



## Review

## On the other hand: Dummy hands and peripersonal space

Tamar R. Makin<sup>a,\*</sup>, Nicholas P. Holmes<sup>b,c</sup>, H. Henrik Ehrsson<sup>d</sup><sup>a</sup> Department of Neurobiology, Life Sciences Institute, Hebrew University, Jerusalem 91904, Israel<sup>b</sup> INSERM U534, Espace et Action, Bron, France<sup>c</sup> Department of Psychology, Hebrew University, Jerusalem 91905, Israel<sup>d</sup> Department of Clinical Neuroscience, Karolinska Institutet, 171 76 Stockholm, Sweden

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## ABSTRACT

Where are my hands? The brain can answer this question using sensory information arising from vision, proprioception, or touch. Other sources of information about the position of our hands can be derived from multisensory interactions (or potential interactions) with our close environment, such as when we grasp or avoid objects. The pioneering study of multisensory representations of peripersonal space was published in *Behavioural Brain Research* almost 30 years ago [Rizzolatti G, Scandolara C, Matelli M, Gentilucci M. Afferent properties of periarculate neurons in macaque monkeys. II. Visual responses. *Behav Brain Res* 1981;2:147–63]. More recently, neurophysiological, neuroimaging, neuropsychological, and behavioural studies have contributed a wealth of evidence concerning hand-centred representations of objects in peripersonal space. This evidence is examined here in detail. In particular, we focus on the use of artificial dummy hands as powerful instruments to manipulate the brain's representation of hand position, peripersonal space, and of hand ownership. We also review recent studies of the 'rubber hand illusion' and related phenomena, such as the visual capture of touch, and the recalibration of hand position sense, and discuss their findings in the light of research on peripersonal space. Finally, we propose a simple model that situates the 'rubber hand illusion' in the neurophysiological framework of multisensory hand-centred representations of space.

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\* Corresponding author. Fax: +972 2 6584985.

E-mail address: [tamar.makin@mail.huji.ac.il](mailto:tamar.makin@mail.huji.ac.il) (T.R. Makin).

## 0. Introduction

Look at the space surrounding your hands and you will experience nothing special as compared to your experience of any other part of space. However, recent advances in neurophysiology, neuropsychology, behavioural sciences, and neuroimaging support the existence of a specialized brain system that represents the sector of space closely surrounding certain body parts (peripersonal space [69,70]). In monkeys, multisensory neurons in this system may respond to visual, tactile, and auditory events, so long as these events occur within the limited sector of space surrounding the monkey's body. By integrating multisensory cues around the body, the peripersonal space system provides information about the position of objects in the surrounding environment with respect to the body. It might therefore play a role in guiding hand actions towards objects within reaching distance [9,29,33,58,59,71]. Moreover, since this multisensory space defines a boundary zone between the body and the environment, some researchers have suggested that it evolved for the execution of defence or object-avoidance movements, in order to protect the body against physical threats [14,15,39]. In this review we will focus on peripersonal space around the hands (peri-hand space [25,26,57]). We will show evidence for the existence of a multisensory representation of space which is specific for events occurring near the hands (i.e., hand-centred space), both in monkeys and in humans. We will also describe how this system may be involved in the multisensory representation of limb position. Interestingly, multisensory integration in hand-centred reference frames may be triggered simply by vision of a dummy hand, provided that the dummy hand is aligned in an anatomically plausible position. Finally, we examine the involvement of peri-hand mechanisms in the "rubber hand illusion" (RHI [8]), an experimental phenomenon in which subjects report feeling as if a dummy hand becomes a part of their own body. We will suggest that this and similar phenomena have close links with multisensory peri-hand space. That is, peripersonal space mechanisms might play a role in the process of attributing body parts to the self.

### 1. Evidence for multisensory integration in peripersonal space

#### 1.1. Evidence from electrophysiological studies

The study of peripersonal space was pioneered with electrophysiological recordings in the monkey premotor cortex [70] (see also [53]). In their study, Rizzolatti and colleagues distinguished between neurons that responded to a visual stimulus only when it was presented close to the monkey (i.e., within its reach), and neurons that responded to the same stimulus when it was presented far away from the monkey. Critically, the population of neurons that responded to visual stimuli within reach typically had visual receptive fields (RFs) that were spatially related to, and largely overlapping with, the same neurons' tactile RFs. Further studies have revealed a network of brain areas with similar multisensory neurons that show visual and sometimes also auditory RFs with a limited extension into the space surrounding the monkey's body. These brain areas include the ventral intraparietal sulcus (VIP [4,5,10,13,20,75]), the parietal area 7b [19,36,48,53,54,72,73] the putamen [35], and perhaps also parts of somatosensory cortex (Brodmann's areas 2 and 5 [49,65] though see [46] for further discussion). These studies reported spatial correspondence between the visual, auditory, and tactile RFs of individual cells—that is, selective neuronal responses to visual and auditory stimuli only when they are presented near to the body, typically approaching or receding from the relevant body part (for reviews, see [12,37,61]). Moreover, a recent study by Avillac et al. [4] showed that when a

visual and a tactile stimulus were presented simultaneously and within a VIP neuron's RF, such bimodal neurons showed evidence of multisensory integration (i.e., they responded in a non-linear way to the combined inputs). These results suggest a possible mechanism for the binding of distinct visual and tactile events occurring within peripersonal space into a single multisensory event, provided that the two stimuli are presented approximately simultaneously and within the same RF.

