QUANTIFYING SELF PERCEPTION: MULTISENSORY TEMPORAL ASYNCHRONY DISCRIMINATION AS A MEASURE OF BODY OWNERSHIP

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ABSTRACT

There are diffuse and distinct cortical networks involved in the various aspects of body representation that organize information from multiple sensory inputs and resolve conflicts when faced with incongruent situations. This coherence is typically maintained as we maneuver around the world, as our bodies change over the years, and as we gain experience. An important aspect of a congruent representation of the body in the brain is the visual perspective in which we are able to directly view our own body. There is a clear separation of the cortical networks involved in seeing our own body and that of another person. For the projects presented in my dissertation, I used an experimental design in which participants were required to make a multisensory temporal asynchrony discrimination after self-generated movements. I measured sensitivity for visual delay detection between the movement (proprioceptive, efferent and afferent information) and the visual image of that movement under differing visual, proprioceptive, and vestibular conditions. The self-advantage is a signature of body ownership and is characterized by a significantly lower threshold for delay detection for views of the body that are considered self compared to those that are regarded as 'other'. Overall, the results from the collection of studies suggest that the tolerance for temporally matching visual, proprioceptive and efferent copy information that informs about the perceived position of body parts depends on: whether one is viewing one's own body or someone else's; the perspective in which the body is viewed; the dominant hand; and the reliability of vestibular cues which help us situate our body in space. Further, the self-advantage provides a robust measure of body ownership. The experiments provide a window on and support for the malleable nature of the representation of the body in the brain.

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1. GENERAL INTRODUCTION

What is self? The question of the sense of self is a rather broad one. It traverses disciplines, can be interpreted in multiple ways, and has been of interest for centuries. For example, Descartes (1637) once wrote “My body is an integral part of ‘me’, in a way that other objects are not. Moreover, the relation between my body and ‘me’ is quite different from the relation between my body and other people”. Although seemingly simple on the surface, differentiating what is considered the ‘self’ and ‘other’ is still being investigated today. The concept of our body is malleable in nature and adapts to changes and experience. There are also times, for example created in experimental settings, where we may not perceive it as it truly is.

The self, being of cross-disciplinary interest, has a mixed ontology. Although there is a philosophical sense of self, a view that identifies self as “a particular, irreducible thing or mental subject”, herein I will speak to the *bodily* sense of self, a view that identifies self with “some set of bodily or mental processes or states” (Sturm, 2012). There are many ways to view our body. It can be seen as a unique object that interacts with the world, it is where our senses originate, and it provides a set of inherent reference frames for many of our actions/movements. Of particular importance to the experiments I present here, our body is the origin of the first-person perspective and when we move or act in the world we do so in such a way that is established by this perspective. Referencing the first-person perspective can help us visually discriminate our body parts from the body parts of others – the sense of body ownership.

For my research projects, I have used an experimental design in which I measure sensitivity for visual delay detection between a self-generated movement (proprioceptive and efferent copy) and the visual image of that movement under differing visual, proprioceptive, and vestibular conditions. In order to detect such a delay, an observer needs to compare their internal representation of their body with the visual feedback. I thus quantify the sense of body ownership by comparing thresholds to the added visual delay and have established the self-advantage as the advantage one has at detecting the visual delay when what is seen matches the internal representation of the body.

1.1. The sense of agency and the sense of body ownership

There are two basic senses we have about the body: agency and body ownership. The sense of agency is the feeling that one can control and move one's body (Gallagher, 2000; Tsakiris, Prabhu, & Haggard, 2006). It constitutes a central representation of a motor signal (efference copy) as well as sensory feedback (afferent signals) (Farrer, Franck, Paillard, & Jeannerod, 2003b). The sense of body ownership is the feeling that the body is uniquely one's own (Gallagher, 2000; Tsakiris et al., 2006). It makes sense that agency and ownership go hand in hand. For example, if I move my hand I have the sense of being the agent of that movement, and since I am the agent then I must own the hand that is moving. Therefore, there are interactions between these two senses. The sense of ownership and correlating motor activity with the visual feedback is also a contributor to the sense of agency. If my hand is moved involuntarily, however, there is no motor command (efference copy), but there would be visual and proprioceptive information (afferent signals) and one could still experience body ownership if these two modalities are not in conflict.

Agency has been experimentally manipulated by comparing self-recognition of one's movements during voluntarily and involuntarily made movements with added temporal and/or spatial conflict (Daprati, Sirigu, & Nico, 2010; Farrer, Bouchereau, Jeannerod, & Franck, 2008; Farrer, Franck, Georgieff, Frith, Decety, et al., 2003a; Franck, 2001; Jeannerod, 2009; Tsakiris, Carpenter, James, & Fotopoulou, 2010a; Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005; van den Bos & Jeannerod, 2002) in attempts to isolate ownership (difference between efferent + afferent information vs afferent information alone). Tsakiris et al. (2005) demonstrated that the efference copy is important to self-body recognition. The participants in their experiment viewed hand movements made by the experimenter or by themselves wearing gloves (to eliminate any differences in the way the hands looked) on a screen in front of them. They were asked if the movement they saw was their own or not. Participants were more accurate in discriminating self/other movements in the active rather than the passive condition. The authors concluded that since an active movement was judged more accurately the efference copy is important because the reafferent sensory information could be used to compare the movement in both cases. This supports findings by others that efference copy is important for the perception of movements (Farrer, Franck, Georgieff, Frith, Decety, et al., 2003a; Leube et al., 2003).

Taken together, the results from these studies suggest that although multisensory congruency is an important part of sensing ownership it is not sufficient –

to determine what is and what isn’t a part of our body, we must compare what is presented to us with a pre-existing representation of our body.

1.2. The representation of the body (or body schema)

From the early 1900s the term “body schema” has been used to describe the representation of our body and has placed an emphasis on proprioception and touch in describing how the brain processes the body (Head & Holmes, 1911). In the literature, this term has also been used interchangeably with body image (Longo, Schuur, Kammers, Tsakiris, & Haggard, 2009), corporeal awareness (Berlucchi & Aglioti, 1997), the bodily self conscious (Aspell et al., 2013; Lenggenhager, Tadi, Metzinger, & Blanke, 2007), or postural schema (Longo, Azañón, & Haggard, 2010). There has been much debate over terminology, however, all the terms equate, to some extent (see Berlucchi & Aglioti, 2010 for a review of the body schema and the differences in popular terminology), to a representation of the body that we have in the brain. Feeling, seeing, moving, and interacting with our body in and with the world develops our body representation. Updating the schema is thought to involve an updating the relationship of our posture and position of the limbs relative to our other body parts. Therefore this representation must be dynamic in nature and must relate our body not only in terms of the relation between its various parts but also relative to the space around us. Locating oneself in space (self-location) is important because we use our body as a reference when interacting with objects and other people in the environment (Lopez, Halje, & Blanke, 2008).

The body schema can be broken down into components (Longo et al., 2010). These components are: (1) Somatosensation, which is defined as “primary sensory processing of somatic stimuli” (Longo et al., 2010) and happens in the primary somatosensory cortices (Kaas, 1983) ; (2) somatoperception, which is defined as “higher level percepts of the body and objects contacting the body” (Longo et al., 2010); and (3) somatorepresentation, which is defined as “abstract knowledge, beliefs, and attitudes about bodies generally and one’s own specifically on-line perception and off-line representation of the body” (Longo et al., 2010). Of key importance to the experiments that I present in this dissertation is somatoperception. Somatoperceptual information processing is the combination of efferent commands, and tactile and proprioceptive afferent inputs to create representations of the posture of the body (or postural schema), the sense of touch on the body surface (or superficial schema), and body shape and size.

1.3. Non-visual cues for constructing the body in the brain

The somatoperceptual inputs to the representation of the body include somatosensory (tactile) and proprioception information. These inputs provide information that helps to locate stimuli on the skin’s surface, judge the size and shape of body parts, and locate the body in space. They are fundamental to being able to move about the world and to recognize what is the self and what is not self.

The sense of touch has a long history and was regarded by Bishop Berkeley (1732/Gallace & Spence, 2014) as the “primary source of sensory information” – without which vision could not work. The skin has a somatotopic representation in the brain, which means that body parts that are near each other on the body are represented near each other in the brain. This somatotopic organization is mapped onto the superficial schema (the representation of the body's surface) (see Medina & Coslett, 2010 for a review). The sense of touch is uniquely our own – stimuli touching our skin cannot be felt by others. The accuracy of perceived size of our body parts has been shown to correlate with the sensitivity of the body part (Longo & Haggard, 2011; Weber, Ross, & Murray, 1996). When afferent information is altered, for example by using anesthesia to numb a finger, the perception of the size of the body part is altered and the estimation of the actual size becomes less accurate (Gandevia & Phegan, 1999). Further, simply vibrating muscles on the arm can alter the perceived size and shape of it (Goodwin et. al., 1972; Lackner, 1988). This suggests that the representation of the body can be quickly changed by acute changes in tactile/afferent information concerning the body-- even in the absence of vision and implies that tactile information is crucial to forming the representation of the body in the brain.

We also need to be able to determine the location of our limbs in space to execute movements and maneuver about the world. In order to determine where the limbs are in space information from the joints and muscles and vision are combined resulting in an estimate of where "I" am in space (Graziano, 1999). The postural schema is used to help in the perception of "the current posture of the body" (Longo et al., 2010). When sighted individuals are asked to locate limbs in space without being able to see the arms performance is poorer when the arm is moved passively (when efferent information is not available), than when the arm can be seen (Mather & Lackner, 1981).

Efferent information, and possibly the sense of being the agent of the movement, provides vital information about the posture of the body when we cannot see the body (Farrer, Franck, Paillard, & Jeannerod, 2003b; Leube et al., 2003; Mather & Lackner, 1981). Given that multiple senses provide different types of information about the same body, it seems likely that the posture of the body can also affect tactile perception on the skin. For example, when the hands are crossed it is more difficult to determine touch position and the timing of touches (Shore, Spry, & Spence, 2002). However, this is not the case for individuals who have been blind since birth who do not exhibit this crossed arms effect (Röder, Rösler, & Spence, 2004).

So the somatoperception of the body schema combines tactile (superficial schema) and proprioceptive (postural schema) information, but it also must take into account visual information/visual experience of the body. When asked to detect the position of our limbs in the dark without visual input we have trouble doing so accurately (Graziano, 1999; Làdavas, Farnè, Zeloni, & di Pellegrino, 2000). This is especially the case when an arm is moved passively to a new location. The lack of a motor command seriously hinders our ability to accurately detect arm position. When a light, however, is attached to the hand the ability to detect arm position improves (Mather & Lackner, 1981). A proprioceptive map of the body could therefore be expected to be of poor resolution and visual-proprioceptive matching to be broadly tuned. Further, when non-informative vision of the arm is available in two-point tactile discrimination there is a significant improvement in spatial resolution (35mm instead of 42mm) suggesting a case for vision in the construction of the representation of the body

(Röder et al., 2004).

Thus we can see that the knowledge of our body is improved by vision of the body. Normally we see the body only from a first-person perspective. What are the implications of this?

1.4. Visual cues for constructing the body in the brain

Another part of somatoperception is the body image. The body image is “a conscious, essentially visual, representation of the body in its canonical position” (Longo, Cardozo, & Haggard, 2008). The canonical position (see Figure 1A) is the default posture of the body that has been postulated to be a statistical estimate of what the most likely position of the limbs with respect to the trunk would be (Bremner, Holmes, & Spence, 2012). This canonical posture is most likely represented in the brain from the first-person perspective (see Figure 1B for an example of a first-person view of the body) – a perspective that is uniquely ‘self’.

A)

B)

Figure 1. A first- person view of the body. A) The canonical posture of the body as seen from the first-person perspective modified from Harris et al., 2015; B) Self-Portrait by Ernst Mach, 1886 (available freely online publicdomainreview.org/collections/self-portrait-by-ernst-mach-1886/).

1.4.1. Neural distinction between the ‘self’ and ‘other’

Being able to distinguish what is not your body is important for determining what is your body. We can visually discriminate ourselves from others, at least from certain views, but how general is this skill? In the literature, the focus has primarily been on face recognition (Gillihan & Farah, 2005). On a cortical level, researchers have identified areas of the brain, through neuroimaging techniques, which are related to face recognition in the inferior occipital gyrus of the occipital lobe, the fusiform gyrus of the temporal lobe and the posterior superior temporal sulcus of the temporal lobe (Pitcher, Walsh, & Duchaine, 2011) and specifically one’s own face in the right hemisphere (van Veluw & Chance, 2013).

There has been a surge in the literature in the exploration of body recognition networks in the brain in recent years. Single cell recording studies in non-human primates have provided evidence for neurons that respond when monkeys are shown images of bodies and body parts (humans and monkeys). Others have found cells in the superior temporal sulcus that code for body postures and actions (Oram, Perrett, & Hietanen, 1993; Perrett et al., 1985).

Discovery of the extrastriate body area (EBA) in the lateral occipitotemporal cortex (Downing, Jiang, Shuman, & Kanwisher, 2001), through neuroimaging techniques with human subjects, has provided a major development in the role of the visual system in the creation of the body representation in the brain. The EBA is selective for human body parts regardless of whether they are presented as photographs, line drawings, stick figures, silhouettes, or still images depicting bodies in motion (Peelen & Downing, 2007). The EBA is not significantly activated for object parts, whole objects, and scrambled control versions of the stick figures. Responses to parts of faces and to mammals show an intermediate level of activation (Peelen & Downing, 2007). This suggests that bodies are distinguishable from other objects in the world and are visually processed with a distinct neural mechanism.

The EBA had been researched primarily using images of bodies and body parts presented in the allocentric perspective. In other words, the images presented were shown to observers in a visual perspective incompatible with ownership of the body or the body parts. Considering the first person perspective is an important vantage point for constructing a body representation, Saxe and colleagues (Saxe, Jamal, & Powell, 2006) looked at whether areas of the brain activated for images of the body were modulated by 'self' perspectives and 'other' perspectives. They looked at the differences in EBA activity between body parts presented in a 'self-congruent' perspective and an 'other' perspective; other areas in the frontal, and parietal cortices were also examined. The right EBA was more active during the presentation of body parts shown in the allocentric perspective and the right dorsal lateral prefrontal cortex (DLPFC) and the post-central gyrus (PCG) were more activated for body parts shown in egocentric viewpoints. Their results coincide with findings from Chan and colleagues (Chan, Peelen, & Downing, 2004) who proposed that the EBA was activated in "social vision". Here, seeing the body in an allocentric perspective would represent social vision. Further, Hodzic and others (Hodzic, Muckli, Singer, & Stirn, 2009) also conducted a neuroimaging study and provided results that complement the study above, where there was a specific distributed network, including parietal and frontal cortex, that was involved when looking at or recognizing one’s own body. What does this suggest? Although bodies are seen as unique objects to us, there is a clear separation of the cortical networks involved in simply seeing a body that could be one’s own (DLPFC and PCG) or that could be another person (EBA) (See Figure 2). However, this can only be true for the relatively small part of our body that can be seen directly.

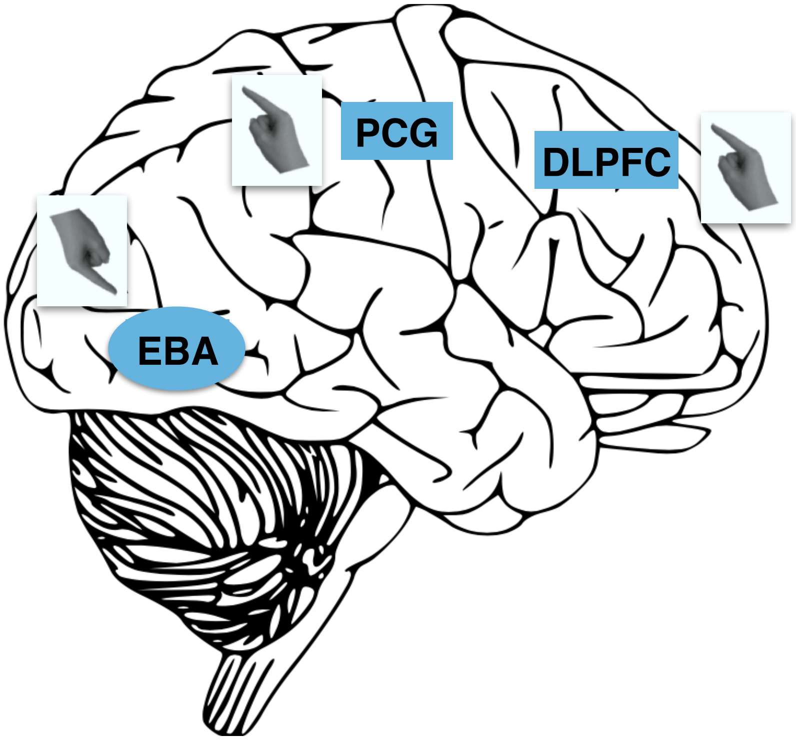

Figure 2. Areas of the brain activated for visual body recognition. The right EBA is activated for the presentation of bodies or body part shown in an allocentric (or other) perspective. The PCG and DLPFC are activated for the presentation of bodies or body parts shown in the egocentric (or self) perspective.

1.4.2. Behavioural distinction between ‘self’ and ‘other’

In a recent study, Conson and colleagues (2010) looked at the ability of individuals to recognize their hands in egocentric (or self) and allocentric (or other) perspectives. They recruited left- and right-handers for the study and showed them images of their own hands and the hands of others in the two differing perspectives. Participants were then asked to make self/not-self judgments as quickly as possible. Importantly, both the dominant and the non-dominant hands of the participants were presented. They found that in the egocentric perspective individuals were more quickly able to recognize their dominant hands compared to the allocentric perspective. The authors referenced the Body Specificity Hypothesis, which states that since we interact with the environment primarily with our dominant hand we would create specific representations of “action- and body-related information” centred on that hand (Casasanto, 2009; Willems & Hagoort, 2009). Therefore, the lowered response times for identifying the dominant hand presented in the expected first-person perspective is most likely due to the fact that it matches the internal representation of the body. This could provide behavioral support for past neuroimaging research claiming that left and right handers have different patterns of activation for areas of the visual cortex that are specifically related to body/ they found a lateralization in activity in this area (Willems, Hagoort, & Casasanto, 2010a; Willems, Peelen, & Hagoort, 2010b).

What happens when we introduce changes of visual perspective during an action control task? Sutter and Musseler (2010) looked at whether the visual perspective in which participants viewed themselves making small finger movements to targets affected their performance. When the perspective changed between trials, the participant must monitor the discrepancies between the tactile/proprioceptive feedback and the visual feedback. Self –perspective movements were identified 89ms faster at moving to the target than when the movements were seen in a perspective reflected about the y-axes. The authors therefore suggested that the participants primarily used visual information, but relied on proprioceptive information when it facilitated the task. Previous studies investigating self recognition during active movement have found misattribution of hand movements to another agent when the participants' movements and the other agents' movements (superimposed over top of their movements) were similar and, in some instances, when there were discrepancies between the movements (Jeannerod, 2003; Fourneret & Jeannerod, 1998; Nielsen, 1963). These results suggest the importance placed upon visual cues when making self/other judgements.

The data from these two experiments provide evidence for the effect of visual perspective for body part recognition and during action control, and suggest a possible quantitative measure for body ownership that I will build on as part of this thesis. Up to this point I have discussed the contributions of vision, somatosensation and proprioception in the construction of the representation of the body, but what about the vestibular system? The vestibular system provides us with the most basic sense of our orientation in space and keeps us upright when moving about the world.

1.5. Vestibular cues for constructing the body in the brain

The literature on the ‘self’ has just recently started to consider the vestibular system as playing an important role in the representation of the body. It is not unreasonable to think that changes in vestibular input would alter feelings about the body. Starting at the beginning of the last century 1905, there have been reports of distorted percepts of the body by patients with lesions that affected vestibular regions of the brain (Bonnier, 1905). The vestibular system provides information as to the orientation of the body with respect to gravity, and thus is important for deciphering where the body is located in space. Directly relevant to the experiments in my dissertation is that patients with vestibular disorders have reported that they experience a lessened sense of agency (Sang, Jáuregui-Renaud, Green, Bronstein, & Gresty, 2006) and ownership (Lopez et al., 2008; Lopez, Bieri, Preuss, & Mast, 2012a).

In the laboratory, experimenters have induced vestibular disruption with either galvanic or caloric vestibular stimulation resulting in the decreased ability to locate limbs in space (Bresciani, Blouin, Popov, & Bourdin, 2002) and altered awareness of the size and shape of our hands (Ferrè, Vagnoni, & Haggard, 2013). Most interestingly though is the increased susceptibility to multisensory illusions of body ownership (see section 1.6.) (Lopez, Lenggenhager, & Blanke, 2010). Taken together, vestibular inputs provide crucial information with respect to self-location, body shape, and body ownership that help create and maintain a coherent representation of the body.

1.6. The multisensory body

As discussed above, the representation of the body, combines tactile, proprioceptive, visual, and vestibular information. It is multisensory experience, therefore, that shapes the body schema (Melzack, Israel, Lacroix, & Schultz, 1997). One of the more current definitions of the body schema is that there are “multiple integrated representations of organized models of ourselves” (Astafiev, Stanley, Shulman, & Corbetta, 2004; Longo et al., 2010) which are created through the combination of proprioceptive, haptic, visual (Serino & Haggard, 2010), and more recently thought to include vestibular signals (Ferrè et al., 2013). Activity in the visual body areas in the brain (e.g., the EBA), for example, has been correlated with limb movement (Astafiev et al., 2004) providing a neural substrate for the interconnectivity of sensory and motor information.

An excellent way to assess the contributions of multisensory input in the creation of the representation of the body is by way of illusions that result from experimentally created conflict between vision, proprioception, and tactile information.

1.6.1 Rubber hand illusion

The Rubber hand illusion (RHI) is a consistently replicated illusion that takes advantage of the multisensory nature of the body schema as it introduces conflict between visual, tactile and proprioceptive information (Armel & Ramachandran, 2003; Botvinick & Cohen, 1998; Costantini & Haggard, 2007; Holmes & Spence, 2005; Makin, Holmes, & Ehrsson, 2008; Tsakiris & Haggard, 2005b; Zopf, Savage, & Williams, 2010).

Interestingly this illusion challenges a participant's sense of body ownership (Botvinick & Cohen, 1998).

Generally, participants are seated with a rubber hand in front of them and beside their real hand, which is hidden from view. The experimenter stimulates the unseen, real arm and the seen, fake arm together with a brush synchronously. After prolonged exposure to the tactile stimulation, participants begin to feel a sense ownership toward the rubber arm (Botvinick & Cohen, 1998). The correlation between the *seen* and *felt* experience leads people to associate the two and assume that they are both coming from their own body.

In a review paper, Tsarkiris et al. (2010) broke down the illusion and proposed a neurocognitive model of body-ownership. Initially, the observer sees the rubber hand and makes a comparison between it and the stored body model (representation of the body in the brain or schema). This body model contains information about the body's structural and visual form, which obviously does not include the rubber hand. Secondly, there is a comparison of the posture of the rubber arm and the current plausible posture of the real arm (body state), which adds a probability that it could be part of your body. Thirdly, there is a comparison between the touch that is felt on the real arm and the touch that is seen on the false arm. The comparisons repeat until "conflict" is resolved (touch referral) and body ownership is sensed or until the information being compared changes. This experimentally induced ownership, however, is dependent on a few things: 1) posture of the dummy arm (anatomical plausibility) (Holmes & Spence, 2007), 2) temporal synchrony of the seen and felt stoking(Bertamini, Berselli, Bode, Lawson, & Wong, 2011; Botvinick & Cohen, 1998; Shimada, Fukuda, & Hiraki, 2009a), (3) ‘realness’ of the dummy hand (Haans, IJsselsteijn, & de Kort, 2008; Press, Heyes, Haggard, & Eimer, 2008; Tsakiris, 2010).

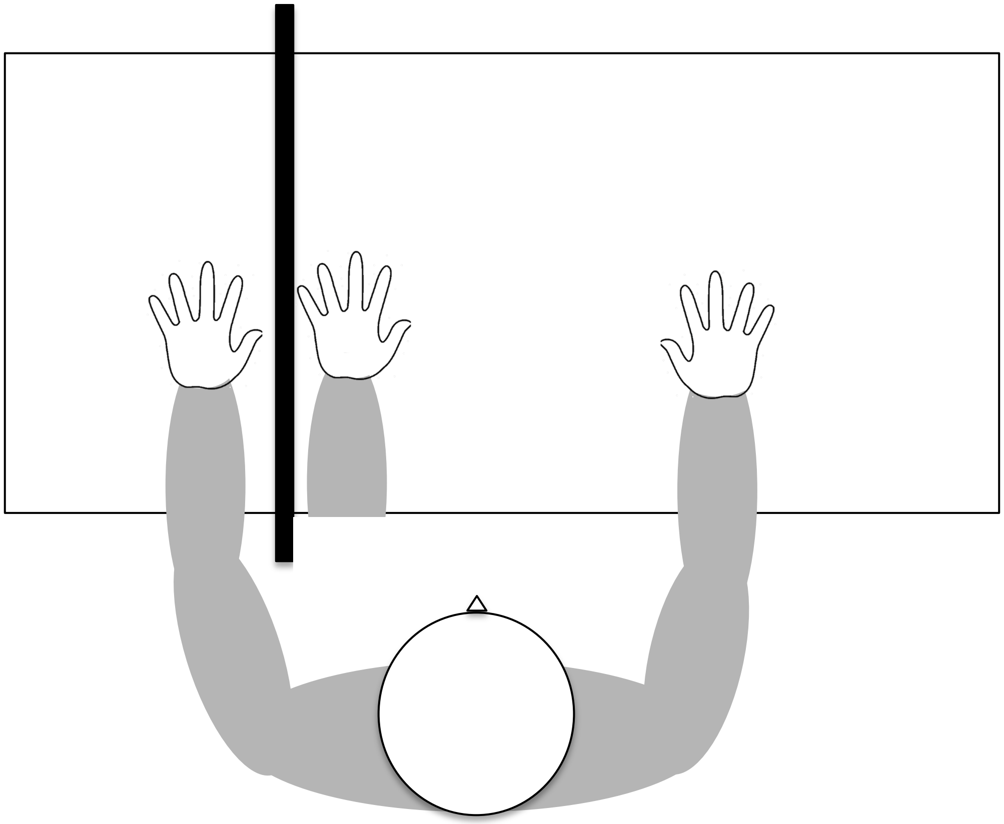

Figure 3. The rubber hand illusion (RHI). In the RHI a participant is seated in front of a dummy hand with one of their hands hidden from view by a screen. The experimenter strokes the real hand and the dummy hand with a paintbrush at the same time. When 1) the hand is placed in an anatomically plausible position, 2) the stroking of the hand and dummy hand are in synchrony, and 3) the dummy hand resembles a real human hand the participant will feel a sense of body ownership over the dummy hand.

Quantification of the outcome – the extent of body ownership – is not straightforward. In order to assess body ownership during the RHI one of three types of measures are typically used. Firstly, researchers tend to rely on a scaled questionnaire measure to assess the extent to which someone feels like the rubber hand is theirs. Many of the questionnaires are adapted from Botvinick and Cohen's (1998) original study which asked participants to rate nine statements about their hand and the rubber hand after prolonged synchronous (or asynchronous) stroking such as: "It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched", "it seemed as though the touch I felt was caused by the paintbrush touching the rubber hand" and "I felt a if the rubber hand were mine." Obviously these are all subjective opinions and as such are vulnerable to suggestibility, trying to please the experimenter, etc. Secondly, the perceived location of the participant's real arm is measured and if the illusion was induced participants tend to feel as though their real arm is closer to that of the rubber hand than it actually is: a phenomenon that has been called proprioceptive drift (Tsakiris, 2010). Thirdly, physiological responses to threat of the dummy hand (such as stabbing it or hitting it with a hammer) have been recorded and when there is a sense of ownership over the dummy hand participants show changes in galvanic skin response (Hägni et al., 2008). Regardless of the type of experimental measure used, researchers have interpreted the results as indicating that the rubber hand was at least partially and temporarily incorporated into the participant's body representation or body schema. The RHI demonstrates successful transfer of ownership to a part of the body, but what about ownership of whole bodies?

1.6.2. Full body illusions

Building upon the RHI, full body illusions use similar multisensory stimulation in order to probe the sense of ownership over a virtual body (Lenggenhager et al., 2007), mannequin, or the participant’s real body presented in an allocentric perspective (Blanke & Metzinger, 2009; Ehrsson, 2007; Lenggenhager et al., 2007). In the more well known “out of body” illusions (Blanke & Metzinger, 2009; Ehrsson, 2007; Lenggenhager et al., 2007) experimenters manipulated visual perspective. Cameras and virtual reality displays were arranged to allow subjects to view themselves from a third person perspective (note that this therefore breaks one of the principles of the RHI). The experimenter then tapped either the back or the chest of the subject with a rod (not in the view of the subject) and ‘tapped’ the back or the chest of the body of the illusory ‘other’ person by making the movement in front of the cameras. Skin conductance responses were recorded while a threat was made to “other body” (the body they see in the third person perspective) after synchronous and asynchronous tapping, body ownership questionnaires were filled out, and proprioceptive drift was calculated (Blanke & Metzinger, 2009; Ehrsson, 2007; Lenggenhager et al., 2007) . The results showed that there was a greater skin conductance response during the synchronous condition, along with greater sense of body ownership and locating the perceived body closer to the ‘other’ body than it actually was. This reinforces the importance of temporal alignment during ownership illusions and how experience alters body ownership.

