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Visual information and rubber hand embodiment differentially affect reach-to-grasp actions

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ABSTRACT

During the "rubber hand illusion" (RHI) participants feel touch originating from an artificial hand, which is felt to belong to the own body. The perceived location of the real hand is shifted towards the location of the artificial hand. However, evidence as to whether the RHI is accompanied by alterations of hand action is mixed. We found that the perceived size of one's own hand was affected by the size of the artificial hand that was used to elicit the illusion. Moreover, we tested a possible transfer of the RHI to a reach-to-grasp action. We observed that hand transport (i.e., reach) errors after RHI induction were independent of artificial hand size, showing that the parameter which is important for these reaching errors is the hand's perceived location. Results thus show that the RHI affects not only perceptual, but also action processing. In contrast, grip aperture was affected by artificial hand size independent of the RHI, suggesting that visual information about hand size affects grasping independent of embodiment of the artificial hand. Grip size increased with artificial hand size; this effect is explained by a higher reliance on proprioceptive information during blind reaching after receiving distorted visual information.

1. Introduction

Our brains are remarkably flexible in what they consider part of our own body. Although we might intuitively feel as if "we never change" – after all, we wake up with the same body each morning –, a large number of experiments have convincingly shown that the brain can consider non-body objects as belonging to, or at least being closely related to the body. One of the most striking demonstrations of such integration processes is the well-known rubber hand illusion (RHI, Botvinick & Cohen, 1998): a participant's hand is hidden from view (for example, by covering it with a box), and an artificial hand is placed in view. Both the (visible) artificial hand and the (hidden) real hand are touched or stroked in synchrony for about a minute. After a few seconds, most participants report a vivid illusion of the artificial hand being their own, and of the touch coming from the location in space at which the artificial hand is touched.

There is some debate about the specific conditions under which the brain incorporates objects into the body. Similar effects as those found for artificial hands have been reported when the table surface rather than an artificial hand was stroked in synchrony with the (hidden) hand (Armel & Ramachandran, 2003). An emotional response, measurable in changes of skin conductance, was observed when a band-aid was violently pulled of the table surface after the illusion had been induced (Armel & Ramachandran, 2003). This emotional response was higher after synchronous than after asynchronous stimulation, indicating an integration of the table according to the same principles as in the case of an artificial hand. However, skin conductance responses obtained when stroking an artificial hand were higher than those obtained after table stroking, possibly indicating that integration of the table was less complete or less strong. Indeed, other researchers have not been able to evoke the RHI with the use of non-hand objects (Holmes, Snijders, & Spence, 2006; Tsakiris & Haggard, 2005). Accordingly, it has been suggested that an object must be perceptually similar to the participant's hand for the illusion to occur (Tsakiris, 2010). Consequently, some characteristics of artificial hands have been investigated with regard to their relevance for the RHI. For example, hand shape and similarity as assessed by third person ratings (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2009) as well as skin complexion or skin color (Holmes et al., 2006) do not seem to influence illusion strength. One of the aims of the current study was to test the influence of similarity of hand size on the RHI.

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A second area of intense research has been the relationship of perception and action in the rubber hand illusion. This relationship can be looked at from different viewpoints. First, one can ask whether motor responses towards the hand affected by the illusion are modulated. Second, one can ask whether movements of the own hand modulate the induction and/or the strength of the illusion. Finally, one can ask whether motor responses executed with the affected hand itself are modulated. We will introduce each of these aspects in turn.

Motor responses towards the affected hand have frequently been used to assess illusion strength. It was originally reported that after synchronous stimulation the location of one's own hand is perceived to have shifted towards the location of the artificial hand (Botvinick & Cohen, 1998); this is often measured by asking participants to point to the affected hand with the other (non-illusion) hand: pointing is biased towards the position of the artificial hand. It has furthermore been suggested that the size of this pointing bias is an indicator of illusion strength based on the finding that the pointing bias correlates with the perceived illusion strength as assessed with questionnaires (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008).

With respect to induction of the illusion, it has been shown that the RHI can be induced not only by tactile stimulation (stroking), but also by passive and active movement of one's finger (Tsakiris, Prabhu, & Haggard, 2006). In the finger movement conditions, participants watched a video image of their hand. If the hand was stroked or passively moved, the perceptual drift (i.e. the shift of localization responses towards the artificial hand) affected only the finger on which the illusion was elicited. In contrast, when the hand was actively moved, drift generalized to the whole hand. The authors therefore suggested that "the sense of agency integrates distinct body-parts into a coherent, unified awareness of the body" (p.423).