Most of the neurons in the studies mentioned above had tactile RFs centred on the monkeys' head, face, neck, torso, or shoulders. Hand- and arm-related visual responses, which are the main focus of studies addressing peripersonal space in humans, are most prominently reported in the monkey ventral premotor (PMv) cortex [28,32,37,38,40], but are also found in more dorsal parts of premotor cortex [30]. Graziano [33] measured the responses of bimodal neurons in PMv to a visual stimulus approaching the monkey along one of several parallel trajectories. A typical neuron responded most to the visual stimulus that most directly approached the tactile receptive field (in the example in Fig. 1, the hand and forearm). However, when the monkey's hand was moved, the neuron's best response shifted with the hand, to the visual stimulus approaching the new location of the hand. This shift in best response was maintained regardless of the position of the monkey's eyes, suggesting a bimodal mechanism for coding visual information in peripersonal space within a hand-centred coordinate system.

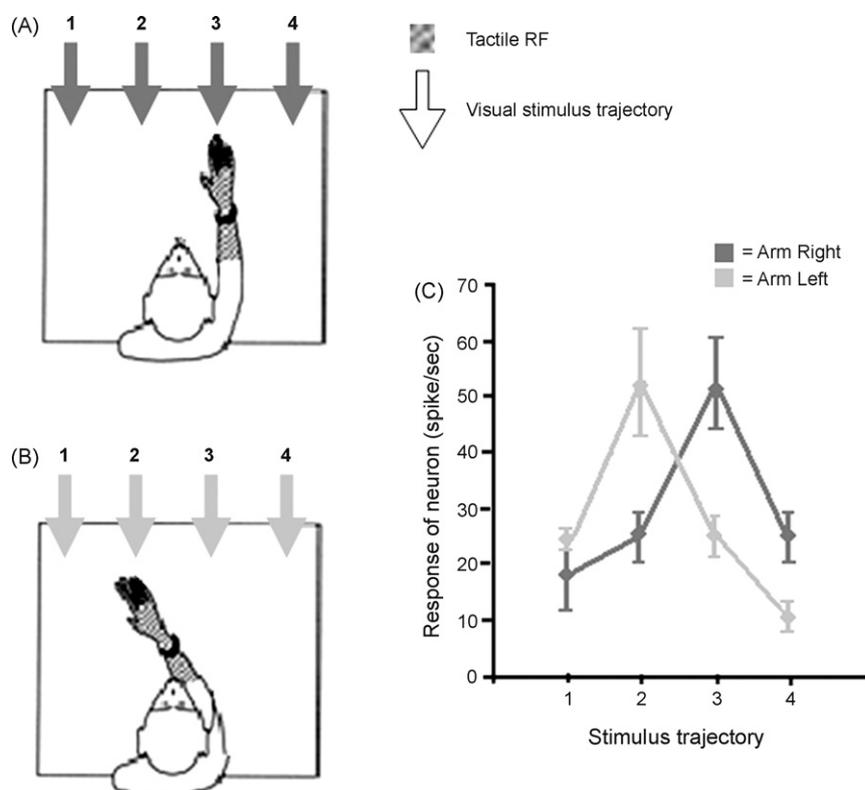
#### 1.2. Evidence from neuropsychological studies in humans

In humans, a major line of evidence for the existence of peripersonal space comes from neuropsychological studies with brain damaged patients. Certain patients with spatial neglect have been reported to show biases in spatial perception of the contralesional (i.e., left) side of peripersonal space, but not of far extrapersonal space [42], or, for the opposite distance-based dissociation [86]. Most of the evidence for mechanisms integrating multisensory information in peri-hand space has been demonstrated with patients suffering from the related neuropsychological phenomenon of extinction. Extinction is a syndrome in which, typically following right hemisphere damage, patients show impaired detection of contralesional (left) stimuli, but only when presented simultaneously with a stimulus on the ipsilesional (right) side.

Studies on patients presenting with extinction have demonstrated that extinction can be induced crossmodally, by using visual and tactile cues [18,52,60]. A visual stimulus applied to the right side of a patient's visual midline can significantly reduce the patient's detection of a simultaneous tactile stimulus presented on the left side. Importantly, extinction has been shown to be more severe for visual stimuli presented near to the patient's right hand, as compared to far from her right hand or near to the right side of her face [25]. Moreover, in a case study in which the patient's hands were held in a crossed posture (such that the left hand was positioned in the right hemispace and vice versa), visual stimulation near the right hand still induced significant extinction of left hand tactile stimuli, even though the (extinguished) tactile stimulus was now in the right hemispace [18], however see also Refs. [16,81]. Together, these findings suggest that crossmodal extinction involves a multisensory mechanism that is specific for the space surrounding certain body parts, specifically peri-hand space.

#### 1.3. Evidence from behavioural studies in humans

Further support for a system of peripersonal space in humans comes from behavioural experiments using the crossmodal congruency task. In this task, subjects are required to discriminate the elevation of vibrotactile stimuli presented either to their thumb



**Fig. 1.** Representation of visual stimuli in hand-centred coordinates. Visual responses of a typical premotor neuron with a tactile RF (hatched) on the forearm and hand, and a visual RF within 10 cm of the tactile RF. On each trial, the arm contralateral to the neuron was fixed in one of two positions: (A) on the right (dark grey symbols and lines), or (B) on the left (light grey symbols and lines) and the visual stimulus was advanced along one of four trajectories (numbered 1–4). (C) Responses of the neuron to the four stimulus trajectories when the arm was visible to the monkey were recorded for both positions. When the arm was fixed on the right, the response was maximal for trajectory 3, which was approaching the neuron's tactile RF. When the arm was fixed on the left, the maximal response shifted with the hand to trajectory 2, which was now approaching the tactile RF. Adapted from Graziano [33].

(‘upper’) or to their index finger (‘lower’) of either hand, while trying to ignore random, non-predictive visual distractors. These distractors are presented in either an upper or a lower location on the same or opposite side of the midline with respect to the vibrotactile target. Previous studies showed that tactile discriminations were slowed by visual stimuli that were incongruent with the correct upper/lower response, and that the greatest slowing occurred when the distractors were presented close to the hand, but regardless of the position of the hand with respect to visual fixation [80]. This crossmodal congruency effect (CCE) is significantly reduced if the visual distractors are presented further from the target hand, for example when presented near to the opposite hand. Thus, the CCE can readily be explained within the framework of multisensory integration in peripersonal space: the visual stimulus becomes more relevant to the tactile task (that is, the visual distractor becomes more effective) when it is presented from within peri-hand space.