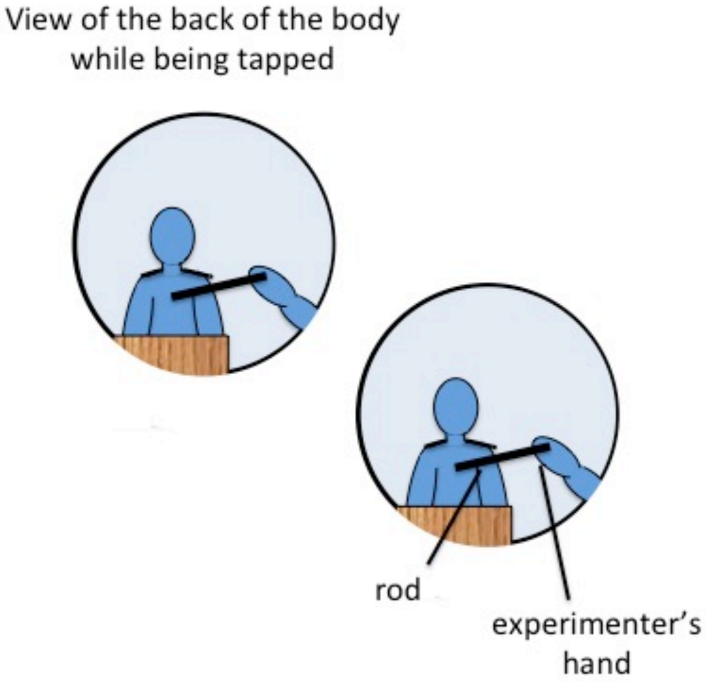

Figure 4. Full body illusions. Participants were tapped with a rod while viewing their body from a third-person or 'other' perspective. Synchronous seen and felt tapping induces illusory ownership over this perspective as reported by questionnaires, proprioceptive drift measures and skin conductance (Blanke & Metzinger, 2009; Ehrsson, 2007; Lenggenhager et al., 2007).

There have been many variations of this illusion produced with parts of whole bodies (Petkova et al., 2011), virtual bodies, and mannequins (Petkova & Ehrsson, 2008). The manipulations in all of these studies provide evidence for the following: 1) the first person perspective is highly influential in determining the location of self in space because seeing oneself in a third person perspective does not elucidate feelings of self until multisensory stimulation is applied while seeing oneself in the third-person perspective; and 2) that the representation of the body is highly malleable and can update and adapt through experience (integration of visual and tactile information in the creation of the representation of self) to incorporate a new perspective as self .

1.6.3. Neural evidence for a multisensory representation of the body in the brain

The multisensory illusions discussed in the previous section rely on the artificial binding of visual, tactile and proprioceptive information concerning the body mimicking the correlation that is normally experienced during the normal development and maintenance of a body representation. When synchronous touch is applied to a seen body part for a short while, there is an undeniable feeling of ownership over said body part and potentially the whole body (Petkova et al., 2011). Neuroimaging studies during multisensory illusions have shown activation in multisensory areas of the brain such as the left ventral premotor cortex, intraparietal cortex, and the temporo-parietal junction Petkova et al., 2011; Petkova & Ehrsson, 2008; Makin, Holmes, & Zohary, 2007; Gentile et al., 2015; Bekrater-Bodmann, Foell, & Kamping, 2011; Ehrsson, Holmes, & Passingham, 2005) suggesting a network of areas that are important in maintaining the representation of our whole body in the brain (See Figure 5). The temporo-parietal junction (TPJ), in particular, has been associated with the first-person (egocentric) perspective in neuroimaging studies (De Ridder, Van Laere, & Dupont, 2007; Ionta, Martuzzi, Salomon, & Blanke, 2014; McCleery, Surtees, Graham, Richards, & Apperly, 2011). Therefore not surprisingly, it has also been correlated with self/other discrimination (Farrer, Franck, Georgieff, Frith, Decety, et al., 2003a). Considering the importance of the egocentric viewpoint in constructing the representation of our body it makes sense that the TPJ plays a role in both. Ionta and colleagues (2014) looked at the brain networks involved in self-location and the first-person perspective and found that the TPJ receives input from intraparietal, occipitotemporal, supplementary motor, and premotor areas in the brain providing evidence for multisensory integration in this area. Further, information from the visual and the vestibular systems, in particular, come together and help us to locate our body in space (Blanke & Metzinger, 2009).

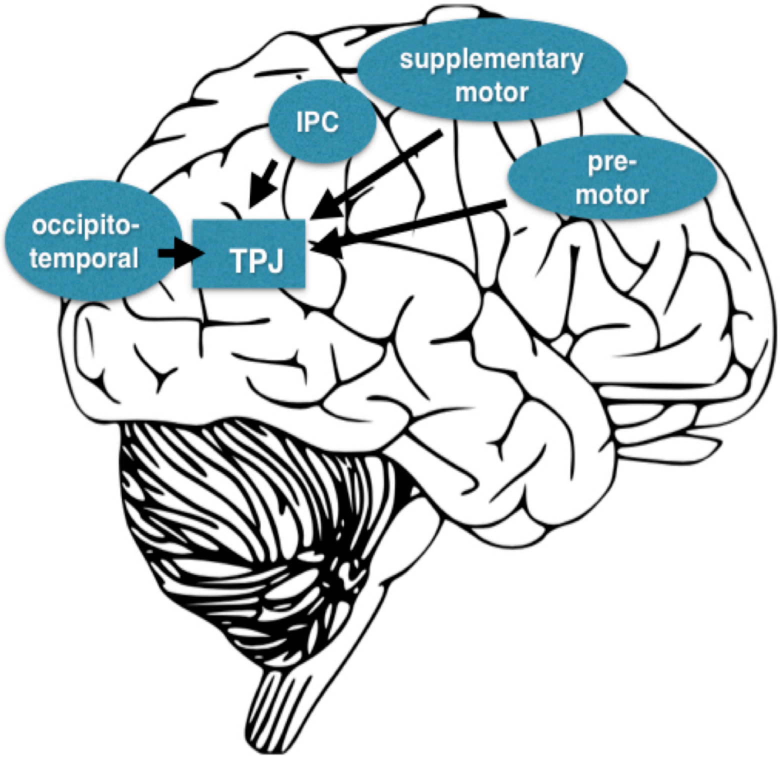

Figure 5. Multisensory brain areas involved in the representation of the body in the brain: The premotor cortex, intraparietal cortex (IPC), and the tempo-roparietal junction (TPJ). The TPJ receives input from various areas in the brain (as depicted by the arrows) corresponding to different senses.

In summary, the TPJ, along with areas such as the posterior parietal cortex, is where multisensory integration of the senses – visual, proprioceptive, auditory, tactile and vestibular – become coherent representations forming a body-centered reference system (Andersen & Buneo, 2002; Avillac, Denève, Olivier, Pouget, & Duhamel, 2005; Azañón, Longo, Soto-Faraco, & Haggard, 2010).

1.7. Purpose

Given the literature reviewed in the sections above, we can conclude that we have a flexible representation of the body in the brain that can, to some extent, be manipulated using artificial cross-modal correlations in neurologically intact adults. Also, brain areas involved form a multisensory network that appears to be the neurophysiological basis. The purpose of the experiments in this thesis was to test and quantify the concept of 'self', by way of the sense of body ownership. This was achieved by manipulating visual, proprioceptive, vestibular, and tactile information. I will quantify the sense of body ownership using a temporal asynchrony detection task (described below), which does not explicitly require participants to consider any aspect of their perception of self. This is therefore a more objective measure of body ownership than simply asking someone if something is perceived as being part of their own body. The task introduces a delay in the visual feedback concerning a voluntary movement made by participants and requires them simply to detect the delay under various conditions.

1.8. General method: Interval forced-choice temporal asynchrony detection under varying visual perspectives

In order to overcome the subjective or possibly biased nature of some of the previous techniques that have been put forward to assess ‘self’ I used an objective psychophysically robust method (two interval forced-choice; 2IFC) where I measured the ability of participants to detect small asynchronies between what was felt and what was seen during a self-generated movement. The displayed movements were subject to temporal manipulation (e.g., adding time delays to the presented live video images) and spatial manipulation (e.g., flipping the presented live video images).

1.8.1.Temporal congruency and the self

Interpreting different sensory modalities as belonging together (or as one event) requires that they happen within a certain temporal window (Spence, Pavani, Maravita, & Holmes, 2004). Temporal congruency promotes binding of the visual, proprioceptive, and efferent signals associated with a self initiated movement. Coherence is therefore an integral factor in creating a sense of self (Gallagher, 2000; Tsakiris et al., 2006). This is a key reason why some multisensory illusions are so powerful – they exploit temporal congruency during the stimulation phase. In the RHI, for example, synchronously seen and felt stroking on the rubber and real hands creates the illusory effect of ownership (Botvinick & Cohen, 1998; Shimada, Fukuda, & Hiraki, 2009). However, when the seen and felt touches are separated in time (more than 300ms; Shimada, Kukuda, & Hiraki, 2009; Bekrater-Bodmann et al., 2014) the illusion is degraded. This is consistent with others who have found that if tactile and visual stimuli happen within a 200ms window we tend to accept that they correspond to a single event (Tipper et al., 2001). In a delay detection task during passive and active movements, Shimada et al. (2010) found that asynchrony was best detected during active movements. During active movements, participants identified the movement as their own only when the visual delay of the presented movement was less than 150ms. This is a considerably shorter delay than the delay needed for the RHI to work (around 300ms; Shimada, Kukuda, & Hiraki, 2009; Bekrater-Bodmann et al., 2014) and most likely due to the available extra efferent information making the system more precise and demanding.

In my experiments I used self-generated movements and varied the amount of added visual delay from approximately 30 to 350ms. This range of delay captures both of the thresholds mentioned above for associating the movement (or body part) as self and extends to temporal delays that would not be associated as self.

1.8.2. Spatial congruency and the self

Just as temporal congruency is an important cue that information from multiple sources should be packaged together, spatial congruency is also an important feature. Even if two pieces of information arrive at the same time, they should probably not be treated as belonging together if they originate from widely separate locations. Not only does the ability to identify static images of one’s body parts and to move one’s hand accurately to a target get degraded if the movements are seen in an incompatible or implausible perspective, but so does the efficacy of the RHI (Costantini & Haggard, 2007; Holmes & Spence, 2007). Being presented with visual stimuli (e.g., hands and bodies) in ergonomically or spatially relevant positions with respect to our own body is important in feeling the sense of ownership over the stimuli. When vision is available to us we compare vision with our other senses. For example, Franck et al. (2001) found that as long as a visual presentation of a hand and arm was within a +/- 15deg rotation from the actual arm then it was still identified as one's own arm.

In my experiments I present participants' movements seen in different visual perspectives. These perspectives were achieved by flipping the presentation of the hand or body about the x- and/or y-axes (See Figure 6 for examples of the hand). If a rotation of more than 15° away from the actual position of the hand is enough to make someone not identify with the hand as theirs (Franck, 2001), any visual manipulation of the images introducing this amount of discrepancy (e.g., flipped by 90° around one of the axes) should then be considered 'other'. Further, as described in section 1.4.1. and 1.4.2., inverting the image of the hand produced differences in self/other performance and differences in brain activation.

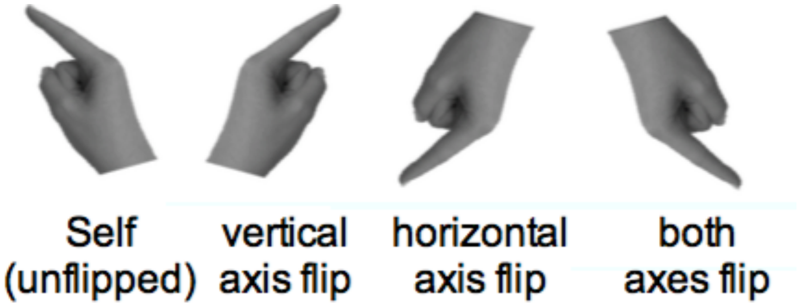

Figure 6. Examples of a right hand in the different visual perspectives. In my experiments participants are shown body parts in varying visual perspectives: 1) the self (or natural) perspective which is the perspective that one would expect to see; 2) a vertical axis flip of the image (flipped along the y axis); 3) the horizontal axis flip of the image (flipped along the x axis); and both axes flip of the image (flipped along the x and y axes). The last three images are interpreted as ‘other’.

1.8.3. The task

I looked for a measure where robust psychophysical techniques could be used. The principle of the task is that the participant makes a decision that is orthogonal to the dimension being tested, for example answering “first” or “second” period when identifying the lowest luminance of a light (Green & Swets, 1966). Here, I used video of self-generated movement with increments of added visual delay. The participants were asked to discriminate this added delay.

The typical response method for ‘self-recognition’ experiments using video stimuli is a yes-no judgement task. Participants were asked to indicate whether the movements they were presented with were in-synch with the felt movement (i.e., “yes, that is me”) or out-of-synch with their felt movement (i.e., “no, that is not me”) to individual videos. Such a measure is vulnerable to response bias in which a participant may not have a *perception* of self but a tendency to *respond* self based on extraneous cues or even just a guess that one or other perspective is the “right answer”. In order to avoid contamination by such a response bias, I employed a two-interval forced choice (2IFC) paradigm. Participants make two movements on each trial, only one of which was delayed. They were then asked to indicate which of the two periods had the added visual delay (See Figure 7 for a schematic of events in a given trial). A set of delays was pre-chosen, limited by the refresh rate of the display screen, and the probability of correct responses were calculated. This method allows for the following: 1) participants are able to compare the delay to a baseline in each trial; 2) reduces likelihood for response bias; and 3) does not require the participant to speculate on which presentation looked more like themselves.

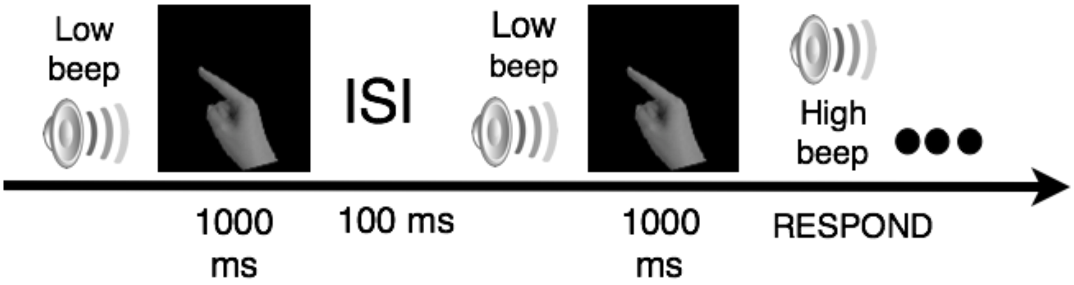

Figure 7. Schematic of a trial in the 2IFC temporal synchrony discrimination task. In any given trial participants made two movements. These movements were separated by an inter-stimulus interval (ISI) of 100ms. In one of the presentations there was an added visual delay to the video of the movement (ranging from 85 to 350ms) and in the other presentation there was no added visual delay. Participants were asked to respond to which of the two presentations had the visual delay, or was not in synchrony with the felt movement. They used foot pedals to respond.

Measuring the tolerance of temporal mismatch between visual and proprioceptive information while making active movements has been used as a measure of body ownership in which perceived synchrony is identified as self and perceived asynchrony is not identified as self (Daprati et al., 2010; Franck, 2001). Further, self-generated movements provide participants with efferent information as well as proprioceptive information, which are both important factors in determining whether you are the agent of the action (Farrer, Franck, Paillard, & Jeannerod, 2003b; Gallagher, 2000; Tsakiris et al., 2005). The sense of agency is an important contributor to the sense of body ownership (Tessari, Tsakiris, Borghi, & Serino, 2010; Tsakiris et al., 2005). I manipulated the perspective in which the movements were displayed to participants (those that could be considered self and other) by positioning a camera close to the line of sight and then flipping the image about the axes (see Figure 6 for examples of the hand in four different perspectives). Visual perspective, as we have seen (sections 1.4. and 1.6.), modulates the ability to distinguish our own body parts from others' (Conson et al., 2010; van den Bos & Jeannerod, 2002), discriminate between left and right hands (Dyde, MacKenzie, & Harris, 2011) and experience the rubber-hand illusion (Costantini & Haggard, 2007; Holmes & Spence, 2007). Therefore, I expected the changes in viewpoint would modulate the ability to detect the delay. Figure 8 provides a schematic of the processes involved in the temporal asynchrony discrimination task under differing visual perspectives.

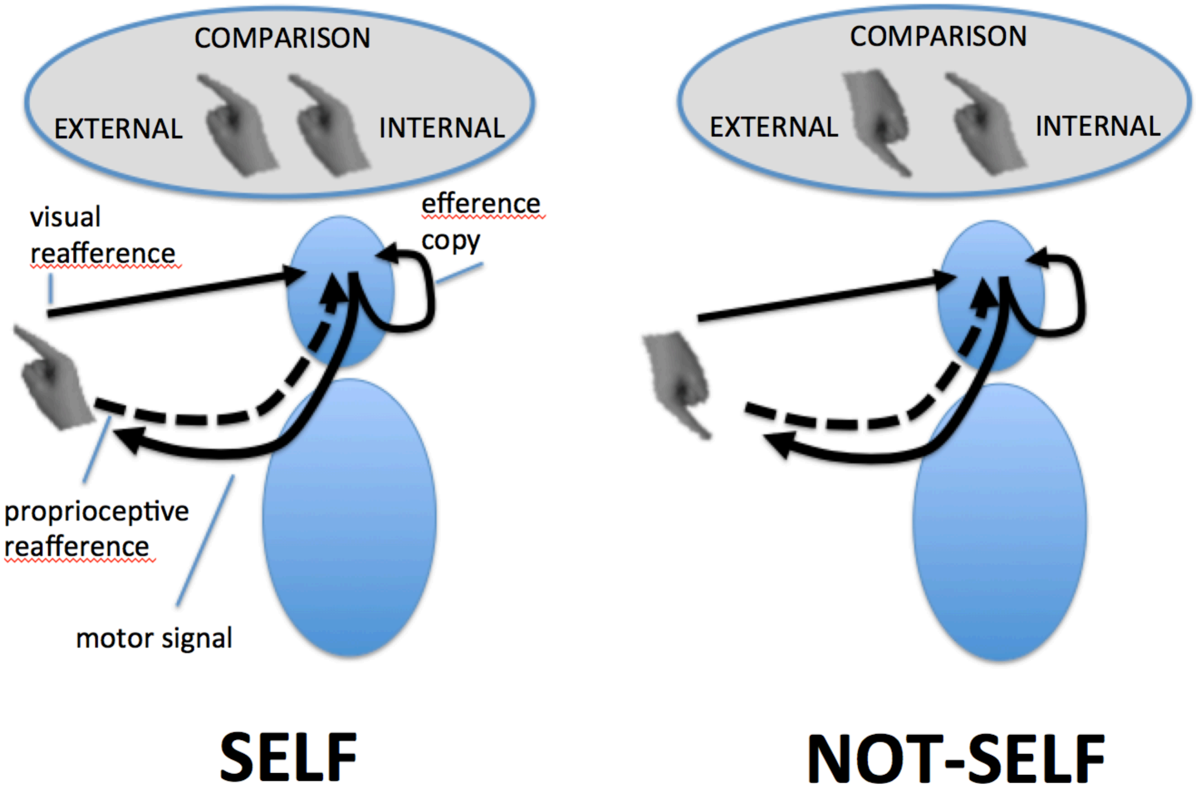

Figure 8. Performing temporal asynchrony discrimination. During active movement, participants know when to expect a movement because of the efference copy. This is then confirmed by proprioceptive and visual reafference. If the reafference does not agree with the expectation, the sense of ownership will be weakened. The comparison is easier if the seen movement matches the internal representation. So in the case of the two images above, it would be easier to detect differences between the seen and the felt movement in the "self" perspective compared to the "non-self" perspective.

1.9. Brief overview of proposed experiments and main hypotheses

The overarching prediction for my experiments was that when the view of the body that was seen matches the internal representation of the body there would be greater sensitivity in detecting the added visual delay. The rationale was that it should be easier to bind visual and motor information if the visual component is aligned with the internal representation of the body in both space and time. Variations in sensitivity for detecting a delay between the view of the movement and the movement itself would depend on the sense of ownership of the body part being viewed and the sense of agency of the body part being moved. From any such variations in sensitivity, in general, I would be able to conclude whether the participants identify the body part moving as self, whereby high sensitivity to temporal delay would suggest ‘self’ and a low sensitivity to temporal delay would suggest ‘other’ or ‘not self’.

My experiments contribute to our understanding of how we represent ourselves in our brain by providing a quantifiable measure of body ownership that has never been used before in live video self-recognition studies. Specifically, I addressed the following:

In Chapter 2, *Detecting delay in visual feedback of an action as a monitor of self recognition*, I looked at the relative roles of vision, proprioception, and efference copy in identifying self. I varied each of these and used the discrimination of temporal delay as a measure. I used unseen discrete or continuous finger movements and presented participants with a view of their movement from egocentric or allocentric perspectives. I then measured the sensitivity with which temporal synchrony discriminations between the movement and the sensory feedback and looked for variation in this sensitivity with visual perspective, movement type, and which hand was moving. I hypothesized that when the sensory information matched the internal representation greater sensitivity in detecting a delay would result.

In Chapter 3, *The role of the viewpoint on body ownership*, I had participants view movements of their hand and head as if seen from three different viewpoints: the direct view (hand movements viewed as if looking down at the hand); the mirror view (hand and head movements viewed as if looking in the mirror) and the behind view (the same hand and head movements as in the mirror but viewed as if from behind). Each of these five live videos was presented in the "natural" or expected perspective or with the video flipped around the horizontal, vertical or both axes to simulate looking at the head or hand of another person; that is, to switch from an egocentric (self) to an allocentric (other) perspective. I hypothesized, that If the natural, unflipped view was regarded as "self" then there would be a self-advantage in which smaller asynchronies would be detected in the unflipped than in the flipped views for the first person view of the body (i.e. looking down at the hands) and for the view in the mirror. There would be no self-advantage, however, for the view of the back.

In Chapter 4, *Disrupting vestibular activity disrupts body ownership*, I sought to confirm the contribution of the vestibular system in the representation of the body. Given that the vestibular system has been linked to registering spatial and temporal aspects of the self (Ferrè, Lopez, & Haggard, 2014; Lopez et al., 2008), I hypothesized that vestibular stimulation would decrease the ability for participants to detect asynchrony when the hand movements are presented in the ‘self’ perspective and not in the ‘other’ perspective.

In Chapter 5, *Inducing ownership over an ‘other’ perspective with a visuo-tactile manipulation*, I introduced synchronous visuo-tactile stimulation (sVTS) and asynchronous visuo-tactile stimulation (aVTS), similar to that used in the RHI and full-body illusions. Live video of participants’ movements were presented in the natural perspective or flipped around both the vertical and horizontal axes, and with varying amounts of delay. I hypothesized that participants who received sVTS, encouraging them to interpret that view as ‘self’, would subsequently show an advantage in detecting temporal asynchrony. Those in the aVTS group would not show a difference in performance between the viewpoints.

2. CHAPTER 2: DETECTING DELAY IN VISUAL FEEDBACK OF AN ACTION AS A MONITOR OF SELF RECOGNITION

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Keywords: crossmodal interactions; visual perspective; self-recognition; body ownership; agency; continuous and discrete movements.

2.1. Abstract

How do we distinguish “self” from “other”? The correlation between willing an action and seeing it occur is an important cue. We exploited the fact that this correlation needs to occur within a restricted temporal window in order to obtain a quantitative assessment of when a body part is identified as “self”. We measured the threshold and sensitivity (d’) for detecting a delay between movements of the finger (of both the dominant and non-dominant hands) and visual feedback as seen from four visual perspectives (the natural view, and mirror-reversed and/or inverted views). Each trial consisted of one presentation with minimum delay and another with a delay of between 33 and 150ms. Participants indicated which presentation contained the delayed view. We varied the amount of efference copy available for this task by comparing performance for discrete movements and continuous movements. Discrete movements are associated with a stronger efference copy. Sensitivity to detect asynchrony between visual and proprioceptive information was significantly higher when movements were viewed from a “plausible” self-perspective compared to when the view was reversed or inverted. Further, we found differences in performance between dominant and non-dominant hand finger movements across the continuous and single movements. Performance varied with the viewpoint from which the visual feedback was presented and on the efferent component such that optimal performance was obtained when the presentation was in the normal natural orientation and clear efferent information was available. Variations in sensitivity to visual/non-visual temporal incongruence with the viewpoint in which a movement is seen may help determine the arrangement of the

underlying visual representation of the body.

2.2. Introduction

We have the awareness that something we are looking at is a part of our own body from experiencing expected sensations correlated with what we are seeing (Gallagher 2000; Tsakiris et al., 2010). Seeing something being touched and feeling synchronous tactile sensations helps create a sense of ownership of the seen item and can even mislead us into thinking that foreign objects, such as rubber hands (the rubber hand illusion; Botvinick & Cohen, 1998; Tsakiris et al., 2010; Tsakiris et al., 2005) or other inanimate objects (Armel & Ramachandran, 2003), are parts of our own body. Similarly, seeing a finger move after we have attempted to move it helps identify it as belonging to us (Tsakiris et al., 2005). This case involves correlating what is seen with the simultaneous sensory and motor information. Identifying sensory and motor information that comes through very different channels as "belonging together" requires, among other things, that they occur in a certain temporal window (Spence et al., 2004). Temporal congruency promotes binding of the visual, proprioceptive, and efferent signals associated with movement and hence assists in creating a sense of self-identification (Gallagher, 2000; Tsakiris et al., 2006). We measured the tolerance to disruption of this temporal congruency by introducing a delay in the visual feedback concerning a voluntary movement and asking people to detect the delay. Our logic was that it should be easier to bind visual and motor information if the visual component was aligned with the internal representation of the body in both space and time. This is therefore a potentially more objective measure of body ownership than simply asking someone if something is perceived as being part of their own body.

2.2.1. The effect of perspective

The visual perspective in which we view a body part modulates the ability to recognize it as our own (Conson et al., 2010). We are able to recognize our dominant hand most quickly when it is seen from an "egocentric" or "plausible self" perspective (i.e., the normal view) compared to when it is seen in some anatomically impossible orientation (referred to as viewing from an "allocentric", "other" or "not self" perspective). As well, the ability to identify a hand as left or right hand (Dyde et al., 2011; Fiorio et al., 2007; Parsons, 1994) and the effectiveness of the rubber hand illusion (Costantini & Haggard, 2007; Holmes & Spence, 2007) is likewise reduced if viewed from an allocentric perspective. The fact that perspective makes a difference suggests that there is an internal representation of the body providing an "expected" view that can be matched to what is actually seen. Varying perspective can therefore be used as an experimental tool to assess the nature of the body's internal representation: the view that is matched against proprioceptive and efferent signals.

2.2.2. Proprioceptive awareness

The ability to detect the position of a limb from proprioceptive information alone is poor (Graziano, 1999; Làdavas et al., 2000). When an arm is moved passively to a new location, such that its position can only be identified by proprioceptive information about joint position and muscle length, participants are significantly less accurate at tracking the arm compared to when a target light is attached to the hand (Mather & Lackner, 1981). A proprioceptive map of the body could therefore be expected to be of poor resolution and visual-proprioceptive matching to be broadly tuned. This is not to say that proprioceptive information is unimportant: loss of the proprioceptive system has devastating consequences for movement control and, particularly relevant here, is associated with a loss of body schema (Cole & Paillard, 1998). The proprioceptive sense thus gives us some information about the position of a moving finger. However, since we are looking at an active finger movement, not only sensory feedback is involved but also information related to the motor signals (Tsakiris et al., 2005).

2.2.3. Awareness of a motor act

The sense of agency, the feeling that one can control and move one's body (Gallagher, 2000; Tsakiris et al., 2010), includes the motor signal (efference copy) as well as sensory feedback (afferent signals) (Farrer et al., 2003). A sense of agency contributes to the sense of ownership and correlating motor activity with visual feedback is thus an important contributor to this sense. Activity in the visual body areas in the brain (e.g., the extrastriate body area) is correlated with limb movement (Astafiev et al., 2004) providing a neural substrate for the interconnectivity of sensory and motor information in the construction of the representation of the body in the brain. Here we quantify the important relationship between the sense of agency and ownership without explicitly asking about either. Instead we look for variations in the sensitivity for detecting a delay between the view of one's finger (ownership if the perspective is correct) and movement of that finger (agency, if it is thought to be one's own finger).

2.2.4. Varying the efferent contribution: continuous vs. discrete movements

Repetitive movements, such as waving one's hand or finger up and down rhythmically, are controlled differently than discrete movements (Spencer, 2003). The use of efference copy to specify timing seems to be most explicit for discrete movements (Spencer, Verstynen, & Brett, 2007). We took advantage of this difference in the weighting assigned to efference copy to assess the contribution of efferent control by comparing performance with repetitive and discrete finger motions. We expected performance to be more sensitive for discrete movements.

2.2.5. The dominant hand

Most people show a preference to use one or other hand (Oldfield, 1971). The Body Specificity Hypothesis (Casasanto, 2009; Willems et al., 2010a; Willems & Hagoort, 2009) proposes that people with dominant right hands interact in different ways with their environment than left-handed people and create different representations of "action- and body-related information". Given the extensive use of the dominant hand, right-handers might be expected to be best at tasks that use their right hand and less so when using their non-dominant left hand. If this were true, then we may expect differences detecting a delayed visual feedback depending on which hand was moving that may be correlated with the reference frame for egocentrically centered body representation. We therefore performed our experiments with both dominant and non-dominant hand movements.

