Left tactile extinction following visual stimulation of a rubber hand

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Summary
In close analogy with neurophysiological findings in monkeys, neuropsychological studies have shown that the human brain constructs visual maps of space surrounding different body parts. In right-brain-damaged patients with tactile extinction, the existence of a visual peripersonal space centred on the hand has been demonstrated by showing that cross-modal visual–tactile extinction is segregated mainly in the space near the hand. That is, tactile stimuli on the contralesional hand are extinguished more consistently by visual stimuli presented near the ipsilesional hand than those presented far from it. Here, we report the first evidence in humans that this hand-centred visual peripersonal space can be coded in relation to a seen rubber replica of the hand, as if it were a real hand. In patients with left tactile extinction, a visual stimulus presented near a seen right rubber hand induced strong cross-modal visual–tactile extinction, similar to that obtained by presenting the same visual stimulus near the patient’s right hand. Critically, this specific cross-modal effect was evident when subjects saw the rubber hand as having a plausible posture relative to their own body (i.e. when it was aligned with the subject’s right shoulder). In contrast, cross-modal extinction was strongly reduced when the seen rubber hand was arranged in an implausible posture (i.e. misaligned with respect to the subject’s right shoulder). We suggest that this phenomenon is due to the dominance of vision over proprioception: the system coding peripersonal space can be ‘deceived’ by the vision of a fake hand, provided that its appearance looks plausible with respect to the subject’s body.

Keywords: peripersonal space; cross-modal extinction; rubber hand; multisensory integration

Abbreviations: RF = receptive field; VC = visually compatible; VI = visually incompatible

Introduction
An increasing amount of neurophysiological evidence suggests that visual peripersonal space, i.e. the space immediately adjacent to the skin surface and surrounding each body part, is coded at the level of single neurones, through the integration of sensory information from different modalities (for a review, see Graziano and Gross, 1998). Single-cell recording studies in monkeys have shown that this multimodal integration occurs in a number of cortical and subcortical structures. The ventral premotor area (approximately corresponding to area F4 of Rizzolatti et al., 1998), the putamen, the postcentral gyrus, the parietal areas 7b and the ventral intraparietal area contain relatively large numbers of neurones that are bimodal. These neurones respond to both tactile and visual stimuli, provided that the visual stimulus is presented within the visual receptive field (RF) extending outwards from the tactile RF of a given neurone (Rizzolatti et al., 1981; Duhamel et al., 1991; Graziano and Gross, 1995; Iriki et al., 1996).

These bimodal cells have visual–tactile RFs distributed predominantly over the face, arm, hand and the upper part of the animal’s body. Across different cerebral sites, bimodal neurones share some basic functional properties: (i) visual and tactile RFs are in spatial register, i.e. visual RFs match the location of tactile RFs on the body surface; (ii) visual RFs have a limited extent in depth, being restricted to the space immediately surrounding the monkey’s hand, face or body; (iii) vision-related activity shows a response gradient, i.e. the discharge decreases as the distance between the visual stimulus and the cutaneous RF increases; and (iv) visual RFs operate in coordinate systems centred on body parts; they remain anchored to the tactile RFs of a given body part when this is moved, and their spatial location does not change when the eyes move. Considered together, these properties indicate that the ventral premotor cortex, the parietal areas and the putamen form an interconnected system for the
integrated (visual–tactile) coding of peripersonal space centred on body parts (Colby et al., 1993; Fogassi et al., 1996; Graziano et al., 1997; Duhamel et al., 1998).

In close agreement with the monkey data, recent studies from our laboratory have provided the first evidence that the human brain forms integrated visual–tactile representations of the peripersonal space surrounding the hand (di Pellegrino et al., 1997a; Ladavas et al., 1998a) and the face (Ladavas et al., 1998b). In these studies, a cross-modal (visual–tactile) stimulation paradigm was used in right-brain-damaged patients with left tactile extinction. The term ‘extinction’ refers to a clinical sign whereby the patient is able to detect a single stimulus presented to the ipsi- or contra-lesional side of the body but fails to report the stimulus delivered to the contralesional affected side when it is presented with a concurrent stimulus on the ipsilesional side.

Although extinction phenomena have long been studied within different sensory modalities (vision, touch, audition and olfaction), they have also been demonstrated to occur between sensory modalities (Mattingley et al., 1997). Most interestingly, recent cross-modal studies in right-brain-damaged patients with tactile extinction have shown that visual stimuli presented near the patient’s ipsilesional hand (or cheek) produce very strong extinction of concurrent tactile stimuli delivered on the contralesional hand (or cheek). In contrast, visual stimuli presented far from the patient’s ipsilesional hand (or cheek) only mildly extinguish tactile stimuli delivered simultaneously on the contralesional side of the body (di Pellegrino et al., 1997a; Ladavas et al., 1998a, b; Farnè and Ladavas, 2000).