#### 1.4. Evidence from an fMRI study in humans

Although there have been a few attempts to study the multisensory space near the face in humans [11,68,77], the neural substrate of human peri-hand space has only been investigated recently [57]. In their fMRI study, Makin and colleagues localized brain areas that showed significantly stronger activation to a visual stimulus when it was approaching the subject's hand, as compared to a similar stimulus moving far from their hands (Fig. 2A). Areas within the premotor cortex, the intraparietal sulcus (IPS), and in the lateral occipital complex (LOC) that showed a significant preference for the near stimulus when it was approaching the hand, did not show

a similar preference in a control experiment, in which the hand was retracted away from both stimuli (Fig. 2B). Since the only difference between the two procedures was the change in hand position, these areas were regarded as representing visual stimuli only when presented in peri-hand space.

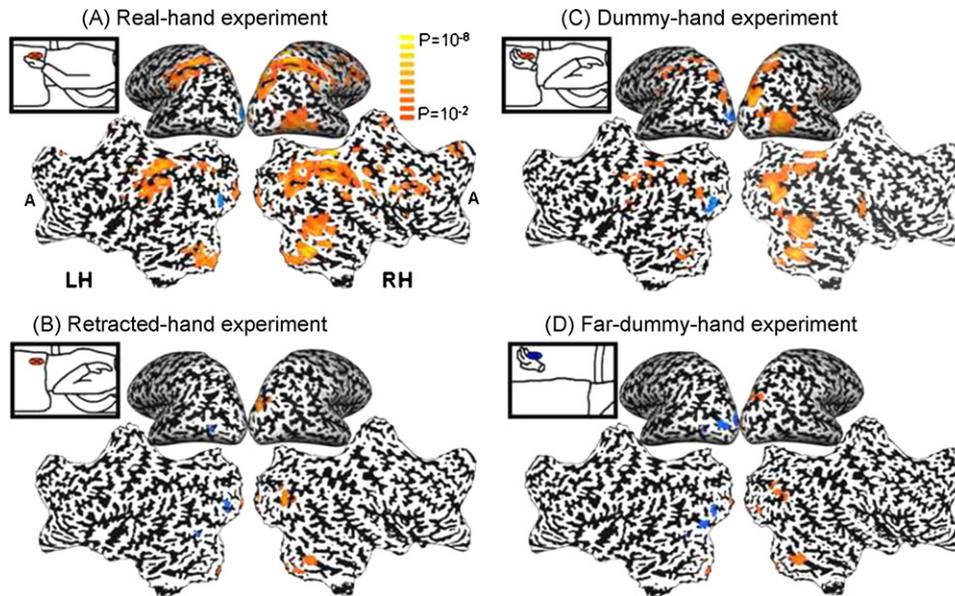
This observation, together with the behavioural evidence reviewed above, strongly suggests that both human and non-human primate brains contain a peripersonal space system that integrates multisensory information in body-part-centred coordinates.

## 2. Determining hand position with multisensory peripersonal space

The extent of peri-hand space must depend upon internal estimates of hand position derived using information gained from multiple sensory modalities. So how does the brain compute the position of the hands and other body parts? In this section, we review evidence showing how neuronal populations within the peripersonal space system (i.e., in premotor and intraparietal cortices) integrate visual and proprioceptive information from the hand to produce an internal estimate of hand position.

### 2.1. Behavioural evidence for the multisensory representation of hand position

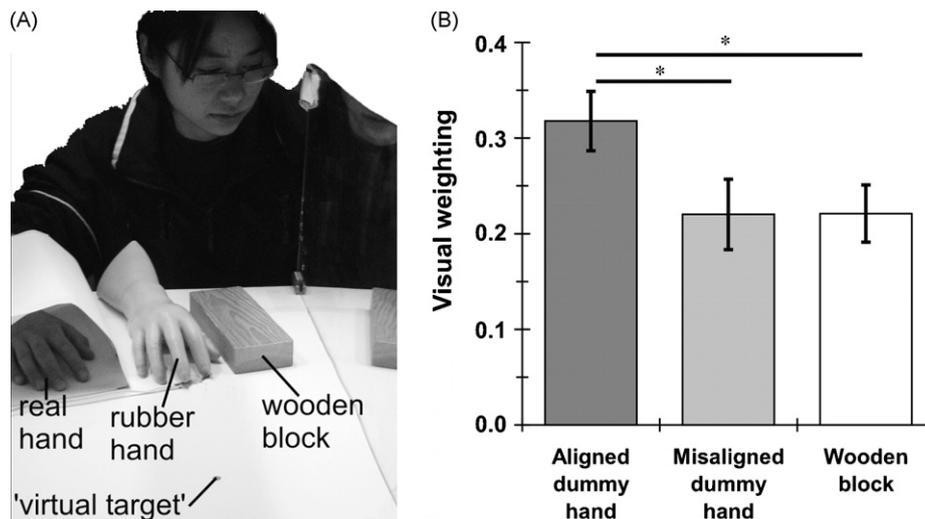
From behavioural experiments we know that central representations of hand position depend upon the integration of sensory information arising from the skin, joints, muscle, eyes, and even the ears [21,51,78]. For example, if visual information about hand position is made, experimentally, to conflict with proprioceptive