2.2.6. Our project

In order to look at the relative roles of vision, proprioception, and efference copy in identifying self, we varied each of these and used the discrimination of temporal delay as a measure. We used unseen discrete or continuous finger movements and presented participants with a view of their movement from egocentric or allocentric perspectives. We measured the sensitivity with which temporal synchrony discriminations between the movement and the sensory feedback could be made and looked for variation in this sensitivity with visual perspective, movement type, and which hand was moving. We hypothesized that when the sensory information matches the internal representation greater sensitivity in detecting a delay should result.

2.3. Method

2.3.1. Participants

10 right-handed adults (6 females, 4 males), mean age of 28.9 (± 10.7) years, participated in this study. All participants took part in all the experiments using both hands in both the continuous and the discrete movement paradigm. Participants gave their informed consent, which conformed to York University ethical guidelines and the Declaration of Helsinki. Handedness was determined by an adapted version of the Edinburgh Handedness Inventory (Oldfield, 1971).

2.3.2. Apparatus

Participants sat on an adjustable chair at a table with their head on a chin rest 50 cm from a LCD display (HP Fv583AA 20” widescreen monitor; 1600 x 900 pixels; 5 ms refresh response time) centred at eye level. They placed their hand on the table shielded from view by black cloth. A PlayStation Eye camera (SCEI; resolution 640x480 pixels @ 30 Hz) was mounted on the front of the chin rest and pointed down at their hand (Figure 9). The camera was angled to capture the view as seen from a “natural” egocentric perspective for the participant as if looking down at their own hand.

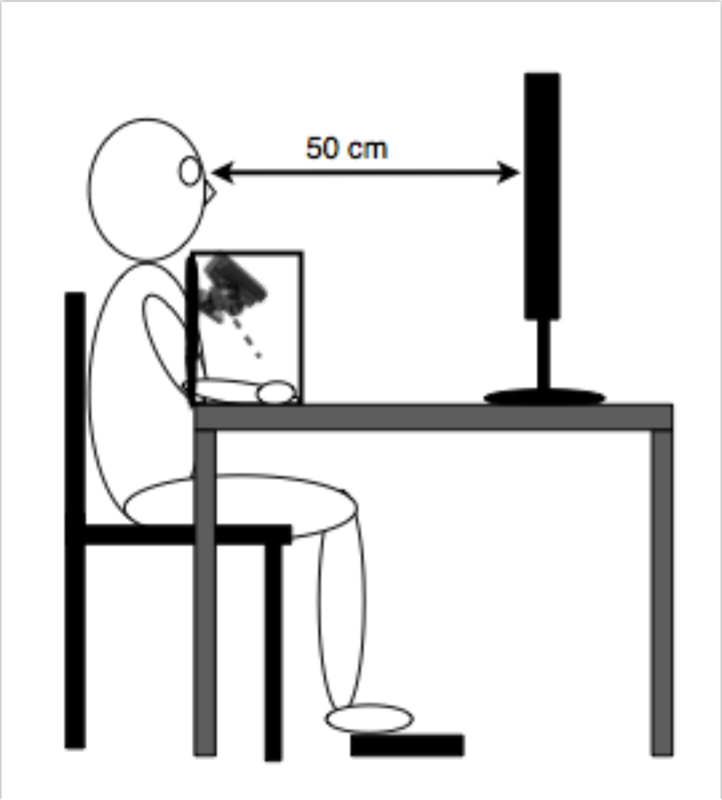


Figure 9. Apparatus: participants sat on an adjustable chair at a table 50 cm from an LCD display centred at eye level. They placed their hand on the table shielded from view by a black cloth. A PlayStation Eye camera was mounted on the front of the chin rest and pointed down at their hand. The camera was angled to capture the view as seen from a ‘‘natural’’ egocentric perspective for the participant as if looking down at their own hand. Participants used foot pedals to make responses.

2.3.4. Introducing a delay in the display

The video signal from the USB camera was fed into an iMAC, read by a Matlab program (version R2009_b) and played through the LCD screen either at a minimal delay, or with an added delay of between 33 and 231 ms. To calibrate the system we had the camera view a flashing LED and compared the voltage across it with its appearance on the screen (measured by a light sensitive diode). This revealed a minimum delay of 85ms ± one-half screen refresh duration and confirmed the delay values we introduced by software. With the minimum system delay, motion on the screen appeared simultaneous. The delays presented in the results have all been corrected by the addition of the system delay.

2.3.5. Finger motions

We used either continuous or discrete movements of the index fingers of both the right and left hands. For continuous movements, participants were required to make a repetitive flexion and extension of their index finger of about 2 cm at 2 Hz. The movements began before they saw their hand on the screen and continued until the hand was no longer visible (1 s presentation time). For discrete movements, participants made a single flexion of their index finger through about 2 cm as soon as they saw their hand on the screen. To reduce between-subject differences in the speed and type of movement all participants went through a 15-trial practice phase for each session during which the experimenter observed and corrected the movement. We ensured that participants avoided touching the table, other fingers, and/or their hand with their index finger during the movement so as not to introduce other tactile cues.

2.3.6. Manipulating the perspective

Through the use of MATLAB and Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997) , participants' movements were displayed on the LCD monitor in one of four perspectives for each of the delays: 1) self perspective (no axis reflection); 2) y-reflection (so that the hand appeared as the opposite hand); 3) x-reflection (so that the hand appeared upside down); and 4) xy-reflection (so that the hand appeared as the opposite hand presented upside down). Viewing conditions 1 and 2 represent egocentric (or "plausible self") viewing perspectives and conditions 3 and 4 represent allocentric (or "other") perspectives. Examples of these views are shown as insets to Figure 10.

2.3.7. Procedure

To explore temporal synchrony discrimination, a 2AFC discrimination paradigm was used. Each trial consisted of two presentations: a minimum-delay presentation (duration 1000ms) and a delayed presentation (duration 1000ms) separated by an inter-stimulus interval (ISI) of 100ms. Whether the delayed presentation or the minimum-delay presentation was displayed first was randomly chosen by MATLAB. There were eight possible differences in visual delays between the two presentations in any given trial: 0, 33, 66, 99, 132, 165, 198, and 231ms. Participants indicated which presentation was delayed using foot pedals (left = first presentation; right = second presentation).

Experiments were run in a counterbalanced block design where either continuous or discrete movements of either the left or right hand were tested in four blocks. For each block, the eight differences of visual delay were presented eight times for the four viewing conditions in a random order resulting in a total of 256 trials. After the first 128 trials, participants were given a break. Each session of 128 trials lasted approximately 15 minutes. Each experiment was repeated for left and right hands, and for continuous and discrete movements resulting in a total of 256*4 = 1024 trials. The entire experiment took two hours to complete.

2.3.8. Data analysis

To assess performance for each visual perspective, we fitted a sigmoidal function to the proportion of times participants correctly chose the delayed presentation as a function of the delay using:

$$y = 0.5 + \frac{0.5}{1 + e^{-\left(\frac{x - x_0}{b}\right)}} \quad \text{……………………………………………………………………………………}(1)$$

where x is the delay, x_0 is the 75% detection threshold and b is the standard deviation.

The sensitivity (d’) values were calculated from the 2AFC discrimination data by dividing the data into trials where the minimum delay was presented first and those where it was presented second. The hit rate was taken from the trials in which the delay was correctly identified as presented in the first presentation; the false positive rate was taken as the rate at which the delay was incorrectly identified as occurring in the first presentation when it actually occurred in the second. These rates were converted into *Z* scores and the difference converted to a d’ score (Macmillan & Creelman, 1991).

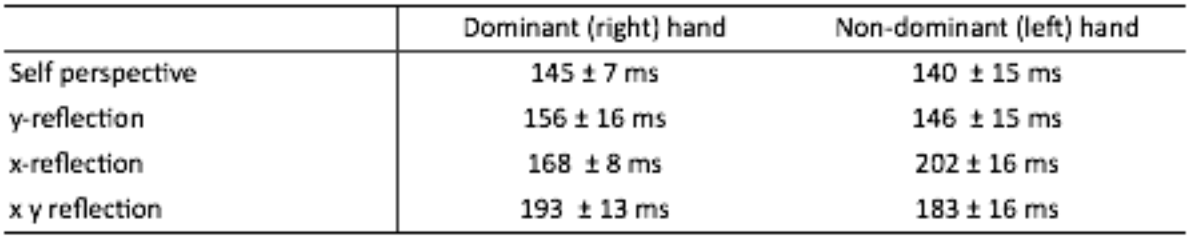
The statistical analysis comprised of repeated measures analysis of variances (ANOVAs). For all tests, alpha was set at $P < 0.05$. All multiple comparisons were carried out with the False Discovery Rate *P* value correction (Benjamini & Hochberg, 1995).

2.4. Results

2.4.1. Detecting visual delays using continuous movement (thresholds)

Figures 10A and B show the mean proportion correct plotted as a function of delay for the data averaged across the 10 participants. For the statistics, each participant's performance was analysed separately. 75% threshold values were extracted from these curves and converted to absolute thresholds by adding the system delay (85ms). The mean thresholds are shown in Table 1.

Table 1. Mean thresholds and standard errors for all conditions tested using continuous movements.



	Dominant (right) hand	Non-dominant (left) hand
Self perspective	145 ± 7 ms	140 ± 15 ms
y-reflection	156 ± 16 ms	146 ± 15 ms
x-reflection	168 ± 8 ms	202 ± 16 ms
x y reflection	193 ± 13 ms	183 ± 16 ms

The values were obtained by adding the system delay (85 ms) to the imposed delay.

A 2 (hands) x 4 (viewing conditions) repeated measures ANOVA revealed a significant main effect of viewing condition ($F_{(3, 27)} = 10.308$, $P < 0.001$, $\eta_p^2 = 0.534$) and no effect of hand ($F_{(1,9)} = 0.183$, P = 0.678, $\eta_p^2 = 0.020$). Pairwise comparisons showed that participants had lower thresholds for detecting an imposed delay while viewing their movement in the "self" perspective compared to the "other" perspective (x- and xy-reflections) ($P < 0.001$ and $P = 0.005$, respectively). Participants also had lower thresholds for detecting the delay when viewing their movement in y-reflection compared to the "other" ($P = 0.005$ and $P = 0.021$, respectively; Figure 10A, B). In other words, when movements were seen in a "plausible self" (self and y-reflection) perspective, participants detected shorter delays (mean threshold 149 ± 13 ms) compared to when movements were seen in an "other" perspective (mean threshold 187 ± 13 ms).

2.4.2. Detecting visual delays in continuous movement (sensitivity)

The same data used for the threshold analysis were converted into sensitivity scores (d'; see methods). A 2 (hands) x 4 (viewing conditions) repeated measures ANOVA revealed a significant effect of perspective ($F_{(3, 27)} = 15.256$, $P < 0.001$, $\eta_p^2 = 0.629$) and no effect of hand ($F_{(1, 9)} = 0.067$, $P = 0.802$, $\eta_p^2 = 0.007$) on sensitivity scores. Pairwise comparisons confirmed the threshold analysis showing that participants were more sensitive at detecting a delay when viewing their movement in the self perspective compared to the "other" perspective ($P < 0.001$ and $P = 0.004$, respectively). Participants were also more sensitive at detecting the delay when viewing their movement in y-reflection compared to the "other" (x- and xy-reflections) viewing conditions ($P = 0.003$ and $P = 0.015$, respectively). Regardless of the hand used, participants performed better (that is, they could detect shorter delays) when their continuous, repetitive movement was viewed from a “plausible self” perspective compared to when it was viewed from an “other” perspective (Figure 10C, D).

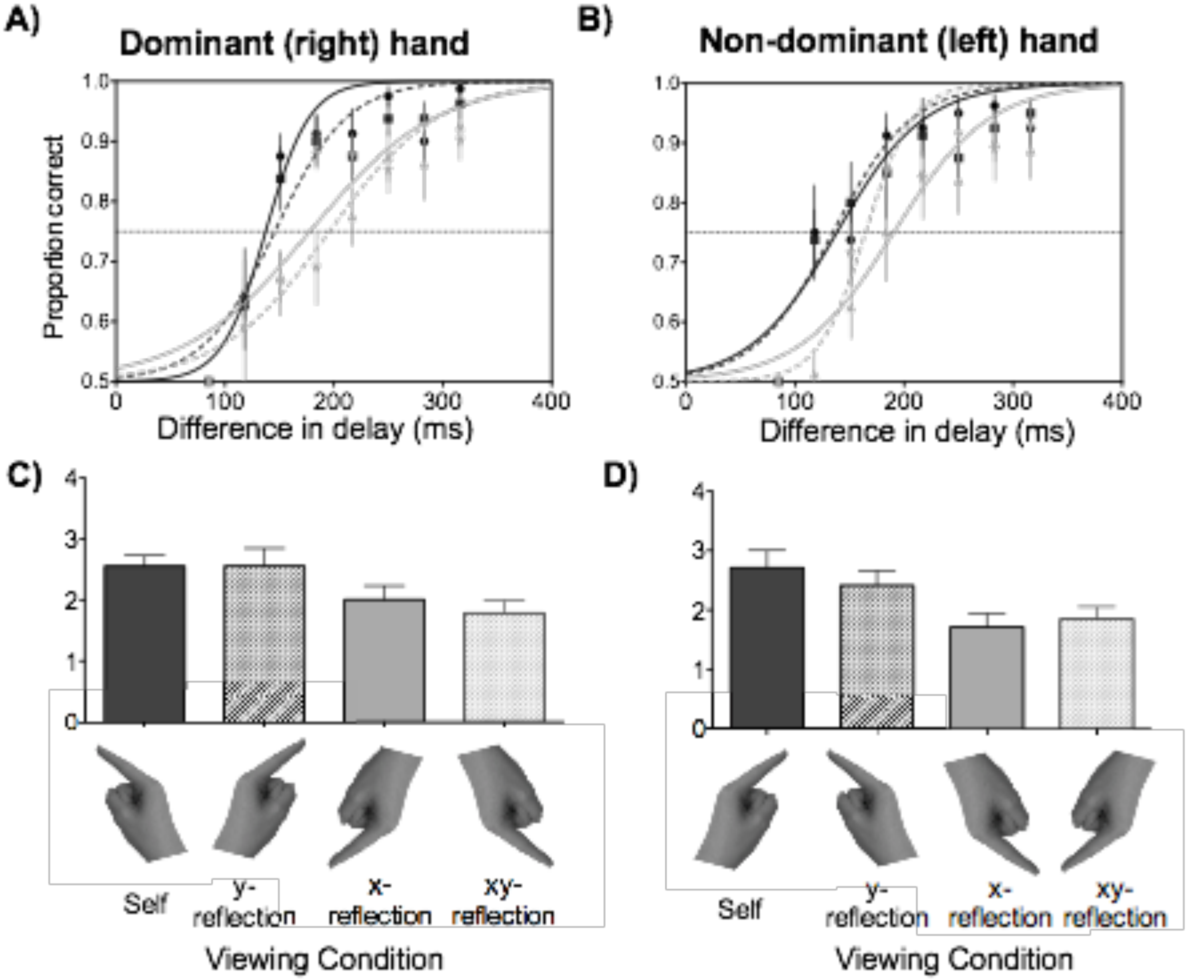
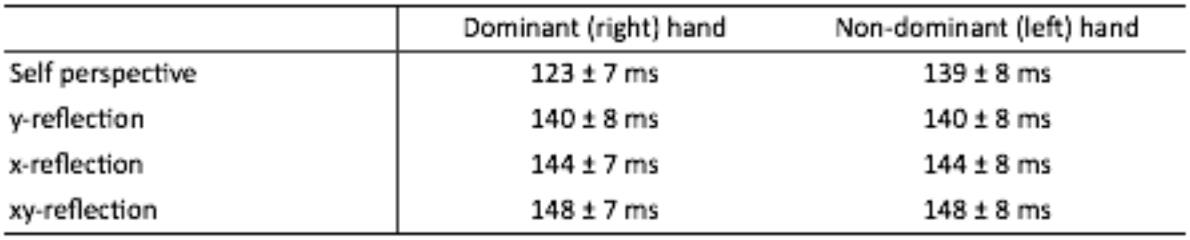


Figure 10. Continuous movement: Plots of the mean proportion correct as a function of the imposed visual delay for the dominant (right) (A) and non- dominant (left) (B) hands. The curves are for self perspective (black solid line and filled circles), y-reflection (black dashed and filled squares), x-reflection (grey solid line and grey circles), and xy-reflection (grey dashed line and grey triangles). The data expressed as mean sensitivity scores (d’) are plotted as bar graphs for the dominant (C) and non-dominant (D) hands. Viewing condition indicated by the insets beneath each column. All error bars are the SE of the mean.

2.4.3. Discriminating visual delay in discrete movement (thresholds)

Figure 11A and B shows the mean proportion correct for detecting a delay in the visual feedback for discrete movements plotted as a function of delay averaged across the 10 participants. For the statistics, each participant's performance was analysed separately. As for the continuous movement analysis, the system delay was added to these values to obtain absolute threshold values. The mean 75% threshold values are shown in Table 2.

Table 2. Mean thresholds and standard errors for all conditions tested using discrete movements.



	Dominant (right) hand	Non-dominant (left) hand
Self perspective	123 ± 7 ms	139 ± 8 ms
y-reflection	140 ± 8 ms	140 ± 8 ms
x-reflection	144 ± 7 ms	144 ± 8 ms
xy-reflection	148 ± 7 ms	148 ± 8 ms

The values were obtained by adding the system delay (85 ms) to the imposed delay.

A 2 (hands) x 4 (viewing conditions) repeated measures ANOVA of the discrete movement data revealed a significant main effect of viewing condition ($F_{(3, 27)} = 8.850$, $P < 0.001$, $\eta_p^2 = 0.496$) and no effect of hand ($F_{(1,9)} = 0.680$, $P = 0.431$, $\eta_p^2 = 0.070$; Figure 11B). Pairwise comparisons showed that participants had lower thresholds when detecting a delay while viewing their movement in the self perspective compared to the "other" perspective ($P = 0.002$ and $P < 0.005$, respectively). Participants also had lower thresholds when detecting the delay when viewing their movement in the y-reflection compared to the “other” (xy-reflection) viewing condition ($P = 0.057$; Figure 11A, B). Further, there was a near-significant difference between the self and y-axis reflection within the “plausible self” perspectives ($P = 0.058$). In other words, when movements were seen in the self-perspective participants detected shorter delays (mean threshold 131 +/- 7 ms) compared to when movements were seen in all other perspectives (mean threshold 144 +/- 8 ms).

2.4.4. Discriminating visual delay in discrete movement (sensitivity)

The same data used for the timing analysis were analysed as sensitivity scores (d’; see methods). Unlike for the continuous movement data, a 2 (hands) x 4 (viewing conditions) repeated measures ANOVA revealed a significant interaction between which hand was used (dominant or non-dominant) for the discrete movement and viewing condition ($F_{(3, 27)} = 6.724$, $P = 0.002$, $\eta_p^2 = 0.428$). Participants performed differently across the viewing conditions depending on the hand with which they performed the movement. To break down the significant interaction, 2 x 2 interaction contrasts were run. The contrasts confirmed that participants performed differently in the self perspective and y-axis reflection conditions for the dominant and non-dominant hand by revealing a significant interaction ($F_{(1, 9)} = 13.190$, $P = 0.005$, $\eta_p^2 = 0.594$). The difference in sensitivity scores between the self perspective and y-axis reflection conditions was greater for the dominant hand than for the non-dominant hand (Figure 11C, D). This difference was also reflected in the threshold data listed in Table 2. In fact, there were no differences for the different viewing conditions for the non-dominant hand. When the non-dominant left hand was y-reflected so that it was seen as the dominant right hand it appeared to inherit the right hand's advantage whereby participants showed higher sensitivity (first two bars in Figure 11D). Further, when comparing the dominant and non-dominant hand across the x-axis and xy-axis refection conditions, we find only a significant main effect of condition where performance was best (regardless of hand) in the x-axis reflection condition ($F_{(1, 9)}$ = 5.847, P = 0.039, η_p^2 = 0.394).

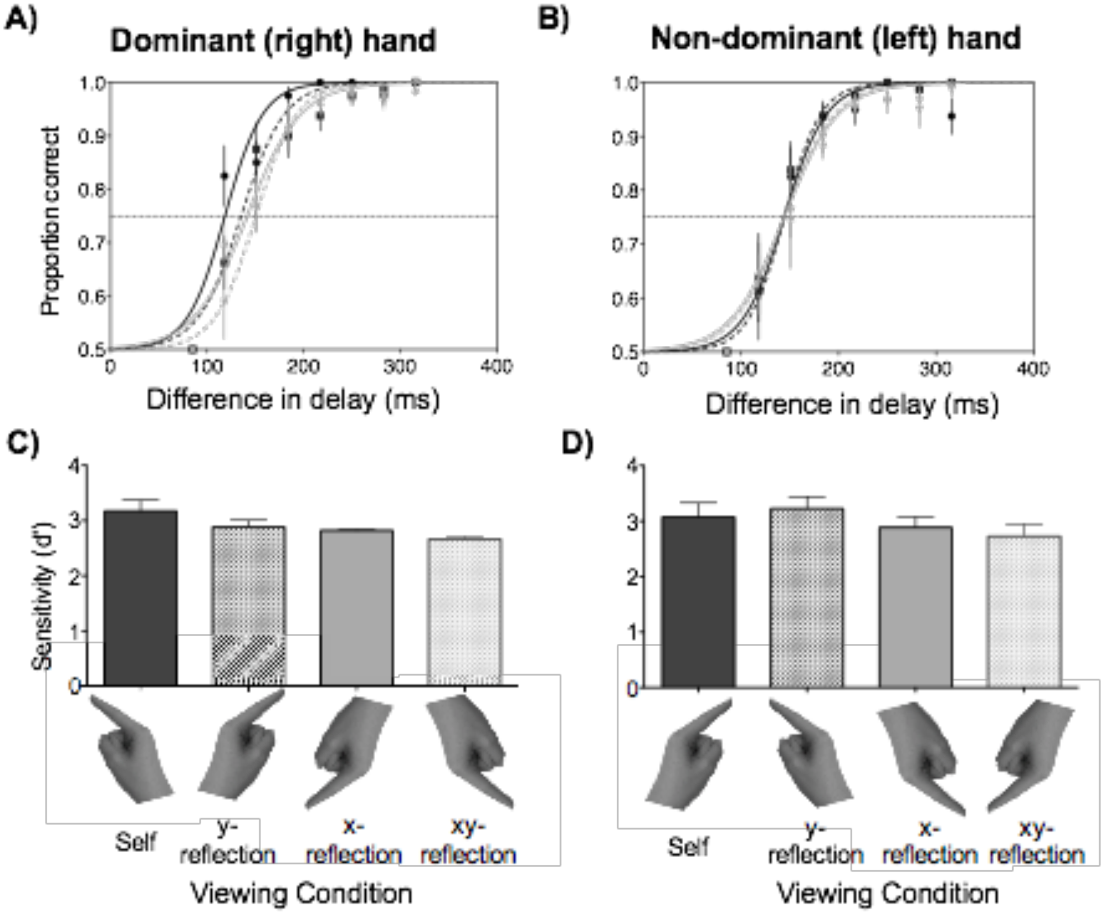


Figure 11. Discrete movement: Plots of the mean proportion correct as a function of the imposed visual delay for the dominant (right) (A) and non- dominant (left) (B) hands. The curves are for self perspective (black solid line and filled circles), y-reflection (black dashed and filled squares), x-reflection (grey solid line and grey circles), and xy-reflection (grey dashed line and grey triangles). The data expressed as mean sensitivity scores (d') are plotted as bar graphs for the dominant (C) and non-dominant (D) hands. Viewing condition indicated by the insets beneath each column. All error bars are the SE of the mean

2.4.5. Continuous versus discrete movements

From the above data, a difference between continuous and discrete movements appeared when comparing the “self” with the y-reflection condition. Therefore, we looked in more detail at these conditions. Figure 12 compares the d’ scores obtained with continuous movement with those from discrete movements for the dominant (Figure 12A) and non-dominant (Figure 12B) hand. A 2 x 2 x 2 repeated measures ANOVA on the d’ scores revealed a significant three-way interaction between the movement (continuous or discrete), hand used (dominant or non-dominant), and visual perspective (no reflection or y-reflection), $F_{(1, 9)} = 16.560$, $P = 0.003$, $\eta_p^2 = 0.648$. That is, the effect of perspective depends on the type of movement and the hand used. To break down this three-way interaction, we ran pairwise comparisons to compare performance across the different movements for both hands and both conditions. There were significant differences between continuous and discrete movements for all comparisons except for the non-dominant hand in the self-perspective condition (dominant hand: self perspective $P = 0.004$ and y-axis reflection $P = 0.022$; non-dominant hand: self-perspective $P = 0.396$ and y-axis reflection $P = 0.023$). Overall, participants were most sensitive at detecting a delay when viewing their dominant hand making a discrete movement.

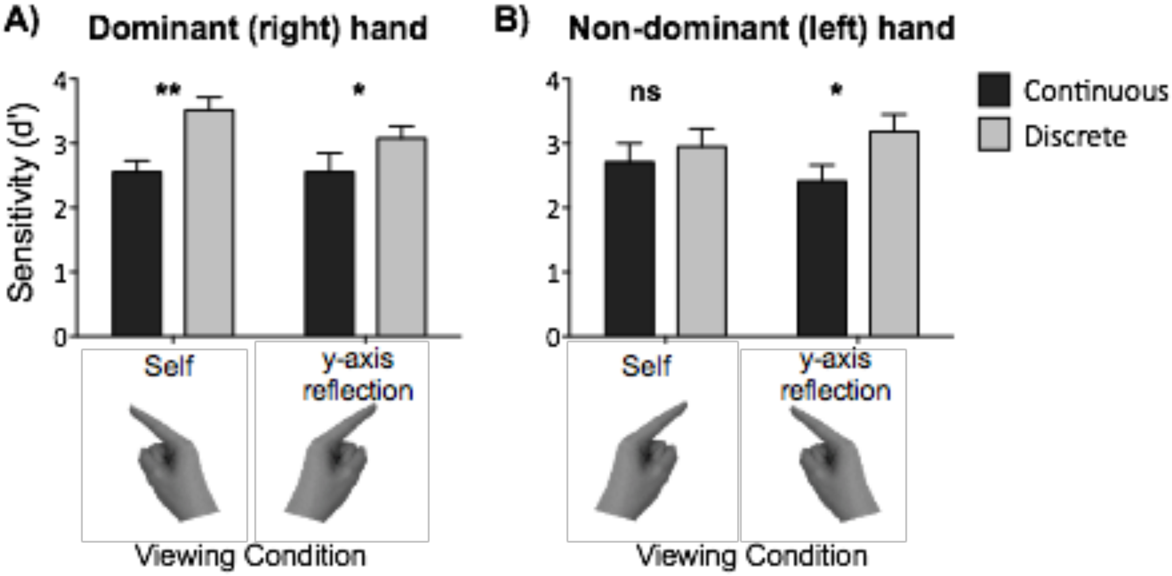


Figure 12. Continuous versus discrete movement: a comparison of the sensitivity to detecting delay for the self and y-reflection views for the dominant (A) and non-dominant (B) hands. All error bars are the SE of the mean.

2.5. Discussion

The current study has shown significant variation in the ability to detect temporal asynchrony between a movement and visual feedback concerning that movement that depended on the visual perspective (egocentric or allocentric), the nature of the movement (continuous or discrete), and the hand used to make the movement (dominant or non-dominant). Performance varied with the perspective from which the visual feedback was presented and on the efferent component such that optimal performance was obtained when the presentation was in the normal natural orientation and clear efferent information was available. In other words, participants were most sensitive when viewing the dominant hand in its natural ("self") perspective making a discrete movement. For this condition, participants could make a reliable discrimination between the minimal delay of 85ms (which appeared simultaneous) and 85+38 =123ms (the mean threshold for the perception of delay). When participants were viewing the dominant hand in its natural perspective making a continuous, repetitive motion (with less access to an efference copy command) the corresponding mean threshold was 85+59 = 134ms, indicating a 21ms improvement attributable to the availability of a clear onset of the movement (efference copy).

2.5.1. An unnatural perspective reduces the ability to detect a delay

Perception of the relative timing of visual and non-visual cues to hand motion depends on whether one is viewing in a "self" (egocentric) or "other" (allocentric) perspective. All conditions provided the participant with an efference copy of their movement, which is deemed as intrinsically important in identifying agency and self

(Gallagher, 2000; Tsakiris et al., 2006). However, when movements were viewed in a “plausible self" perspective, there was a higher sensitivity to delay between visual and non-visual cues, suggesting an enhanced sense of ownership (Gallagher, 2000) and a better ability to match the image presented on the screen in an egocentric perspective to the visual motion expected. Participants performed best (regardless of the type of movement) when the hand was viewed in the self or plausible self-perspective. This is in line with previous research which revealed that the rubber hand illusion was not effective when the observer saw the rubber hand in a spatially or anatomically incongruent posture (Costantini & Haggard, 2007; Holmes & Spence, 2007). The pattern of performance for our cross-modal task replicates a similar pattern of performance found in the detection of self while viewing static images in which performance was best when images were presented in a self (or egocentric) perspective (Conson et al., 2010). However, this study used only a subjective method of report. We conclude that variation in temporal synchrony discrimination provides quantitative evidence for an internal representation of the body providing an “expected” perspective that can be matched to what is actually seen.

2.5.2. The contribution of a clear efferent component

Discrete motion is associated with more efferent activity and a sharper onset of that activity than is present while maintaining a repetitive, continuous movement (Spencer et al., 2007). Sensitivity for detecting a delay in visual feedback was greater for discrete movements thus suggesting a role of efference copy ("forward model"; Wolpert, 1997). Delays could be detected on average 22ms earlier if the movement was discrete.

We thus conclude that having such a clean efferent component may have made it possible to detect shorter delays between the “efferent plus proprioceptive” and the visual feedback. This is reminiscent of the 29ms advantage for detecting an active rather than a passive finger movement measured by Winter et al., (2008) and Lau et al., (2004). Of course this advantage would have been constant across perspectives.