This pattern of results is what should be expected if an ipsilesional visual stimulus presented near the body were processed in an integrated visual–tactile system coding peripersonal space, like that described in monkeys. Due to this sensory integration, a visual stimulus presented near ipsilesional parts of the body would strongly activate the corresponding somatosensory representation of those body parts, thus extinguishing the contralesional tactile stimulation. On this account, the finding that cross-modal effects are mainly segregated in the space near the body has been taken as evidence of the existence of an integrated visual–tactile system responsible for coding visual peripersonal space in humans. Moreover, this integrated system appears to operate in body part-centred coordinates. When the patient’s hands are crossed along the midsagittal plane, tactile stimuli delivered to the left hand (in the right hemisphere) are extinguished by visual stimuli presented near the right hand (in the left hemisphere), showing that cross-modal effects remain anchored to the moved hand (di Pellegrino et al., 1997a).

However, the hands are moved continually in space and the brain has to compute their spatial position to update the visual mapping of space surrounding the hand as posture changes. The position of the hand in space can be computed by the joint contribution of at least two types of sensory information, i.e. vision and proprioception (Rossetti et al., 1995). In the monkey, visual and proprioceptive cues about arm position converge on bimodal visual–tactile neurones, some of which also respond to peripersonal visual stimuli when the monkey’s vision of the arm is prevented (Graziano et al., 1994). However, when information about arm position is provided by proprioception alone, the bimodal cells’ responsiveness to peripersonal visual stimuli is considerably reduced (Graziano, 1999) or even extinguished (MacKay and Craik, 1987), suggesting that visual information about a given body part might be more relevant than proprioceptive information.

In agreement with these neurophysiological data, a recent study conducted by Ladavas and colleagues on right-brain-damaged patients with tactile extinction showed that proprioception alone is not sufficient to activate the representation of the hand-centred visual peripersonal space (Ladavas et al., 2000). In this study, visual stimuli were presented near or far from the patient’s ipsilesional hand while unseen tactile stimuli were concurrently delivered to the patient’s contralesional hand. Vision of the ipsilesional hand was either allowed or impeded. When vision of the hand was prevented, the amount of cross-modal extinction did not vary as a function of the distance of the visual stimulus from the patient’s ipsilesional hand (i.e. near versus far). In other words, when hand position was specified only by proprioceptive cues, cross-modal extinction was not segregated in the peripersonal space. In contrast, when vision of the hand was allowed, tactile stimuli were more consistently extinguished by visual stimuli presented near to rather than far from the patient’s ipsilesional hand. These results demonstrate that the additional information provided by vision of the hand is necessary to obtain cross-modal effects segregated in the peripersonal space (Ladavas et al., 2000).

In the present study we investigated whether visual information about hand position in space, besides being necessary, can also be sufficient for mediating the integrated processing of visual–tactile input in the peripersonal space. Both animal and humans studies strongly support this hypothesis. In monkeys, some bimodal visual–tactile neurones in the ventral premotor area were shown to respond to visual stimuli presented near a seen fake arm while vision of the real arm was prevented (Graziano, 1999). In this study, the stuffed arm of a monkey, of the same species as the tested animal, was placed on a horizontal panel covering the animal’s real arm. The proximal end of the detached arm was not visible to the monkey and was aligned with the animal’s shoulder, whereas the distal part of the seen stuffed arm was either spatially aligned with the hidden monkey’s hand or orientated slightly to the left. The responses of the bimodal neurones were influenced by the seen position of the fake arm. That is, the neuronal response to visual stimuli presented near the stuffed arm varied according to its spatial orientation, showing that the visual RFs of bimodal cells remained anchored to the position of the seen arm even if the monkey’s real arm position did not change (Graziano, 1999).

In humans, vision dominates many aspects of sensory perception, whereas proprioception seems to be more
recessive, being overwhelmed by vision when discrepant information is provided. In some circumstances, the ‘visual bias of proprioception’ (Hay et al., 1965) can be strong enough to induce healthy subjects to perceive their hand in the position occupied by a seen rubber hand (Botvinick and Cohen, 1998; Pavani et al., 2000). Botvinick and Cohen demonstrated that, after subjects had looked at a rubber hand being stroked with a paintbrush while receiving a synchronous stroke on their own hidden hand, they experienced the illusion that tactile sensations came from the seen rubber hand, which they felt as belonging to themselves (Botvinick and Cohen, 1998). When required to indicate the felt position of their hidden hand they pointed towards the rubber hand position, showing that this illusion results from distorted proprioceptive information. Interestingly, Pavani and colleagues have shown that this illusory effect disappears when the rubber hands are seen by subjects in an implausible posture with respect to their own body, i.e. when they are not aligned with subjects’ shoulders (Pavani et al., 2000).