Maybe the most interesting aspect of the action-perception relationship of the RHI is how actions of the affected hand are modulated: do the perceptual changes (e.g. the perceived altered location of the hand) influence the planning and execution of hand actions? From a theoretical standpoint, a connection between perceptual and motor processes would not be a trivial result: it is commonly assumed that the brain features two different processing routes, one occipito-temporal route which mediates perceptual processes, and a second, occipito-parietal–frontal route which mediates action (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). Besides dissociations of these two processing streams in neuropsychological patients, one major source of evidence for this hypothesis has been a dissociation of the influence of visual illusions on perception versus on action (Bruno, 2001; Goodale & Westwood, 2004). Although these results have been challenged (Bruno, 2001; Franz, 2001; Franz, Hesse, & Kollath, 2009), the idea of two processing streams is still highly influential. Accordingly, an equivalent distinction has been proposed for body processing, separating perceptual aspects of body processing, the "body image", from action-related aspects of body processing, the "body schema" (e.g. de Vignemont, 2010; Kammers, van der Ham, & Dijkerman, 2006; Newport, Pearce, & Preston, 2010). For example, in two related studies, Kammers et al. (Kammers, de Vignemont, Verhagen, & Dijkerman, 2009) (Kammers, Verhagen, et al., 2009) tested whether the RHI disappeared when the hand for which the illusion had been induced (the "illusion hand") was actively moved. In the first study (Kammers, de Vignemont, et al., 2009), participants made two successive pointing movements either with the illusion hand, or with the unaffected hand. Pointing movements were as accurate for the illusion hand as they were for the unaffected hand. At the same time, even if both successive pointing movements were executed with the illusion hand, a subjective RHI remained (though diminished). Perception and action for the RHI were thus dissociated in this study. These results were corroborated by the second study (Kammers, Verhagen, et al., 2009), in which the authors disrupted processing in the intraparietal lobule with repetitive transcranial magnetic stimulation (rTMS) and showed that this disruption lead to a decrease in the location bias towards the artificial hand, but did not influence pointing responses. These results are at odds with previous reports (Botvinick & Cohen, 1998) about an influence of the RHI on pointing responses; the authors suggested that this difference may be explained by the requirements for the pointing response: in Kammers et al.'s studies, participants made fast movements which were presumably not corrected during execution (referred to as "ballistic" by the authors), whereas Botvinick and Cohen required slow, controlled, non-ballistic responses.

The present study aimed to bring together two aspects discussed so far: how similar the artificial hand must be for the RHI to emerge, and, how the RHI influences actions executed with the affected hand. To this end, we attempted to induce the RHI with differently sized artificial hands, one very large and one very small, and asked participants to make reaching and grasping actions.

A manipulation of artificial hand size for the RHI has previously been investigated. In one study, the perceptual location bias of the real towards the artificial hand was elicited when the artificial hand was either as large or larger than the real hand, but not when it was smaller (Pavani & Zampini, 2007), although the subjective illusion, assessed with a questionnaire, did not differ for different artificial hand sizes. However, another study found pointing responses equally affected for both hand sizes (Haggard & Jundi, 2009). In contrast, participants in this latter study perceived the weight of briefly lifted objects differently after RHI induction with a large, but not with a small hand (Haggard & Jundi, 2009). A third study induced the RHI with a large or small artificial hand and then asked participants to compare the size of a small disk touched with the fingers of the affected hand with a reference disk felt with the other, unaffected hand (Bruno & Bertamini, 2010). The disk was judged larger after induction of the RHI with a large artificial hand than with a small hand. The results were interpreted as an influence of an altered representation of the hand on active touch. Given the complexity of active touch, one might suggest that the RHI here affected not only perception but also action, possibly due to the interaction necessary to integrate finger movement and tactile perception. In contrast to the results of Pavani and Zampini as well as Haggard and Jundi, the effect was stronger for a small than for a large artificial hand. Unfortunately, a questionnaire assessing illusion strength was given only at the very end of the experiment, referring to both large and small artificial hands at once.

The influence of the RHI on perceived object size suggests that the RHI does not just globally affect perception of the hand, but more specifically affects perception of the fingers. This was tested more directly by manipulating both the participants' as well as the artificial hand's finger posture during RHI induction (Kammers, Kootker, Hogendoorn, & Dijkerman, 2010). When reaching for a cylinder with closed eyes, maximum grip aperture – the largest distance between index finger and thumb during the grasping movement – was larger both when the real and the artificial hand's fingers were held far apart during RHI induction than when they were held closer together. Thus, grip aperture was not only influenced by the size of the object to be grasped, but also by (real and illusory) hand posture at the start of the movement.

In the present study, we tested the effect of artificial hand size on grasping movements by testing whether it modulates grip aperture during a grasping movement, similar to finger posture in Kammers et al.'s (2010) study. Following previous studies (Bruno & Bertamini, 2010; Haggard & Jundi, 2009), we hypothesized that manipulating the size of an artificial hand for the RHI would influence the perceived size of one's own hand. Such an illusion could potentially influence hand action: when adjusting the distance between thumb and index finger during grasping with a precision grip, finger aperture would have to be larger when the hand were small than when it were large. We therefore induced a RHI using both a very small (primary school child size) and a very large (hand size of a tall man) artificial hand and asked participants