**Fig. 2.** Human brain areas showing selectivity for a visual stimulus presented near both the real hand and a dummy hand. Differential fMRI activation for “near” vs. “far” stimuli on representative inflated and unfolded maps of the right and left hemispheres. Areas in orange show preference for a 3D ball stimulus approaching the “near” target: (A) Next to the subject’s hand. (B) In the same position as (A), but while the subject’s hand was retracted away. (C) When a dummy hand was placed by the near target, while the subject’s own hand was retracted. (D) When a dummy hand was placed by the “far” target, while the subject’s own hand was retracted. Areas in blue show preference for a ball approaching the “far” target. Note that mere presence of the dummy hand modulated activity in the pIPS and LOC in a similar way to the real hand, as long as the dummy was placed in an anatomically plausible position. Data redrawn from Makin et al. [57]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

information, for example by using prisms [74], virtual environments [31], or a mirror reflecting the opposite hand [44,45,47,79], reaching movements made by the optically displaced hand may be disrupted. When Holmes et al. [45] asked subjects briefly to view a right hand placed in front of a parasagittally aligned mirror, then reach for an unseen target behind the mirror (see Fig. 3A), their reaching movements were biased equally by visual exposure to a reflection of their real right hand and of a dummy right hand

(although there was a trend towards a greater effect of the real hand). By contrast, passive visual exposure to the reflection of a wooden block or an incompatibly aligned dummy hand (i.e., facing palm-up rather than palm-down like the subject’s real hand) had smaller effects on subsequent reaching movements (i.e., had a smaller visual bias of hand position) than exposure either to the real hand or to the dummy hand. This result suggests that, for visual information to influence hand position representation, it is suffi-



**Fig. 3.** Viewing a compatibly aligned dummy hand before reaching biases the integration of vision and proprioception towards vision. (A) Subjects gazed into a mirror, viewing a reflection either of their real hand, a dummy rubber hand, or a wooden block. After 10 s, they made a reaching movement with their unseen left hand towards a target behind the mirror (seen only as a ‘virtual target’ reflected in the mirror). Changing the initial position of the subject’s left hand (i.e., moving it closer to or further from the mirror) changed the relative positions of the real (proprioceptive) and the apparent (visual) hands. These visual-proprioceptive mismatches had varying effects on the subject’s subsequent reaching movements. (B) Relative visual weighting of reaching movements. Viewing a compatibly aligned dummy hand had significantly greater effects ( $*p < .05$ ) on the mean ( $\pm$ S.E.M.) terminal error of reaching movements (i.e., on the felt initial position of the reaching hand) than viewing either a dummy hand rotated along its long axis by  $180^\circ$  (misaligned) or a wooden block. Dummy hands in compatible postures lead to an increase in the weighting of visual information over proprioceptive information in determining hand position prior to movements. This increased visual weighting is reflected in less accurate reaching movements. Figure adapted and redrawn from Holmes et al. [45].

cient that the visual image of the hand only approximately resembles certain aspects of the veridical hand—specifically its posture.

Other behavioural experiments have focused on the question of how and when visual and proprioceptive information is fused [85]. An interesting and well-replicated finding is that vision and proprioception may be combined optimally to produce a better estimate of hand position than what is possible if relying on vision or on proprioception alone. Specifically, this integration seems to depend upon a weighted sum of both visual and proprioceptive information about hand posture [43,79,85]. This makes intuitive sense: such ‘optimal integration’ would improve the accuracy of limb localization, which is important for everyday motor tasks in which visual and proprioceptive information is predominantly veridical. But how is this integration reflected in the peri-hand mechanisms discussed here? We next turn to this question.

## 2.2. Determining hand position with multisensory peri-hand brain activity

The question of how multisensory cortical neurons combine visual and proprioceptive information from the hand was addressed in the electrophysiological study conducted by Graziano [33] mentioned earlier. He took advantage of the peripersonal space properties of these neurons to make inferences about the representation of hand position during various experimental manipulations of visual and proprioceptive feedback. Specifically, Graziano measured the best response of bimodal neurons (with tactile RFs centred on the monkey’s hand and arm) to an identical set of visual stimuli approaching the hand, with respect to systematic changes in the static position of the monkey’s arm (proprioceptive manipulation; see Section 1.1 and Fig. 1 for details). Neurons with visual RFs that were anchored to the tactile RFs showed a shift in their best response with the hand when it was moved. Interestingly, when an artificial monkey’s hand was placed above the monkey’s static hand (which was now hidden from view), and the position of the visible artificial hand was manipulated, some of the visual responses shifted with the artificial hand to its new position. This suggests that, at least for some neurons, illusory visual information about hand position was sufficient to induce shifts in peri-hand space. Thus, these findings show that some bimodal neurons may predominantly rely on visual information to estimate hand position and thereby to define peripersonal space.

Makin et al. [57] tested for the existence of similar responses in human multisensory brain areas. The question again was whether peri-hand areas would change their responses due to experimental manipulations of visual and proprioceptive feedback. For this purpose, a dummy hand was positioned resting on the subject’s thigh, while their real hand was retracted away from the dummy, and positioned near their shoulder. Visual stimuli were presented both near to and far from the dummy hand. The results of this experiment can be seen in Fig. 2C: the preference for the stimulus approaching the dummy hand was remarkably similar in the posterior part of the intraparietal sulcus and the lateral occipital cortex, in both amplitude and spatial extent, to that shown for the real hand (Fig. 2A). Thus, just like in Graziano’s [33] study, the visual information provided by the dummy hand changed the representation of the hand in peripersonal space brain areas. Furthermore, when the dummy hand was placed far from the subject’s body (Fig. 2D), the preference for the stimulus approaching the dummy hand did not exceed that for the far stimulus in the retracted-hand experiment (Fig. 2B), which was identical in all but the presence of the dummy hand.

Perhaps the most striking aspect of these results is that viewing visual stimuli near a dummy hand is sufficient to change the representation of hand position in peri-hand brain areas. This implies that the visual information from the dummy hand is weighted heav-

ily when combined with the proprioceptive information about the position of the hand, but only when the dummy hand is placed in an anatomically plausible position and posture.