These findings suggest that the vision of a hand can largely dominate over proprioception when constructing a representation of the space near the body. Here we investigated the hypothesis that, despite incongruent proprioceptive information about the subject’s hand position in space, the vision of a rubber hand might mediate the activation of the corresponding representation of visual peripersonal space. We also predicted that this phenomenon should occur when the rubber hand is spatially aligned with the subject’s shoulder and that it should disappear under conditions of extreme conflict between the seen and felt positions of the hand.

To test these hypotheses, a group of right-brain-damaged patients with tactile extinction were tested in two experimental settings, using a cross-modal stimulation paradigm. In the first setting, visual stimuli were presented near or far from the patient’s ipsilesional hand, and in the second the visual stimuli were always presented far from the patient’s ipsilesional hand (which was placed behind the patient’s back) but near a rubber hand that could be visually aligned or misaligned with the patient’s ipsilesional shoulder. In both situations, unseen tactile stimuli were delivered on the patient’s contralesional hand.

According to our hypotheses, stronger cross-modal extinction was expected after presentation of visual stimuli near the patient’s real hand than far from it. Strong cross-modal extinction, similar to that induced by visual stimuli presented near the patient’s real hand, was also expected after stimulation of the rubber hand, but only when it was aligned with the patient’s shoulder.

**Method**

**Subjects**

A group of 10 consecutive neurological patients gave their informed consent to participation in the study. All patients were right-handed and had suffered a unilateral stroke in the right hemisphere, as confirmed by CT scanning. Nine patients had hemiplegia of the left arm, while one patient (R.L.) had only a mild left motor deficit. On clinical examination, the patients were alert and well oriented in time and space, and showed no sign of anosognosia or supernumerary limb phenomenon. Since the illusory perception of a phantom limb has been reported as a consequence of some right cerebral lesions (Halligan et al., 1993; Mazzoni et al., 1997), the absence of this delusion was ascertained. None of the patients complained about the felt or seen perception of a supernumerary limb, either spontaneously or after an explicit request. Before the experiment, each patient underwent a standard battery of tests for the assessment of neglect, including two cancellation tests (letters and bells), line bisection and two subtests taken from the BIT (Behavioural Inattention test) (Wilson et al., 1987): Picture Scanning and Menu Reading.

The presence of left unimodal extinction was assessed by using standard confrontation techniques. Visual extinction was tested by the experimenter moving one index finger in the left or right visual hemifield or in both hemifields simultaneously. Tactile extinction was tested by manually delivering brief, light touches on the dorsum of the patient’s left or right index finger or on both index fingers simultaneously. There were 20 trials of each type of stimulation (unilateral left, unilateral right and bilateral). Visual and tactile extinction were assumed to be present when a patient made significantly more contralesional omissions for bilateral than for unilateral stimuli, provided that omissions on single contralesional stimulation did not exceed 20% of trials.

At the time of testing, five patients showed signs of left visual neglect, while visual extinction was present in three patients; most importantly for the purpose of the present study, all patients showed left tactile extinction, and none of them had obvious somatosensory loss.

Details of the patients’ age and sex and additional clinical and neuroradiological information are provided in Table 1.

<table>
<thead>
<tr>
<th>Patient</th>
<th>Sex</th>
<th>Age (years)</th>
<th>Education (years)</th>
<th>Months after stroke</th>
<th>Lesion site*</th>
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<tbody>
<tr>
<td>R.L.</td>
<td>M</td>
<td>67</td>
<td>13</td>
<td>12</td>
<td>T, (P, O)</td>
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<tr>
<td>V.G.</td>
<td>M</td>
<td>64</td>
<td>5</td>
<td>7</td>
<td>F, T, P</td>
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<tr>
<td>B.L.</td>
<td>M</td>
<td>70</td>
<td>5</td>
<td>12</td>
<td>F, P, O</td>
</tr>
<tr>
<td>C.N.</td>
<td>M</td>
<td>64</td>
<td>5</td>
<td>12</td>
<td>F, P, BG, Ic</td>
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<tr>
<td>N.A.</td>
<td>M</td>
<td>55</td>
<td>5</td>
<td>8</td>
<td>Ic, BG</td>
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<tr>
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<td>M</td>
<td>47</td>
<td>11</td>
<td>21</td>
<td>F, T</td>
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<tr>
<td>D.M.A.</td>
<td>F</td>
<td>48</td>
<td>5</td>
<td>8</td>
<td>T, P</td>
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<tr>
<td>P.B.</td>
<td>F</td>
<td>62</td>
<td>8</td>
<td>19</td>
<td>F, P, Th</td>
</tr>
<tr>
<td>B.M.</td>
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<td>5</td>
<td>P, O</td>
</tr>
<tr>
<td>C.M.</td>
<td>F</td>
<td>60</td>
<td>12</td>
<td>5</td>
<td>F, P</td>
</tr>
</tbody>
</table>