2.5.3. Dominant versus non-dominant hand

Participants were most sensitive at detecting a delay when viewing their dominant hand making a discrete movement compared to a continuous movement. Further, we found that participants showed less of a difference in performance between the “plausible self” conditions (self perspective and y-reflection) during a discrete movement when performing that movement with the non-dominant hand. Thus subjects were best at cross-modal asynchrony detection when moving their dominant hand in a discrete movement. This is consistent with previous self recognition experiments which indicated superior recognition of movement of the dominant hand (Conson et al., 2010) and the Body Specificity Hypothesis (Casasanto, 2009).

It is possible that when participants perform a continuous movement (typical for bimanual tasks, Swinnen, 2002) they consider the right and left hands as yoked or working in tandem. Under these conditions, the advantage would be compatible with our observation that participants did not show a difference between the two “plausible self” (self and y-reflection) perspectives during continuous movements performed with the non-dominant hand. In contrast, during the discrete movements, which are typical of goal-directed movements, participants may consider the left and right hands as different/separate. Goal-directed movements are typically initiated and performed by the dominant hand because they often require greater precision (Bryden et al., 2000).

Our results provide further evidence that handedness could possibly define the reference frame for egocentrically centered body representation and create different representations of “action-and body-related information” (Conson et al., 2010). Past neuroimaging research has shown that the dominant hand provides the basis for left and right handers having different patterns of activation in areas of the visual cortex that are specifically related to body (Willems et al., 2010; Willems et al., 2009a; Willems et al., 2009b).

2.5.4. Neural correlates of self recognition

The discovery of an area in the brain responsive to views of the body (extrastriate body area: EBA; Downing et al., 2011) has provided a possible neural substrate for how the body may be represented in the brain. The EBA responds selectively to views of human body parts regardless of whether they are presented as photographs, line drawings, stick figures, silhouettes, or still images depicting bodies in motion (see review in Peelen, 2007). It does not respond selectively based on perspective, lending doubt as to whether it may be involved in representing one’s own body. However, EBA activity has been correlated with motor imagery of the movements of a limb suggesting that integration of visual, efference, and proprioceptive information tantalizingly suggestive of an involvement in creating a representation of one’s body in the brain (Astafiev et al., 2004). We suggest that the EBA may be particularly active during the combination of agency and ownership employed in this study, possibly underpinning the enhanced sensitivity to discrepancy between motor and visual correlates of finger movements when viewed in the natural perspective. Another area that might be involved in the recognition of these finger actions is in the parietal. Reduction of activity in parietal and frontal cortices has been correlated with difficulties in recognizing self actions in schizophrenia (Maruff et al., 2005).

2.5.5. Conclusion

We manipulated the recognition of “self” by varying the visual perspective in which participants saw their movements and the quality of efferent information available by varying the nature of the movement. Overall, we find that egocentric perspectives of self are very important. We are able to discriminate asynchrony from our proprioceptive information and visually presented information more efficiently when our movements are seen in a plausible self perspective and when efferent information is most distinctive during a discrete movement. Further, there is a clear difference in whether the dominant hand provides an advantage in detecting asynchrony during a discrete movement compared to a continuous movement. Together, these data contribute to the evidence for the roles of both vision and information about posture/movement from proprioceptive and motor systems in the development of representations of self (body schema).

2.6. Acknowledgements

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3. CHAPTER 3: THE ROLE OF THE VIEWPOINT ON BODY OWNERSHIP

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3.1. Abstract

People are more sensitive at detecting asynchrony between a self-generated movement of the hand and delayed visual feedback when what they see matches the expected "self" perspective rather than an "other" perspective (Hoover & Harris, 2012). We take this as corresponding to the ability to distinguish self from others and call it the "self advantage": a measure of body ownership. What about views of the body that cannot be seen directly? Here we assessed the effect of familiarity of the view of the body on the self advantage. Participants performed self-generated hand and head movements viewed directly, in a mirror, and from behind with a variable delay added to the visual feedback. Each view was shown either in the natural perspective or flipped about the vertical or horizontal axes to provide a view from another perspective. Thresholds for detecting a delay in visual feedback were calculated. Dependency of the self advantage on perspective was most evident for views of the body that are seen most often. Results support the importance of correlating visual feedback with movement information in creating the sense of body ownership.

3.2. Introduction

Seeing and feeling a self-initiated movement is a strong indicator that the body part that we see moving belongs to us (Gallagher, 2000; Tsakiris et al., 2005; Tsakiris 2010; Walsh et al., 2011). This sense of agency and the associated feeling of ownership derive from a correlation between the motor and proprioceptive signals and the visual feedback confirming the expected outcome (Tsakiris et al., 2005; Tsakiris, 2010). Artificially created synchrony between seeing and feeling an event can trick us into feeling ownership over rubber hands (Botvinick & Cohen 1998; Tsakiris & Haggard, 2005; Tsakiris et al., 2010) and even inanimate objects (Armel & Ramachandran, 2003). Temporal synchrony alone, however, is not sufficient for knowing what is self. We usually experience our body and its movements from a first-person (egocentric) perspective and from this we build up an expected view of ourselves, constrained by anatomical limits and by how much of our body we can ever see. Here we investigate the significance of visual perspective of self-generated movement on body ownership of views of the body that cannot normally be seen and for which we therefore have no chance to build up an expected view.

Matching the consequences of our actions with what we expect is an important part of controlling our actions. Information comes from proprioception and from an efferent copy of the motor command signal, both of which can be matched to visual feedback. The successful completion of this loop provides a basis for constructing and updating the perception of self. When a person views their hand from an anatomically plausible perspective they are better at making laterality judgements (Parsons, 1994;

Fiorio et al., 2007; Dyde et al., 2011), self-other judgements (Conson et al., 2010), finger movements to targets (Sutter & Müsseler, 2010), and at detecting multisensory asynchrony (Hoover & Harris, 2012) than they are when the hand is seen in an anatomically implausible perspective. Furthermore, the effectiveness of body ownership illusions, such as the rubber hand illusion, is lessened if the rubber hand is not at least approximately aligned with the actual hand (Costantini & Haggard, 2007; Holmes & Spence, 2007). This suggests that a uniquely egocentric visual perspective is required to generate the feeling of ownership and self identity. Is there an “anatomically plausible” perspective for body parts that cannot be seen directly? We consider the front and back of the head. Neither view can be seen directly, but we are familiar with the view of the front of the head because of our daily use of mirrors. Is this view adequate to provide a quantifiable sense of identifying the face in the mirror as our self?

The link between the mirror and the self is one that has been made since ancient times (Bartsch, 2006) and the ability to identify the person in the mirror as oneself has been used as evidence that humans (and some non-human primates) demonstrate self-awareness (Gallup, 1970; Bertenthal & Fischer, 1978; Nielsen et al., 2006). The process by which one equates an image in the mirror to oneself involves prior experience in which the visual information seen in a mirror is correlated with other sensorimotor information about movement or tactile information experienced for example while shaving, combing one’s hair, or putting on makeup. This is, in essence, similar to how we use multisensory cues in creating the sense of ownership over other body parts but with one integral difference. The difference is that we must correlate these sensorimotor experiences with visual information seen now from an allocentric perspective. Therefore, interpreting the image in a mirror is a special case that in some sense combines both egocentric and allocentric perspectives.

Measuring the tolerance of temporal mismatch between visual feedback, efferent copy, and proprioceptive information concerning self-generated movement can be used as a measure of body ownership (Daparti et al., 1997; Franck et al., 2001; Hoover & Harris, 2012). When sensory information matches the expected self perspective, it provides a signature self advantage in which the asynchrony can be detected about 40ms sooner than when viewed from some other perspective. Using the self advantage as a probe, we asked whether, when you see yourself in a mirror or from an unfamiliar viewpoint, do you truly attribute what you see as being yourself? Using a live video to which we could add delays, we had participants view movements of their hand and head as if seen from three different viewpoints: the direct view (hand movements viewed as if looking down at the hand); the mirror view (hand and head movements viewed as if looking in the mirror) and the behind view (the same hand and head movements as in the mirror but viewed as if from behind). Each of these five live videos was presented in the “natural” or expected perspective described above or with the video flipped around the horizontal, vertical or both axes to simulate looking at the head or hand of another person; that is, to switch from an egocentric (self) to an allocentric (other) perspective. If the natural, unflipped view were regarded as “self” then, following the logic of Hoover and Harris (2012), there should be a self advantage in which smaller asynchronies can be detected than in the flipped views.

3.3. Materials and Methods

3.3.1. Participants

10 right-handed adults (7 females, 3 males), with a mean age of 29.8 (± 5 SD) years, participated in this study. All participants took part in all five blocks of the experiment and gave their informed consent. The experiment was approved by the York University office of research ethics and followed the guidelines of the Declaration of Helsinki. Handedness was determined by an adapted version of the Edinburgh Handedness Inventory (Oldfield, 1971).

3.3.2. Apparatus and camera viewpoints

For hand movements seen in the direct view, participants sat on an adjustable chair at a table with their head on a chin rest 50 cm away from a LCD display (HP Fv583AA 20” widescreen monitor; 1600 x 900 pixels; 5ms refresh response time) centred at eye level. They placed their hand on the table shielded by a black cloth. A PlayStation Eye camera (SCEI; resolution 640x480 @ 30 Hz) was mounted on the front of the chin rest pointing down at their hand (Camera A in. Figure 13). The camera was angled to approximately capture the view seen by participants looking down at their own hand.

For the hand and head movements seen in the mirror view, participants sat 50cm away from the display and were not restrained by a chin rest. The camera was mounted to the LCD display and angled to capture the view as if they were looking in a mirror (Camera B in Figure. 13).

For the hand and head movements seen in the behind view, participants sat 50cm away from the display and were not restrained by the chin rest. The camera was mounted on a post positioned 40cm directly behind the participants’ head (Camera C in Figure 13).

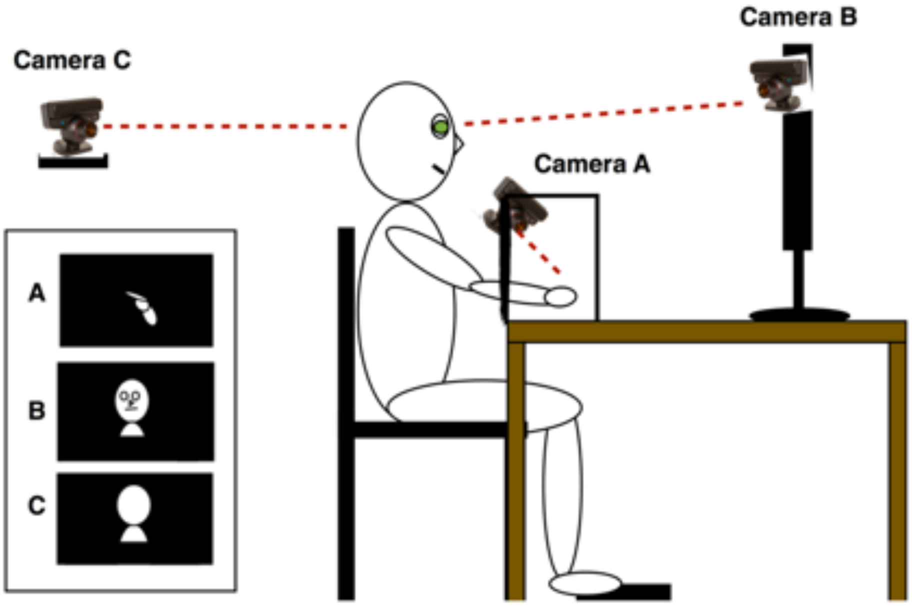

Figure 13. Apparatus: participants sat on an adjustable chair at a table 50 cm from an LCD display centered at eye level. PlayStation Eye cameras (see text) were used. Camera A was mounted on the front of the chin rest and pointed down at the participant's hand, Camera B was mounted on the LCD display pointed at the participant's face, and Camera C was mounted on a post directly behind the participant pointed at the participant's back. Insets show the view on the monitor for each camera.

3.3.3. Introducing a delay in the display

The video signal from the USB camera was fed into a computer (iMac 11.2, mid 2010), read by MATLAB (version R2009_b) and played through the LCD screen at either a minimal system delay, or with an added delay of between 33 and 264ms. To calibrate the system we had the camera view a flashing LED and compared the voltage across it with its appearance on the screen measured by a light sensitive diode. This revealed a system delay of 85ms ± one-half camera refresh duration and confirmed the delay values we introduced by the software.

3.3.4. Movements

For all hand movements, participants performed a single flexion of the right index finger through approximately 2cm both when their hand was on the table or held up by the side of their head. They made the movement as soon as they saw their hand on the screen in a given trial. Participants avoided touching the table, other fingers, or their face with their index finger during the movement so as to not introduce additional tactile cues. For the head movements, participants performed a single, small roll of the head of approximately 5° to either the left or the right while looking straight ahead. To reduce between-subject differences in the speed and type of movement, all participants went through a 15-trial practice phase for each of the movements during which the experimenter observed and corrected movement.

3.3.5. Manipulating the visual perspective

In order to display the movements in the four perspectives, video images were flipped and delayed using the Psychophysics Toolbox extension of Matlab subroutine *PsychVideoDelayLoop.* This program implemented a realtime video feedback loop in which the video images could be flipped about the horizontal, vertical, both or neither axes. Delays were introduced in 33ms increments (Brainard, 1997; Pelli, 1997) to match the rate of image capture of the camera. These manipulations are illustrated as inserts in Figures. 14 and 15.

3.3.6. Procedure

To explore temporal synchrony detection, a two-interval forced choice paradigm was used. Each trial consisted of two 1s periods separated by an inter-stimulus interval of 100ms. One interval contained a minimal-delay presentation of the movement while the other contained a delayed presentation. Which presentation was displayed first was chosen randomly. There were nine possible differences in visual delay between the two periods: 33, 66, 99, 132, 165, 198, 231, 264, and 297ms (corresponded to an integral number of camera frames). Participants responded by means of foot pedals (Yamaha FC5). They kept their feet on the foot pedals for the entirety of the block and raised their left foot to indicate that the delay was in the first period or their right to indicate the second period.

Each of the five movement/viewpoint combinations were run in separate blocks. For each block, the nine visual delays were presented eight times for each of the four perspectives (flip conditions) in a random order resulting in a total of 9x8x4=288 trials. Blocks were broken down into 144 trial sessions, each lasting approximately 20 minutes. The 10 sessions of 144 trials were run in a counterbalanced order separated by at least an hour.

3.3.7. Data analysis

To compare performance across conditions we fitted a logistic function[1] to the proportion of times participants correctly chose the delayed period as a function of the delay using:

$$y = 0.5 + \frac{0.5}{1 + e^{-\left(\frac{x - x_0}{b}\right)}} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(1)$$

where x is the delay, x_0 is the 75% threshold value, and b is the standard deviation.

The statistical analysis comprised of repeated measures analyses of variances (ANOVAs) and paired samples t-tests. For ANOVA tests, alpha was set at $P < 0.05$. All a priori multiple comparisons were performed using one-tailed Student's T tests and corrected using the false discovery rate P values (Benjamini & Hochberg, 1995).

3.4. Results

Figure 14 shows the proportion of times participants correctly identified the interval with the delay plotted as a function of the total delay (system delay plus added delay) averaged across 10 participants for each condition. Psychometric functions are plotted through these average data. Mean thresholds are shown in Table 3.

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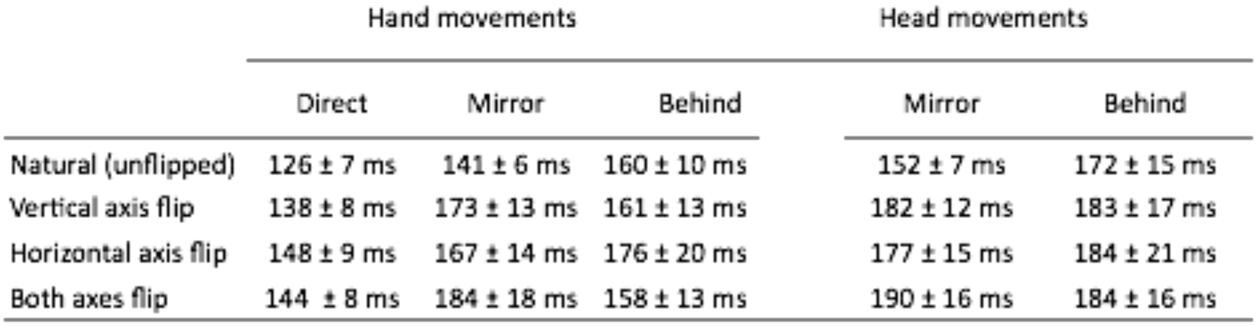
[1] In the published version the function was incorrectly named cumulative Gaussian

Table 3. Mean thresholds and standard errors for the hand and head movements tested



	Hand movements			Head movements	
	Direct	Mirror	Behind	Mirror	Behind
Natural (unflipped)	126 ± 7 ms	141 ± 6 ms	160 ± 10 ms	152 ± 7 ms	172 ± 15 ms
Vertical axis flip	138 ± 8 ms	173 ± 13 ms	161 ± 13 ms	182 ± 12 ms	183 ± 17 ms
Horizontal axis flip	148 ± 9 ms	167 ± 14 ms	176 ± 20 ms	177 ± 15 ms	184 ± 21 ms
Both axes flip	144 ± 8 ms	184 ± 18 ms	158 ± 13 ms	190 ± 16 ms	184 ± 16 ms

The values were obtained by adding the system delay (85 ms) to the added delay.

3.4.1. Discriminating visual delays for hand movements

A one-way repeated measures ANOVA revealed a significant main effect of perspective when participants viewed their hand movements in the direct view ($F_{(3, 27)}$ = 9.45, P = 0.01, η_p^2 = 0.51; see Figure 14A). The threshold for detecting the delay was significantly lower for the natural (unflipped) perspective (*M* ± *SE* = 126 ± 7 ms) compared to the other perspectives (vertical axis flip *M* ± *SE* = 138 ± 8 ms, *M* ± *SE* difference = 12 ± 5 ms, P = 0.02; horizontal axis flip *M* ± *SE* = 148 ± 9 ms, *M* ± *SE* difference = 22 ± 7 ms, P = 0.01; and both axes flip *M* ± *SE* = 144 ± 8 ms, *M* ± *SE* difference = 18 ± 6 ms, P = 0.01) thus confirming the self advantage (Hoover & Harris, 2012).

Interestingly, the same effect of perspective was found when participants made hand movements while looking at their hand raised up beside their head in the mirror view ($F_{(3, 27)}$ = 4.12, P = 0.02, η_p^2 = 0.31; see Figure 14B). Again, the threshold was lower for the natural (unflipped) perspective (*M* ± *SE* = 141 ± 6 ms) compared to the other perspectives (vertical axis flip *M* ± *SE* = 173 ± 13 ms, *M* ± *SE* difference = 32 ± 11 ms, P = 0.03; horizontal axis flip *M* ± *SE* = 167 ± 14 ms, *M* ± *SE* difference = 26 ± 13 ms, P = 0.03; and both axes flip *M* ± *SE* = 184 ± 18 ms, *M* ± *SE* difference = 43 ± 18 ms, P = 0.03). That is, the view of the hand in the mirror was still associated with a perspective-dependent self advantage. There was, however, no such self advantage when participants viewed their hand movements in the behind view where thresholds for detecting asynchrony were similar across all perspectives ($F_{(3, 27)}$ = 1.32, P = 0.29, η_p^2 = 0.13; see Figure 14c).

Analysis of the standard deviations of the psychometric functions showed no significant differences between the perspectives for the direct and mirror views ($F_{(3, 28)}$ = 1.11, P = 0.36 and $F_{(3,28)}$ = 0.88, P = 0.46 respectively). There was, however, a just-significant effect of perspective for the behind view ($F_{(3,28)}$ = 2.64, p = 0.05) where the vertical axis flip slope was considerably lower (*M* ± *SE* = 17 ± 4 ms; solid light curve in Figure 14C) than the three other slopes (unflipped *M* ± *SE* = 36 ± 5 ms; horizontal axis flip *M* ± *SE* = 42 ± 8 ms; and both axes flip *M* ± *SE* = 41 ± 7 ms).

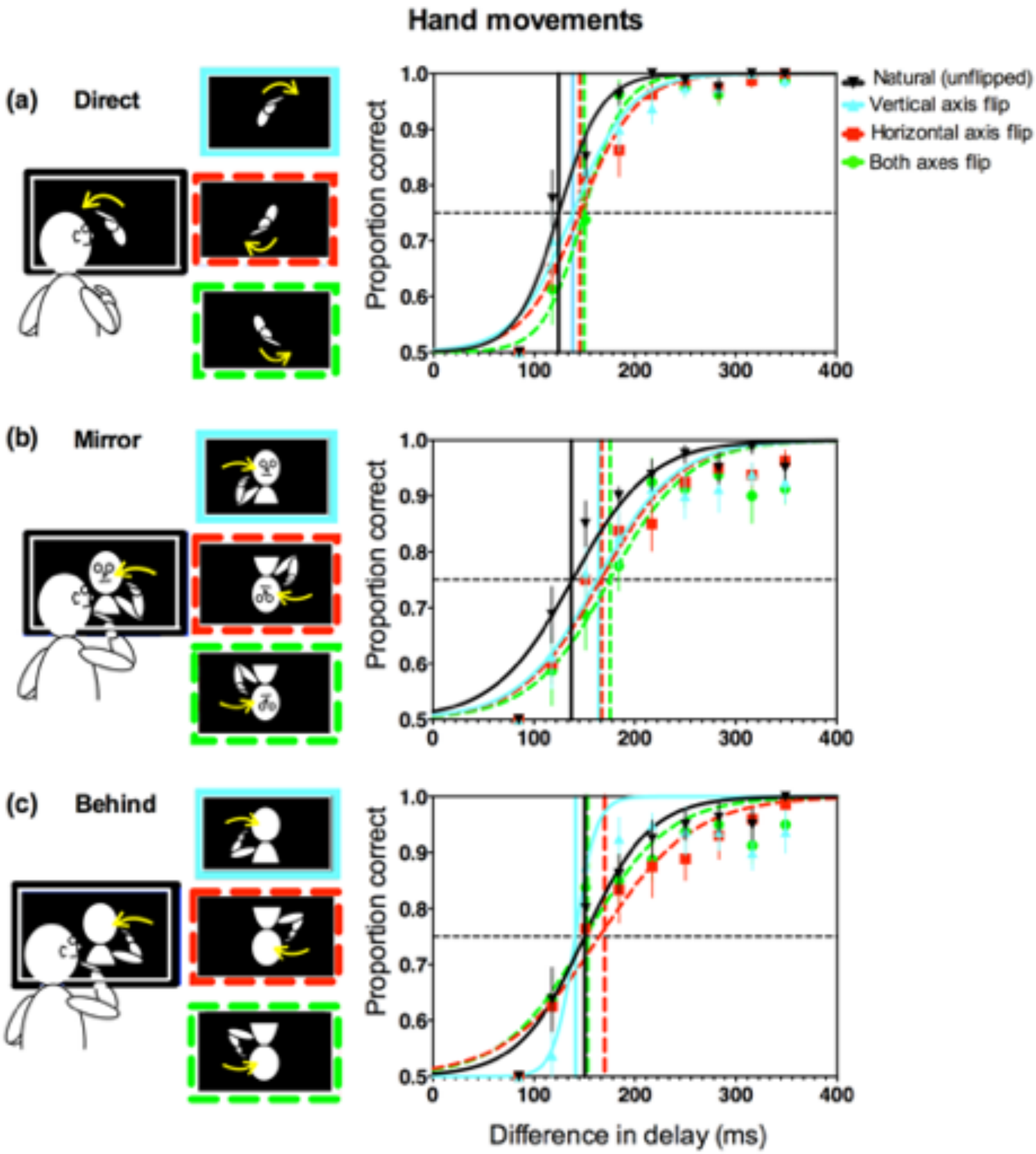


Figure 14. Detecting an added delay to the visual feedback for hand movements viewed in the direct view (A), in the mirror view (B) and in the behind view (C). Mean proportion correct is plotted as a function of the imposed visual delay. The sigmoidal curves plotted through the data are for the natural (unflipped) perspective (solid dark

lines and filled inverted triangles), the video flipped around the vertical axis (solid light lines and filled circles), flipped around the horizontal axis (dashed dark lines and filled squares), and flipped around both axes (dashed light lines and filled triangles). Vertical lines represent the 75% threshold and the horizontal dashed line represents the 75% criterion. Error bars represent SEM.

3.4.2. Discriminating visual delays for head movements

A one-way repeated measures ANOVA revealed a significant main effect of perspective when participants saw their head movements in the mirror view ($F_{(3, 27)}$ = 3.26, P = 0.04, η_p^2 = 0.27; see Figure 15A). The threshold for the natural (unflipped) perspective (that is, the view expected when looking in a mirror) was lower (*M* ± *SE* = 152 ± 7 ms) than for the other perspectives (vertical axis flip *M* ± *SE* = 182 ± 12 ms, *M* ± *SE* difference = 30 ± 9 ms, P = 0.03; horizontal axis flip *M* ± *SE* = 177 ± 15 ms, *M* ± *SE* difference = 25 ± 12 ms, P = 0.03; and both *M* ± *SE* = 190 ± 16 ms, *M* ± *SE* difference = 38 ± 16 ms, P = 0.03): the self advantage prevailed. There was, however, no such self advantage when participants saw their head movements in the behind view ($F_{(3, 27)}$ = 0.50, P = 0.68, η_p^2 = 0.05; see Figure 15B).

Analysis of the standard deviations of the psychometric functions showed no significant difference between perspectives for the mirror and behind views ($F_{(3, 28)}$ = 1.393, p = 0.27 and $F_{(3,28)}$ = 0.81, p = 0.5 respectively).

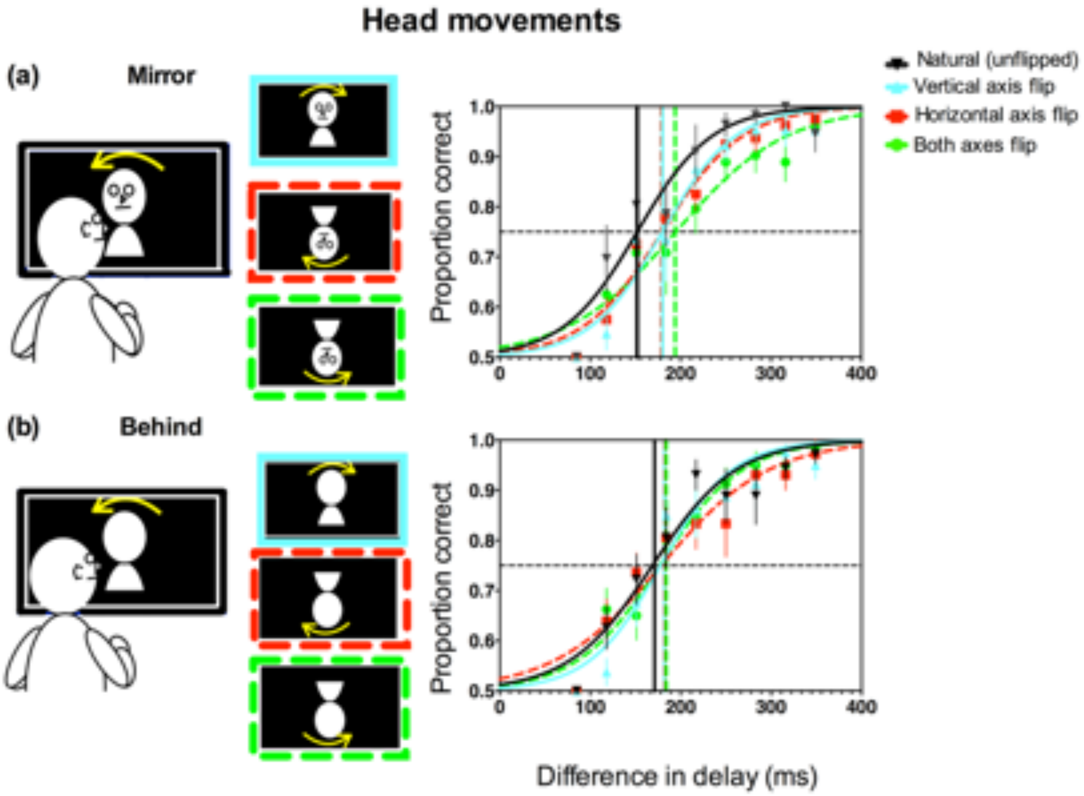


Figure 15. Detecting an added delay to the visual feedback for head movements viewed in the mirror view (A) and in the behind view (B). Mean proportion correct is plotted as a function of the imposed visual delay. The sigmoidal curves plotted through the data are for the natural (unflipped) perspective (solid dark lines and filled inverted triangles), with the video flipped around the vertical axis (solid light lines and filled circles), flipped around the horizontal axis (dashed dark lines and filled squares), and flipped around both axes (dashed light lines and filled triangles). Vertical lines represent the 75% threshold and the horizontal dashed line represents the 75% criterion. Error bars represent SEM.

3.4.3. Is temporal delay better detected for views of the body experienced most often?

We compared the performance at detecting delays in visual feedback for the natural (unflipped) perspectives (solid dark lines in Figure 14A-C and Figure 15A,B) for each movement and viewpoint. For hand movements, a one-way repeated measures ANOVA revealed a significant main effect of view ($F_{(2, 18)} = 13.22$, $P < 0.001$, $\eta_p^2 = 0.6$) with a linear trend between the natural, mirror, and behind views of the body ($F_{(1, 9)} = 35.38$, $P < 0.001$, $\eta_p^2 = 0.8$). The mean thresholds for the natural perspectives differed from one another (direct view was 15 ± 5ms lower than the mirror view, $P = 0.02$; direct view was 34 ± 6ms lower than the behind view, $P < 0.001$; and the mirror view was 19 ± 8ms lower than the behind view, $P = 0.02$). Thresholds for detecting asynchrony between hand movement and visual feedback were lowest when the body was seen from the direct view. Analysis of the standard deviations of the psychometric functions showed no significant difference between the views ($F_{(2, 18)} = 0.51$, $p = 0.61$).

