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The role of distance from the body and distance from the real hand in ownership and disownership during the rubber hand illusion

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ABSTRACT

A key tool for investigating body ownership is the rubber hand illusion, in which synchronous multisensory feedback can induce feelings of ownership over a fake hand. Much research in the field aims to tease apart the mechanisms that underlie this phenomenon. Currently there is conflicting evidence as to whether increasing the distance between the real and fake hands (within reaching space) can reduce the illusion. The current study examines this further by modulating, not only the absolute distance between the real and fake hands but also their relative distance from body midline. It is found that the strength of the illusion is reduced only when the fake hand is both far from the real hand and far from the trunk; illusion scores over a fake hand in the same position can then be increased by moving the real hand nearer. This is related to peripersonal space surrounding the trunk and the hand. Subjective disownership of the real hand, and proprioceptive drift measures were also taken and may be driven by different mechanisms.

1. Introduction

The rubber hand illusion (RHI) is a phenomenon in which neurologically healthy individuals can be induced to feel ownership over a non-corporeal fake hand (Botvinick & Cohen, 1998). This is achieved by touching the seen fake hand and the unseen real hand in synchrony. When the touch is asynchronous, or the position of the fake hand is not compatible with that of the body, the illusion is abolished. Mechanisms underlying the RHI are thought to involve integration of visual, tactile and proprioceptive signals (Botvinick & Cohen, 1998) resulting in feelings of ownership demonstrated by questionnaire responses and an apparent remapping of actual limb position towards the location of the fake hand measured with perceptual judgments of hand position (Tsakiris & Haggard, 2005) and reaching (Newport, Pearce, & Preston, 2010).

Multisensory encoding of limb position for both real and fake limbs has been associated with the human parietal and premotor cortex using fMRI (Ehrsson, Spence, & Passingham, 2004; Lloyd, Shore, Spence, & Calvert, 2003). Single cell recordings with monkeys have also identified neurons in these areas that fire in response to visual and tactile stimuli near to and touching the hand. In many instances the visual receptive fields of these neurons radiate out, at least in part, from the tactile receptive field on the skin and are based on egocentric body-centred coordinates; following the hand through different positions independent of eye and head movements (Graziano, Hu, & Gross, 1997) or the monkey's position in the room (Fogassi et al., 1996). The area of space surrounding the body that is captured by the bimodal neurons (peripersonal space) is thought to be important for defensive behaviour, object avoidance (Graziano & Cooke, 2006) and also for the self-attribution of body parts (Makin, Holmes, & Ehrsson, 2008).

To date the exact relationship between peripersonal space and body ownership remains unclear. In humans and monkeys peripersonal space around the hand (perihand space) can be remapped, not only in accordance with the different positions of the actual limb, but also to incorporate a fake hand placed in a compatible position with the body (Graziano, 1999; Makin, Holmes, & Zohary, 2007). Remapping of perihand space does not, however, necessarily indicate ownership. Makin et al. (2007) found similar activations in the posterior parietal cortex and the right lateral occipital cortex when viewing an object close to a fake hand compared to when close to the real hand in the same location. Such activations were not observed with no hand present or when the fake hand was outside reaching space. It was suggested that these areas respond to visual information concerning hand position (with separate activations in the ventral premotor cortex responding proprioceptive information) despite no attempt to induce the RHI and post-experiment questioning revealing that participants did not feel any ownership over the fake hand. Furthermore, tools that do not resemble hands are thought to extend peripersonal space following use (Farnè & Làdavas, 2000; Iriki, Tanaka, & Iwamura, 1996, but see Holmes, 2012 for an alternative argument), yet to induce ownership over an external object that object needs to resemble a part of the body (Tsakiris, Carpenter, James, & Fotopoulou, 2010). However, we do not tend to mistake a hand over the other side of the

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room as our own just because it looks like a hand. Intuitively, in order to feel like a seen hand is part of our body, it needs to be spatially close to us. Indeed, Lloyd (2007) found that proximity of the fake hand to the real limb position played a key role in the RHI, finding that distances greater than 27.5 cm lead to a significant reduction in illusion strength. The author related this effect to size of visual receptive fields of the bimodal neurons found in monkeys (perihand space).

A more recent study by Zopf, Savage, and Williams (2010) did not find a reduction in RHI strength with distances of up to 45 cm between the real and fake hands. This was said to indicate that there is no reduction in the illusion within reaching space. The authors instead suggested that the reduced illusion previously found at smaller distances (Lloyd, 2007) was not actually due to the distance between the real and fake hands, but a result of the rubber hand crossing the midline, which has subsequently been found to abolish the proprioceptive drift in the RHI (Cadieux, Whitworth, & Shore, 2011; Folegatti, Farnè, Salemme, & de Vignemont, 2012). Furthermore, most bimodal neurons identified in primates had a boundary extending beyond 30 cm and many didn't have a clear border at all (Fogassi et al., 1996). However, recent evidence from human subjects suggests that distance from the body, even within reaching space, may change the way stimuli are processed by the brain. For example, a slight leftward bias observed in healthy controls when completing a line bisection task in near space has been found to gradually shift rightwards with an increasing distance of the task stimuli (from peri- to extra-personal space) (Longo & Lourenco, 2006; Varnava, McCarthy, & Beaumont, 2002). This shift in attentional bias was thought to reflect a transition of processing from the right hemisphere for peripersonal space to the left hemisphere for extrapersonal space. Importantly, this transition was found to begin within reaching space.