*BG = basal ganglia; F = frontal; Ic = internal capsule; O = occipital; P = parietal; T = temporal; Th = thalamus. Cortical areas indicated in brackets for patient R.L. refer to a lesion following a vascular accident 10 years previously.
Rubber hand and visual–tactile extinction

Fig. 1 (A–E) The five experimental conditions (viewed from above) used in the study. Shaded areas represent the patient’s (P) and experimenter’s (E) body parts occluded from view. ‘Tactile’ and ‘visual’ refer to the type of stimulus applied by the experimenter to the patient’s right (R) and left (L) hand, according to the experimental conditions (see text for details).

Apparatus and procedure

Subjects sat at a table in front of the experimenter with the left hand resting palm-down on the table surface, in the left hemispace. Depending upon the experimental condition, each subject’s right hand was placed on the table top, in a symmetrical position with respect to the left hand and ~40 cm from it (conditions 1 and 2), or it was placed behind the subject’s back (conditions 3, 4 and 5). To prevent direct vision of the arms, the subject wore an apron made of white fabric, like a barber’s. They fixated a red dot, aligned with their midsagittal axis, marked on the table surface 35 cm from the front edge of the table (Fig. 1). At the beginning of each trial, the experimenter checked that the subject was gazing at the fixation dot.

When required, a life-sized aesthetic prosthesis of a right hand, wrist and forearm was placed on the table. This was a vivid, realistic three-dimensional rubber hand, whose feminine or masculine appearance varied according to subject’s sex (Fig. 2A and B).

A cardboard shield (width 20 cm, depth 40 cm, height 12 cm) prevented the subjects from viewing tactile stimuli delivered to their hands (Fig. 1A) or to their left hand only (Fig. 1B–E). Tactile stimulation was applied silently by means of a synthetic monofilament fibre, similar to a Frey hair, mounted on a plastic rod which was handled by the experimenter. At the beginning of each session, the tactile sensitivity of each subject’s left hand was assessed with a set of probe fibres of different diameters (0.4, 0.6 and 1 mm; 4 cm long), which exerted a pressure of 20, 45 and 95 g, respectively. For each subject, the diameter of the probe fibre for which there was a minimum of 80% of left single detections was chosen. This probe fibre was used in all experimental conditions. According to this criterion, subjects N.A. and C.M. were tested with a pair of 0.4 mm diameter...
fibres (20 g); subjects B.A. and D.M.A. were tested with a pair of 1 mm diameter fibres (95 g), and a pair of 0.6 mm diameter fibres (45 g) was employed for testing all the remaining subjects.

Tactile stimuli, both for sensitivity assessment and experimental testing, consisted of brief touches (<1 s) delivered on the dorsal aspect of the second phalanx of subject’s index finger. Visual stimuli consisted of rapid flexion–extension of the examiner’s index finger (~5 cm of excursion).

In each experimental condition, four types of stimulation were delivered: unilateral left or right stimulation, bilateral simultaneous stimulation, or no stimulation at all (catch trials). For each type of stimulation, 20 trials were performed according to a fixed random sequence. Each subject was tested twice (with an interval of ~1 week between sessions) in the following five conditions (Fig. 1), which were run at random in separate blocks. In the first condition, only unimodal tactile stimulation was given, whereas cross-modal visual–tactile stimulation was used in all remaining conditions.

In condition 1, both of the subject’s hands rested on the table surface and were covered by a cardboard shield. Tactile stimuli were delivered to the left, right or both index fingers simultaneously (Fig. 1A).

In condition 2 (peripersonal), both of the subject’s hands rested on the table surface, but only the left, contralesional hand was covered by the shield (Fig. 1B). Subjects saw their right hand and wrist protruding from under the edge of the white fabric of the apron. Tactile stimuli were delivered to the left hand, whereas visual stimuli were presented near the right hand, ~10 cm above the dorsal aspect of subject’s index finger.