A similar story was found for head movements where a paired t-test showed that threshold for the natural (unflipped) perspective was 20 ± 10ms lower when the head movement was seen in the mirror view than when it was seen in the behind view ($t_{(9)} = -1.92$, $P = 0.04$). Analysis of the standard deviations of the psychometric functions showed no significant difference between the views ($t_{(9)} = 0.36$, $p = 0.72$).

3.4.4. Differences between hand and head movements

Repeated measures ANOVA's revealed no significant difference between detecting delays for head or hand movements seen in the mirror view ($F_{(1,9)} = 1.93$, $p = 0.2$, $=0.18$) or in the behind view ($F_{(1, 9)} = 3.49$, $p = 0.10$, $= 0.279$), although the thresholds for the head movements ranged from 6 to 26ms longer than the thresholds for the hand movements.

3.5. Discussion

This study demonstrates significant variation in the ability to detect a temporal asynchrony between a movement and its visual feedback depending on the perspective from which the movement was viewed (manipulated by the various flips of the video image we employed) and previous experience of the view. A self advantage in detecting delays viewed from the natural perspective was evident only for the direct view (looking down at the hand) or viewing indirectly (looking at the hand or head in the mirror), and not for a view of the body that is never seen (looking at the hand or head from behind). We interpret the variation of performance across viewing perspectives as reflecting when the visual feedback matches the internal representation of the body and the view is thus recognized as being of the “self”.

There was no clear systematic variation in the slopes (standard deviations) of the psychometric functions with perspective for any of the viewpoints. In particular, the natural perspective was not associated with lower standard deviations than the other perspectives. Neither was there a systematic variation in the standard deviations between the views. This suggests that the difficulty of the task was equivalent in all conditions and that there was no variation in the reliability of the sensory information involved. Rather, the self advantage results instead from the information needed to the task being available faster.

The self advantage in detecting delay in visual feedback about a movement when it is viewed in the natural perspective is an objective measure of body ownership through agency (Hoover & Harris, 2012). Variation in performance with perspective has also been found in self-other recognition of hands and feet (Saxe et al., 2006; Conson et al., 2010), when judging which hand is portrayed in a static image (Parsons, 1994; Dyde et al., 2011), and for the rubber hand illusion (Costantini & Haggard, 2007; Holmes & Spence, 2007). So interpreting the self advantage as indicating ownership is clear when looking directly at one's own body. But why might a similar advantage be given to views of the face seen in a mirror?

3.5.1. Mirror viewing

Identifying the face in the mirror as being one's own has long been regarded as an ultimate test of self-recognition. Thus, countless hours have been spent trying to get various species to indicate that they can recognize themselves in mirrors by, for example, seeing if they could remove tags that could only be seen in a mirror (Gallup, 1970; Bertenthal & Fischer, 1978; Nielsen et al., 2006). Of course humans can perform this task with ease, but the present study is the first objective demonstration that the face in the mirror is given preferential treatment.

Mirrors allow us to match personal sensorimotor events with simultaneous visual information seen from an allocentric perspective. Since mirrors are used on a daily basis it is likely that we create an internal representation of our face that combines egocentric and allocentric perspectives. Interestingly, performance at detecting delays while viewing the natural perspective in the mirror view (hand 141ms; head 152ms) falls between performance while viewing the direct (hand 126ms) and the behind (hand 160ms; head 172ms) views in the natural perspective. This indicates that there is possibly less of a sense of ownership for the face-in-the-mirror than for the hands. Faces are highly ecological and provide very strong cues to self-identification relying heavily on featural configuration. Thus, when a face is inverted it is harder to identify changes in these configurations (Yin, 1969; Leder & Bruce, 2000; Thompson, 1980). Our data suggest that when the face-in-the-mirror is viewed upside down, the consequent reduction in performance is a quantifiable estimate of this reduction in identifiability and ownership.

3.5.2. Viewing invisible views

There was no self advantage when detecting visual feedback asynchrony for head or hand movements viewed in the behind view. This suggests an absence of an internal visual representation of this viewpoint of our body – all such presentations could best be considered as “other”. Of course, we cannot see ourselves from behind so it is unlikely that we would recognize the image as corresponding to ourselves. But what then does this mean for our sense that the back is part of our self? Recent studies have suggested a special connection between the front and back of the body (D'Amour & Harris, 2014). Perhaps non-visible parts of the body are pinned to surfaces that are visible; but this is not enough to provide a self advantage.

3.5.3. Conclusion

We have examined three views of the body: the direct view of the hand, the mirror view of the face and hand, and the view from behind. We have demonstrated a progressively weaker effect of varying the visual perspective from which these views are seen in the ability to detect temporal asynchrony between self-initiated movements and visual feedback concerning the movement for these three views. We interpret this as indicating that body parts that can be seen directly are treated as more part of the self than other body parts. We conclude that the sense of self is linked with the sight of self.

3.6. Acknowledgements

This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) grant to LRH. AENH held a PGS-D2 NSERC graduate scholarship.

4. CHAPTER 4: DISRUPTING VESTIBULAR ACTIVITY DISRUPTS BODY OWNERSHIP

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Keywords: cross-modal interactions; body ownership; visual perspective; body representation; vestibular cues; proprioception

4.1. Abstract

People are more sensitive at detecting asynchrony between a self-generated movement and visual feedback concerning that movement when the movement is viewed from a first-person perspective. We call this the “self advantage” and interpret it as an objective measure of self (Hoover & Harris, 2012; 2014). Here we ask if disruption of the vestibular system in healthy individuals affects the self advantage. Participants performed finger movements while viewing their hand in a first-person (“self”) or third-person (“other”) perspective and indicated which of two periods (one with minimum delay and the other with an added delay of 33 – 264ms) was delayed. Their sensitivity to the delay was calculated from the psychometric functions obtained. During the testing, disruptive galvanic vestibular stimulation (GVS) was applied in five-minute blocks interleaved with five minutes of no stimulation for a total of 40 minutes. We confirmed the self advantage under no stimulation (31ms). In the presence of disruptive GVS this advantage disappeared and there was no longer a difference in performance between perspectives. The threshold delay for the “other” perspective was not affected by the GVS. These results suggest that an intact vestibular signal is required to distinguish “self” from “other” and to maintain a sense of body ownership.

4.2. Introduction

The representation of body in the brain, sometimes referred to as the body schema, is created through convergence of proprioceptive, haptic, and visual signals (see: Serino & Haggard, 2010 for a review). Recently the vestibular system has been implicated in a previously unsuspected role in the development of the body schema (Lopez, Schreyer, Preuss, & Mast, 2012). For example, individuals with vestibular disorders, such as vestibular vertigo or vestibular deafferentation, tend to misrepresent the size, shape, and location of their body parts even though the vestibular system provides no information of direct relevance to making these judgments (Lopez, Halje, & Blanke, 2008; Sang, Jáuregui-Renaud, Green, Bronstein, & Gresty, 2006; Lopez & Blanke, 2007; Schilder, 1935). Healthy individuals with no vestibular symptoms can also be made to show degraded performance on tasks that require knowledge about their body and self by adding temporary, disruptive galvanic vestibular stimulation (GVS). For example, Bresciani and colleagues (2002) found that unilateral GVS disrupted reaching movements toward the side being stimulated and created a less accurate estimate of where the hands were in space. More remarkably, caloric vestibular stimulation affects the ability to discern the size and shape of a participant’s own hands (Lopez et al., 2012) and increases susceptibility to self-attribution illusions such as the rubber-hand illusion (Lopez, Lenggenhager, & Blanke, 2010). Taken together, these observations suggest that intact vestibular background activity is integral for creating and maintaining a coherent representation of the self and that losing this signal undermines a person’s perception of self. However, reliable, quantitative assessments of how a person perceives themselves as themselves is lacking and studies have generally been restricted to using questionnaires or self report measures.

Previous studies investigating self recognition during active movement have found misattribution of hand movements to another agent when the participants' movements and the other agents' movements (superimposed over top of their movements) were similar and, in some instances, when there were discrepancies between the movements (Nielsen, 1963; Forneret & Jeannerod, 1998; see Jeannerod, 2003 for a review). These results suggest the importance placed upon visual cues when making self/other judgements. Visual perspective, in particular, has been shown to modulate the ability to recognize our own body parts from others' (van den Bos & Jeannerod, 2002; Conson, Aromino, & Trojano, 2010), discriminate between left and right hands (Dyde, MacKenzie, & Harris, 2011), and experience the rubber-hand illusion (Holmes & Spence, 2007). We have previously shown that visual perspective also affects the threshold for detecting a temporal mismatch between a self-generated movement (e.g., of the finger) and visual feedback of the movement (Hoover & Harris, 2012; 2014). We found that when body movements are seen from a first-person perspective (e.g., when looking down at your own hands) there is a signature self advantage in detecting the delay: asynchrony is detected approximately 40ms faster when viewed from this "self perspective" than when movements are viewed from a perspective considered third-person or other (e.g., upside down) (Hoover & Harris, 2012; 2014). Self-generated movements provided participants with efferent information as well as proprioceptive information, which are important factors in determining whether you are the agent of the action (Gallagher, 2000; Farrer et al., 2003; Tsakiris et al., 2005). In turn, the sense of agency is an important contributor to the sense of body ownership (Tsakiris et al., 2010). The advantage in asynchrony detection thresholds suggests an enhanced sense of body ownership when an action is viewed in a self perspective. This measure can therefore be taken as an objective measure of body ownership.

Given that the vestibular system has been linked to registering spatial and temporal aspects of the self (Ferrè, Vagnoni, & Haggard, 2013; Lopez et al., 2008) we examined whether disruption of vestibular activity using GVS in healthy individuals affected the self advantage in temporal asynchrony detection.

4.3. Methods

4.3.1. Participants

9 right-handed adults, with a mean age of 29 (± 12 SD) years, participated in this study. The experiment was approved by the York University office of research ethics and followed the guidelines of the Declaration of Helsinki. Handedness was determined by an adapted version of the Edinburgh Handedness Inventory (Oldfield, 1971).

4.3.2. Galvanic vestibular stimulation

The vestibular stimulation consisted of a small current applied through electrodes positioned on the mastoid processes behind the ears. A reference electrode was placed in the centre of the forehead. The electrodes were 3.25 cm diameter round carbon-conductor electrodes (9000 series electrodes; Empi Recovery Sciences, St. Paul, Minnesota, USA). The vestibular stimuli were generated by a GVS system (Good Vibrations Engineering Ltd., Nobleton, Ontario, Canada) controlled by a PC. Our vestibular stimulus was a sum-of-sines waveform with dominant frequencies at 0.16, 0.32, 0.43, and 0.61 Hz (maximum current limited to +/- 5 mA) which has shown to be disruptive to the vestibular system (MacDougall, Moore, Curthoys, & Black, 2006; Moore et al., 2006). Bilateral, bipolar stimulation was applied in 5-minute blocks interleaved with 5-minute blocks without stimulation so that data collected with and without GVS were interleaved over the total experimental time of 40 minutes.

4.3.3. Apparatus and stimuli

Participants sat on an adjustable chair at a table with their head on a chinrest 50 cm away from a LCD display (HP Fv583AA 20” widescreen monitor; 1600 x 900 pixels; 5 ms refresh response time) centred at eye level as shown in Figure 16. They placed their hand on the table shielded from view by a black cloth. A PlayStation Eye camera (SCEI; resolution 640x480 @ 30 Hz) was mounted on the front of the chinrest and pointed down at their hand. The camera was angled to capture the view as seen from a “natural” egocentric perspective as if participants were looking down at their own hands.

The video signal from the camera was fed into a computer (iMAC11, 2, mid 2010), read by MATLAB (version R2009_b) and played through the LCD screen at either a minimal delay, or with an added delay of between 33 and 264ms. To calibrate the system we had the camera view a flashing LED and compared the voltage across it with its appearance on the screen measured by a light sensitive diode. This revealed a minimum delay of 85ms ± one-half camera refresh duration and confirmed the delay values we introduced with the software.

We asked participants to perform a single flexion of the right index finger through approximately 2cm. They made the movement as soon as they saw their hand on the screen in a given trial. Participants avoided touching the table or other fingers with their index finger during the movement so as to not introduce additional tactile cues. To reduce between-subject differences in the speed and type of movement, all participants went through a 15-trial practice phase during which the experimenter observed and corrected movement prior to testing. Video images were manipulated using the Psychophysics Toolbox extension of MATLAB subroutine *PsychVideoDelayLoop* (Brainard, 1997; Pelli, 1997). Participants were presented with two views of their movements: 1) a "self" perspective (the expected first-person perspective), and 2) an "other" perspective (the unexpected third-person perspective where the video images are flipped around the x and y axes so that it was upside down and back to front). Examples of these views are shown in insets in Figure 17.

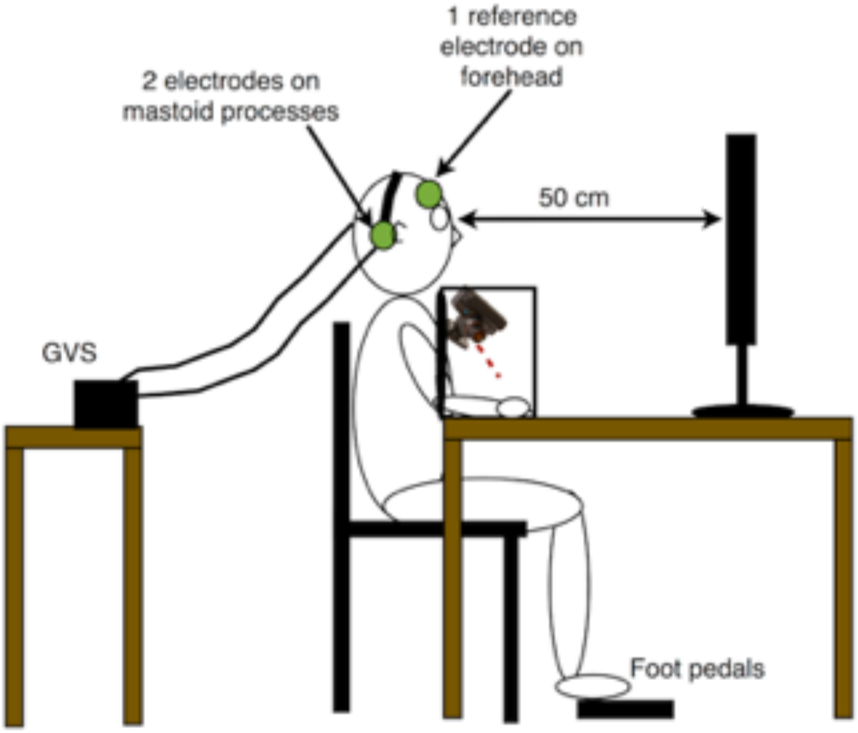


Figure 16. Apparatus: participants sat on an adjustable chair at a table 50 cm from an LCD screen centred at eye level. The right hand was placed on the table shielded from direct view by a black cloth. A Playstation Eye camera was mounted on the front of a chinrest and pointed down to capture the view as seen from a natural self-perspective. Two stimulating electrodes were placed on the mastoid processes behind the ears and one reference electrode was placed on the center of the forehead. The electrodes were connected to a GVS generator. Foot pedals were used to make responses.

4.3.4. Procedure

To assess the thresholds for detecting temporal synchrony, a two-interval forced choice (2IFC) discrimination paradigm was used. Each trial consisted of two 1s periods separated by an inter-stimulus interval of 100ms: in one period a minimal-delay presentation of the movement was shown and in the other, the presentation was delayed by a variable amount. Whether the minimal-delay presentation or the delayed presentation was displayed first was randomly chosen by MATLAB. There were nine possible differences in visual delays in any given trial: 0, 33, 66, 99, 132, 165, 198, 231, and 264ms corresponding to a delay of an integral number of video frames. Participants indicated which presentation was delayed using foot pedals (Yamaha FC5): left for first and right for second. The experiment was run in a block design where GVS was applied in five-minute blocks interleaved with five minutes of no stimulation for a total of eight blocks taking 40 minutes in total. Five participants started with a control block and 4 participants started with a GVS block. In total, the nine differences in visual delay were presented eight times for the two visual perspectives in a random order with and without GVS resulting in a total of 288 trials.

4.3.5. Data analysis

To explore differences in performance across conditions we fitted logistic functions[2] to the proportion of times participants correctly chose the delayed period as a function of the delay using:

---

[2] This function was incorrectly named cumulative Gaussian in the published version

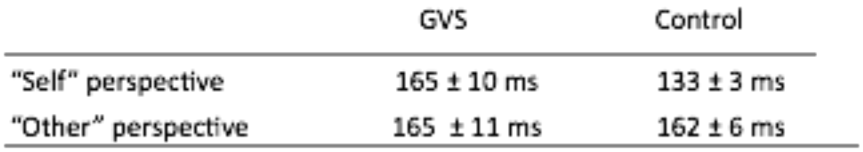
$$y = 0.5 + \frac{0.5}{1 + e^{-\left(\frac{x - x_0}{b}\right)}}$$

………(1)

where x is the delay, x_0 is the 75% threshold and b is the standard deviation. The statistical analysis comprised of repeated measures analysis of variances (ANOVAs) and paired t-tests. For all tests, alpha was set at $P < 0.05$.

4.4. Results

Figure 17 shows the mean proportion of trials in which the participants correctly identified the presentation with the delay, plotted as a function of the total delay (system delay plus added delay), averaged across the nine participants for the two experimental conditions (with and without GVS) and the two perspectives of the movement ("self" and "other"). Illustrative psychometric functions are plotted through these average data for the four conditions. Threshold values for detecting the added visual delay were defined as the 75% point of this curve. Each participant's performance was analysed separately for the statistical tests. The mean thresholds and standard errors are shown in Table 4.



	GVS	Control
“Self“ perspective	165 ± 10 ms	133 ± 3 ms
“Other” perspective	165 ± 11 ms	162 ± 6 ms

Table 4: Mean detection thresholds averaged across all participants, with SEs. The values were obtained by adding the system delay (85 ms) to the delay added to the video.

A 2x2 repeated measures ANOVA revealed a significant interaction between the perspective of the hand (“self” vs “other”) and whether GVS was applied or not, $F_{(1, 8)}$ = 12.54, P = 0.008, η_p^2 = 0.61. In the absence of GVS, when participants saw their hand in the expected “self” perspective they were better at detecting the delay, showing a self advantage of 29ms on average compared to when the hand was viewed in the “other” perspective ($t_{(8)}$ = 5.70, p = 0.001, d= 4.03). The presence of disruptive GVS increased the threshold to detect asynchrony in the “self” perspective by 32ms compared to the no-GVS condition ($t_{(8)}$ = 3.17, p = 0.01, d= 2.24) thus eliminating the self advantage that was apparent in the control condition. Critically, GVS did not affect performance while participants viewed their movements in the “other” perspective: the GVS “self” perspective showed no significant difference in performance from either the control or the GVS “other” perspective (GVS “self” vs GVS “other” $t_{(8)}$ = 0.10, p =0.92, d = 0.07; GVS “self” vs control “other” $t_{(8)}$ = 0.46, p = 0.66, d = 0.35).

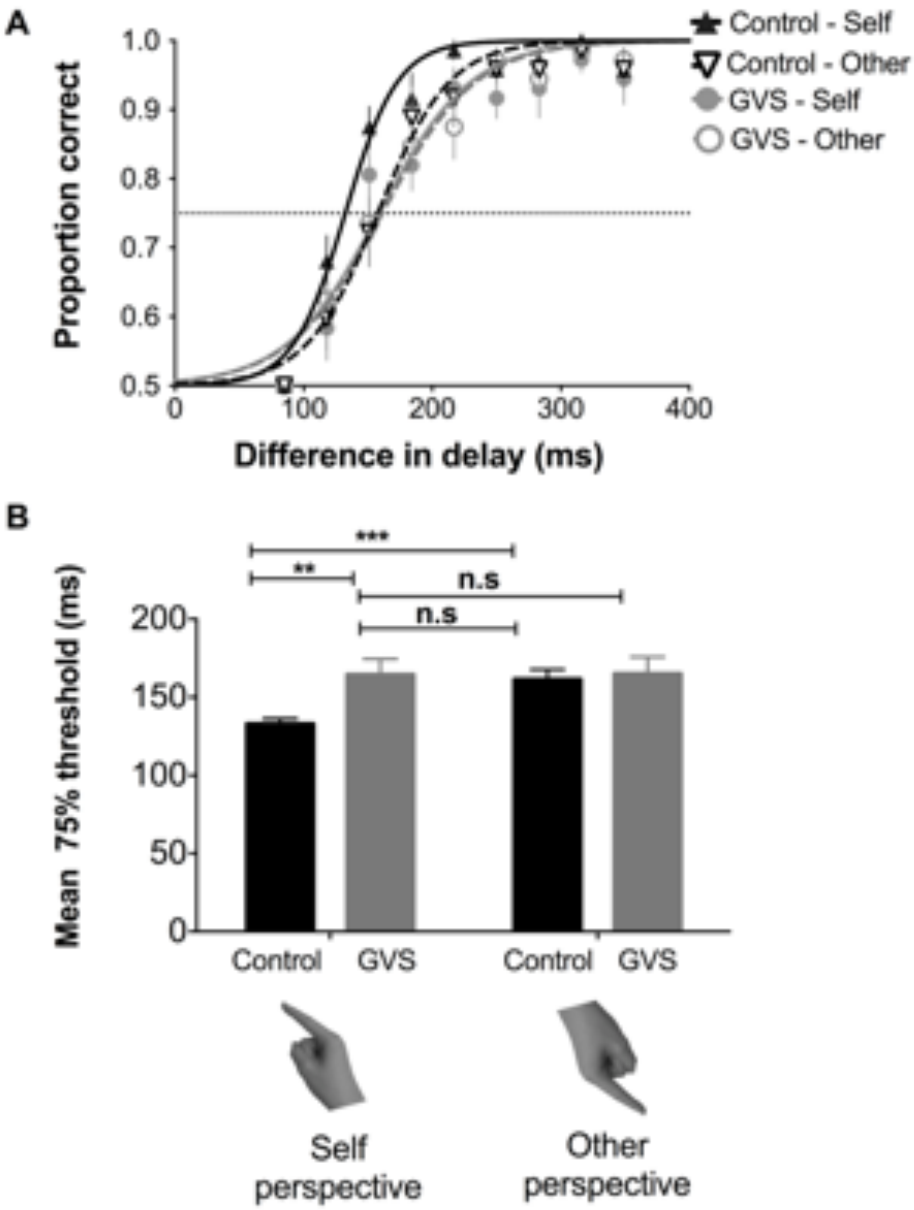


Figure 17. A) Thresholds for detecting an imposed visual delay in the visual feedback concerning a self-generated movement. The mean proportion correct is plotted as a function of the imposed visual delay. The curves are psychometric functions fitted through the data for the “self” perspective (solid black line and black triangles), the “other” perspective (dashed black line and inverted white triangles), GVS “self”

perspective (solid grey line and grey circles), and GVS “other” perspective (dashed grey line and white circles). B) The mean 75% thresholds averaged from the fits to the individual participant’s data in the control condition (black bars) and the GVS condition (grey bars) for the “self” and “other” perspectives. Error bars are SEMs. n.s $p > 0.05$ ** $p = 0.01$ *** $p = 0.001$.

Analysis of the slopes of the psychometric functions (b, see methods) showed no significant effect (F (3, 316) = 2.40, p = 0.07), although there was a trend in which the "self" perspective without GVS tended towards being lower (20.3 ± 3 ms) than the other three conditions (GVS "self" = 35.9 ± 6 ms; GVS "other" = 36.5 ± 5 ms; and control "other" = 27.9 ± 5 ms).

4.5. Discussion

Here we showed that disruptive vestibular stimulation affected the ability to detect temporal asynchrony between a self-generated movement and visual feedback about the movement but solely when self-generated movement was seen in the expected "self" perspective. We replicated our previous finding of a self advantage where one is more sensitive to a temporal mismatch when the hand is shown in the expected "self" perspective and showed that this self advantage is completely abolished by disruptive GVS. Since threshold for detecting a delay for movements seen from the "other" perspective were unaffected by GVS, the GVS was clearly not exerting its effect by, for example, degrading the visual scene by eye movements or any other such indirect influence. Does this effect indicate a reduced sense of body ownership or a reduced sense of agency?

The sense of agency - the sense of being in control of your intended actions (Gallagher, 2000) - contributes to the sense of body ownership (van den Bos & Jeannerod, 2002) but can be dissociated from it. Patients with vestibular disorders have reported that they experience a lessened sense of agency (Sang et al., 2006) and sense of agency can be felt for objects that are not seen as part of the body (such as using a computer mouse to control a cursor on a screen; Balslev, Cole, & Miall, 2007). The current study required participants to compare efferent and proprioceptive information concerning the self-generated finger movement with visual information. It may be that the noisy vestibular information from the artificial vestibular stimulation caused participants to be less aware of their movements – reducing the sense of agency. However, one would expect that if our effect disrupted the ability to compare visual with proprioceptive/efferent signals (i.e., the sense of agency), both the “self” and “other” perspectives would be equally affected. Since this was not the case and the “other” judgments were unaffected, it seems improbable that the disruptive GVS affected the sense of agency but rather that our task is probing the sense of body ownership.

The fact that disruptive vestibular stimulation only affected performance when the hand was seen from the first-person perspective suggests that the vestibular system plays a role in providing some kind of grounding information to the multisensory representation of the body in the brain. This is in line with other research investigating the contribution of the vestibular system to the ownership of a body part seen in a first-person perspective. Ferrè and colleagues (2014) found that in the presence of vestibular stimulation, participants were more apt to identify characters drawn on their forehead as being from the self-perspective rather than from the third-person perspective. This propensity for responding to the first person-perspective during a graphesthesia task also suggests, but in a more indirect way than the present study, that vestibular inputs are an integral component of the development of the body representation in the brain.

When movements are seen in the "self" perspective, the self- advantage we report here of 29ms (comparable to the 40ms we reported previously, Hoover & Harris, 2012), provides a quantitative example of how the sense of body ownership aids performance (Gallagher, 2000). This enhancement suggests that participants are better able to detect temporal asynchrony between making a movement and seeing the movement when the visual information matches their internal representation of their hand moving. When disruptive GVS is applied, it seems that the disruption of the vestibular signal creates a reduced sense of body ownership – thus eliminating the self advantage. Under this interpretation our observation provides a quantitative measure of the effect of vestibular input on body ownership which is consistent with other more qualitative reports of vestibular stimulation leading to a lessened sense of self (Ferrè et al., 2014; Lopez et al., 2008; Lopez, 2013) and being more susceptible to the rubber hand illusion (Lopez et al., 2010).

4.6. Acknowledgements

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5. CHAPTER 5: INDUCING OWNERSHIP OVER AN ‘OTHER’ PERSPECTIVE WITH A VISUO-TACTILE MANIPULATION

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Keywords: cross-modal interactions; body ownership; visual perspective; body representation; proprioception

5.1. Abstract

Seeing our body from a ‘self’ perspective while performing a movement improves our ability to detect asynchrony between the visual and proprioceptive information concerning that movement: a signature of enhanced body ownership referred to as the ‘self advantage’. We consequently experience no self advantage when seeing our body from an ‘other’ perspective. Here we ask whether introducing visuo-tactile stimulation (VTS), similar to that used in the rubber hand illusion to invoke ownership over a dummy hand, would produce a self-advantage when viewing the body from a typically ‘other’ perspective. Prior to the experiment, participants watched a live video of their own back using a camera mounted behind them while their back was tapped with a rod for two minutes. The video was either synchronous (sVTS) or asynchronous (aVTS) with the tapping. Participants then raised their hands and made a stereotyped finger movement that they watched from the same camera either in the original, natural perspective or upside down. Participants indicated which of two periods (one with minimum delay and one with an added delay of 33 to 264ms) appeared delayed. Sensitivity was calculated using psychometric functions. The sVTS group showed a self-advantage of about 45ms in the natural visual condition compared to the upside down condition, whereas the aVTS group showed no difference between the two conditions. Synchronous visuo-tactile experience increased the feeling of ownership over a typically ‘other’ perspective in a quantifiable way indicating the multisensory and malleable nature of body representation.

5.2. Introduction

The first-person perspective is our visual frame of our body in the world. It provides us with information about body ownership (Gallagher, 2000) and our body location in space (Haggard, Christakou, & Serino, 2007; Serino et al., 2013). The first-person perspective is therefore an important component in the construction of the representation of the body in the brain. When seeing a static image of a hand, for example, from an egocentric vantage point we are better able to determine that this is our hand as opposed to someone else's (Conson et al., 2010; van den Bos & Jeannerod, 2002). We also do better at making laterality judgements (Dyde et al., 2011; Fiorio et al., 2007; Parsons, 1994) and when moving our fingers to a target (Sutter & Müsseler, 2010). This identification of ownership is reflected in our ability to detect an added visual delay in the visual feedback concerning a self-generated finger movement when the hand is seen in the first-person perspective compared to another view (Hoover & Harris, 2012). This improved ability to detect asynchrony in the 'self' perspective is called the self-advantage and is a quantitative measure of body ownership.

