THE ROYAL SOCIETY
FirstCite® e-publishing

Received 1 January 2003
Accepted 29 January 2003
Published online

Projecting sensations to external objects: evidence from skin conductance response

K. Carrie Armel* **and V. S. Ramachandran**

Brain and Perception Laboratory, Psychology Department, University of California at San Diego, La Jolla, CA 92093-0109, USA

Subjects perceived touch sensations as arising from a table (or a rubber hand) when both the table (or the rubber hand) and their own real hand were repeatedly tapped and stroked in synchrony with the real hand hidden from view. If the table or rubber hand was then 'injured', subjects displayed a strong skin conductance response (SCR) even though nothing was done to the real hand. Sensations could even be projected to anatomically impossible locations. The illusion was much less vivid, as indicated by subjective reports and SCR, if the real hand was simultaneously visible during stroking, or if the real hand was hidden but touched asynchronously. The fact that the illusion could be significantly diminished when the real hand was simultaneously visible suggests that the illusion and associated SCRs were due to perceptual assimilation of the table (or rubber hand) into one's body image rather than associative conditioning. These experiments demonstrate the malleability of body image and the brain's remarkable capacity for detecting statistical correlations in the sensory input.

Keywords: body image; skin conductance response; hand illusion; table illusion; logic of perception; phantom limbs

1. INTRODUCTION

There is a sense in which one's body image is itself a 'phantom': one that the brain constructs for utility and convenience. A striking illustration comes from studies of amputees who experience phantom limbs. We had patients insert their 'good arm' and phantom arm through two holes in the front of a 'virtual reality box'. The roof of the box was removed and inside a vertical mirror divided the holes in the sagittal plane. The patients viewed the reflection of their intact hand in the mirror, thus creating the illusion of observing two hands. Several subjects viewing the reflection while the intact arm was touched reported feeling the touch on the phantom limb (Ramachandran *et al.* 1995).

Studies on intact individuals also illustrate the importance of visual feedback in constructing body image and localizing body parts. Tastevin (1937) showed that people mistook a plastic finger extending beyond a cloth as their own when the latter was concealed several centimetres away. In another study, subjects compensated for manual errors performed by a hand mistaken to be their own (Nielson 1963). Welch (1972) suggested that this misidentification is cognitively impenetrable. He demonstrated that even when subjects knew they were viewing an experimenter's finger, rather than their own adjacent occluded finger, they felt as though the former was their own.

The usual explanation for these findings is that vision has higher reliability and spatial acuity than proprioception, so the brain gives more weight to visual information. Thus, people localize a body part to its apparent visual location, particularly when the visible location falls within the possible range dictated by proprioception. Although this theory has not been carefully tested, some support for it lies in the fact that placing the fake hand perpendicular to the subject's real, occluded hand does seem to destroy the illusion that a fake hand is one's own. This has been documented in intact (Pavani *et al.* 2000) and brain-damaged people (Farne *et al.* 2000), and suggested by neurophysiological recordings in monkeys (Graziano 1999).

This paper is concerned with two closely related illusions that were reported recently. In the first one, a fake hand is placed on the table. The subject sits next to it and places his own corresponding hand (say his right hand) next to it. A vertical partition is then placed on the table in between the real and fake hands so that the subject's view of his real hand is occluded but he can see the fake hand. While the subject looks at the fake hand, the experimenter applies a long sequence of randomly placed strokes and taps on it while at the same time the hidden real hand is stroked and tapped in synchrony (Botvinick & Cohen 1998). The subject then experiences the uncanny illusion that the touch sensations are actually felt in the spatial location of the dummy hand—not from the hidden real hand! The authors interpret this as an example of the brain's tolerance for discrepancy between vision and proprioception, with vision dominating in most situations (Rock & Victor 1964; Ramachandran & Rogers-Ramachandran 1996).

The second effect, which was observed in our laboratory (Ramachandran *et al.* 1998), is even more surprising. The subject's real hand is hidden by a partition as in the previous experiment. However, instead of using a dummy hand, we simply stroked and tapped the table in precise synchrony for about a minute. To our astonishment, subjects often reported sensations arising from the table surface, despite the fact that it bears no visual resemblance to a hand. Whereas Botvinick & Cohen (1998) interpret their results in terms of resolving incongruities between visual versus proprioceptive location of the hand, our table

* Author for correspondence (carrie@ucsd.edu).

experiment would lead us to argue that the illusion arises mainly from the 'Bayesian logic' of all perception; the brain's remarkable ability to detect statistical correlations in sensory inputs in constructing useful perceptual representations of the world—including one's body. It is especially intriguing that this bizarre perceptual representation (assimilating the table into one's body image) is so resistant to 'top-down' knowledge of the absurdity of the situation.

The main questions we set out to answer are: in what sense does the subject really incorporate the table or fake hand into his body image? What are the limits of this ability? How much incongruity of appearance can be tolerated? Does distance matter? If you looked through a telescope at the moon and used an optical trick to stroke and touch it in synchrony with your hand, would you 'project' the sensations to the moon?

To measure the extent to which subjects incorporated the external objects into their body image, they rated the vividness of the illusion. We also recorded skin conductance response (SCR), a physiological measure of psychological and autonomic arousal. This provided an objective test of whether the table had indeed become informationally 'coupled' with subjects' body image, or whether subjects were simply being metaphorical or responding to task demands when they reported the table or fake hand felt like their own. If the external objects became integrated into their body image, would they be aroused when the table or fake hand was 'injured', in the same way that anticipation of bodily harm to oneself produces arousal? Finally, variations in the control conditions were used to test whether this arousal could be attributed merely to associative conditioning (a type of learning where one stimulus comes to predict the occurrence of another through repeated pairings).