## 2.3. Using behavioural peri-hand paradigms to study the representation of hand position

The effect of visual input on the central hand representation and peri-hand space is also evident in behavioural experiments. First, Farnè et al. [27] examined whether a dummy hand can activate peri-hand space sufficiently in order to induce crossmodal extinction. In their experiment, visual stimuli were presented near to a dummy right hand, while the patient’s real right hand was held behind their back. The visual stimuli were indeed successful in extinguishing tactile stimuli applied concurrently to the patient’s left hand, so long as the dummy hand was in plausible anatomical alignment with the patient’s shoulder. When the dummy hand was positioned unnaturally (i.e., misaligned with the shoulders), extinction was reduced to the same extent as for a “regular” far visual stimulus.

Second, Pavani et al. [66] used the crossmodal congruency task for a similar purpose: these authors placed dummy hands near the visual distractors, with both dummy hands and distractors positioned above the subject’s occluded hands. When the dummy hands were aligned in an anatomically compatible orientation with respect to the subject’s hands, and “holding” the distractor lights, the CCE was increased with respect to a control condition without dummy hands. Furthermore, when the dummy hands were misaligned with respect to the veridical position of the subjects’ hands, there was no increase of the CCE above the “no dummy hands” condition (for further support and an extension of these results, see [3]). Thus, when realistic but non-veridical visual feedback of hand position was given, the central representation of hand position was significantly affected, representing the subjects’ real hand as being closer to the dummy hand than it actually was.

## 3. Integrating multisensory cues in peri-hand space across time—the rubber hand illusion

Because peripersonal space represents a boundary zone between one’s own body and the external environment, it could also have a role in the self-attribution of sensory signals. Botvinick and Cohen [8] reported that viewing a dummy hand being stroked by a paintbrush in synchrony with feeling strokes applied to one’s corresponding real, but occluded hand (using a second, unseen paintbrush) can create an illusion that the rubber hand “senses” the touch, i.e., that there is a displacement of the felt location of the touch from the hidden real hand to the visible dummy hand. The subject in this illusion experiences just one unified multisensory event (the brush seen and felt touching the dummy hand), rather than two separate unimodal events (seeing one brush and feeling the other brush). In addition there is a change in position sense of the real hand so that the subject experiences that her hand is closer to or even ‘inside’ the dummy hand. Interestingly, the subject also reports that she feels as if the dummy hand is her own hand. This set of phenomena, known collectively as the rubber hand illusion, is abolished when the two paintbrushes stroke the real and the dummy hands asynchronously. That is, temporal synchronicity between seen and felt events induces the illusory binding of those events onto the visible dummy hand, which is now experienced as one’s own. Further studies over the years have both confirmed and extended these findings using a variety of methods, including intermanual pointing or verbal reporting of the illusory felt hand position [17,55,82,84], skin conductance responses [1], somatosensory evoked potentials and EEG [50,67], transcranial magnetic stimulation [76], positron emission tomog-

raphy (PET) [83], and fMRI [22–24,56], see also [34] for related electrophysiological results.

Botvinick and Cohen [8] proposed a simple connectionist model for the rubber hand illusion, suggesting that it arises as the result of a constraint-satisfaction process between vision, touch, and proprioception, relying upon the structured correlations that normally obtain between these senses. In the RHI, in order to resolve the conflict between vision and touch, position sense is distorted. In the remaining part of this article we will argue for the view that peripersonal mechanisms are an integral part of the RHI, and that one gets a more complete explanation of the illusion within the framework of multisensory integration in peri-hand space.

### 3.1. The RHI in the framework of multisensory peripersonal space: a model

For clarity, we will start by outlining a preliminary model of the RHI that involves multisensory integration in peri-hand space (Fig. 4). Visual information from the dummy hand and proprioceptive information from the hidden real hand are conveyed to multisensory brain areas where hand position is computed. This could involve neuronal populations in posterior parietal cortex including the intraparietal sulcus, the premotor cortex, and the cerebellum [23,41,56,57]. So long as the dummy hand is situated in an anatomically plausible position, the integration of sensory information is weighed heavily in favour of vision (in particular when the real hand is static as is typically the case in studies of the RHI). In these circumstances, as we showed in the second part of this review, visual stimuli presented near the dummy hand should be sufficient to trigger peri-hand mechanisms: the seen brushstrokes on the dummy hand are processed as if they were occurring close to the real hand. Thus, once the space around the dummy hand is represented as peri-hand space, the seen stroke of the brush on the dummy hand is represented in reference frames centred on and with respect to the dummy hand. Simultaneously, the felt touches of the brush stroking the real hand will also activate the same bimodal mechanism. This conjunction of visual and tactile sensory information in hand-centred coordinates signals the occurrence of a single visual–tactile event [4] on the dummy hand. Thus, the sensation of touch is referred from the hidden real hand to the seen dummy hand.

It should be pointed out that this binding of vision and touch does not seem to require a complete behavioural recalibration of position sense (i.e., as demonstrated with verbal or manual reports of the felt hand position). It is sufficient with a partial recalibration in peri-hand space areas for the visual and tactile events to be mapped in peripersonal space and to be bound together onto the dummy hand. Consequently, the referral of touch to seen stimulation on the rubber hand might in itself be sufficient to induce an illusory feeling of ownership over the dummy hand, which further increases the weighting of vision over touch and proprioception in hand position estimation. In this section, we review recent behavioural and imaging experiments on the RHI in the light of this model.

