimage disruption provides converging evidence that feeling of ownership plays a crucial mediating role in the integration of vision and proprioception.

Interestingly, relocation of the target hand did not affect the initial appearance of the afterimage. The initial appearance of the two hands in each afterimage was identical in all relocation conditions (although there was a trend suggesting a slight decrease in clarity after active relocation, the size of this was effect was very small). This is striking considering that new proprioceptive information *during* the afterimage can overwrite the visual information. Why then would new proprioceptive information available *before* occurrence of the afterimage not affect the initial appearance of the relocated limb in the afterimage?

One reason could be that relocation movements did not cause *temporally coinciding* mismatch between visual and proprioceptive information. The moment new proprioceptive information is made available while the afterimage is visible, the latter is disrupted (if the participant experiences ownership over the visible hand). This hypothesis is in line with the observation that temporal synchrony is crucial for feeling of ownership to occur in the rubber hand illusion (Botvinick & Cohen, 1998). Furthermore, research with prism lenses has shown that although the brain combines proprioceptive and visual information in an optimal way, mutual calibration is not necessary for a coherent percept of the location of the hand (Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006): seeing one's own hand does not immediately lead to recalibration of proprioceptive information, allowing some variation between the two without altering our coherent sense of hand location.

In sum, the present study investigated the integration of proprioception and vision in light of two subcomponents of embodiment: agency and ownership. We showed that feeling of agency is not a necessary condition for hand movement to disrupt the visual representation of a hand in an afterimage, suggesting that afferent proprioceptive signals rather than efference copy mechanisms drive the interaction between proprioception and vision. Importantly, we found that relocation of the participant's hand prior to the formation of the afterimage resulted in reduced (passive relocation) or even eliminated disruption (active relocation) of the afterimage during subsequent continuous proprioceptive update. This finding, linked to the corresponding reduction in the subjective experience of feeling of ownership over the visible hand, suggests that higher order top-down influences mediate visuo-proprioceptive integration. Even with your hand in sight, relocation places it out of mind, such that its outdated visual appearance need not be overwritten by new proprioceptive information.

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