Condition 3 (extrapersonal) was similar to condition 2, except that the right hand was placed behind the subject’s back. Tactile stimuli were delivered to the left hand covered by the shield, whereas visual stimuli were presented far from the right hand, in the same spatial position as in condition 2 (Fig. 1C).
Conditions 4 and 5 were similar to condition 3, with the exception that a prosthesis of the right hand was placed on
the table surface, as a rubber substitute for the subject’s right
hand. In condition 4 (visually compatible, VC), the rubber
hand had the same spatial location and orientation as the
subject’s real hand in condition 2, i.e. it was protruding from
under the white fabric and was symmetrically located with
respect to the subject’s left hand and forearm. In this condition
the rubber hand was aligned with the subject’s ipsilesional
shoulder, and its open end (near the elbow) was hidden by
the apron (Fig. 1D). In condition 5 (visually incompatible,
VI), the location of the rubber hand on the table top was the
same as in condition 4, but its orientation was orthogonal
with respect to the subject’s left hand. The rubber hand was
thus misaligned with respect to the subject’s ipsilesional
shoulder, and both the forearm and the open end of the
artificial arm (near the elbow) could be seen by the subject
(Fig. 1E). In conditions 4 and 5, tactile stimuli were delivered
to the left hand, which was covered by the shield, whereas
visual stimuli were presented near the rubber hand, ~10 cm
above the dorsal aspect of the index finger, in the same
spatial position as in condition 2.

The subjects were required to respond verbally to what
they felt (unimodal condition 1), or to what they felt or saw
(cross-modal conditions 2–5), by reporting the side of the
stimulation with the words ‘left’, ‘right’, ‘both’ or ‘none’,
regardless of the modality of the stimulus. To check for
confusion when using these verbal labels, subjects were also
required to accompany the verbal response by orienting their
head towards the left, right or both sides. In both conditions
involving vision of the rubber hand (conditions 4 and 5),
patients were asked whether they were aware of the fact that
the rubber hand was not their own, but a replica. They were
also asked to report the location of their own right hand.

Results

For each subject, responses to a total of 800 trials were
obtained across the two sessions, 40 per type of stimulation
in each condition. The patients’ performance on unilateral
left tactile stimulation was close to normal, confirming that
the tactile sensitivity of the contralesional hand was not
impaired. The percentage accuracy in unilateral left tactile
detection did not vary between unimodal condition 1 and
cross-modal conditions 2–5. Performance on unilateral right
stimulation, both tactile and visual, was without error. The
number of ‘false alarms’ in catch trials did not exceed 3%
of the total number of trials. All patients reported verbally
that the rubber hand was not their own, and they correctly
reported that their right hand was located behind their back.

Figure 3 shows group mean percentages of correct left
tactile detection as a function of the type of stimulation
delivered in experimental conditions. The subjects’ mean
accuracy percentages were transformed into arcsin values
and submitted to repeated measures ANOVA (analysis of
variance), with type of stimulation as the within-subjects
factor (unilateral and bilateral tactile stimulation; visual–
tactile stimulation within peripersonal and extrapersonal
space; and visual–tactile stimulation in visually compatible
and incompatible rubber hand position). The main factor,

type of stimulation, was highly significant \( F(5,45) = 28.82, \)
\( P < 0.0001 \) and it was further explored by using the
Newman–Keuls post hoc test. In this paper, cross-modal
effects mediated by vision of the real hand are presented
separately from cross-modal effects mediated by vision of
the rubber hand. A further section provides a statistical
comparison between the cross-modal effects mediated by the
real and rubber hands.

Patient’s hand

Left tactile stimuli were significantly more likely to be
reported in unilateral than in bilateral tactile trials [91% (SD = 8)
and 29% (SD = 16) accuracy, respectively, \( P < 0.0001 \), showing a consistent unimodal tactile extinction.

The patients’ ability to report a single tactile stimulus
on the left hand (91%) was reduced by the simultaneous
presentation of a visual stimulus near their right hand [41%
(SD = 18), \( P < 0.0001 \)] or far from it [74% (SD = 12),
\( P < 0.001 \)]. Crucially, the last two conditions differed
significantly (41 versus 74%, \( P < 0.0002 \)). In addition, cross-
modal extinction found in the near space (41% detection)
was not significantly different from unimodal tactile
extinction (29% detection). In contrast, the latter was
significantly different from the amount of cross-modal
extinction found in the far space (74% detection, \( P < 0.0001 \)).
Stronger cross-modal extinction in near than in far space
was shown by all patients, and the difference between these
conditions varied from 12.5 to 57.5%.