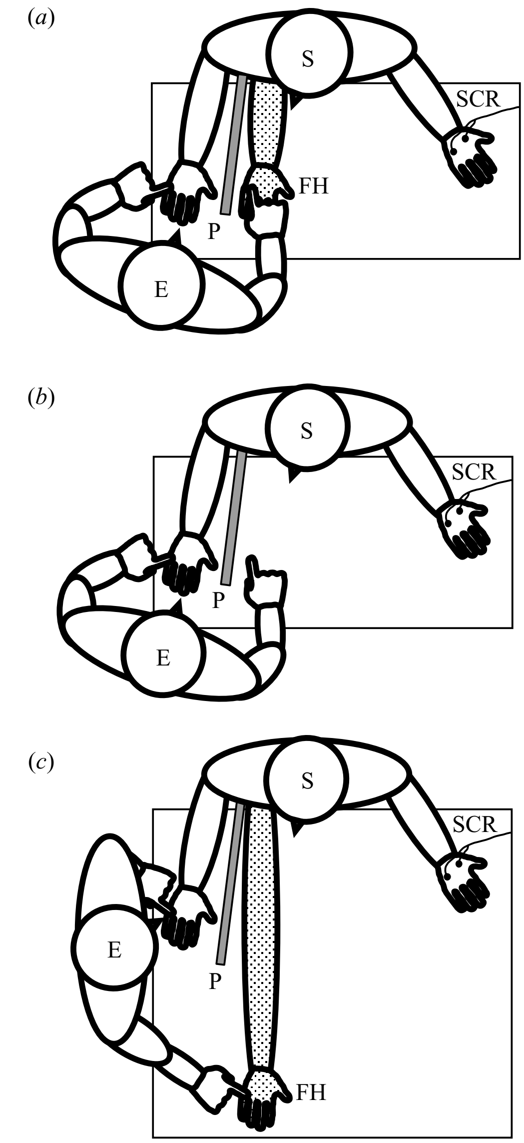

Figure 1. The conditions (viewed from above). In all experiments, subjects received the fake hand condition (*a*). In experiment 2 (form manipulation), subjects also received the table condition (*b*). In experiment 3 (location manipulation), subjects received the distant hand condition (*c*) rather than the table condition. Abbreviations: E, experimenter; S, subject; P, partition; FH, fake hand; SCR, SCR electrodes.

2. METHOD

(a) *Participants*

University of California at San Diego undergraduates were recruited from the Psychology Department human subjects pool and were given class credit for their participation. They were naive about the purpose of the experiment. Different subjects were tested in each experiment. Sixteen participated in experiment 1, and 24 in experiments 2 and 3. The age of the subjects ranged from 18 to 23 years (mean of 20.2 years; s.d. = 1.8).

(b) *Procedure*

Subjects sat upright at a table with a 40 cm × 60 cm sagittal partition extending from their right collar-bone onto the table. The subject's right arm lay palm face down on the right side of the partition, and a rubber right hand and a fake 'arm' (created from a folded sheet of cloth that was the length of the subject's arm) occupied the left side of the partition (depicted in figure 1*a*). This set-up occluded the subject's real right hand and arm from view, while allowing the subject to view the fake hand in a position similar to their real hand. To minimize any contribution the subject's real left hand could have on the illusion, it was located on the table palm face up, *ca*. 60 degrees to the left of the subject's torso. Subjects watched continuously as the fingers of the fake hand and hidden real hand were simultaneously stroked, tapped and lifted in synchrony.

Pilot work showed that after 2.5 min of such stimulation subjects reported a compelling illusion of the tactile and proprioceptive sensation emerging from the fake hand rather than from their own hidden hand. We then carried out experiments to answer three questions.

(i) Experiment 1: if a finger of the fake hand is bent backwards to seem painful, does the subject register an SCR? In other words, to what extent is the hand assimilated into the subject's body image? To address this, after *ca*. 2.5 min of the touching procedure, both the real and fake fingers were lifted, but only the fake finger was bent into a 'painful' position. SCR was recorded at this point, and after several seconds a free response description of the experience and an intensity rating of the vividness of the illusion were obtained.

(ii) Experiment 2: would subjects still experience the illusion if the form of the external object was manipulated? To explore this, a barren table was stroked and tapped in the same manner and in the same relative locations as the real hand (depicted in figure 1*b*). Before beginning the stroking, band-aids were placed on both the real hand and the table, and subjects were told that the band-aid would be pulled off the table but not off their real hand. At the end of the 2.5 min touching period, in lieu of pulling back a fake finger, the band-aid was pulled partly off of the table. This 'table' condition was preceded by one in which a fake hand, rather than a table, was touched (as in experiment 1).

(iii) Experiment 3: would subjects still experience the illusion if the location of the external object was manipulated? Each subject viewed touch to a fake hand in a 'realistic' location in one condition, and then to a distant fake hand in another (depicted in figure 1*c*). The fake arm was extended 3 feet (0.91 m), so that it lay 3 feet (0.91 m) beyond the real hand. In the distant fake hand manipulation, a fake finger was bent back for the painful stimulus, as in experiment 1.