In the experiment by Zopf et al. (2010), in which distance between the real and fake hands was found to not affect the RHI, the fake hand was always closer to the trunk than the real hand (medial position). Therefore, although the fake hand may have been far from the real hand it remained close to another part of the body (the trunk). Some bimodal neurons have been found with receptive fields that encompass space on and around *both* the trunk and the arm (Fogassi et al., 1996), such that in the set-up described Zopf et al. (2010), although the fake hand may have been far away in terms of peri*hand* space, it is not further away in terms of peri*personal* space. Moreover, studies that have investigated ownership over two fake hands simultaneously have found that relative distance of the real and fake hands from the body midline is important for illusion strength. For example, when given a choice of two synchronous fake hands equidistant either side of the (hidden) real hand, the hand that is nearer to the body was preferred when planning reaching movements, such that participants reach as though their hand was located nearer to the medial fake hand, although there was no significant difference in questionnaire judgments (Newport et al., 2010). Another experiment using a similar paradigm investigated the ease of which the illusion could be abolished by encroaching the fake limb with a stick (Preston & Newport, 2011a). It was found that the illusion over a fake hand at a medial position relative to the real hand was more robust than for a laterally positioned fake hand, which was readily 'disowned' following encroachment.

As well as owning a fake hand, recent studies have also found evidence for disowning the real hand during the RHI, suggesting that the representation of the real hand is replaced, at least in part, by the new representation of the fake hand (Barnsley et al., 2011; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008; Moseley et al., 2008). Ownership over more than one left (Newport et al., 2010) or right (Ehrsson, 2009) fake hand has been demonstrated, which suggests that disownership of the real hand is not essential when inducing the RHI. Moreover, no significant disownership of the real hand was found during a version of the RHI in which the real hand remains visible, even though ownership over the fake hand is still induced (Guterstam, Petkova, & Ehrsson, 2011). Despite not being essential for ownership over a fake hand, disownership may still occur to some extent during the RHI when the real hand is unseen. The continued ownership over a medially positioned fake hand, despite encroachment that destroys ownership for a fake hand in a lateral position (Preston & Newport, 2011a) may suggest that any disownership that does occur will do so more readily when the real hand is further from the body midline compared to the fake hand.

In addition to questionnaire responses, the RHI is often also measured by proprioceptive drift in which the perceived position of the real limb drifts towards that of the fake hand following synchronous (illusion) stroking and not asynchronous (no illusion) stroking. However, recently the validity of proprioceptive drift as a measure of ownership has been questioned suggesting that the two processes are driven by different mechanisms (Rohde, Di Luca, & Ernst, 2011). Supporting this, Zopf et al. (2010) found slightly differing patterns between the two measures when modulating the distance between the real and fake hands. It was found that synchrony of multisensory feedback was only important when the hands were far apart. When the hands were close, there was no significant difference between synchronous stroking and asynchronous stroking as both lead to a similar degree of proprioceptive drift towards the fake hand. This was in contrast to the subjective questionnaire reports, which were modulated by multisensory feedback in all conditions.

As well as absolute distance between the real and fake hands, relative distance between the hands and body midline may also modulate proprioceptive drift. In the absence of visual feedback of the limb, proprioceptive signals degrade, resulting in a shift in perceived limb position towards the trunk (Wann & Ibrahim, 1992). Afferent signals from the limb are also found to degrade during visual and proprioceptive conflict (Jones, Wessberg, & Vallbo, 2001) similar to that which occurs in the RHI when the visible (owned) rubber hand is in a different location to that of the felt real hand. Therefore, because the RHI is most often conducted with the fake hand at a medial position relative to the real hand, this reduction of afferent signals may lead to a perceived shift towards the body through mechanisms unrelated to body ownership. Therefore, the traditional RHI set-up may serve to exacerbate effects of proprioceptive drift during the illusion, and thus, if the fake hand is placed at a lateral position (further from the trunk), proprioceptive drift (towards the fake hand) may be impeded. Indeed, the effect of the illusion over a laterally placed fake hand on reaching movements is found to be abolished in favour of a medially positioned fake hand, despite both hands being subjectively owned to a statistically equivalent degree (Newport et al., 2010).

The current study aimed to directly test the contributions of proximity to the real hand and proximity to the trunk in the RHI. The fake hand was placed in full view on a raised surface in front the participants at one of three locations relative the body midline: *Near*, *Mid* and *Far*. The RHI was then induced with the real hand positioned at different locations relative to the body and the fake hand. Based on our current understanding of peripersonal space it was predicted that subjective responses measuring the strength of the illusion would only be reduced when the fake hand is both far from the real hand and the trunk. Similarly, it is predicted that disownership of the real hand would be modulated by spatial position of the real and fake hands particularly in relation to the body midline, with disownership occurring more readily when the fake hand is nearer to the midline than the real hand. It is also predicted that proprioceptive drift towards the fake hand will be reduced when the fake hand is further from body midline than the real hand. Furthermore, in line with findings by Zopf et al. (2010), small distances between the real and fake hands are expected to correspond with a reduced importance of synchronous multisensory feedback for proprioceptive drift.