Rubber hand

The patients’ accuracy in reporting a single tactile stimulus
on their left hand (91%) was reduced by the simultaneous
presentation of a visual stimulus near the rubber hand, arranged in the VC [49% (SD = 13), \( P < 0.0001 \)] or VI orientation [71% (SD = 16), \( P < 0.001 \)]. However, patients showed stronger cross-modal extinction in the VC condition than in the VI condition (49 and 71%, respectively, \( P < 0.003 \)). This effect was present in all patients, and the difference between these two conditions ranged from 7.5 to 37.5%.

It is worth noting that the cross-modal extinction found both in the VC condition (49% detection) and in the VI condition (71% detection) was significantly less than unimodal tactile extinction (29% detection, \( P < 0.01 \) and \( P < 0.0001 \) for the two comparisons, respectively).

**Patient’s hand versus rubber hand**
The comparison between the amount of cross-modal extinction found for the real hand in the peripersonal condition and that found for the rubber hand in the VC condition did not reveal any significant difference (41 versus 49% detection). In contrast, when the rubber hand was in the VI condition, cross-modal extinction was significantly less than that obtained for the real hand in the peripersonal condition (71 versus 41%; \( P < 0.0002 \)). This effect was manifest in eight out of 10 patients, and the difference between these two conditions ranged from 17.5 to 72.5%. Moreover, the amount of cross-modal extinction found in the rubber hand VI condition was very similar to that obtained when the visual stimulus was presented far from the real hand (74 versus 71% detection).

**Discussion**
The present study provides the first evidence that the human brain can form visual representations of the peripersonal space of a non-owned body part, such as a rubber hand, as if it were a real hand. This claim is strongly supported by the pattern of distribution of cross-modal visual–tactile extinction found with the patient’s real hand and with its rubber substitute. In agreement with previous results from our laboratory (Ladavas et al., 1998a), a tactile stimulus delivered on the contralesional hand was more consistently extinguished by a concurrent visual stimulus presented near the patient’s ipsilesional hand than far from it. Although in some of our earlier studies (Ladavas et al., 1998a, 2000), and in more recent unpublished work from this laboratory, a few right-brain-damaged patients with tactile extinction did not show segregation of cross-modal extinction in the peripersonal space, it is interesting to note that in the present study this segregation was present in all subjects.

Moreover, strong cross-modal extinction was also found when patients who had their right hand placed behind their back were presented with a rubber hand that was spatially aligned with their shoulder and thus appeared in a plausible orientation relative to their body. In this VC condition, patients consistently failed to report a tactile stimulus delivered on their contralesional hand when a visual stimulus was presented simultaneously near the rubber hand. Interestingly, the amount of cross-modal extinction found in this condition was similar to that obtained when a visual stimulus was presented near the patient’s right hand.

In contrast, weak cross-modal extinction was found when a visual stimulus was presented either far from the patient’s real hand or near the rubber hand when the latter was not aligned with the subject’s shoulder and thus appeared in an implausible orientation with respect to their body. The amount of cross-modal extinction found in this VI condition was similar to that found in the condition in which the patient’s hand was visually stimulated outside the peripersonal space.

The cross-modal effects obtained by visually stimulating the real hand and the rubber hand will be discussed separately in the next two sections.

**Real hand**
The presence of strong cross-modal extinction in the space near the patient’s hand confirms the existence of a hand-centred visual peripersonal space in humans. The study of models of selective attention (Duncan, 1980; Duncan and Humphreys, 1989; Driver et al., 1997) has led to the suggestion that unimodal extinction reflects a difference in strength between competitive weights assigned to ipsi- and contralesional stimuli for access to limited attentional resources (di Pellegrino and De Renzi, 1995; Driver, 1998; Berti et al., 1999). In patients with extinction, the ipsilesional stimulus would benefit from a higher weight relative to the contralesional stimulus; as a result, when two simultaneous stimuli are engaged in competition, the contralesional stimulus will lose, appearing to be extinguished by the ipsilesional stimulus (Ward et al., 1994; di Pellegrino et al., 1997b).