(c) *Design and control conditions*

In experiment 1, each subject received the fake hand condition and its control condition, which were counterbalanced across subjects (illustrated in figure 2*a*). In experiment 2, subjects then received the table condition and its control, which were also counterbalanced across subjects. Thus, each subject received all four conditions, in one of four possible orders, as illustrated in figure 2*b*. A similar design was used in experiment 3, as seen in figure 2*c*, except that instead of receiving the table conditions they received the distant fake hand conditions.

The control conditions were identical to the experimental conditions except for one manipulation that diminished the vividness of the illusion. The control conditions were as follows.

(i) Control experiment 1. We refer to the control condition for experiment one as the delayed synchrony condition. Here, touch to the real hand was identical to that on the fake hand, but touch to the real hand occurred *ca.* 1 s after the touch occurred on the fake hand.

(ii) Control experiment 2. In the control condition for experiment two, the real hand was made visible by removing the partition that occluded the real hand. Subjects were instructed to look back and forth between the real hand and the fake hand, or table, *ca.* every 5 s (this timing was briefly practised before the experiment began). Furthermore, the real and fake hand (or real hand and location where the table was touched) were close enough together so that they could be seen simultaneously even while looking at one or the other. The fake finger was bent back or band-aid pulled, while the subject viewed the fake hand or table. To ensure the subject was only attending to this external object, the experimenter occluded the subject's real finger at this time (with the experimenter's hand, which was already holding the subject's real finger).

(iii) Control experiment 3. In the control condition for experiment three, touch applied to the fake and real hands was asynchronous. That is, touch to each was random and there was no correlation between the two sequences.

The main purpose of the control conditions was to allow us to compare SCRs due primarily to surprise with those due to the real anticipation of pain. If subjects exhibit SCRs to *any* surprising event, we would have expected arousal due to surprise in both the experimental conditions and control conditions. However, if subjects genuinely assimilated the fake hand into their body image in the experimental condition, they should

(*a*)

	condition		condition
order A		order B	
fake hand	1. synchronous	fake hand	1. delayed synchronous
	2. delayed synchronous		2. synchronous

(*b*)

	condition		condition
order A		order B	
fake hand	1. real hidden	fake hand	1. real visible
	2. real visible		2. real hidden
table	3. real hidden	table	3. real hidden
	4. real visible		4. real visible
order C		order D	
fake hand	1. real hidden	fake hand	1. real visible
	2. real visible		2. real hidden
table	3. real visible	table	3. real visible
	4. real hidden		4. real hidden

(*c*)

	condition		condition
order A		order B	
fake hand	1. synchronous	fake hand	1. asynchronous
	2. asynchronous		2. synchronous
distant fake hand	3. synchronous	distant fake hand	3. synchronous
	4. asynchronous		4. asynchronous
order C		order D	
fake hand	1. synchronous	fake hand	1. asynchronous
	2. asynchronous		2. synchronous
distant fake hand	3. asynchronous	distant fake hand	3. asynchronous
	4. synchronous		4. synchronous

Figure 2. Experimental design for all experiments. (*a*) In experiment 1, basic hand illusion, subjects watched a fake hand as it was touched in synchrony with their real, hidden hand. This condition was counterbalanced with a control in which touch on the real hand was identical to touch on the fake hand, but touch on the real hand was delayed by *ca.* 1 s. Each subject received both conditions. (*b*) In experiment 2, form manipulated, subjects watched a fake hand as it was touched in synchrony with their real, hidden hand. This condition was counterbalanced with a control condition in which the real hand was visible. Next, subjects watched the table as it was touched in synchrony with their real, hidden hand. This table condition was also counterbalanced with a control in which the real hand was visible. Each subject received all four conditions, in one of four possible orders, as indicated by the quadrants above. (*c*) In experiment 3, location manipulated, subjects watched a fake hand as it was touched in synchrony with their real, hidden hand. This condition was counterbalanced with a control condition in which the hands were touched asynchronously. Next, the fake arm was extended so that the fake hand lay 3 feet (0.91 m) beyond the real hand. Subjects watched the distant fake hand as it was touched in synchrony with their real, hidden hand. This condition was counterbalanced with a control in which the real and fake hands were touched asynchronously. As above, each subject received all four conditions.

Table 1. Means and standard errors of the means for intensity ratings (1–10) and SCRs (log (microsiemens + 1)) for all experiments.
(Intensity ratings: 1, the fake hand felt nothing like one's own; 10, the fake hand felt exactly like one's own.)

condition	mean intensity (s.e.m.)	mean SCR (s.e.m.)
experiment 1: basic hand illusion (delayed synchrony control)		
fake hand	7.75 (0.29)	0.39 (0.07)
fake hand control	2.05 (0.33)	0.18 (0.05)
experiment 2: form manipulated (real hand visible control)		
fake hand	7.35 (0.44)	0.34 (0.05)
fake hand control	4.19 (0.61)	0.24 (0.05)
table	4.38 (0.56)	0.24 (0.05)
table control	3.02 (0.53)	0.11 (0.04)
experiment 3: location manipulated (asynchronous control)		
fake hand	7.69 (0.30)	0.45 (0.06)
fake hand control	2.58 (0.39)	0.26 (0.05)
distant fake hand	5.75 (0.49)	0.35 (0.06)
distant fake hand control	1.75 (0.32)	0.21 (0.05)

exhibit larger SCRs from anticipating personal injury in this condition. Furthermore, to minimize surprise SCRs, subjects were shown the injurious actions before beginning the experiment and were assured that these would not be performed on their real hand.