The malleable nature of the representation of the body in the brain has been exposed by ingenious experiments that introduce conflicting visual, tactile, and/or proprioceptive sensory information that challenge a participant's sense of body ownership. In the rubber hand illusion (RHI; Botvinick & Cohen, 1998; Tsakiris et al., 2010a; Tsakiris & Haggard, 2005b), for example, the experimenter strokes the participant's hand (hidden from view) and a dummy rubber hand synchronously to provide a misleading visual-tactile correlation. Many people report feeling as though the dummy hand is their own hand, or that their real hand is closer to the dummy hand than it actually is (Botvinick & Cohen, 1998). The RHI only occurs if the seen stroking of the dummy hand and the felt stroking of the real hand are synchronous. When the visuo-tactile components are separated by more than approximately 300ms, individuals do not assign ownership to the rubber hand (Shimada et al., 2009). Further, the RHI is diminished if the dummy hand is not aligned in an anatomically plausible position (Costantini & Haggard, 2007; Holmes & Spence, 2007). Both the binding of the visual and tactile information and an anatomically possible position of the hand are necessary for the developing a sense of ownership over a dummy hand.

Previously, we have shown that detecting temporal asynchronies between visual and proprioceptive information during self-initiated hand or head movements viewed from behind (via a video camera) shows no self advantage, in contrast to when viewing parts of the body that are seen all the time (natural, egocentric view looking down at the body) or some of the time (face in the mirror). We concluded that unseen views of the body may not be independently represented visually (Hoover & Harris, 2014). This is inline with others who have shown that simply detecting a tactile stimulus on parts of the body that cannot bee seen directly (e.g., back of the neck) is more difficult than on parts that can be seen (e.g., hands) (Tipper et al., 2001) and with the initial absence of ownership over indirect views of real or virtual bodies in full body illusion (Ehrsson, 2007; Lenggenhager et al., 2007). An illusion equivalent to the RHI, called the whole-body illusion or the out-of-body illusion, is evoked when seeing the body presented in a third person perspective (from behind) being tapped at the same time as feeling the tap.

The synchrony of the seen and felt taps induces the sense of self-identification with the virtual body and the sense of the real body being located outside of itself (Blanke & Metzinger, 2009; Ehrsson, 2007; Lenggenhager et al., 2007). This change in self-location is typically analysed with self-report questionnaires similar to RHI questionnaires or by skin conductance responses when the seen body is threatened (Ehrsson, 2007; Petkova et al., 2011; Guterstam & Ehrsson, 2012; Preston et al., 2015).

Here, we introduced synchronous visuo-tactile stimulation, similar to that used in the RHI and full-body illusions, and had participants make temporal discrimination judgments that we have previously used to quantify body ownership without explicitly asking about it (Hoover & Harris, 2012; 2014; 2015a; Hoover, Elzein, & Harris, 2016). Participants performed self-generated finger movements while viewing their arms, hands and bodies from behind (Figure 18). The live movements were presented in the natural perspective or flipped around both the vertical and horizontal axes, and with varying amounts of delay. We hypothesized that participants who received synchronous visuo-tactile stimulation encouraging them to interpret that view as 'self' would subsequently show an advantage in detecting temporal asynchrony thus providing a quantitative assessment of the induced body ownership in the full-body illusion, whereas those in the asynchronous visuo-tactile stimulation group would not show such an advantage. We also predicted that asynchronous visuo-tactile stimulation would evoke no difference in performance between the viewpoints.

5.3. Methods

5.3.1. Participants

20 right-handed adults, with a mean age of 24 (± 4 SD) years, participated in this study. Half of the participants were recruited through the York University undergraduate participant pool and awarded class credit for their participation. The remaining participants were recruited through word of mouth on campus. They were randomly divided into two groups of ten. Each group had five participants from each pool. The experiment was approved by the York University office of research ethics and followed the guidelines of the Declaration of Helsinki. All participants gave informed consent. Handedness was determined by an adapted version of the Edinburgh Handedness Inventory (Oldfield, 1971).

5.3.2. Apparatus

Participants sat on an adjustable chair at a table 50 cm away from a LCD screen (HP Fv583AA 20” widescreen monitor; 1600 x 900 pixels; 5ms refresh response time). Participants placed their heads at the entrance to a cylindrical shroud that was mounted in front of the LCD screen so that they could not see their body directly and all surrounding visual distractions from the laboratory room were obscured (Figure 18A). A PlayStation Eye camera (SCEI; resolution 640x480 @ 30 Hz) was mounted to a pole 40cm behind the participant’s head. Since the camera was positioned behind the participants, the visual image presented on the LCD screen was of the back of their head, shoulders, and upper back. The LCD screen was hidden from view of the camera with a surround of black foamcore.

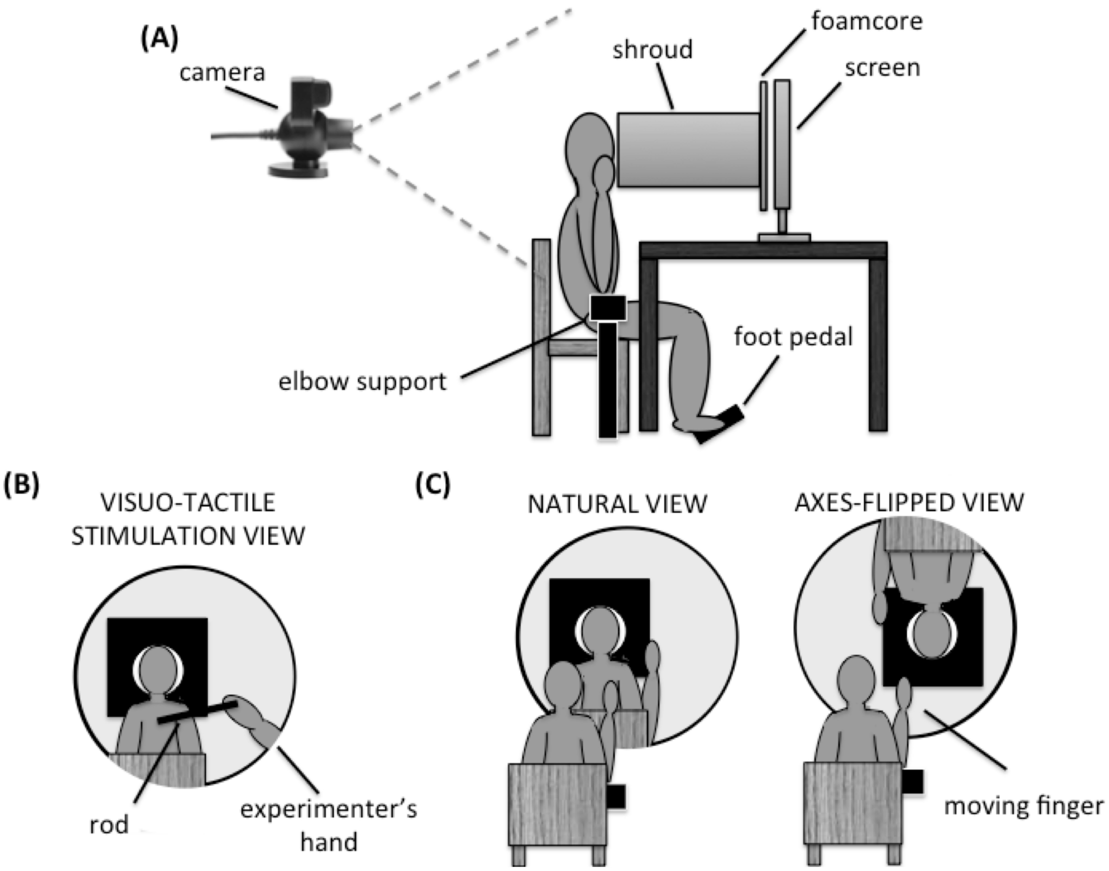

Figure 18. Apparatus: (A) Participants sat on an adjustable chair 50cm away from the LCD screen and placed their head in a shroud that was mounted in front of the screen. A PlayStation Eye camera was mounted to a pole 40cm behind the participant head. Since the camera was positioned behind the participants, the visual image presented on the LCD screen was the back of their heads, shoulders, and upper back. Insets (B) shows what was presented on the LCD screen during the VTS phase. The back of the participant's head, their shoulders and back, and the experimenter's arm with the rod are visible. Inset (C) shows what was visible on the LCD screen during the experiment for the natural and axes flipped views.

The video signal from the camera was fed into a computer (iMAC11, 2, mid 2010), read by MATLAB (version R2009_b), and played through the LCD screen at either a minimal delay, or with an added delay of between 33 and 389ms. Calibration of the system (see Hoover & Harris, 2012; 2014) revealed a minimum delay of 85ms ± one-half camera refresh duration and confirmed the delay values we introduced with the software.

5.5.4. Movement

While resting their right elbow on an armrest, participants held their right hand and forearm up beside their head in view of the camera and performed a single flexion of the right index finger through approximately 2 cm taking about 1 s to do so. This same active finger movement used in our previous studies (Hoover & Harris, 2012; 2014; Hoover et al., 2016). Participants were prompted to start the movement after hearing a beep and as soon as the image appeared on the screen in a given trial. Participants avoided touching the shroud, their face or other fingers to avoid introducing other tactile cues. Each participant had a 15 trial practice phase where the experimenter observed and corrected movements prior to testing to ensure consistency of speed and type of movement.

5.3.5. Stimuli

Live video images were manipulated using the Psychophysics Toolbox extension of

MATLAB subroutine *PsychVideoDelayLoop* (Brainard, 1997; Pelli, 1997). Participants were presented with two views of their movements: 1) a natural, expected view of the body seen from behind, as if they were viewing their body while sitting behind themselves, and 2) an unexpected view of the body from behind where the live video images were flipped around the horizontal and vertical axes so that the video was upside down and back-to-front. Examples of these views are shown in insets in Figure 18C.

5.3.6. Visuo-tactile stimulation

Each block of trials started with a two-minute visuo-tactile stimulation (VTS) period. The experimenter stood behind and off to the right side of the participant and tapped the upper center of the participant's back just below the neck with a rod (see Figure 18B) in a consistent tapping pattern at approximately 60 taps per minute. The experimenter's hand, the rod and the point at which they were touched on the back were visible on the video images presented on the LCD screen in the natural view. Participants were randomly assigned to one of two experimental groups: (1) the synchronous visuo-tactile stimulation (sVTS) group and (2) the asynchronous visuo-tactile (aVTS) group. The synchronous group saw the touch on the LCD screen at the same time (with the system's minimum delay) as they felt the touch. The asynchronous group saw the touch on the LCD screen with varying time delays and lengths of delay presentation within the stimulation session. This was done so that there was no association made between a specific delay and the touch (see Pfeiffer, Schmutz, & Blanke, 2014). Each two-minute stimulation period (for the aVTS group only) was divided into 11 segments of time (10, 5, 20, 10, 20, 5, 10, 20, 5, 10, and 5s) and visual delays between 85 and 382 ms were assigned to each of the 11 segments (349, 184, 283, 382, 316, 151, 85, 382, 184, 349, 217 ms). This was to make sure that there could be no association between an added delay and the amount of time for which each delay was experienced.

5.3.7. Procedure

We used a two-interval forced choice (2IFC) discrimination paradigm to assess temporal asynchrony discrimination. Each trial had two 1s periods separated by an inter-stimulus interval of 100ms: one period had a minimal-delay presentation of the video of them making a finger movement, and the other period had a presentation delayed by a variable amount. The period in which the minimal-delay and the added delay appeared was chosen randomly by MATLAB. There were nine possible differences in visual delays in any given trial: 0, 33, 66, 99, 132, 165, 198, 231, and 264ms corresponding to a delay of an integral number of video frames. Participants used foot pedals (Yamaha FC5) to indicate which of the two periods had the added delay: left for first and right for second.

The experiment was run in four blocks. Each block was preceded by two minutes of synchronous or asynchronous VTS (depending on group assignment) followed by 36 trials, which took about six minutes. The nine differences in visual delay were presented eight times in each of the two views (natural or flipped) randomly interleaved for a total of 144 trials for each participant.

5.3.8. Data analysis

Detection thresholds were obtained for each participant and condition by fitting a logistic function to the proportion of times they correctly chose the delayed period plotted as a function of the delay using:

$$y = 0.5 + \frac{l-0.5}{1+e^{-\left(\frac{x-x_0}{b}\right)}} \qquad \text{...(1)}$$

where L is the performance rate when the delay was clearly detectable and was set to ≤ 1, x is the delay, x_0 is the 75% threshold and b is the slope of the function. The lapse rate was 1-L. The statistical analysis comprised of analysis of variances (ANOVAs) and t-tests. Multiple comparison p-values were corrected with the false discovery rate method (Benjamini & Hochberg, 1995). For all tests, alpha was set at $p < 0.05$.

5.4. Results

Figure 19A plots the mean response rate as a function of delay for the natural and flipped views following either sVTS or aVTS. A 2 x 2 between-within ANOVA revealed a significant interaction between VTS group (synchronous vs asynchronous) and the view (natural vs axes flipped), $F_{(1, 18)}$, 5.95, $P = 0.03$, $\eta_p^2 = 0.25$. (Figure 19B). The sVTS group was able to detect the visual delay at a lower threshold for the natural view (the view they had experienced while being tapped) than for the axes-flipped view, showing an advantage of 45ms ($t_{(9)} = 2.51$, $p = 0.03$, Cohen's $d = 1.16$. The aVTS group showed no difference between the views, ($t_{(9)}$ = 0.37 p = 0.72, Cohen's d = 0.05): there was no advantage to seeing the movements from the natural view.

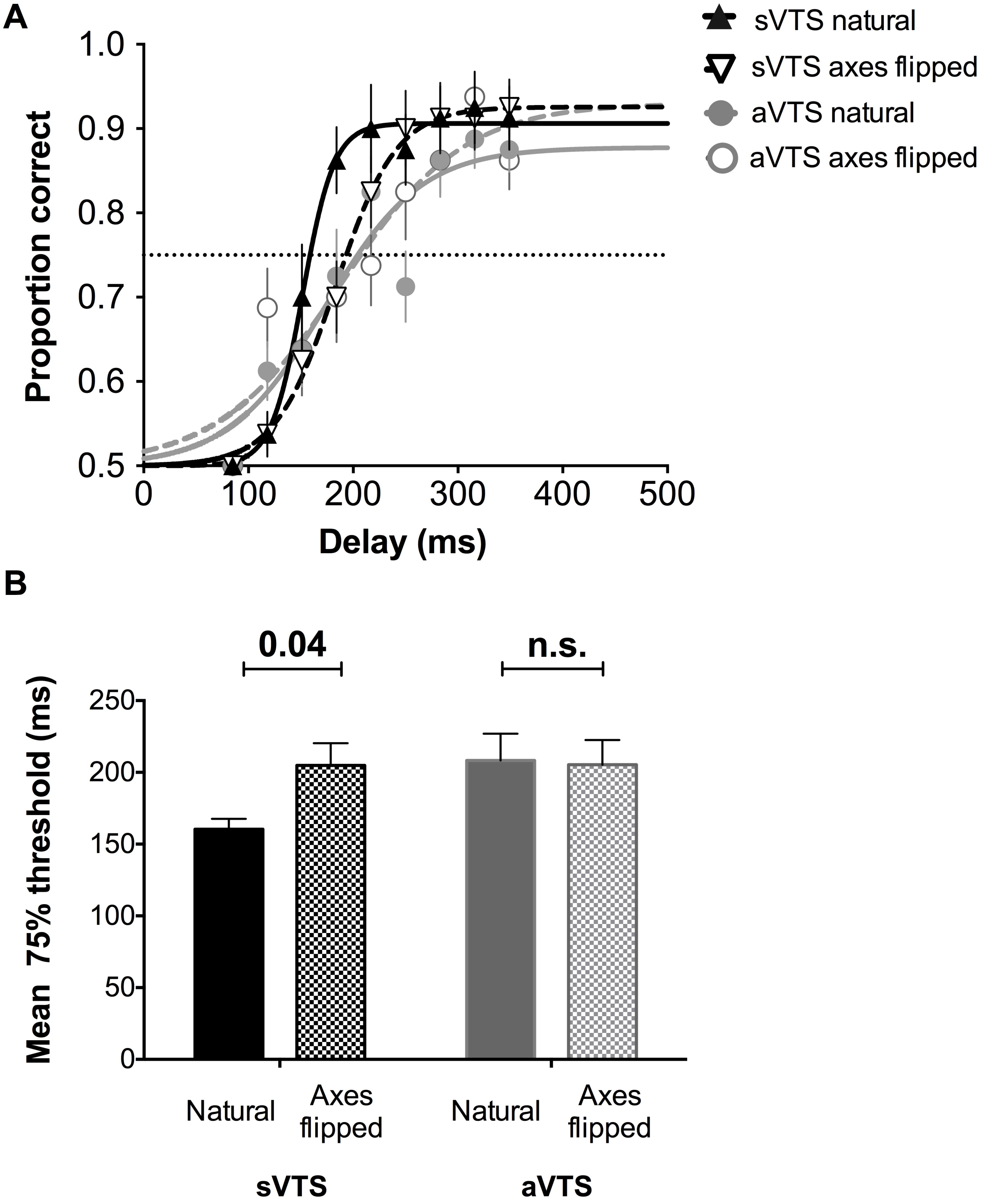

Figure 19. (A) Thresholds for detecting the added visual delay in the visual feedback for self-generated movement. The mean proportion correct is plotted as a function of the added visual delay. The curves are logistic functions (see text) fitted through the data for the synchronous visuo-tactile stimulation group (sVTS) natural view (solid black line and black triangles), the sVTS group axes flipped view (dashed black line and inverted white triangles), the asynchronous visuo-tactile stimulation group (aVTS) natural view (solid grey line and grey circles), and the aVTS group axes flipped view (dashed grey line and white circles). (B) The mean 75% thresholds averaged from the fits to the individual participant's data for the sVTS group (black bars) and the aVTS group (grey bars) for the two views. Error bars are SEMs.

Analysis of the slopes of the psychometric functions (b, see methods) showed no significant interaction $F_{(1, 18)} = 1.16$, $P = 0.30$, $\eta_p^2 = 0.06$, effect of view, $F_{(1, 18)}$, 0.04, $P = 0.86$, $\eta_p^2 = .00$, or effect of group $F_{(1, 18)}$,= 1.21, $p = 0.29$, $\eta_p^2 =0.10$.

5.5. Discussion

After viewing the back of their body from a third-person perspective and seeing themselves being touched by a rod that they could also feel, participants were able to detect a shorter visual-proprioceptive delay than if what they saw was not synchronized to what they felt. sVTS generated a 45ms advantage for detecting the delay for the experienced, natural view whereas aVTS created no such advantage. This advantage is comparable to the 18 – 29 ms self-advantage we have reported previously (Hoover et al., 2016; Hoover & Harris, 2012; 2015a; 2015b) when the perspective and view of the body match the internal representation of the body. Interestingly, our observations show that a first-person perspective is not a sine qua non for evoking the sense of self. Petkova and colleagues (2011) found that although a first-person perspective helps evoke a stron sense of ownership, the feeling of ownership over a just one part of a mannequin body generalized to ownership over the entire mannequin body. In our task although participants are detecting delay in the movement of only a finger we interpret this as corresponding to ownership over the entire back view of the body.

We have previously shown that when viewing the self from the back while making hand movements there is no difference in thresholds for detecting differences in delay between the upright, natural view of the body compared to an inverted, unexpected view of the body (Hoover & Harris, 2015a). To draw direct comparisons between the previous study and the present one, we calculated difference scores between delay detection thresholds for the axes-flipped and the natural views in the sVTs and aVTS conditions in the present study, and the back view with no VTS from Hoover et al. (2004). The difference scores are shown in Figure 20. A significant one-way ANOVA revealed a significant between groups effect ($F_{(2, 29)} = 5.41$, $p = 0.01$). The aVTS difference score (-2.9 ±8ms) was no different from the difference score for the back view in the previous study (-2.2±6ms; Mean difference = 0.75, SE = 16.5, $p = 0.96$, $d = 0.03$) (Hoover & Harris, 2015a) but both scores were significantly different from the sVTS difference score (44.5±18ms; mean difference = 47.4, SE = 16.5, $p = 0.009$, $d = 1.09$ and mean difference = 46.6, SE = 16.5, $p = 0.008$, $d= 1.12$, respectively). This confirms that when felt tapping is not synchronous with the seen tapping during the stimulation period (aVTS), thresholds are effectively the same as after receiving no tapping at all prior to performing the delay detection task. This observation emphasizes the need for synchronous multisensory experience (sVTS) to create a sense of ownership over an otherwise non-self representation of the body.

Although out display was a live video, it was viewed in 2D. It is possible that our values might even be an underestimate and the evoked self-advantage could have been even larger if we had used a 3D display such as a VR system (Ijsselteijn et al., 2006; but c.f., Zopf et al., 2015). Our results are consistent with a plethora of multisensory illusions in which feelings of ownership are invoked over dummy hands (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005b), other people's faces (Dobricki & Mohler, 2015; Paladino, Mazzurega, Pavani, & Schubert, 2010; Tajadura-Jiménez, Lorusso, & Tsakiris, 2013), virtual bodies (Blanke & Metzinger, 2009; Ehrsson, 2007; Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2009), and mannequins (Pomes & Slater, 2013; Petkova, 2011; Preston, Kuper-Smith, & Ehrsson, 2015; Petkova & Ehrsson, 2008).

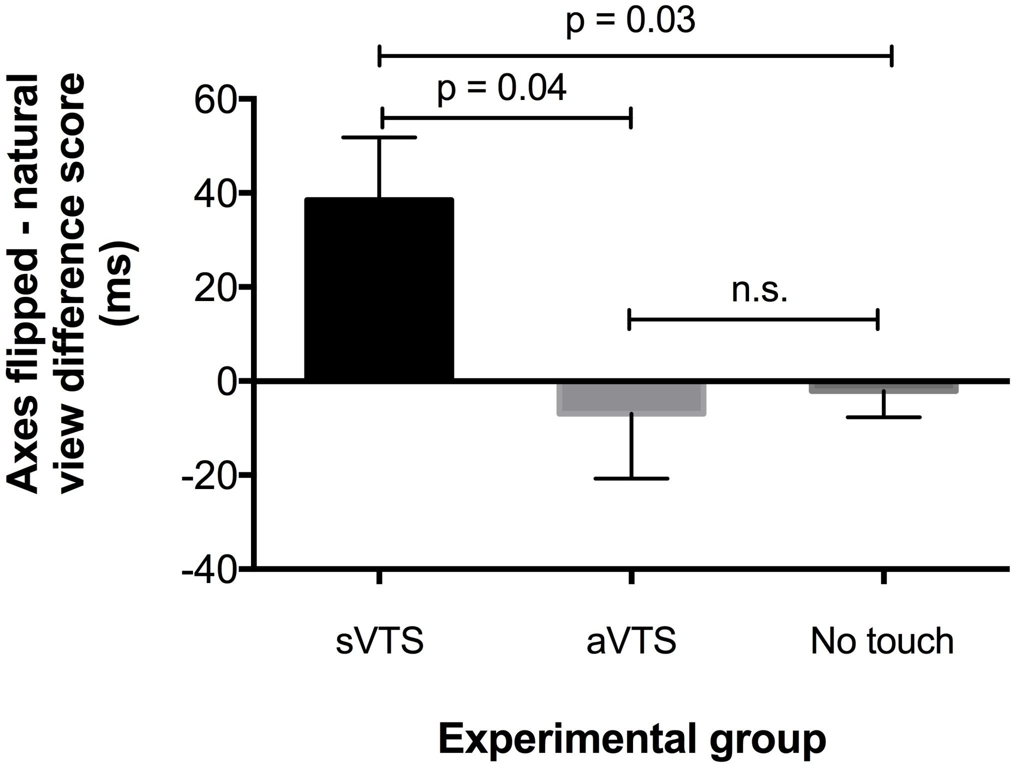

Figure 20. Difference scores were calculated for the sVTS (black bar), aVTS (gray bar), and a no touch condition (light gray bar; data from Hoover & Harris, 2015a) by subtracting the threshold for natural view from the axes-flipped view. There was a significant effect across the groups ($F_{(2, 29)} = 5.03$, $p = 0.02$) where the aVTS difference

score was no different from the no touch difference score. Both scores were significantly lower than the sVTS difference score. Error bars are SEMs.

The strength of our method is that, without explicitly asking whether our participants identified with the back view of the body shown to them in the third-person perspective, we were able to assess their sense of ownership over that view of the body. Measuring the threshold for delay detection provides an objective behavioural measure that is superior to subjective, self-identification questionnaires (Ehrsson, 2007; Lenggenhager et al., 2007; Petkova et al., 2011) that are susceptible to task-compliance, cognitive bias, and confabulation. Monitoring one's own body movements has been established as an important contributing factor to body ownership and subsequently self-recognition (see Jeannerod, 2003 for a review; "Limited conscious monitoring of motor performance in normal subjects," 1998; Nielsen, 1963). Therefore measuring threshold differences in seen and felt self-generated movements provides a quantitative objective method to complement questionnaire, proprioceptive drift, and skin conductance measures.

5.5.1. Neurophysiological correlates of self-perception

Neuroimaging studies have found differential activation depending on synchrony between a movement and the corresponding visual feedback. During the presentation of synchronous visual and proprioceptive information during hand movements, which would invoke body ownership, bilateral superior/middle parietal areas are activated (Shimada, Hiraki, & Oda, 2005). In contrast, during the presentation of asynchronous visual and proprioceptive information, which would inhibit the sense of body ownership, right inferior parietal areas were activated (Shimada et al., 2005; Tsakiris, Longo, & Haggard, 2010b). Such differential activation can be interpreted as corresponding to regarding body parts as either part of the 'self' or part of an 'other'. Further, full-body illusions have been shown to activate multisensory areas of the brain such as the putamen, left ventral premotor cortex, and intraparietal cortex (Petkova et al., 2011; Gentile et al., 2015; Petkova & Ehrsson, 2008; Bekrater-Bodmann, Foell, & Kamping, 2011; Ehrsson, Holmes, & Passingham, 2005; Gutertam et al., 2015) suggesting a network of areas that are important in maintaining the representation of our whole body in the brain. Our study suggests that this network is plastic and can be expanded to incorporate new body parts (such as rubber hands or the back of the body) in response to new information indicating that they should be regarded as part of the self.

5.5.2. Conclusion

We have demonstrated that synchronous visual and tactile experience can elucidate feelings of ownership over a typically 'other' view of the self. The ability to detect temporal asynchrony provides an objective measure of body ownership with which we can track the malleability of the representation of the body in the brain.

5.6. Acknowledgements

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6. CHAPTER 6: GENERAL DISCUSSION

The suite of experiments I present here has contributed to the literature on the 'self' in a fundamental way. I have successfully used a quantitative experimental method that explicitly assesses body ownership. I have manipulated visual, proprioceptive, vestibular, and tactile senses in varying ways as described in the method sections of each of the experimental chapters (sections 2.3, 3.3, 4.3, and 5.3) in order to probe the representation of the body in the brain. As Descartes (1637) once wrote "My body is an integral part of 'me', in a way that other objects are not. Moreover, the relation between my body and 'me' is quite different from the relation between my body and other people". Together, my data provide a window into what of the body we consider as 'self' and subsequently what we consider as 'other': a topic that has been pondered for centuries.

6.1. A measure of perceptual sensitivity for body ownership

I am the first to use the 2IFC task for self-recognition during active, real-time movement with delay detection. The 2IFC task provides a measure of perceptual sensitivity that is less vulnerable to response bias. Temporal synchrony judgements have been used before to evaluate movement recognition (Farrer et al., 2008; Jeannerod, 2009; Shimada, Qi, & Hiraki, 2010; van den Bos & Jeannerod, 2002), however, generally in these studies participants were asked to make a self/not self (or yes/no) judgement about the movement that they saw. Shimada and colleagues (2010), for example, showed participants their own right index finger movements, which were captured by a video camera and reflected to the participants using a double-sided mirror, presented with an added visual delay ranging between 118 and 352ms (including the inherent delay of the system). Participants were asked to make judgements about delayed and not-delayed trials. The average PSE for active movements was 231ms suggesting that added visual delays of less than around 230ms are undetectable. The undetectable system delay and asking participants to identify the delay are features of both my studies and the ones described above. The major difference, however, is that I used a 2IFC method. Instead of using simple yes-no judgments I presented my participants with two intervals. One interval of any given trial showed movements with just the inherent system delay of 85ms, and the other had an added visual delay ranging up to approximately 350ms (depending on the specific experiment). The 2IFC is less vulnerable to response bias, as it provides a baseline (no delay) for participants to compare with the delayed interval.

6.2. Major Findings

In the task I used for all the experiments described here, I measured the ability to detect an added visual delay during active movements while viewing the motion from different perspectives (and/or views) of the body. From the results of this series of experiments, I suggest that participants were more able to discern the added visual delay during the movement when the presented view of the body matched that of the internal representation of the body thus giving us a window on the form of that representation. Participants made two movements in each trial and compared what they saw with what they experienced to determine which of the two presentations of movements had the added visual delay. I then calculated the threshold (75% correctly identifying the delay) by using a logistic function and compared thresholds across variables and groups. On average, there was an increase in sensitivity to delay of approximately 25-45ms for the special cases in which one saw the 'self'. I have called this increase the self-advantage and regard it as a signature of body ownership. In the following sections I will outline my major findings, the special cases in which a self-advantage was found, and situate my research within the current literature on the self.