The fact that cross-modal visual–tactile extinction is segregated mainly into the space near the hand can be explained by referring to the activity of an integrated visual–tactile system coding for peripersonal space, similar to that found in monkeys (Ladavas et al., 1998a, b; Farnè and Ladavas, 2000). Due to this peripersonal sensory integration, only visual stimuli presented near the ipsilesional hand would produce strong activation of its somatosensory representation. This strong representation would then win the competition with the weaker somatosensory representation of the contralesional hand, evoked by a simultaneous tactile stimulus, thus leading to stronger cross-modal extinction in the near hand in the far space. Remarkably, in the present study and in previous studies (di Pellegrino et al., 1997a; Ladavas et al., 1998a, b), we found that the degree of cross-modal extinction due to peripersonal visual stimulation is similar to the level of unimodal extinction induced by bilateral tactile stimulation. This suggests that a visual stimulus presented in the peripersonal space acts as if it were tactile.

A complementary competitive account that should be considered in discussing these findings is the integrated
Rubber hand

The present study makes an important step forward by showing that, in humans, visual–tactile sensory integration can occur in the peripersonal space of an artificial hand as if this hand were a personal belonging. When the rubber hand was spatially aligned with the patient’s shoulder, a visual stimulus presented close to the rubber hand induced powerful cross-modal extinction of a simultaneous contralesional tactile stimulus. In this VC condition, cross-modal effects were as robust as those found by visually stimulating the patient’s hand in the peripersonal space.

How can this phenomenon arise? In keeping with the hypothesis outlined in the introduction, we suggest that the integrated visual–tactile system, which is responsible for coding the hand-centred peripersonal space in humans, derives information about the spatial position of a hand (and its proximity to a visual stimulus) primarily through vision. When there is a conflict between vision and proprioception, the former dominates. Due to this dominance of vision over proprioception, a rubber hand appearing in a plausible posture relative to the subject’s shoulder can deceive the integrated visual–tactile system in such a way that a visual stimulus that is presented far from the patient’s real hand is processed as if it were in the peripersonal space. This dominance of visual cues about hand position in mediating cross-modal visual–tactile integration is in agreement with neurophysiological (MacKay and Crammond, 1987; Graziano et al., 1994; Graziano, 1999) and neuropsychological evidence (Ladavas et al., 2000).

Although prima facie this deception may seem surprising, it can be better conceived as the result of a normal adaptive process. Because the visual response of the monkey’s bimodal neurones does not change after repeated stimulation (Graziano et al., 1997), it has been suggested that the functional properties of these neurones are hard-wired and that the spatial correspondence between visual and tactile RFs can be calibrated through experience, perhaps within a critical period early in life (Salinas and Abbott, 1995; Graziano et al., 1997). In the case of hand-centred bimodal neurones, the obvious crucial experience through which spatial calibration is achieved consists of repeated exposure to visual stimuli approaching the hand, and vice versa. On almost all of these occasions, both the visual stimulus and the hand are under visual control, and the felt position of the hand is congruent with its seen position. Thus, the deception operated by a rubber hand seems to reflect a sort of impenetrability of the integrated visual–tactile system to discrepant information provided by proprioception. In Bayesian terms, proprioception will normally have little chance of being dissociated from vision.

However, the present results show that this impenetrability to proprioceptive information is not complete. Indeed, the amount of cross-modal extinction found in the rubber hand VC condition, although similar to that obtained with the patient’s hand, was less than the amount of unimodal extinction produced by bilateral tactile stimulation. Conversely, the latter did not differ from the cross-modal extinction produced by visual stimuli presented near the patient’s real hand. This result suggests that discrepant information provided by proprioception, with respect to the seen position of the rubber hand, could have played some role in the VC condition. The role played by proprioception becomes critical when visual and proprioceptive cues about hand position convey extremely discrepant information, which shows the extent to which visual information can be ‘accepted’ by the sensory integrating system. If the rubber hand appears in a spatial arrangement that is not plausible with respect to the current position of the subject’s body and shoulder (VI condition), the system is no longer deceived by the seen rubber hand, and the integrated processing of visual–tactile inputs in the peripersonal space is impeded. Cross-modal extinction was substantially reduced by presenting patients with the rubber hand located in the same spatial position but not aligned with the shoulder. Since the spatial arrangement was the critical difference between the VC and VI conditions, the possibility of visually attributing the rubber hand to the body seems to be a key factor leading to the integration of visual–tactile inputs in the peripersonal space. This attribution, however, might have occurred at an implicit level, as shown by the fact that the patients never reported explicitly false beliefs about belonging concerning the rubber hand.