Two of the control conditions allowed us determine whether associative conditioning could account for subjects' arousal when the fake hand was injured. The logic was as follows: if the arousal was due to associative conditioning, then in experiment two subjects should have had equally large SCRs when the partition was removed compared with when it was present. Pairing the seen and felt touch alone would be sufficient for associative conditioning to occur, and viewing or not viewing the real hand is irrelevant. If viewing their real hand were to diminish subjects' arousal, then we could conclude the arousal was genuinely due to assimilation of the hand (or table) into the subjects' body image. Experiment one also tested the associative conditioning hypothesis. That is, given that conditioning can occur with a lag of up to 1 s between stimuli (e.g. Manns *et al.* 2000), and that touch to the real hand was delayed by *ca.* 1 s, SCR in this control condition should have been as large as with the synchronous touch if the illusion was merely due to associative conditioning.

(d) *Measures*

(i) *Self-report*

After each condition, free response descriptions of the experience and an intensity rating were obtained to determine the degree to which subjects identified with the fake hand. Intensity ratings were elicited with the request: 'please rate how much the rubber hand felt like your own on a scale of 1–10, with a 1 meaning the hand felt nothing like your hand and a 10 meaning it felt exactly like your own'.

(ii) *SCR*

We wanted to ensure that subjects were not just being metaphorical or responding to task demands when they said, 'the rubber hand felt like my own'. Because the anticipation of pain produces autonomic nervous system (ANS) arousal, we measured identification with the fake hands by recording autonomic responses to the fake hands being harmed. SCR was used as the measure of ANS arousal because it is not easily prone to movement artefacts, and of the physiological measures it is the best predictor of psychological arousal (Lang *et al.* 1993). Also, subjects cannot voluntarily control their SCRs so the SCR results (unlike self-reports of emotional arousal) cannot be 'faked' or be the result of task demands.

SCR was recorded with Ag–AgCl electrodes from the thenar and hypothenar eminences of the left hand. Data were recorded through Biopac's MP100 acquisition unit, and analysed with their AcqKnowledge v. 3.4.1 software. SCRs were quantified in the following manner: the amplitude of the largest SCR greater than 0.03 microsiemens that occurred 1–5 s from injury to the fake hand or table was scored as a response to that stimulus. Following standards set by Venables & Christie (1980), SCR magnitudes were recorded, meaning that SCR amplitudes of zero were included in analyses. Based on their pre-established criteria, subjects who exhibited SCR magnitudes of zero to all stimuli were classified as SCR non-responders and were excluded from analyses.

(iii) *Additional measures*

To determine whether identification with the fake hand could produce a misperception of body location, we used a protractor to measure the actual and perceived magnitude that the real finger was bent back in the fake hand condition in 13 subjects.

To quantify the illusion's tolerance for visual inconsistencies (in addition to performing the form and location manipulations), we determined whether there were correlations between subjects' intensity ratings for the fake hand condition and their skin tone or hand size. We compared the skin tone of 15 subjects to that of the fake hand by rating tones on a scale of seven flesh-coloured swatches. For hand size, we measured circumference at the widest part of the hand.

3. RESULTS

(a) *Free response*

The illusion was very vivid for many subjects as evidenced by remarks such as, 'wow', 'that was bizarre' or 'oh my God!' Some subjects reported that the illusion was so convincing that they found themselves wondering why their hand was so white or how they had bruised their hand (there was a small ink smudge on the fake hand). Furthermore, during pilot work many subjects behaved as if they anticipated pain when the rubber finger was bent back: they laughed nervously, widely opened their eyes,

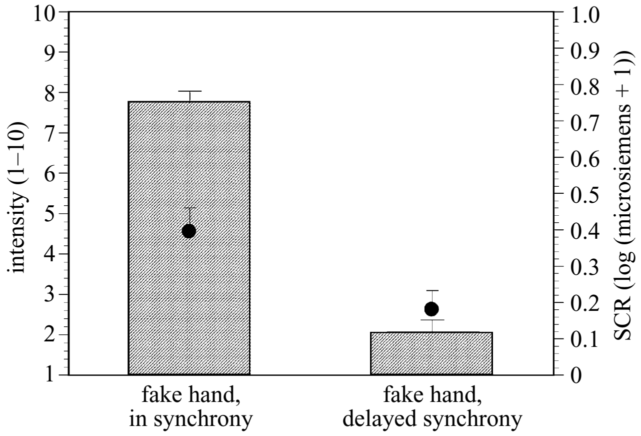

Figure 3. Intensity ratings (grey bars) and SCRs (black circles) for experiment 1, in which synchronous touch to the real hand was delayed by 1 s in the control condition. Error bars represent one standard error of the mean. Intensity ratings: 1, the fake hand felt nothing like one's own; 10, it felt exactly like one's own.