6.1.1. An upside-down hand is not considered self

Which views of the body are treated as self? Is it necessary to see the body part as being anatomical attached to you? Simply flipping the presentation of a hand on its axes changes how we view this hand – it goes from being attributed to oneself to being seen as belonging to another person. When right-handed people were asked to make finger movements while viewing their hand as if they were looking down at it (this view is commonly referred to as either the egocentric, natural, or first-person view) they showed a self-advantage for temporal asynchrony detection. This advantage was lost when their movements were shown in an unexpected view (unnatural, third person or allocentric view; Figure 11A in Chapter 2 for an example). I will speak to how hand dominance and the type of movement used changed performance in the following section (6.1.2). Here, I focus solely on the results from the dominant hand making discrete movements (Chapter 2, dark gray line in Figure 11A and dark gray bar in Figure 11C). These results are robust and are reproduced using the same conditions but different participants in Chapters 3 and 4 (Chapter 3, black line in Figure 14A; Chapter 4 black line in Figure 17A) and in a paper of mine that is not included in this dissertation looking at the differences between right- and left-handers (Hoover et al., 2016).

The significant variation in performance, specifically the self-advantage of 25-45ms in delay detection, I found was dependent on whether the visual perspective of the hand was egocentric or allocentric. The improved performance for the upright hand is in line with many other studies that looked at self-recognition (Conson et al., 2010), laterality judgements (Dyde et al., 2011), and mental rotation (Parsons, 1994) of static images of the hand where participants all performed at higher levels when hands were shown upright and not inverted. My studies, however, provide an implicit, quantifiable measure of self-recognition during active movements. This will be discussed at greater lengths below.

Why would the inversion of a hand make such a difference as the information content of the images is the same? To answer this we could consider the rubber hand illusion (see 1.5.1. for an explanation of that task) under differing hand postures (Costantini & Haggard, 2007; Ehrsson, Spence, & Passingham, 2004; Tsakiris & Haggard, 2005b). When the dummy hand and real hand are not aligned in space (for example, dummy had placed at a rotation of 90°) the effect of the RHI is diminished. The RHI relies on multisensory integration of synchronous vision and touch in order to induce feelings of ownership over the dummy hand. However, if it were solely dependent on this type of bottom up process then changing the posture of the hand would not diminish the effect – after all, the correlation between the senses would be the same. Spatial misalignment diminishing the illusion suggests a top-down process as well and, considering the illusion plays with the sense of body ownership, suggests that a stored representation of the body must be compatible with the seen body for the illusion to be effective. If there is conflict between the internal representation and what is seen the illusion is not felt. We interpret the results from asynchrony detection while looking down at the hand in this same manner – when the hand that is seen does not match what we have stored in our body schema (e.g., when the view of the hand is flipped) there is no advantage in delay detection.

The experiments described above to which I have compared my results, however, provided participants with static views of the hand and the participants did not perform movements. In my experiments participants were asked to judge the timing of their active movements with respect to live video feed (with varying visual delays). Although the visual manipulations of the video images flipped along the x, y, and xy axes are similar to the visual stimuli in the static images, hand movements provide added proprioceptive information as well as the sense of agency.

When making an active movement there is not only a motor command, but also efferent and afferent information. The sense of agency, the sense that one is the agent of one's movements (Gallagher, 2000), is also present during active movements unlike when viewing static images. Many studies have attempted to tease apart the contribution of the sense of agency (motor command and efferent copy) by looking at differences between active and passive movements (Farrer et al., 2008; Jeannerod, 2009; Shimada et al., 2010; Tsakiris et al., 2005; Tsakiris & Haggard, 2005a). During self-other discrimination, participants tended to make fewer attribution errors when making active movements than they do during passive movements. However, when judging temporal asynchrony participants were able to detect smaller delays during active versus passive movements (Shimada et al., 2010). This suggests that although agency provides added information it does not make the temporal window smaller for detecting asynchronies between the visual and proprioceptive information. In all of my studies, participants performed active movements (I never manipulated the sense of agency) therefore by manipulating the visual perspective (or viewpoint) I exclusively addressed the sense of body ownership. Further, in a 3D virtual reality replication of my study presented in Chapter 2, Zopf and colleagues (2010) confirmed an 18ms advantage for an upright hand compared to an upside down hand when detecting added visual delays. They conferred that anatomical plausibility of an upright hand aided the temporal asynchrony detection.

To summarize, there is a self-advantage in the detection of multisensory discord, specifically between vision and proprioception, during active movements when movements are seen in a perspective that matches that of the internal representation of the self. Further, this increase in sensitivity to visual delay of 20 – 45ms can be seen as a quantifiable measure of body ownership – one that is without subjective bias.

6.1.2. The self-advantage for the dominant hand is movement dependent

Not only do we see our movements from an egocentric perspective, there is a special role for the dominant hand in the creation of body representation. In my experiment outlined in Chapter 2, I looked at the difference in performance in delay detection for right-handers when they move their dominant (right) hand and when they move their non-dominant (left) hand. Interestingly, I found that only during discrete movements (single flexion of the finger) and not during continuous movements (repetitive finger movements) did right-handers show a self-advantage for the dominant (not the non-dominant) hand making the movements. The differences between the two types of movements will be discussed below.

The majority of people show a right-hand preference (Annett, 1985; Oldfield, 1971). This asymmetric preference of the right hand over the left hand has been linked to differences in performance between the two hands during motor tasks (see Goble & Brown, 2008). The dominant right hand tends to be stronger (Farthing, Chilibeck, & Binsted, 2005) and faster when performing tasks (J. Annett, Annett, Hudson, & Turner, 1979), as well as being more precise (Heuer, 2007) than the left hand for fine motor tasks. Right-handers also show performance biases for the right hand for hand laterality judgements (Dyde et al., 2011; Gentilucci, Daprati, & Gangitano, 1998; Ní Choisdealbha, Brady, & Maguinness, 2011) and during mental rotation tasks (Takeda, Shimoda, Sato, Ogano, & Kato, 2010) where aspects of the right hand were identified with greater speed and accuracy. When asked to imagine other people making movements, right-handers tended to imagine more of the actions being performed with a right hand (Marzoli, Menditto, Lucafò, & Tommasi, 2013) and during a pointing task to targets on the body without vision of the body right-handers pointed more rightward (Hach & Schütz-Bosbach, 2010). This suggests that right-handers have a strong rightward bias that may actually affect the way in which their entire body is represented.

Casasanto (2009) proposed that given the extensive use of the right hand, right-handers interact with their environment in a different manner than their left-handed counterparts. His Body Specificity Hypothesis suggests that the dominant hand provides a frame of reference for the representation of the entire body and its actions in the brain (Casasanto, 2009; Willems et al., 2010a). For example, when making self/not self judgments of pictures of hands, Conson and colleagues (2010) found that right-handers more quickly identified their own dominant right-hand compared to their non-dominant left hand. The authors suggested that the motor experiences from using the dominant hand provide a frame of reference for the body and the body's actions. These dominant hand specific experiences would then provide improved ability to distinguish between the self and an "other" when presented with images (or in the case of my experiments, live-video feed of active movements) of the dominant hand. This Body Specificity Hypothesis predicts that there would be a self-advantage for right-handers using and seeing only their dominant hand and not the non-dominant hand in my study and that is exactly what I found -- a self-advantage only for dominant hand movements while viewing movements in self-perspective.

Of importance, though, is that this exclusive dominant hand self-advantage was only present during discrete movement and not for the continuous movement. During the continuous movements both the right and left hand movements presented in both upright perspectives (natural and y-axis reflection; see Figure 10) showed significantly lower thresholds compared to the inverted perspectives (x- and xy-axes reflections; see Figure 10). I suggest that this is most likely due to some differences between the two types of movements. When participants performed a discrete movement they were prompted to initiate the movement when they saw the hand shown on the display. Whereas, when they performed the continuous movements participants initiated the movement prior to seeing the hand on the display and continued to make the same movement repeatedly until the trial ended. Thus there was a distinct visual onset of the movement for the discrete trials, which provided participants with sharply timed efferent information. This was not the case for the continuous movement. The thresholds for the discrete movement and the continuous movement viewed in self-perspective were 123ms and 145ms, respectively. The difference was 22ms, which is similar to a 29ms advantage when detecting active finger movements over passive finger movements (Winter et al. 2008; Lau et al. 2004). Therefore, we can conclude that clear efferent information provides a slight advantage overall, but why was there not a dominant hand advantage for the continuous movements?

Right-handers use their dominant hand for more accurate and precise movements (Bryden et al., 2000). Goal directed movements have distinct start and end times. Therefore discrete movements could be considered as goal directed movements and using the dominant hand for such a movement would be advantageous while performing tasks. Continuous movements could be associated more with less precise bimanual tasks (Swinnen, 2002) in which the dominant and non-dominant hands work together or are yoked together. When a participant was presented with the hand in an upright perspective *but* flipped as if it was their other hand (y-reflection of the right hand), it could be interpreted as the left hand moving in phase with the right hand (hidden from view). This would explain why the self and y-reflection presentation of the movements did not differ. These perspectives are both upright and could be deciphered as plausible self-perspectives (see Figure 10).

The results presented in Chapter 2 show that there is a special case for the dominant hand in the creation of the representation of the body and this is most likely due in part to the way in which right-handers interact with their environment supporting Casasanto's Body Specificity Hypothesis.

6.1.3. Disruption to vestibular system makes you less sure of your 'self'

Up to this point I have discussed the visual and proprioceptive senses and their contribution to the sense of self, but other senses are also integrated in order to create a full representation of the body in the brain. In Chapter 4, I found that applying galvanic vestibular stimulation during the temporal asynchrony detection task affected thresholds for detecting visual/proprioceptive delays during finger movements displayed in the self-perspective. Detection with views in the other perspective were not affected (Chapter 4; Figure 17).

When the vestibular reference was disrupted under disruptive GVS participants did not detect delays any differently in the self and other conditions: the self-advantage was abolished. In the control condition (with no GVS – trials interleaved), the signature self-advantage was found where the visual delay was detected for smaller delays when the movements were displayed in the self-perspective compared to the other perspective. The vestibular system, therefore, provides information concerning the body that helps one differentiate between self and other. What sort of reference might the vestibular system provide?

Patients with vestibular disorders, such as vestibular vertigo or vestibular deafferentation, have reported distorted percepts of their body and/or body parts suggesting the vestibular system maintains a coherent schema of the body. Along with misperceiving the size and shape of the body and its parts (Lopez, Halje, & Blanke, 2008; Sang, Jáuregui-Renaud, Green, Bronstein, & Gresty, 2006; Lopez & Blanke, 2007; Schilder, 1935) some vestibular patients have reported feeling that their body is not whole (Vallar & Papagno, 2003), feeling as though they are outside of their body (Brugger, 1997), and the loss of the feeling that they are in control of their actions (Sang et. al, 2006). Since vestibular patients have shown distortions in the representation of the body would introducing noise to the vestibular system affect healthy participants in a similar way?

In previous studies, vestibular input has been experimentally manipulated by using either galvanic or caloric stimulation in healthy participants. Disruptive GVS (such as passing +ve current through one ear and –ve through the other) produces illusory tilting of the head, even when the head is stabilized with a head rest, which suggests that disruption to the vestibular system demonstrates a disconnect between the actual posture of the body and the perceived posture of the body. Inline with the results from my study, Lopez and colleagues (2012b) found that participants under GVS distorted the perception of the size and shape of their own hands. Vestibular stimulation also reduces accuracy at pointing to tactile stimuli on the hand (Ferrè et al., 2013). Further, others have found that a lessened sense of self (Ferrè et al., 2014; Lopez et al., 2008; Lopez,

2013) and a greater susceptibility to multisensory illusions, such as the RHI (Lopez et al., 2010). Taken together, the vestibular contribution seems to bear considerable weight in the development of the sense of the body and subsequently the self. It integrates with proprioceptive, visual, and tactile cues.

As we have seen in the last two sections, changes in visual perspective affects the ability to discern visual delay during active movements for our hands as if seen in a natural, egocentric perspective. If these changes in visual perspective suggest that vision is so important, what can we say about parts of our body that we cannot see?

6.1.4. No sense of ownership for views of the body that are rarely seen

The first-person perspective, as we have seen, is integral when distinguishing between the self and other. When the visual component is aligned with the representation of the body (the view of the hand matched up with what we expect) there is an added benefit when detecting asynchrony between visual and proprioceptive information during active movements. But what about when there can be no direct vision (such as for the face) or even no vision at all (such as for the back)? In Chapter 3, I looked at two additional views of the body: the view you see when looking in the mirror (see Figures 15B and 16A, Chapter 3) and the view someone else would see of your body from behind (allocentric view; see Figures 15C and 16B, Chapter 3).

Firstly, I found that there was systematic variation in performance across the viewpoints for the natural perspective (the upright expected perspective) where delay was detected at lower thresholds for the direct view of the hand, higher thresholds for the allocentric viewpoint from behind, and intermediary thresholds for the mirror viewpoint (see Figures 15A, B and C, Chapter 3). This suggests that visual experience (familiarity) is important for deciding what is represented as the body. Secondly, there was a self-advantage for both the egocentric and mirror views of the body, which was evident from the significantly lower threshold in the expected perspectives compared to the other perspectives (x, y, and xy axes flipped). The back view, however, showed no such advantage as participants detected the delay at similar thresholds for all four perspectives. Given this result, I conclude that the back view of one's body is normally regarded as 'other'.

These results are in line with a study done by Tipper and colleagues (2001) who found that it is more difficult (longer latencies) to detect tactile stimuli on parts of the body that cannot be viewed directly (e.g., the back of the neck) compared to parts of the body that can be viewed directly (e.g., hands; Tipper et al., 2001). Even the simple act of being able to see a body part (e.g., image of the hand on a display) without orienting the eyes to the actual body part improves the ability to detect tactile stimuli (Tipper et. al., 1998; Maravita et. al., 2000). This suggests that visual experience, and to some extent body part familiarity, is enough to improve somatoperception.

Seeing the body from the first-person vantage point is such a strong cue to self that even inanimate mannequins can be experimentally manipulated into becoming 'self' – induced body ownership if seen from the right angle in VR (Petkova & Ehrsson, 2008). Identifying virtual bodies as self was more effective when the body was presented in the first-person and not third-person viewpoint (Petkova et al., 2011; Slater et al., 2009). Further, as discussed in section 6.1.1., there are differentially activated areas of the brain for self and other (Saxe et al., 2006). Given the separation between such cortical networks, it is possible that detection of smaller visual and proprioceptive disparities is more finely tuned for events that we relate to the self, compared to those we relate to another person.

What implications does the visually absent back of the body have on our perception of our whole body? For example, D'Amour and Harris (2014) have suggested that there is a special connection between the front and back of the body. This would suggest that the 'other' part of our body is pinned to the 'self' part of our body. But how does one bring parts of the body that are previously missing from this representation of the body into the visually driven body image?

6.1.5. Multisensory stimulation induces body ownership of an 'other'

In Chapter 3, I found that back views of the body, regardless of body part moving (hand or head), awarded no self-advantage. This result suggests that this view of the body is not visually represented in the body schema. Although participants knew that this was their body they demonstrated no advantage over this view (as seen by no differences in delay detection thresholds) and therefore I concluded that the back view of the body was seen at least to some extent as other and not self. In Chapter 5, I employed a multisensory stimulation technique to induce ownership for this otherwise "other" view of the body. After experiencing synchronous multisensory stimulation (tapping on the participants back while they viewed themselves from behind being tapped), participants were better able to detect temporal asynchrony for the natural perspective of the back of the body compared to the axes flipped presentations (see

Figure 19): in other words they developed a self-advantage that they didn’t previously have. A control group received asynchronous multisensory stimulation and never showed an advantage for the natural perspective over the axes flipped perspective.

My study fits into an extensive array of studies that exploit multisensory integration in order to provoke participants to adopt a new extremity (Botvinick & Cohen, 1998), someone else’s face (Sforza, Bufalari, Haggard, & Aglioti, 2010; Tajadura-Jiménez et al., 2013), the back view of the body (Ehrsson, 2007; Lenggenhager et al., 2007), virtual bodies (Petkova et al., 2011), and mannequins (Petkova & Ehrsson, 2008). By allowing participants to experience simultaneous, multisensory events while watching it happen from behind themselves (using a video camera) they were able to detect shorter delays (the classic signature SA) when the displayed view of the body matched the view they experienced. I conclude that synchronous visuo-tactile stimulation induced ownership, which is evident by a self-advantage of 45ms (see Figure 19). The results from my study provide further evidence for the malleability of the representation of the brain and how multisensory stimulation (new information about the self) is incorporated into an updated self.

What is considered self can be extended to include rubber hands, virtual bodies, and even to include parts of the body that are not visually represented, such as the back, through synchronous multisensory experience.

6.3. Possible limitations

There are some limitations to the studies I conducted with respect to 1) the method; 2) the timing of delays; 3) the visual stimuli; 4) the participants; and 5) the lack of control conditions. Although 2IFC is a robust psychophysical method because it takes twice as long to complete a trial than a simple yes/no judgement task I only collected eight data points per difference of delay in any given condition. One mistake in response could have had effects on the curves used to calculate thresholds.

The inherent system delay was approximately 85ms and although this was within the range of delay that is undetectable to human observers it still was different than looking at genuinely live movements. Further, the added visual delay increments were linked to the refresh rate of the screen, which was approximately 33ms. Having greater control over the delay could have allowed me more precise measurement and smaller incremental steps in the temporal component of the visual stimuli.

The visual stimuli were displayed in black and white and not colour. Colour images might have increased the degree to which ownership was felt over the views of the body parts and possibly decreased thresholds. However, as some studies have suggested, if participants are able to feel ownership over inanimate rubber hands and gloved hands then black and white images may not haven been too much of a hindrance. Further, for all the hand movements conditions in my studies (Chapters 2, 3, and 4) there could have been greater care in setting up the apparatus so that the hands were shown in the same spatial location as the hand making the movement (See Shimada et al., 2010). In a temporal delay detection task Keetels and Vroomen (2012) compared performance when the hands were seen on a LCD display like in my studies and using mirrors and LCD displays to create a more spatially aligned set up. They found no significant different in performance. Given our extensive use of trackpads and mice controlling cursors on computer screens it is reasonable to regard seeing our movements in such a set up as a ‘natural’ view.

Another limitation to my initial experiment (Chapter 2) was that I did not have a control condition for movements on the screen that was not a body part. For example, I could have used a rod that moved with the finger movements. In the replication of my study, Zopf and colleagues (2015) used 3D virtual reality where participants wore gloves that were connected to the computer. There were points on the glove that were connected to create either a virtual reality hand or points of light along the fingers as a control. They found that delay detection was significantly enhanced for the virtual hand compared to the control. This suggests that the self-advantage I found in my studies was indeed body specific.

Finally, the people who participated in my studies were undergraduate and graduate students for the most part. A more diverse sample of the population may have changed the results. I might have also been able to look for a correlation between age and threshold.

6.4. Future Research

There are many possible directions in which the studies presented in this dissertation could be developed. In my experiments, I presented the body movements in four different perspectives (See Figure 6 in Chapter 2 for examples) that were based on flips about the horizontal and vertical axes. It would be informative to present the body parts in smaller degrees of rotations to be able to determine the tuning of where exactly the hand is regarded as “self”. I could compare delay detection thresholds and use the self-advantage as a measure of body ownership for a range of shifts of the orientation of the video – not just the 90° used in this dissertation. This would reveal the actual tuning and position of the internal representation of the body. Along these same lines, I only used three viewpoints of the body (looking down at the hand, looking at the face in the mirror, and looking at the body from behind) and it would be interesting to extend the viewpoints to include such views as profile views of the body and looking down at the legs. This would provide a more complete picture of what perspectives and viewpoints of the body that are represented in the body image.

If I were to look at delay detection from viewpoints of the body that include the legs, the natural next step would be to have participants discriminate temporal asynchrony during leg/foot movements. Would there be a self-advantage for the feet? Would footedness (similar to handedness) affect the ability for one to discriminate delay? Would people that have more experience looking at their legs/feet, such as ballet dancers, have a self-advantage over those of us that do not pay that close attention to those movements?

The self-advantage could also be useful in clinical settings. For example, people who suffer from schizophrenia are more likely to have a skewed perception of the body, the self, and the senses of agency and ownership (Jeannerod, 2009). Given that this test measures the sense of body ownership without directly asking questions that relate to the self, it could provide a objective measure of what parts of the body they consider to be self. Further, could the implementation of visuo-tactile stimulation (along the lines described in chapter 5) help to update or strengthen their representation of their body?

6.4. Conclusion

For the projects presented in my dissertation, I used an experimental design in which participants were required to make multisensory temporal asynchrony discrimination after self-generated movements. I measured sensitivity for visual delay detection between the movement (proprioceptive, efferent and afferent information) and the visual image of that movement under differing visual conditions.

Vision of the body, mainly our first-person perspective of it, provides input for the creation of the multiple representations of the body that we have (See Figure 21). These representations, namely the postural and superficial schemas, come together to provide us with a template as to what we consider to be our body – the self.

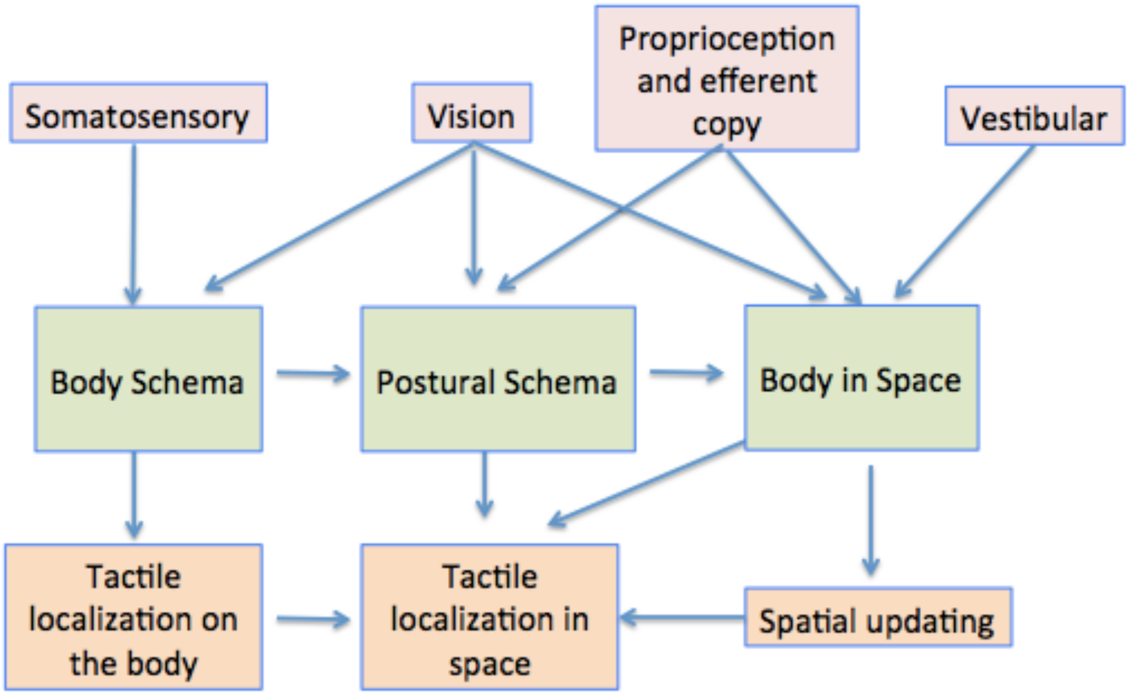

Figure 21. Schematic of the components that make up the representation of the brain. Somatosensory, visual, proprioceptive, and vestibular inputs create representations of the body that aid in the localization of tactile stimuli on the body, and where the body is in space (adapted from Harris et. al., 2015).

The lowered threshold for detecting added visual delay during self-generated movement, the self-advantage, is indicative to what we consider self and subsequently not-self. Thus the self-advantage is an implicit measure of body ownership, which is a key sense of self. Overall, the results from this dissertation suggest that the tolerance for temporally matching visual, proprioceptive and efferent copy information that informs about the perceived position of body parts depends on: whether one is viewing one’s own body or someone else’s; the view we have of the body; the dominant hand; the reliability of vestibular cues which help us situate our body in space; and congruent multisensory experience. The experiments provide support for the malleable nature of the representation of the body in the brain.

7. BIBLIOGRAPHY

Andersen, R. A., & Buneo, C. A. (2002). Intentional maps in posterior parietal cortex. *Annual Review of Neuroscience*. http://doi.org/10.1146/annurev.neuro.25.112701.142922

Annett, J., Annett, M., Hudson, P. T., & Turner, A. (1979). The control of movement in the preferred and non-preferred hands. *The Quarterly Journal of Experimental Psychology*, *31*(4), 641–652. http://doi.org/10.1080/14640747908400755

Annett, M. (1985). Left, Right, Hand and Brain. Psychology Press.

Armel, K. C., & Ramachandran, V. S. (2003). Projecting sensations to external objects: evidence from skin conductance response. *Proceedings. Biological Sciences / the Royal Society*, *270*(1523), 1499–1506. http://doi.org/10.1098/rspb.2003.2364

Aspell, J. E., Heydrich, L., Marillier, G., Lavanchy, T., Herbelin, B., & Blanke, O. (2013). Turning body and self inside out: visualized heartbeats alter bodily self-consciousness and tactile perception. *Psychological Science*, *24*(12), 2445–2453. http://doi.org/10.1177/0956797613498395

Astafiev, S. V., Stanley, C. M., Shulman, G. L., & Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions.

Nature Neuroscience, *7*(5), 542–548. http://doi.org/10.1038/nn1241

Avillac, M., Denève, S., Olivier, E., Pouget, A., & Duhamel, J.-R. (2005). Reference frames for representing visual and tactile locations in parietal cortex. *Nature Neuroscience*, *8*(7), 941–949. http://doi.org/10.1038/nn1480

Azañón, E., Longo, M. R., Soto-Faraco, S., & Haggard, P. (2010). The Posterior Parietal Cortex Remaps Touch into External Space. *Current Biology : CB*, *20*(14), 1304–1309. http://doi.org/10.1016/j.cub.2010.05.063

Balslev, D., Cole, J., & Miall, R. C. (2007). Proprioception contributes to the sense of agency during visual observation of hand movements: Evidence from temporal judgments of action. *Journal of Cognitive Neuroscience*, *19*(9), 1535–1541. doi:10.1126/science.7569931

Bartsch S (2006) The Mirror of the Self. University of Chicago Press

Bekrater-Bodmann, R., Foell, J., & Kamping, S. (2011). The Importance of Ventral Premotor Cortex for Body Ownership Processing. The Journal of Neuroscience : the Official Journal of the Society for Neuroscience, 31(26), 9443–9444. http://doi.org/10.1523/JNEUROSCI.2302-11.2011

Bekrater-Bodmann, R., Foell, J., Diers, M., Kamping, S., Rance, M., Kirsch, P., et al. (2014). The Importance of Synchrony and Temporal Order of Visual and Tactile Input for Illusory Limb Ownership Experiences – An fMRI Study Applying Virtual Reality. PloS One, 9(1), e87013. http://doi.org/10.1371/journal.pone.0087013

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 289–300.

Berlucchi, G., & Aglioti, S. M. (1997). The body in the brain: neural bases of corporeal awareness. *Trends in Neurosciences*, *20*(12), 560–564.

Berlucchi, G., & Aglioti, S. M. (2010). The body in the brain revisited. *Experimental Brain Research Experimentelle Hirnforschung Expérimentation Cérébrale*, *200*(1), 25–35. http://doi.org/10.1007/s00221-009-1970-7

Bertamini, M., Berselli, N., Bode, C., Lawson, R., & Wong, L. T. (2011). Consciousness and Cognition. *Consciousness and Cognition*, *20*(4), 1108–1119. http://doi.org/10.1016/j.concog.2011.04.006

Bertenthal, B.I. & Fischer, K.W. (1978) Development of self-recognition in the infant. *Developmental Psychology,* 14:44–50. doi: 10.1037/0012-1649.14.1.44

Blanke, O., & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends in Cognitive Sciences*, *13*(1), 7–13.

Bonnier, P. (1905). L'Aschématie [Asomatognosia]. *Revue Neurologique*, 12, 605–609.

Botvinick, M., & Cohen, J. (1998). Rubber hands "feel" touch that eyes see. *Nature*, *391*(6669), 756. http://doi.org/10.1038/35784

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.

Bremner, A. J., Holmes, N. P., & Spence, C. (2012). Development of multisensory representations of the body and the space around the body. In A. J. Bremner, D.J. Lewkowicz, & C. Spence (Eds.), *Multisensory Development* , 113 -136. Oxford: Oxford University Press.

Bresciani, J. P., Blouin, J., Popov, K., Bourdin, C., Sarlegna, F., Vercher, J. L., & Gauthier, G. M. (2002). Galvanic vestibular stimulation in humans produces online arm movement deviations when reaching towards memorized visual targets. *Neuroscience Letters*, *318*(1), 34–38.

Bryden P.J., Pryde, K.M., & Roy, E. A. (2000) A Performance Measure of the Degree of

Hand Preference. *Brain Cognition* 44:402–414.

Casasanto, D. (2009). Embodiment of abstract concepts: good and bad in right- and left-handers. *Journal of Experimental Psychology General*, *138*(3), 351–367. http://doi.org/10.1037/a0015854

Chan, A. W.-Y., Peelen, M. V., & Downing, P. E. (2004). The effect of viewpoint on body representation in the extrastriate body area. *Neuroreport*, *15*(15), 2407–2410.

Cole J & Paillard J (1998) Living without touch and peripheral information about body position and movement: studies with deafferented subjects. pp 245-266. In: J. Bermudez (Ed) *The body and the self*. Cambridge, Mass:MIT Press.

Conson, M., Aromino, A. R., & Trojano, L. (2010). Whose hand is this? Handedness and visual perspective modulate self/other discrimination. *Experimental Brain Research Experimentelle Hirnforschung Expérimentation Cérébrale*, *206*(4), 449–453. http://doi.org/10.1007/s00221-010-2418-9.