The phenomenon of self-attribution of a rubber hand in the condition of intermodal visual–tactile matching is less rare than one might expect, even in healthy individuals. Recently, it has been shown to occur in normal subjects who were looking at touches delivered to a seen rubber hand while, at the same time, they were feeling touches on their hidden hand (Botvinick and Cohen, 1998). After a few minutes of adaptation to this procedure, the subjects’ responses to a questionnaire revealed that they experienced...
the illusion that the rubber hand was their own, and that they were feeling touches on the rubber hand. The connectionist model devised by these authors suggested that the illusion was made possible through a distortion of position sense. Interestingly, this model featured a layer of units whose properties were similar to those described above for bimodal neurones; that is, they responded to both tactile and visual inputs.

In a closely related study, Pavan and colleagues provided more objective evidence of illusory self-attribution of rubber hands (Pavan et al., 2000). They showed that normal subjects erroneously localized tactile stimuli, delivered to their hidden hands, on hand-shaped rubber gloves that were located above their hands. However, this ‘visual capture of touch’ depended critically upon the spatial orientation of the rubber gloves with respect to the subject’s body. Tactile stimuli were captured by the seen rubber gloves only if these were superimposed on the subject’s hands and aligned with their shoulders. When the rubber gloves were misaligned with respect to the subject’s shoulders, the tactile stimuli were no longer captured by the seen position of the gloves.

Indeed, vision of a body part seems to provide information that is crucial not only for deception but also for the enhancement of tactile sensitivity in normal subjects (Tipper et al., 1998) as well as in neurological patients (Ladavas et al., 1998a, 2000). By taking advantage of the rubber hand illusion, Rorden and colleagues showed that the impaired tactile sensitivity of a patient with hemisensory loss could be improved by attaching a light to the rubber hand (Rorden et al., 1999), thus extending knowledge about a phenomenon firstly reported by Halligan and collaborators (Halligan et al., 1996, 1997). Again, the patient’s tactile sensitivity was improved only when the rubber hand was superimposed and aligned with subject’s hidden hand.

The present results are in general agreement with these findings. The construction of a visual peripersonal space relative to a rubber hand, as revealed through cross-modal extinction, seems to be tightly bound to the spatial orientation of the rubber hand. However, it is important to emphasize that, in our study, the visually compatible and incompatible arrangements of the rubber hand were both completely incongruent with respect to the real position of the patient’s right hand. In both cases, this hand was located behind the patient’s back. This means that, in the phenomenon we found, vision of a hand largely dominates over proprioception.

In fact, it is widely accepted that our sensory experience is dominated by vision (for review, see Posner et al., 1976). This is particularly true of senses with low spatial resolution, such as proprioception, haptic exploration and kinaesthesia (Rock and Victor, 1964; Hay et al., 1965; Dassonville, 1995). Visual information invariably seems to overwhelm proprioception, even when there is a large amount of conflict (Warren and Cleaves, 1971; Mon-Williams et al., 1997). In normal subjects, visually displacing the position of the hand in space by the use of prisms affects hand localization (Rossetti et al., 1995) as well as the felt position of the limb (Welch et al., 1979; Shimojo, 1987). In these situations of visual–proprioceptive conflict, people report that they feel their hand where they see it, suggesting that vision provides a primary input for somatosensory perception (Mon-Williams et al., 1997). While the natural drift of proprioception can be stopped by a brief glimpse of the limb (Wann and Ibrahim, 1992), the spatial resolution of position sense is even lower when a limb is kept passively in a constant position, especially when posture is non-optimal (Paillard and Brouchon, 1968; Rossetti et al., 1994), as was the case in the present study.

Given the recessive nature of proprioception and the fact that, on most occasions, vision and proprioception convey congruent information, it is conceivable that the seen position of the rubber hand could have attracted the felt position of the patient’s hand, but only in the visually compatible condition.

In conclusion, the present study considerably extends the notion of visual dominance over proprioception by showing that vision largely replaces proprioception in representing the visual peripersonal space of a rubber hand. We have demonstrated that in humans, as in monkeys (Graziano, 1999), a seen fake hand can deceive the integrated visual–tactile system coding peripersonal space and appear as a real hand. These findings strongly support the idea that the visual peripersonal space represented in the human brain is in many ways similar to that described in monkeys. It would be of great interest to verify whether, in monkeys, the visual responses of bimodal neurones are reduced when a seen fake arm is no longer visually attributable to the monkey’s body, as suggested by the results of the present study.

Acknowledgements

We thank all the subjects for their collaboration. We also thank Jon Driver for helpful comments on an earlier version of the manuscript and Francesca Frassinetti for her assistance in reading CT scans. The aesthetic prostheses were kindly provided by the Officine Ortopediche Rizzoli, Bologna. This work was supported by grants from MURST and CNR.

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Rubber hand and visual–tactile extinction 2359


Received February 7, 2000. Revised June 19, 2000. Accepted July 4, 2000