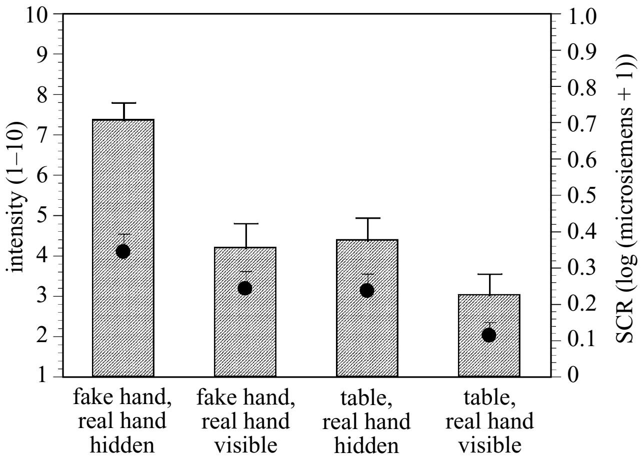

Figure 4. Intensity ratings (grey bars) and SCRs (black circles) for experiment 2, in which form of the hand was manipulated. Error bars represent one standard error of the mean.

flinched, and even pulled their real hand away from the experimenter (sufficient instruction prevented subject noise and movement during the experiments reported here). Two out of 120 study and pilot subjects even reported *feeling* pain when the fake finger was bent back.

(b) *Intensity ratings and SCR*

Mean intensity ratings and SCRs for the three experiments can be viewed in table 1. Figures 3–5 illustrate that, according to both intensity and SCR measures, subjects identified with the rubber hand or table more in the experimental than in the control conditions. This conclusion was supported statistically with planned two-tailed *t*-tests. Two subjects out of the 66 recruited were classified as non-responders and excluded from analyses.

(i) *Experiment 1: delayed synchrony control*

Mean intensity and mean SCRs are presented in figure 3. It can be seen that subjects identified with the fake hand

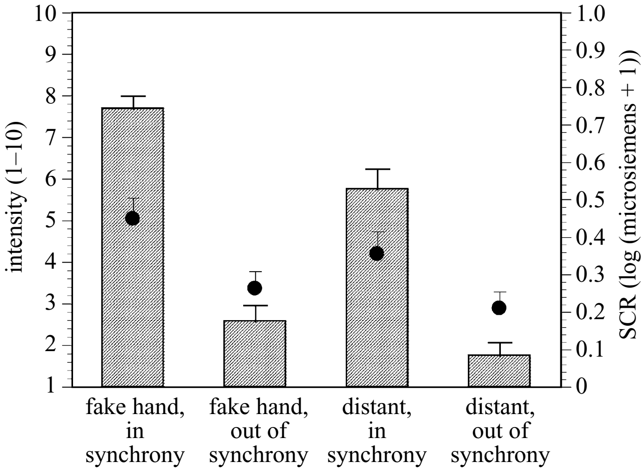

Figure 5. Intensity ratings (grey bars) and SCRs (black circles) for experiment 3, in which location was manipulated. Error bars represent one standard error of the mean.

more in the conditions when touch was synchronized compared with when it was synchronized but delayed. Comparisons were significant for both intensity ratings ($t_{10} = 11.25$, $p < 0.0001$)[1] and SCR ($t_{15} = 4.29$, $p < 0.001$).

(ii) *Experiment 2: form*

Mean intensity and SCRs are presented in figure 4. In a comparison of the fake hand condition and its control in which the partition was removed, both intensity ratings ($t_{20} = 5.11$, $p < 0.0001$) and SCR ($t_{23} = 2.61$, $p < 0.05$) were significantly different. In a comparison of the conditions in which the table and real hand were touched with the partition in place or removed, intensity ratings ($t_{23} = 3.21$, $p < 0.005$) and SCR ($t_{23} = 2.20$, $p < 0.05$) were also significantly different. It may be noted that the fake hand condition was significantly more effective at inducing the illusion than the table (both conditions with the partition) when measured by intensity ratings ($t_{23} = 4.22$, $p < 0.001$), but only marginally so for SCR ($t_{23} = 2.07$, $p = 0.05$).

(iii) *Experiment 3: location*

Mean intensity and mean SCRs are presented in figure 5. It can be seen that subjects identified with the fake hand and the distant fake hand, as measured by both self-report and SCR, more in the conditions when touch was synchronized than when not synchronized. This was statistically supported in a comparison of the fake hand and its control condition for both intensity ratings ($t_{19} = 9.95$, $p < 0.0001$) and SCR ($t_{23} = 3.62$, $p < 0.01$). In a comparison of the synchronous and asynchronous distant fake hand conditions, intensity ratings ($t_{23} = 9.64$, $p < 0.0001$) and SCR ($t_{23} = 2.20$, $p < 0.05$) were also significantly different. However, the 'anatomically correct' fake hand condition was significantly more effective than the distant fake hand condition (both conditions with synchronous touch), for intensity ratings ($t_{23} = 3.63$, $p < 0.01$), but not for SCR ($t_{23} = 1.31$, n.s.).

(c) *Additional measures*

The illusion's vividness was also demonstrated by the fact that subjects felt that their real finger was bent farther back than in reality while they were viewing the bent fake finger (at the end of the fake hand condition). The fake finger was bent back *ca*. 90°, the real finger bent back *ca*. 18.8° (s.d. = 4.2), but it was perceived that the real finger was bent back *ca*. 40.8 degrees (s.d. = 19.3). The difference between the actual and perceived magnitude of bending was significant ($t_{12} = 4.12$, $p < 0.01$).