### 3.2. Dissociations between hand position drifts, the felt position of touches, and hand ownership

According to the model suggested by Botvinick and Cohen [8], once proprioceptive, tactile, and visual space are aligned to the dummy hand, such that one feels somatic sensations as if arising from the dummy hand, just as one does from a real hand, then the person will say ‘this is my hand’. But what is the exact relationship between these reports of ownership and the sensory shifts? Some evidence suggests that the visually induced recalibration of felt

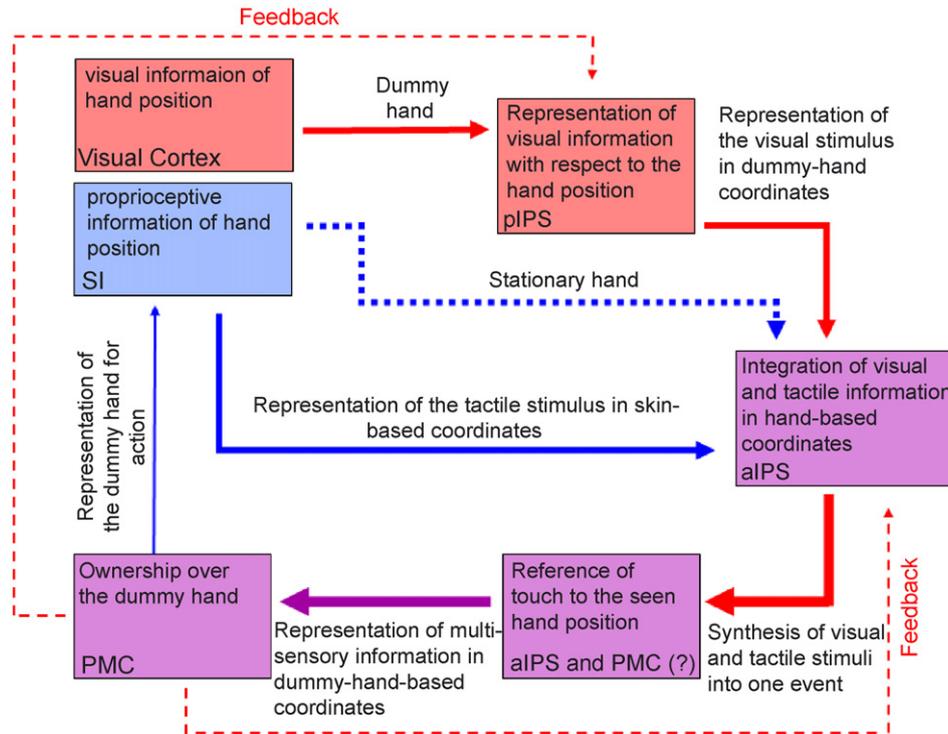
hand position can occur independently of the illusion of ownership. For example, the mirror reflection of a dummy hand positioned so as to create illusory visual hand position information, induces a significant drift in felt hand position (as measured with reaching movements), while the same subjects showed only weak illusions of ownership over the mirrored dummy hand (as measured with questionnaire reports [45], see Fig. 3). Similarly, RHI questionnaire studies which showed strong agreement with the ownership statement (“I felt as if the rubber hand was my own hand”), generally disagreed with the statement describing drifts in the felt position of the hand (“I felt as if my hand was drifting toward the rubber hand”) [8,22,23,66]. Furthermore, the felt hand position drift can also be dissociated from the visual capture of touch: the former is never complete, but subjects only report a drift of about 15–30% of the full distance between the real hand and the dummy hand [17,24,82,84], which corresponds well with the magnitude of proprioceptive drift in the mirror-illusion [45]. However, as revealed by questionnaires, subjects generally displace the felt touch to the location of the dummy hand, and not to an intermediate location between the real hand and the dummy hand. This raises questions about whether a simple recalibration of position sense can fully explain the illusion.

Finally, the time courses of these three dissociated phenomena support our proposed model: while in those subjects who are susceptible to the illusion, the referral of touch occurs as early as 6 s after the onset of simultaneous stroking [55], Ehrsson et al. [23] reported that the RHI typically takes about 11 s to occur. As for the changes in felt hand position, while Holmes et al. [45] reported rapid initial changes (following as little as 4–6 s of passive visual exposure to real hands) that may precede the onset of the RHI, other groups reported that felt hand position drift continues to increase after the illusion has begun [8,82,83]. It is therefore likely that further shifts in the felt position of the real hand towards the dummy hand occur after the onset of both the referral of touch to the dummy hand, and the illusion of ownership over the dummy hand. It is important to note that the exact temporal relationships between the drift in felt hand position, the referral of touch to the dummy hand, and the reported ownership over the dummy hand have not yet been clarified. This should be an important goal for future behavioural experiments.

The model we present here suggests that the referral of touch towards the dummy hand, which may be a result of the processing of peri-hand space mechanisms [4], might in itself be sufficient to induce a (bottom-up) feeling of ownership over the dummy hand. In this model, the feeling of ownership, caused at least partially by bimodal integration, may also be a catalyst for further changes in the felt position of the hand.

### 3.3. Constraints upon the RHI

We will next examine some of the constraints on the RHI and see how they fit with our suggested model. Apart from multisensory temporal synchronicity, the strength or occurrence of the RHI is limited by several other constraints: first, the occurrence of the RHI depends on the alignment between the actual position of the subject’s hand and the seen position of the dummy hand. When the dummy hand is positioned in an anatomically implausible posture (e.g., rotated by 90° beyond the maximum elbow rotation [66,82], or by 180° [23,56]), the RHI effects are abolished. And indeed, according to our model, peri-hand mechanisms will only bind synchronous visual and tactile events if they are both located near to the visible hand and if the visible hand is in an anatomically congruent position. Second, according to Lloyd [55], the occurrence of the RHI is limited by the distance between the dummy hand and the subject’s real hand: by parametrically manipulating the distance between the two hands, Lloyd found a significant decrease in