Conson, M., Mazzarella, E., & Trojano, L. (2009). Numbers are represented in egocentric space: effects of numerical cues and spatial reference frames on hand laterality judgements. Neuroscience Letters, 452(2), 176–180. http://doi.org/10.1016/j.neulet.2009.01.043

Costantini, M., & Haggard, P. (2007). The rubber hand illusion: Sensitivity and reference frame for body ownership. *Consciousness and Cognition*, *16*(2), 229–240. http://doi.org/10.1016/j.concog.2007.01.001

D'Amour ,S, & Harris, L.R. (2014). Vibrotactile masking through the body. *Experimental Brain Research*, 232:2859–2863. doi: 10.1007/s00221-014-3955-4

Daprati, E., Sirigu, A., & Nico, D. (2010). Body and movement: Consciousness in the parietal lobes. *Neuropsychologia*, *48*(3), 756–762. http://doi.org/10.1016/j.neuropsychologia.2009.10.008

De Ridder, D., Van Laere, K., Dupont, P., Menovsky, T., & Van de Heyning, P. (2007). Visualizing Out-of-Body Experience in the Brain. *New England Journal of Medicine*, *357*(18), 1829–1833. http://doi.org/10.1056/NEJMoa070010

Descartes, R. 1637/1958: Dioptric. New York: Modern Library.

Dobricki, M., & Mohler, B. J. (2015). Self-Identification With Another's Body Alters Self-Other Face Distinction. *Perception*, *44*(7), 814–820. http://doi.org/10.1177/0301006615594697

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science (New York, NY)*, *293*(5539), 2470–2473. http://doi.org/10.1126/science.1063414

Dyde, R., MacKenzie, K., & Harris, L. R. (2011). How well do you know the back of your hand? Reaction time to identify a rotated hand silhouette depends on whether it is interpreted as a palm or back view. *Journal of Vision*, *11*(11), 868–868. http://doi.org/10.1167/11.11.868

Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science (New York, NY)*, *317*(5841), 1048. http://doi.org/10.1126/science.114217

Ehrsson, H. H., Holmes, N. P., & Passingham, R. E. (2005). Touching a Rubber Hand: Feeling of Body Ownership Is Associated with Activity in Multisensory Brain Areas. The Journal of Neuroscience : the Official Journal of the Society for Neuroscience, 25(45), 10564–10573. http://doi.org/10.1523/JNEUROSCI.0800-05.2005

Farrer, C., Bouchereau, M., Jeannerod, M., & Franck, N. (2008). Effect of distorted visual feedback on the sense of agency. *Behavioural Neurology*, *19*(1-2), 53–57.

Farrer, C., Franck, N., Georgieff, N., Frith, C. D., Decety, J., & Jeannerod, M. (2003a). Modulating the experience of agency: a positron emission tomography study.

NeuroImage, *18*(2), 324–333.

Farrer, C., Franck, N., Paillard, J., & Jeannerod, M. (2003b). The role of proprioception in action recognition. *Consciousness and Cognition*, *12*(4), 609–619.

Farthing, J. P., Chilibeck, P. D., & Binsted, G. (2005). Cross-education of arm muscular strength is unidirectional in right-handed individuals. *Medicine and Science in Sports and Exercise*, *37*(9), 1594–1600.

Ferrè, E. R., Lopez, C., & Haggard, P. (2014). Anchoring the Self to the Body: Vestibular Contribution to the Sense of Self. *Psychological Science*. http://doi.org/10.1177/0956797614547917

Ferrè, E. R., Vagnoni, E., & Haggard, P. (2013). Vestibular contributions to bodily awareness. *Neuropsychologia*, *51*(8), 1445–1452. http://doi.org/10.1016/j.neuropsychologia.2013.04.006

Fiorio, M., Gambarin, M., Valente, E. M., Liberini, P., Loi, M., Cossu, G., et al. (2007). Defective temporal processing of sensory stimuli in DYT1 mutation carriers: a new endophenotype of dystonia? *Brain : a Journal of Neurology*, *130*(Pt 1), 134–142. http://doi.org/10.1093/brain/awl283

Fourneret, P., & Jeannerod, M. (1998). Limited conscious monitoring of motor performance in normal subjects. Neuropsychologia, 36(11), 1133–1140. http://doi.org/10.1016/S0028-3932(98)00006-2

Franck, N. (2001). Defective Recognition of One's Own Actions in Patients With Schizophrenia. *American Journal of Psychiatry*, *158*(3), 454–459. http://doi.org/10.1176/appi.ajp.158.3.454

Gallace, A., & Spence, C. (2014). In touch with the future: The sense of touch from cognitive neuroscience to virtual reality. Oxford: Oxford University Press.

Gallagher, I. (2000). Philosophical conceptions of the self: implications for cognitive science. *Trends in Cognitive Sciences*, *4*(1), 14–21.

Gallup, G.G. (1970). Chimpanzees: Self-Recognition. *Science* 167:86–87. doi: 10.1126/science.167.3914.86

Gandevia, S. C., & Phegan, C. M. L. (1999). Perceptual distortions of the human body image produced by local anaesthesia, pain and cutaneous stimulation. *The Journal of Physiology*, *514*(2), 609–616. http://doi.org/10.1111/j.1469-7793.1999.609ae.

Gentile, G., Björnsdotter, M., Petkova, V. I., Abdulkarim, Z., & Ehrsson, H. H. (2015).

Patterns of neural activity in the human ventral premotor cortex reflect a whole-body multisensory percept. NeuroImage, 109, 328–340. http://doi.org/10.1016/j.neuroimage.2015.01.008

Gentilucci, M., Daprati, E., & Gangitano, M. (1998). Right-handers and left-handers have different representations of their own hand. *Brain Research Cognitive Brain Research*, *6*(3), 185–192.

Gillihan, S. J., & Farah, M. J. (2005). Is self special? A critical review of evidence from experimental psychology and cognitive neuroscience. *Psychological Bulletin*, *131*(1), 76–97. http://doi.org/10.1037/0033-2909.131.1.76

Goble, D. J., & Brown, S. H. (2008). The biological and behavioral basis of upper limb asymmetries in sensorimotor performance. *Neuroscience and Biobehavioral Reviews*, *32*(3), 598–610. http://doi.org/10.1016/j.neubiorev.2007.10.00.

Goodwin, G.M., McCloskey, D.I., & Matthews, P.B.C. (1972). Proprioceptive illusions induced by muscle vibration: Contribution by muscle spindles to perception? *Science,* 175, 1382–1384.

Graziano, M. S. (1999). Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proceedings of the National*

Academy of Sciences of the United States of America, *96*(18), 10418–10421.

Green, D. M., and J. A. Swets. "Signal detection theory and psychophysics. 1966." New York 888 (1966): 889.

Guterstam, A., Bjornsdotter, M., Gentile, G., and Ehrsson, H. (2015). Posterior cingulate cortex integrates the sense of self-location and body ownership. *Current Biology*, 25: 1416 - 1425.

Guterstam, A., and Ehrsson, H. (2012). Disowning one's seen real body during an out-of-body illusion. *Brain and Cognition*, 21:1037 - 1042.

Haans, A., IJsselsteijn, W. A., & de Kort, Y. A. W. (2008). The effect of similarities in skin texture and hand shape on perceived ownership of a fake limb. *Body Image*, *5*(4), 389–394. http://doi.org/10.1016/j.bodyim.2008.04.003

Hach, S., & Schütz-Bosbach, S. (2010). Brain and Cognition. *Brain and Cognition*, *72*(3), 408–418. http://doi.org/10.1016/j.bandc.2009.12.001

Haggard, P., Christakou, A., & Serino, A. (2007). Viewing the body modulates tactile receptive fields. *Experimental Brain Research*, *180*(1), 187–193. http://doi.org/10.1007/s00221-007-0971-7

Hägni, K., Eng, K., Hepp-Reymond, M.-C., Holper, L., Keisker, B., Siekierka, E., & Kiper, D. C. (2008). Observing Virtual Arms that You Imagine Are Yours Increases the Galvanic Skin Response to an Unexpected Threat. *PLoS ONE*, *3*(8), e3082.

Harris, L. et al., (2015). How our body influences our perception of the world. *Frontiers in Psychology*, *6*. http://doi.org/10.3389/fpsyg.2015.00819

Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain : a Journal of Neurology*, *34*(2-3), 102.

Heuer, H. (2007). Control of the dominant and nondominant hand: exploitation and taming of nonmuscular forces. *Experimental Brain Research*, *178*(3), 363–373. http://doi.org/10.1007/s00221-006-0747-5

Hodzic, A., Muckli, L., Singer, W., & Stirn, A. (2009). Cortical responses to self and others. *Human Brain Mapping*, *30*(3), 951–962. http://doi.org/10.1002/hbm.20558

Holmes, N. P., & Spence, C. (2005). Visual bias of unseen hand position with a mirror: spatial and temporal factors. *Experimental Brain Research*, *166*(3-4), 489–497. http://doi.org/10.1007/s00221-005-2389-4

Holmes, N. P., & Spence, C. (2007). Dissociating body image and body schema with rubber hands. *Behavioral and Brain Sciences*, *30*(02), 211. http://doi.org/10.1017/S0140525X07001501

Hoover, A. E. N., & Harris, L. R. (2012). Detecting delay in visual feedback of an action as a monitor of self recognition. *Experimental Brain Research*, *222*(4), 389–397. http://doi.org/10.1007/s00221-012-3224-3

Hoover, A. E. N., & Harris, L. R. (2015a). The role of the viewpoint on body ownership. *Experimental Brain Research*, 1–8. http://doi.org/10.1007/s00221-014-4181-9

Hoover, A. E. N., & Harris, L. R. (2015b). Disrupting Vestibular Activity Disrupts Body Ownership. *Multisensory Research*, *28*(5-6), 581–590. http://doi.org/10.1163/22134808-00002472

Hoover, A. E. N., Elzein, Y., & Harris, L. R. (2016). Left-handers show no self-advantage in detecting a delay in visual feedback concerning an active movement. *Experimental Brain Research*. http://doi.org/10.1007/s00221-016-4595-7

IJsselsteijn, W.A., de Kort, Y. A. W., and Haans, A. (2006). Is this my hand I see before me? The rubber hand illusion in reality, virtual reality, and mixed reality. *Presence Teleoperators Virtual Environments*, 15: 455 - 464.

Ionta, S., Martuzzi, R., Salomon, R., & Blanke, O. (2014). The brain network reflecting bodily self-consciousness: a functional connectivity study. *Social Cognitive and Affective Neuroscience*. http://doi.org/10.1093/scan/nst185

Jeannerod, M. (2003). The mechanism of self-recognition in humans. *Behavioural Brain Research*, *142*(1-2), 1–15.

Jeannerod, M. (2009). The sense of agency and its disturbances in schizophrenia: a reappraisal. *Experimental Brain Research*, *192*(3), 527–532. http://doi.org/10.1007/s00221-008-1533-3

Kaas, J. H. (1983). What, if anything, is SI? Organization of first somatosensory area of cortex. *Physiological Reviews*, *63*(1), 206–231.

Keetels, M., & Vroomen, J. (2012). Exposure to delayed visual feedback of the hand changes motor-sensory synchrony perception. *Experimental Brain Research*, *219*(4), 431–440. http://doi.org/10.1007/s00221-012-3081-0

Làdavas, E., Farnè, A., Zeloni, G., & di Pellegrino, G. (2000). Seeing or not seeing where your hands are. *Experimental Brain Research*, *131*(4), 458–467. http://doi.org/10.1007/s002219900264

Lau, H.C., Rogers, R.D., Haggard, P., & Passingham, R.E. (2004). Attention to intention. *Science* 303:1208 - 1210.

Leder H., & Bruce, V. (2000). When inverted faces are recognized: the role of configural information in face recognition. *Quarterly Journal of Experimental Psychology-A* 53:513–536. doi: 10.1080/713755889

Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video Ergo Sum: Manipulating Bodily Self-Consciousness. *Science*, *317*(5841), 1096–1099. http://doi.org/10.1126/science.1143439

Leube, D. T., Knoblich, G., Erb, M., Grodd, W., Bartels, M., & Kircher, T. T. J. (2003). The neural correlates of perceiving one's own movements. *NeuroImage*, *20*(4), 2084–2090.

Longo, M. R., & Haggard, P. (2011). Weber's illusion and body shape: Anisotropy of tactile size perception on the hand. *Journal of Experimental Psychology Human Perception and Performance*, *37*(3), 720–726. http://doi.org/10.1037/a0021921

Longo, M. R., Azañón, E., & Haggard, P. (2010). More than skin deep: body representation beyond primary somatosensory cortex. *Neuropsychologia*, *48*(3), 655–668. http://doi.org/10.1016/j.neuropsychologia.2009.08.022

Longo, M. R., Cardozo, S., & Haggard, P. (2008). Visual enhancement of touch and the bodily self. *Consciousness and Cognition*, *17*(4), 1181–1191. http://doi.org/10.1016/j.concog.2008.01.001

Longo, M. R., Schuur, F., Kammers, M. P. M., Tsakiris, M., & Haggard, P. (2009). Self awareness and the body image. *Acta Psychologica*, *132*(2), 166–172. http://doi.org/10.1016/j.actpsy.2009.02.003

Lopez, C., Bieri, C. P., Preuss, N., & Mast, F. W. (2012a). Tactile and vestibular mechanisms underlying ownership for body parts: a non-visual variant of the rubber hand illusion. *Neuroscience Letters*, *511*(2), 120–124. http://doi.org/10.1016/j.neulet.2012.01.055

Lopez, C., Halje, P., & Blanke, O. (2008). Body ownership and embodiment: vestibular and multisensory mechanisms. *Clinical Neurophysiology*, *38*(3), 149–161. http://doi.org/10.1016/j.neucli.2007.12.006

Lopez, C., Lenggenhager, B., & Blanke, O. (2010). How vestibular stimulation interacts with illusory hand ownership. *Consciousness and Cognition*, *19*(1), 33–47. http://doi.org/10.1016/j.concog.2009.12.003

Lopez, C., Schreyer, H.-M., Preuss, N., & Mast, F. W. (2012b). Vestibular stimulation modifies the body schema. *Neuropsychologia*, *50*(8), 1830–1837. http://doi.org/10.1016/j.neuropsychologia.2012.04.008

MacDougall, H. G., Moore, S. T., Curthoys, I. S., & Black, F. O. (2006). Modeling postural instability with Galvanic vestibular stimulation. *Experimental Brain Research*, *172*(2), 208–220. doi:10.1007/s00221-005-0329-y

Macmillan, N. A., & Creelman, D. C. (1991). Detection theory: a user's guide, New Jersey: Lawrence Erlbaum Associates, Inc.

Makin, T. R., Holmes, N. P., & Ehrsson, H. H. (2008). On the other hand: dummy hands and peripersonal space. *Behavioural Brain Research*, *191*(1), 1–10. http://doi.org/10.1016/j.bbr.2008.02.041

Makin, T. R., Holmes, N. P., & Zohary, E. (2007). Is that near my hand? Multisensory representation of peripersonal space in human intraparietal sulcus. *The Journal of Neuroscience : the Official Journal of the Society for Neuroscience*, *27*(4), 731–740. http://doi.org/10.1523/JNEUROSCI.3653-06.2007

Maruff, P., Wood, S.J., Velakoulis, D., Smith, D.J., Soulsby, B., Suckling, J., Bullmore, E.T.,

& Pantelis, C. (2005). Reduced volume of parietal and frontal association areas in patients with schizophrenia characterized by passivity delusions. P*sychological Medecine*, 35: 783-9

Marzoli, D., Menditto, S., Lucafò, C., & Tommasi, L. (2013). Imagining others' handedness: visual and motor processes in the attribution of the dominant hand to an imagined agent. *Experimental Brain Research*, *229*(1), 37–46. http://doi.org/10.1007/s00221-013-3587-0

Mather, J. A., & Lackner, J. R. (1981). The influence of efferent, proprioceptive, and timing factors on the accuracy of eye-hand tracking. *Experimental Brain Research Experimentelle Hirnforschung Expérimentation Cérébrale*, *43*(3-4), 406–412.

McCleery, J. P., Surtees, A. D. R., Graham, K. A., Richards, J. E., & Apperly, I. A. (2011). The Neural and Cognitive Time Course of Theory of Mind. *Journal of Neuroscience*, *31*(36), 12849–12854. http://doi.org/10.1523/JNEUROSCI.1392-11.2011

Medina, J., & Coslett, H. B. (2010). From maps to form to space: touch and the body schema. *Neuropsychologia*, *48*(3), 645–654. http://doi.org/10.1016/j.neuropsychologia.2009.08.017

Melzack, R., Israel, R., Lacroix, R., & Schultz, G. (1997). Phantom limbs in people with congenital limb deficiency or amputation in early childhood. *Brain : a Journal of Neurology*, *120 (Pt 9)*, 1603–1620.

Moore, S. T., MacDougall, H. G., Peters, B. T., Bloomberg, J. J., Curthoys, I. S., & Cohen, H. S. (2006). Modeling locomotor dysfunction following spaceflight with Galvanic vestibular stimulation. *Experimental Brain Research*, *174*(4), 647–659. doi:10.1007/s00221-006-0528-1

Nielsen, T. I. (1963). Volition: A new experimental approach. *Scandinavian Journal of Psychology*, *4*(1), 225–230.

Ní Choisdealbha, Á., Brady, N., & Maguinness, C. (2011). Differing roles for the dominant and non-dominant hands in the hand laterality task. *Experimental Brain Research Experimentelle Hirnforschung Expérimentation Cérébrale*, *211*(1), 73–85. http://doi.org/10.1007/s00221-011-2652-9

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113.

Oram, M. W., Perrett, D. I., & Hietanen, J. K. (1993). Directional tuning of motion-sensitive cells in the anterior superior temporal polysensory area of the macaque. *Experimental Brain Research*, *97*(2), 274–294.

Paladino, M.-P., Mazzurega, M., Pavani, F., & Schubert, T. W. (2010). Synchronous multisensory stimulation blurs self-other boundaries. *Psychological Science*, *21*(9), 1202–1207. http://doi.org/10.1177/0956797610379234

Parsons, L. M. (1994). Temporal and kinematic properties of motor behavior reflected in mentally simulated action. *Journal of Experimental Psychology Human Perception and Performance*, *20*(4), 709–730.

Peelen, M., & Downing, P. E. (2007). The neural basis of visual body perception. *Nature Reviews Neuroscience*, 8(8):636-48.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442.

Perrett, D. I., Smith, P. A., Mistlin, A. J., Chitty, A. J., Head, A. S., Potter, D. D., et al. (1985). Visual analysis of body movements by neurones in the temporal cortex of the macaque monkey: a preliminary report. *Behavioural Brain Research*, *16*(2-3), 153–170.

Petkova, V. I., & Ehrsson, H. H. (2008). If I were you: perceptual illusion of body swapping. *PloS One*, *3*(12), e3832. http://doi.org/10.1371/journal.pone.0003832

Petkova, V. I., Björnsdotter, M., Gentile, G., Jonsson, T., Li, T.-Q., & Ehrsson, H. H. (2011). From Part- to Whole-Body Ownership in the Multisensory Brain. *Current Biology*, 21(13), 1118–1122. http://doi.org/10.1016/j.cub.2011.05.022

Pfeiffer, C., Schmutz, V., & Blanke, O. (2014). Visuospatial viewpoint manipulation during full-body illusion modulates subjective first-person perspective. *Experimental Brain Research*, *232*(12), 4021–4033. http://doi.org/10.1007/s00221-014-4080-0

Pitcher, D., Walsh, V., & Duchaine, B. C. (2011). The role of the occipital face area in the cortical face perception network. *Experimental Brain Research*, *209*(4), 481–493. http://doi.org/10.1007/s00221-011-2579-1

Pomés, A., & Slater, M. (2013). Drift and ownership toward a distant virtual body. *Frontiers in Human Neuroscience*, 7:908.

Preston, C., Kuper-Smith, B.J., & Ehrsson, H. (2015). Owning the body in the mirror: The effect of visual perspective and mirror view on the full-body illusion, Scienctific Reports, *5*. http://doi.org/10.1038/srep18345

Press, C., Heyes, C., Haggard, P., & Eimer, M. (2008). Visuotactile Learning and Body Representation: An ERP Study with Rubber Hands and Rubber Objects. *Journal of*

Cognitive Neuroscience, *20*(2), 312–323. http://doi.org/10.1073/pnas.97.17.9777

Ramachandran, V. S., & Hirstein, W. (1998). The perception of phantom limbs. The D. O. Hebb lecture. Brain : a Journal of Neurology.

Roder, B., Rosler, F., & Spence, C. (2004). Early Vision Impairs Tactile Perception in the Blind, *14*(2), 121–124. http://doi.org/10.1016/j.cub.2003.12.054

Sang, F. Y. P., Jáuregui-Renaud, K., Green, D. A., Bronstein, A. M., & Gresty, M. A. (2006). Depersonalisation/derealisation symptoms in vestibular disease. *Journal of Neurology*.

Saxe, R., Jamal, N., & Powell, L. (2006). My body or yours? The effect of visual perspective on cortical body representations. *Cerebral Cortex (New York, NY : 1991)*, *16*(2), 178–182. http://doi.org/10.1093/cercor/bhi095

Serino, A., & Haggard, P. (2010). Touch and the body. *Neuroscience and Biobehavioral Reviews*, *34*(2), 224–236. http://doi.org/10.1016/j.neubiorev.2009.04.004

Serino, A., Alsmith, A., Costantini, M., Mandrigin, A., Tajadura-Jiménez, A., & Lopez, C. (2013). Bodily ownership and self-location: components of bodily self-consciousness. *Consciousness and Cognition*, *22*(4), 1239–1252.

http://doi.org/10.1016/j.concog.2013.08.013

Sforza, A., Bufalari, I., Haggard, P., & Aglioti, S. M. (2010). My face in yours: Visuo-tactile facial stimulation influences sense of identity. *Social Neuroscience*, *5*(2), 148–162. http://doi.org/10.1080/17470910903205503

Shimada, S., Fukuda, K., & Hiraki, K. (2009). Rubber hand illusion under delayed visual feedback. *PloS One*, *4*(7), e6185. http://doi.org/10.1371/journal.pone.0006185

Shimada, S., Hiraki, K., & Oda, I. (2005). The parietal role in the sense of self-ownership with temporal discrepancy between visual and proprioceptive feedbacks. *NeuroImage*, *24*(4), 1225–1232. http://doi.org/10.1016/j.neuroimage.2004.10.039

Shimada, S., Qi, Y., & Hiraki, K. (2010). Detection of visual feedback delay in active and passive self-body movements. *Experimental Brain Research Experimentelle Hirnforschung Expérimentation Cérébrale*, *201*(2), 359–364. http://doi.org/10.1007/s00221-009-2028-6

Shore, D. I., Spry, E., & Spence, C. (2002).Confusing the mind by crossing the hands. *Cogn Brain Res*, *14*(1), 153 - 163.

Slater, M., Marcos, D. P., & Ehrsson, H. (2009). Inducing illusory ownership of a virtual body. Frontiers in ….

Spence, C., Pavani, F., Maravita, A., & Holmes, N. P. (2004). Multisensory contributions to the 3-D representation of visuotactile peripersonal space in humans: evidence from the crossmodal congruency task. *Journal of Physiology, Paris*, *98*(1-3), 171–189. http://doi.org/10.1016/j.jphysparis.2004.03.008

Spencer, R. M. C. (2003). Disrupted Timing of Discontinuous But Not Continuous Movements by Cerebellar Lesions. *Science*, *300*(5624), 1437–1439. http://doi.org/10.1126/science.1083661

Spencer, R., Verstynen, T., & Brett, M. (2007). Cerebellar activation during discrete and not continuous timed movements: An fMRI study. *NeuroImage,* 36(2):378-387.

Sturm, T. (2012). The Self Between Philosophy and Psychology: The Case of Self-Deception. Psychology Press.

Sutter, C., & Müsseler, J. (2010). Action control while seeing mirror images of one's own movements: effects of perspective on spatial compatibility. *Quarterly Journal of Experimental Psychology (2006)*, *63*(9), 1757–1769. http://doi.org/10.1080/17470210903511244

Swinnen, S. P. (2002). Intermanual coordination: from behavioural principles to neural-network interactions. *Nature Reviews Neuroscience*, *3*(5), 348–359. http://doi.org/10.1038/nrn807

Tajadura-Jiménez, A., Lorusso, L., & Tsakiris, M. (2013). Active and passive-touch during interpersonal multisensory stimulation change self-other boundaries. *Consciousness and Cognition*, *22*(4), 1352–1360. http://doi.org/10.1016/j.concog.2013.09.002

Takeda, K., Shimoda, N., Sato, Y., Ogano, M., & Kato, H. (2010). Reaction time differences between left- and right-handers during mental rotation of hand pictures. *Laterality*, *15*(4), 415–425. http://doi.org/10.1080/13576500902938105

Tessari, A., Tsakiris, M., Borghi, A. M., & Serino, A. (2010). The sense of body: a multidisciplinary approach to body representation. *Neuropsychologia*, *48*(3), 643–644. http://doi.org/10.1016/j.neuropsychologia.2009.12.004

Thompson, P. (1980). Margaret Thatcher: a new illusion. *Perception* 9:483–484.

Tipper, S., Phillips, N., Dancer, C., Lloyd, D., Howard, L., & McGlone, F. (2001). Vision influences tactile perception at body sites that cannot be viewed directly. *Experimental Brain Research*, *139*(2), 160–167. http://doi.org/10.1007/s002210100743

Tsakiris, M. (2010). My body in the brain: a neurocognitive model of body-ownership. *Neuropsychologia*, *48*(3), 703–712. http://doi.org/10.1016/j.neuropsychologia.2009.09.034

Tsakiris, M., & Haggard, P. (2005a). Experimenting with the acting self. *Cognitive Neuropsychology*, *22*(3-4), 387–407. http://doi.org/10.1080/02643290442000158

Tsakiris, M., & Haggard, P. (2005b). The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology Human Perception and Performance*, *31*(1), 80–91. http://doi.org/10.1037/0096-1523.31.1.80

Tsakiris, M., Carpenter, L., James, D., & Fotopoulou, A. (2010a). Hands only illusion: multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. *Experimental Brain Research Experimentelle Hirnforschung Expérimentation Cérébrale*, *204*(3), 343–352. http://doi.org/10.1007/s00221-009-2039-3

Tsakiris, M., Haggard, P., Franck, N., Mainy, N., & Sirigu, A. (2005). A specific role for efferent information in self-recognition. *Cognition*, *96*(3), 215–231. http://doi.org/10.1016/j.cognition.2004.08.002

Tsakiris, M., Longo, M. R., & Haggard, P. (2010b). Having a body versus moving your body: Neural signatures of agency and body-ownership. *Neuropsychologia*, *48*(9), 2740–2749. http://doi.org/10.1016/j.neuropsychologia.2010.05.021

Tsakiris, M., Prabhu, G., & Haggard, P. (2006). Having a body versus moving your body: How agency structures body-ownership. *Consciousness and Cognition*, *15*(2), 423–432. http://doi.org/10.1016/j.concog.2005.09.004

van den Bos, E., & Jeannerod, M. (2002). Sense of body and sense of action both contribute to self-recognition. *Cognition*, *85*(2), 177–187.

van Veluw, S. J., & Chance, S. A. (2013). Differentiating between self and others: an ALE meta-analysis of fMRI studies of self-recognition and theory of mind. *Brain Imaging and Behavior*, *8*(1), 24–38. http://doi.org/10.1007/s11682-013-9266-8

Walsh, L.D., Moseley, G.L., Taylor, J.L., & Gandevia, S.C. (2011). Proprioceptive signals contribute to the sense of body ownership. *Journal of Physiology*, 589:3009–3021. doi: 10.1113/jphysiol.2011.204941

Weber, E. H. (1996). De subtilitate tactus (H. E. Ross, Trans.). In H. E. Ross & D. J. Murray (Eds.), E. H. Weber on the tactile senses, 2nd ed (pp. 21–128). London: Academic

Press. (Original work published 1834)

Willems, R. M., & Hagoort, P. (2009). Hand preference influences neural correlates of action observation. *Brain Research*, *1269*, 90–104. http://doi.org/10.1016/j.brainres.2009.02.057

Willems, R. M., Hagoort, P., & Casasanto, D. (2010a). Body-Specific Representations of Action Verbs: Neural Evidence From Right- and Left-Handers. *Psychological Science*, *21*(1), 67–74. http://doi.org/10.1177/0956797609354072

Willems, R. M., Peelen, M. V., & Hagoort, P. (2010b). Cerebral lateralization of face-selective and body-selective visual areas depends on handedness. *Cerebral Cortex*, *20*(7), 1719–1725. http://doi.org/10.1093/cercor/bhp234

Winter, R., Harrar, V., Gozdic, M., & Harris, L.R. (2008). The relative timing of active and passive touch. *Brain Research*, 1242:54 - 58.

Wolpert, D. M. (1997). Computational approaches to motor control. *Trends in Cognitive Sciences*. Elsevier Science.

Yin RK (1969) Looking at upside-down faces. *Journal of Experimental Psychology (General)*, 81:141145.doi:10.1037/h0027474

Yen Pik Sang, F. (2006). Depersonalisation/derealisation symptoms in vestibular disease. *Journal of Neurology, Neurosurgery & Psychiatry*, *77*(6), 760–766.

Zopf, R., Savage, G., & Williams, M. A. (2010). Crossmodal congruency measures of lateral distance effects on the rubber hand illusion. *Neuropsychologia*, *48*(3), 713–725. http://doi.org/10.1016/j.neuropsychologia.2009.10.028

Zopf, R., Friedman, J., and Williams, M.A. (2015). The plausibility of visual information for hand ownership modulates multisensory synchrony perception. *Experimental Brain Research*, 233:2311 - 2321.