Additional support for the illusion's resistance to visual discrepancies includes its insensitivity to skin tone, hand size, and whether subjects had distinguishing characteristics not present on the fake hand. Subjects vividly experienced the illusion (intensity rating mean of 7.8) even though their skin tone (mean of 4; s.d. = 1.3) compared with the rubber hand (skin tone of 2) was significantly darker ($t_{14} = 5.68$, $p < 0.0001$). Furthermore, skin tone did not correlate with intensity of the illusion ($r_{14} = -0.142$, $p = 0.62$). Size also had little effect: circumference of the subjects' hands did not correlate with intensity of the illusion ($r_{14} = -0.318$, $p = 0.25$), and subjects experienced the illusion vividly (mean of 7.8) even though circumference of the fake hand (23.0 cm) compared with the subjects' real hands (mean of 21.29 cm, s.d. = 1.81 cm) was 2 cm larger on average: a significant difference ($t_{14} = 2.71$, $p < 0.05$). In fact, subjects with the smallest hands (18.0 cm long × 17.5 cm wide and 20.0 cm × 17.0 cm) perceived the illusion very vividly (7.5 and 8 intensity ratings, respectively). The illusion also seemed resistant to other visual inconsistencies: for instance, subjects who had warts or who wore nail polish experienced it.

(d) *Phenomenological observations*

The illusion is surprisingly insensitive to discrepancies in visual appearance between the hand and the external objects. By contrast, the precise synchrony between seen and felt touch, and the precise nature of the seen and felt touch, had a strong effect on the illusion's vividness. Subjects reported that the more random and unpredictable the touch (if synchronized), the more vivid the illusion. Also, proprioceptive stimulation seemed particularly effective given many subjects spontaneously reported that having their fingers lifted and knuckles pushed was extremely effective in enhancing the illusion, while stroking of the fingers was less effective.

Also critical was consistency in the precise nature of the seen and felt touch. That is, discrepant types of touch information (touch to a hairy versus smooth hand, touch to the skin versus wood of a table) diminished the illusion. Four subjects with particularly hairy hands, out of 120 study and pilot subjects, spontaneously reported that the illusion was ruined when their hand was touched in areas of high hair density. Given the robustness of the illusion to visual inconsistencies, it is possible that under these circumstances it was actually a mismatch in the expected (from visual information) versus felt *type* of touch, rather than just the visual inconsistencies of hair versus no hair, that diminished the illusion. That is, somatic sensation from areas of high and low hair density feels different, and so subjects experienced a discrepancy between the expected sensation from touch to the smooth fake hand and the experienced one from their own hairy hand. Similarly, subjects frequently reported that the table illusion was vivid when the touch was received through a common covering—the band-aids—but weak in its absence. In the latter case there may have been a discrepancy between the expected sensation from viewing touch to the hard table and the actual sensation of touch to soft flesh. It would be interesting to determine if the illusion becomes more vivid if a rubber sheet, which is soft and pliable (and feels 'skin-like'), is touched in place of a table.

Subjects were asked about specific sensations in the table and distant fake hand manipulations. Upon questioning regarding the latter, five out of five subjects reported that the hand felt dislocated or at a distance from them, and not as though it had lengthened. Upon questioning five subjects in the table experiment, four reported that the 'image' of the hand on the table felt well delineated, while one reported that the borders of the perceived hand felt diffuse. Two out of the five reported that the 'invisible' hand seemed to be above the table, two reported that the hand felt flat on the table (or under the table but pressed flat against it), and one reported that his hand seemed to be below the table with substantial depth.

Subjects also reported other odd sensations, and these were much more frequently reported in the experimental than in the control conditions. Specifically, subjects commonly reported coldness, numbness ('like novocaine'), tingling, or tickling in their hand, as well as feeling that things were 'confusing', 'in a state of chaos' or 'did not make sense'. It is possible that these peculiar sensations arise when the brain tries to integrate contradictory sensory information. Five subjects in the study also reported odd body location sensations, such as having two right hands or sensing the rubber hand (which was assimilated into their body image) moving.

4. DISCUSSION

What is most surprising about this illusion is that a lifetime of experience should be negated by just a few minutes of the right kind of sensory stimulation. One's body image, despite its appearance of durability, is a transitory internal construct that can be easily and profoundly modified. Subjects on average rated the vividness of the fake hand feeling like their own as a 7.6 on a scale where a 10 indicated it felt exactly like their real hand—and the ratings were significantly higher than in the comparable control conditions for all three experiments. Even more convincing is the fact that subjects rated the touch sensations in the table and distant hand conditions as significantly more intense than in their respective control conditions.

How can we be sure that the subjects were not simply being metaphorical or responding to task demands, when they said 'it feels like the fake hand/table is my hand'? Subjects got SCRs, which cannot be voluntarily controlled, in all three experiments when the fake hand or table were injured, and they got significantly larger ones in the experimental conditions. This suggests that the fake hand had become assimilated into subjects' own body images. The consistency between intensity ratings and SCRs suggests the former were not simply due to task demands, and that subjects meant it when they said the hand or table felt like their own (given SCR is not under volitional control). Furthermore, when subjects identified with the fake hand, they estimated that their real finger was bent into a position between that of their real and the fake finger, suggesting the visual information from the fake hand affected their own body image. Finally, subjects were naive in that (i) they were debriefed only at the end of the experiment; (ii) free-response self-reports were obtained before the first ratings for 'how intensely does the hand feel like your own' (these self-reported sensations were very vivid and subjects usually conveyed surprise); and (iii) intensity ratings were obtained only after the subject received the experimental fake hand condition (in which the hand felt like the subject's own), so as to not bias subjects' interpretations while experiencing this condition.