**Fig. 4.** A model of the rubber hand illusion involving multisensory peri-hand mechanisms. A schematic diagram illustrating a possible shared mechanism between multisensory peri-hand processing and the RHI. Arrows represent transformation of visual (red), somatosensory (blue) and multisensory (purple) information from unimodal areas to multisensory peri-hand area aIPS and to premotor cortex (PMC). The relative weighting between visual and proprioceptive (dotted line) contributions of the hand position is context-dependent (lower ratings for proprioception if the hand is stationary, for example). The result of this weighting is a central hand representation that is partially shifted towards the dummy hand. Consequently, visual information of the seen brush stroke on the dummy hand will be represented in (visual) dummy hand coordinates in the pIPS. This visual information will be conveyed to aIPS where it will be integrated with tactile information concerning the felt brush stroke. The result of this integration is one coherent multisensory event, represented in dummy hand coordinates (possibly in the PMC), and perceived as the illusion of referred touch. One major result of the re-mapping of touch to the dummy hand using peri-hand space mechanisms is the illusion of ownership over the dummy hand in PMC, which is also independently connected to unimodal areas. This illusion subsequently reinforces the dominance of visual information near the dummy hand in multisensory areas (visual feedback in dotted red arrows, proprioceptive shifts in blue). The drift in the felt position of the hand towards the dummy hand begins almost immediately upon visual feedback of the dummy hand, and continues throughout the generation and maintenance of the RHI, and after the onset of the illusion of ownership. Red, blue and purple boxes represent visual, somatosensory and multisensory brain areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

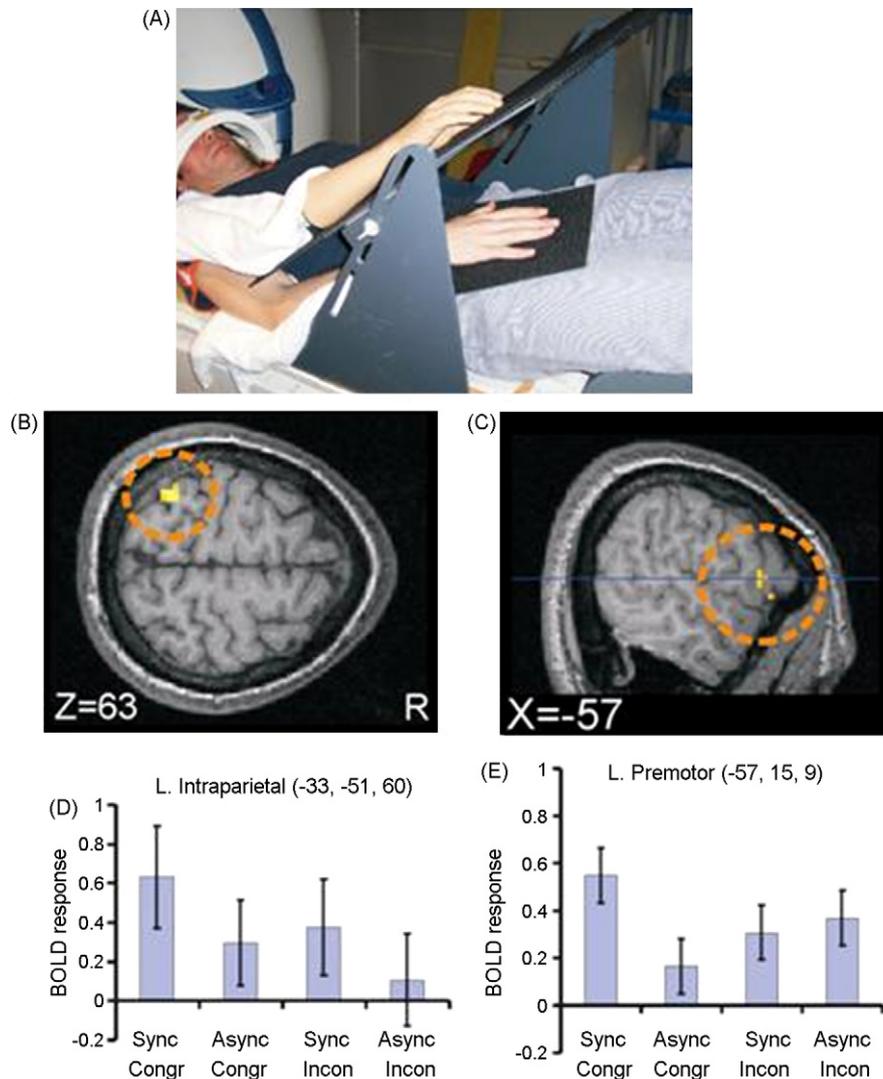
illusion strength (compared to the minimal separation) for separations greater than 27.5 cm. The non-linear decay of illusion strength with spatial distance converges with both electrophysiological [28] and neuropsychological [52] studies that measured the extent of peri-hand space. Lloyd suggested that the exponential decay of illusion strength with distance may reflect the response properties of bimodal visuo-tactile cells encoding peri-hand space: when the dummy hand is placed outside the initial (i.e., un-shifted) peri-hand space, the visual stimulus near the dummy hand is not represented by peri-hand multisensory mechanisms, and therefore no referred tactile sensation to the dummy hand can be elicited.

While the position of the dummy hand in Lloyd's study [55] was always anatomically plausible, the further away the dummy hand was placed from the real hand, the more its posture with respect to the shoulder differed from that of the real hand. This increasing angular difference, which was not accounted for in Lloyd's study, could have interacted with the effect of the lateral separation. An elegant study that deals with this possibility is the recent paper by Costantini and Haggard [17]. They investigated the effect of small variations in the position of the dummy hand, the real hand, and the direction of the brush strokes on the occurrence and strength of the RHI. When either the orientation of the real hand or the direction of the stroking stimulus was rotated by 10°, the RHI (as measured by verbal reports of felt hand position) was not abolished. However, when both the direction of the stimulus and the position of the hand were rotated in opposite directions, such that the felt stimulus was

spatially aligned with the visual stimulus on the dummy hand (i.e., aligned in external coordinates), but misaligned with respect to the hand (i.e., misaligned in hand-based coordinates), the RHI was significantly reduced. That is, spatial compatibility *per se* between the directions of visual and tactile stimuli is not sufficient to elicit the RHI. The position of these stimuli seems to be critical only when represented with respect to the position of the hand, and not with respect to the absolute position of the stimuli in external space. This finding supports our contention that, rather than simple recalibration of hand position based on multisensory synchrony (e.g. [1,8]), hand-centred peripersonal mechanisms are intimately involved in generating the RHI.