(a) *Underlying mechanism*

We suggest that the principle underlying this illusion is Bayesian perceptual learning—that two perceptions from different modalities are 'bound' when they co-occur with a high probability. In the hand illusion, the seen and felt touch were bound because of their temporal synchrony. This differs from Botvinick & Cohen's (1998) explanation that the illusion mainly represents tolerance to discrepancies between the seen and felt position of the hand.

The brain's remarkable capacity for extracting statistical correlations in sensory input is most apparent in the table condition. In the hand experiments, given the visual similarity between the fake and real hand, it is not unreasonable for the brain to tolerate some level of discrepancy between the felt position of the hand and its apparent visual location. (Indeed, Graziano (1999) has shown specific cells in the macaque to be responsive to the visual appearance of both a monkey's real hand and a proximate fake one.) This argument, however, is difficult to apply to the case of the table; indeed, we would argue that the assimilation of the table into the body image is dictated exclusively by the Bayesian logic underlying all perception; in this case the brain's tendency to take advantage of statistical correlations (even when they do not 'make sense' from the cognitive point of view and contradict a lifetime of experience with our own bodies). Thus instead of emphasizing the visual resemblance of the fake hand to the real hand (Tastevin 1937; Welch 1972; Botvinick & Cohen 1998), we would place emphasis primarily on the synchronicity of stimulation.

It is especially surprising that the brain can tolerate even absurd distortions of body position as in the distant fake hand experiment. With simultaneous touch to the real and fake hands, subjects were able to assimilate a fake hand extended to the anatomically impossible distance of 3 feet (0.91 m). By contrast, in other experiments where the fake hand was mislocated and only visual cues were available (no simultaneous touch occurred), subjects failed to incorporate the fake hand into their body image (Farne *et al.* 2000; Pavani *et al.* 2000). It may be noted that differences in the limb orientation could also play a part in whether or not subjects identified with the fake hand: the arm was perpendicular to the real arm in these other experiments.

Graziano *et al.* (2000) provides additional support that statistical information is important in coding limb position. Their experiment showed that coincident tactile and visual information alters neural response properties for positional coding. Monkeys first viewed a fake arm while their real arm was occluded (visual cues only). When synchronous touch was introduced, four out of five neurons previously responsive only to the position of the real arm began to respond to the visual appearance of the fake arm. Future experiments should elucidate the relative contribution of visual resemblance versus synchrony to the hand illusion.

Pilot work and subjective reports indicated that the more random and unpredictable (but synchronized) the stroking sequence, the more striking the illusion. Why does this happen? When the touching is more random, the probability declines that a mere coincidence can explain the synchronous touch felt on your hand and that seen on the table or the rubber hand. The high probability of the seen and felt touch co-occurring facilitates the percepts from the different modalities becoming more tightly 'bound', hence the enhanced vividness that the seen and felt touch are from the same source. Thus, the brain deems this coincidence highly unlikely, and finds it much more probable that the external objects are part of your body image.

How precise is the temporal coding of this information? In other words, how close does the coincidence of seen and felt touch need to be for one to experience the illusion? To test this, our control condition in experiment one consisted of touch on the real hand that was identical to that on the fake hand but delayed by *ca.* 1 s. It seems that the integration is fairly precise: there was a significant difference, for both intensity ratings and SCR, between synchronous and delayed synchronous touch. Also, mean intensity and SCR for the delayed synchrony condition were as low as those for the fake hand control conditions in the other experiments, suggesting it was equally effective as a control. Thus the brain is very sensitive to slight asynchronies or perturbations. As anecdotal testament to this, subjects periodically reported that the experimenter had briefly ruined the illusion when she 'messed up' the synchronous touch.

(b) *Alternative explanations*

Is it possible this cross-modal integration between vision and touch occurs via associative conditioning: that is, do subjects merely expect injury because all of the touch up to the point of injury is identical? We think this unlikely for two reasons. First, in experiment 1, touch was synchronous in the control condition in which the partition was removed. If the illusion was induced exclusively by associative conditioning, subjects should have had just as large SCRs in the no partition condition as all of the touch up to the point of 'injury' is identical. Second, conditioning can occur with a lag of up to 1 s between stimuli (e.g. Manns *et al.* 2000). Given touch to the real hand was delayed by *ca.* 1 s in experiment 1, this should have been sufficient time for trace conditioning to occur, yet the illusion was substantially diminished.

It is also unlikely that these effects are due to attentional modulation. In the control condition for experiment 1, shifting gaze reduced the time spent looking at the rubber hand, which may have reduced attention allocated to the rubber hand. Is it possible that this diminished attention in and of itself (rather than diminishing the illusion) was sufficient to reduce the intensity ratings and SCRs? We think that this is not the case for two reasons. First, taking into consideration findings from all three experiments, it is not the most parsimonious account. That is, in the other experiments, subjects also showed larger SCRs in the experimental compared with the control conditions, and in those experiments the subjects never shifted gaze from the fake hand because their real hands were always hidden. Second, if simple Hebbian learning were responsible for the SCRs, then receiving the additional visual information from the real hand regarding synchronous touch (control for experiment 1) should have served to enhance the SCRs rather than diminish them.