### 3.4. Neuroimaging and behavioural evidence linking peri-hand space mechanisms to ownership

Recent fMRI evidence supports the view that the RHI critically depends upon multisensory integration in peripersonal space. Ehrsson et al. [23] manipulated independently the synchronicity between tactile and visual stimuli and the congruency in orientation between the real and the dummy hand, in order to determine the respective contributions of these two variables to RHI-related brain activity. This 2 × 2 factorial design allowed them to distinguish between areas in the posterior IPS and LOC that were associated with the underlying conditions necessary for the onset of the RHI (i.e., a conjunction between the main effects of (a) hand ori-



**Fig. 5.** Activity in multisensory areas representing peri-hand space during the rubber hand illusion. (A) The position of the subject and the dummy hand in the scanner environment. (B) Activity in the left (contralateral) intraparietal cortex during the illusion, (C) activity in the ventral premotor cortex ( $p < 0.05$  after small volume correction). The mean ( $\pm$ S.E.M.) BOLD response amplitude in the ROIs B and C is plotted for each condition in D and E (respectively), and as can be seen, the greatest response was observed in the illusion condition (Sync Congr). The coordinates refer to Montreal Neurological Institute standard space.

entation congruency and (b) bimodal stimulus synchronicity), and areas within the ventral aspect of the premotor cortex that were associated with the reported feeling of ownership over the dummy hand (i.e., assessed by the interaction between hand orientation and stimulus synchronicity). In a separate analysis, Ehrsson and colleagues identified activity within the anterior part of the IPS preceding the onset of the RHI, which might play a role in the continued multisensory integration of stimuli with respect to the hand (Fig. 5).

Importantly, the RHI-related activation in the premotor cortex was also found to correlate positively with the subjective strength of the illusion across subjects as rated after the scan. These observations, both the pattern of responses with respect to the manipulation of temporal and spatial congruency, and the anatomical localization of the activations in multisensory hand-centred areas, fit well with the assertion that the RHI is mediated by multisensory mechanisms of peripersonal space. These brain imaging findings have been replicated several times with fMRI [22,24,55], although a recent positron emission tomography study failed to do so [83] perhaps due to the poorer sensitivity of PET, or to differences in the design with respect to the fMRI studies. Together with the findings of Makin and colleagues (as described in Sections 1 and 2 of

this review) these results indicate dissociation between the roles of posterior parietal cortex and PMv. PPC seems to integrate multisensory information with respect to the dummy hand, starting before illusion onset. The PMv shows additional, multisensory, responses during the period when people experience the illusion. This could be explained by the enhancement of the responses of bimodal neurons once their reference frame is centred on the dummy hand. It might therefore be that the posterior parietal cortex is more involved in the resolution of the conflict between visual and tactile information, and the recalibration of the visual and tactile coordinate systems, whereas the premotor cortex could mediate the referral of touch, by binding the visual and tactile events in hand-centred coordinates, thereby resulting in the participant saying “it feels like my hand” (i.e., body ownership). However, further studies are required in order to determine the roles of posterior parietal and premotor cortices in the visual referral of touch and the relationship between the neural correlates of the referral of touch and the association of ownership over the dummy hand.

Peripersonal space is important for our ability physically to interact with objects in our immediate surroundings, so it is not surprising that the processes of multisensory integration critical

for body ownership would take place in the premotor cortex. Similarly, work on kinaesthetic illusions has demonstrated that activity in the primary motor cortex is closely related to the perception of limb movement [62–64]. It is thus possible that bodily sensations related to ownership are processed in frontal motor areas contrary to the traditional wisdom that somatic sensations are generated by activity in the parietal lobes. Indeed, two recent studies have reported that damage to the premotor cortex after stroke can cause asomatognosia [2,7], a condition where the patients often deny owning their paralysed limbs [6]

Suggestive evidence from the crossmodal congruency task also supports an association between the RHI and peri-hand space mechanisms: Pavani et al. [66] showed that the magnitude of the CCE correlated with subjective ratings of agreement with statements describing the referral of touch to and the feeling of ownership over the dummy hands. That is, stronger spatial binding of multisensory information may result in referred touch and the conscious sensation of ownership over the dummy hands (see also Ref. [87] for complementary results). The CCE might therefore offer a direct behavioural link between peri-hand space mechanisms and the RHI, although further studies should establish whether enhanced CCEs lead to increased feelings of ownership or vice versa, whether this association depends on which sensory modality is attended or task-relevant, and whether other factors can modulate the relationship between the CCE and the RHI.

#### 4. Summary

We have reviewed recent evidence for multisensory integration in body-centred reference frames in the primate brain, with a focus on recent human neuroimaging and behavioural studies. We have further suggested that the conceptual framework of multisensory integration in peri-hand space might provide us with a more complete understanding of the RHI. Specifically we have emphasized that these mechanisms, grounded in physiological studies of active neuronal populations in the cerebral cortex, can extend our understanding of body ownership beyond the connectionist model suggested by Botvinick and Cohen [8]. Importantly, because the model we have outlined is based on results from neurophysiology as well as from experimental psychology, it may be more likely to generate fruitful predictions and to guide the design of future experiments in both brain and cognitive sciences.

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