(c) *Neural basis*

There are several reasons, including findings from our own pilot work, to suspect that rostral premotor frontal cortex mediates the illusion. First, neurons in frontal area five (located in this area of frontal cortex) of macaques exhibit properties necessary for the hand illusion: they use visual and tactile information to represent body position, and they exhibit 'mirror' properties: for example, they are active both when an individual makes a movement *and* when they watch another individual make that movement (Di Pellegrino *et al.* 1992; Gallese *et al.* 1996). Second, in a paradigm similar to our own, when macaques viewed a stuffed arm of its own species above their occluded real arm, neurons coded the location as a combination of the proprioceptive information from the real arm and visual information from the stuffed arm (Graziano 1999). Third, in humans, the homologous area 44 seems to exhibit mirror properties given that the area exhibited significant and equal activation in an fMRI experiment when subjects moved their own finger versus when they observed another's finger moving (Iacoboni *et al.* 1999). Finally, extensive pilot work in our laboratory touching the face (nose, cheek, chin), arm (front and back), hand (front and back) and fingers demonstrated that the illusion was most vivid with touch to the fingers, hence our use of this stimulation for our experiment. This finding is consistent with neural response properties in frontal area five: according to recording studies in monkeys, stimulation of the fingers is the most effective somatosensory stimulation for inducing activity in this brain region (Di Pellegrino *et al.* 1992; Gallese *et al.* 1996; Fadiga *et al.* 2000).

(d) *Conclusion*

Taken collectively, our experiments suggest that the so-called body image, despite all its appearance of durability and permanence, is a transitory internal construct—a temporary shell—that can be profoundly altered by the stimulus contingencies and correlations that one encounters. In addition to demonstrating the malleability of body image, this simple illusion also illustrates an important principle underlying perception: that the mechanisms of perception are mainly involved in extracting statistical correlations from the world to create a model that is temporarily useful.

It is possible that further investigation into the malleability of body image will help us to understand other phenomena, such as body dysmorphic disorder and anorexia nervosa. Understanding how we identify with external objects may also provide insight into the neural basis of empathy.

We thank John Wixted for his advice about statistical analyses.

ENDNOTE

[1]Degrees of freedom for the comparisons of intensity ratings of the fake hand versus fake hand control conditions were smaller than $n-1$. This is because the first few subjects who received the fake hand control before the fake hand condition were not asked for their control intensity ratings (so as not to bias self-reports in the subsequent fake hand condition). This procedure biased the results against us given that subjects gave higher intensity ratings for the control condition if they received it before experiencing the fake hand condition. Subsequent subjects who received the control condition first were asked for their control ratings after giving their fake hand condition self-reports.

REFERENCES

Botvinick, M. & Cohen, J. 1998 Rubber hands 'feel' touch that eyes see. *Nature* **391**, 756.

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V. & Rizzolatti, G. 1992 Understanding motor events: a neurophysiological study. *Exp. Brain Res.* **91**, 176–180.

Fadiga, L., Fogassi, L., Gallese, V. & Rizzolatti, G. 2000 Visuomotor neurons: ambiguity of the discharge or 'motor' perception? *Int. J. Psychophysiol.* **25**, 165–177.

Farne, A., Pavani, F., Meneghello, F. & Ladavas, E. 2000 Left tactile extinction following visual stimulation of a rubber hand. *Brain* **123**, 2350–2360.

Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. 1996 Action recognition in premotor cortex. *Brain* **119**, 593–609.

Graziano, M. S. 1999 Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position *Proc. Natl Acad. Sci.* **96**, 10 418–10 421.

Graziano, M. S., Cooke, D. F. & Taylor, C. S. R. 2000 Coding the location of the arm by sight. *Science* **290**, 1782–1786.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C. & Rizzolatti, G. 1999 Cortical mechanisms of human imitation. *Science* **286**, 2526–2528.

Lang, P. J., Greenwald, M. K., Bradley, M. M. & Hamm, A. O. 1993 Looking at pictures: affective, facial, visceral, and behavioral reactions. *Psychophysiology* **30**, 261–273.

Manns, J. R., Clark, R. E. & Squire, L. R. 2000 Parallel acquisition of awareness and trace eyeblink classical conditioning. *Learning and Memory* **7**, 267–272.

Nielsen, T. I. 1963 Volition: a new experimental approach. *Scandinavian J. Psychol.* **4**, 225–230.

Pavani, F., Spence, C. & Driver, J. 2000 Visual capture of touch: out-of-the-body experiences with rubber gloves. *Psychol. Sci.* **11**, 353–359.

Ramachandran, V. S. & Rogers-Ramachandran, D. 1996 Synaesthesia in phantom limbs induced with mirrors. *Proc. R. Soc. Lond.* B **263**, 377–386.

Ramachandran, V. S., Rogers-Ramachandran, D. & Cobb, S. 1995 Touching the phantom limb. *Nature* **377**, 489–490.

Ramachandran, V. S., Hirstein, W. & Rogers-Ramachandran, D. 1998 Phantom limbs, body image, and neural plasticity. *Int. Brain Res. Org.* **26**, 10–11.

Rock, I. & Victor, J. 1964 Vision and touch: an experimentally created conflict between the two senses. *Science* **143**, 594–596.

Tastevin, J. 1937 En partant de l'experience d'Aristotle. *L'Encephale* **1**, 57–84.

Venables, P. H. & Christie, M. J. 1980 Electrodermal activity. In *Techniques in psychophysiology* (ed. I. Martin & P. H. Venables), pp. 3–67. New York: Wiley.

Welch, R. B. 1972 The effect of experienced limb identity upon adaptation to simulated displacement of the visual field. *Perception and Psychophysics* **12**, 453–456.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.