

That's My Hand! Activity in Premotor Cortex Reflects Feeling of Ownership of a Limb

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When we look at our hands, we immediately know that they are part of our own body. This feeling of ownership of our limbs is a fundamental aspect of self-consciousness. We have studied the neuronal counterparts of this experience. A perceptual illusion was used to manipulate feelings of ownership of a rubber hand presented in front of healthy subjects while brain activity was measured by functional magnetic resonance imaging. The neural activity in the premotor cortex reflected the feeling of ownership of the hand. This suggests that multisensory integration in the premotor cortex provides a mechanism for bodily self-attribution.

The experience that the body is part of the self is critical for our daily interaction with the outside world and is a fundamental aspect of self-consciousness. Many of us take this ability for granted, but under certain pathological conditions (1–4) people demonstrate an inability to identify their own limbs as belonging to themselves. Although these observations suggest that the frontal and parietal lobes are somehow involved in the self-attribution of limbs, the underlying neural mechanism remains uncertain.

We used functional magnetic resonance imaging (fMRI) to investigate the brain mechanisms of the feeling of ownership of seen body parts. We manipulated ownership by making use of a perceptual illusion: the rubber hand illusion (5). During the experiment, the subject's real hand is hidden out of view (under a table) while a realistic life-sized rubber hand is placed in front of the subject. The experimenter uses two small paintbrushes to stroke the rubber hand and the subject's hidden hand, synchronizing the timing of the brushing as closely as possible. After a short period, the majority of subjects have the experience that the rubber hand is their own hand and that the rubber hand senses the touch (5, 6). This illusion happens as a result of the interaction of vision, touch, and position sense (proprioception) and the dominance of vision over proprioception (5).

To manipulate the feeling of ownership, we took advantage of the fact that the rubber hand illusion is only elicited when synchronous brushstrokes are applied to the real and fake hand (5, 6) and when the rubber hand is aligned with the subject's own hand (7). Thus, we defined four conditions where we

systematically manipulated the orientation of the seen rubber hand (aligned with the subject's own hand or rotated 180°, pointing toward the subject) and the timing of the brushstrokes applied to the real and fake hand (synchronous or alternating brushstrokes). In this 2 × 2 factorial design with four conditions—Synchronous Congruent, Asynchronous Congruent, Synchronous Incongruent, and Asynchronous Incongruent—the activation associated with the feeling of ownership of the fake hand corresponds to the interaction between hand orientation and brushstroke timing (8) (fig. S1).

We hypothesized that the multisensory activity in the parietal and premotor cortex would reflect the feeling of ownership of a seen hand. It has been suggested that the body is distinguished from the external world by its participation in specific types of multisensory perceptual correlations (5, 9–11). Self-attribution depends on a match between the look and feel of the body part. Relevant to this hypothesis is

the observation that neuronal populations in the parietal and ventral premotor cortex represent both the seen and felt position of the arm (12–16). But although these studies show that limb position can be computed in these areas on the basis of multisensory information, they do not inform us as to whether the activity in these areas is related to the conscious experience of ownership of the seen limb. This is because it is not possible to know what monkeys feel when looking at a fake limb (14, 15) and the feeling of ownership of the limbs was not experimentally manipulated in the human studies (16).

Before the brain scan, we tested the subjects to make sure that they experienced the rubber hand illusion (8) (fig. S2). The participants felt the illusion more strongly in the Synchronous Congruent condition relative to the other three control conditions [$P < 0.05$ (8)].

We looked for brain activity related to the illusion in three ways. First, we analyzed the areas in which there was activity during the illusion condition that could not be accounted for by the summation of the effects of seeing the arm in a congruent position and feeling the synchronous brushstrokes [the interaction term (8)]. Such activity was detected in the bilateral inferior part of the precentral sulcus ($P < 0.001$; Fig. 1) (table S1). The posterior bank of this sulcus corresponds to ventral premotor area 6, and the anterior bank to the posterior part of area 44. We also observed activation that reflected the illusion condition in the bilateral frontal operculum, which is a region located adjacent to the premotor cortex and area 44.

We then searched for areas in which the activity was related to the strength of the illusion as rated by the subjects just after the scan [using a linear regression analysis (8)]. The subjects who reported the strongest illusion during the Synchronous Congruent condition relative to the control conditions also

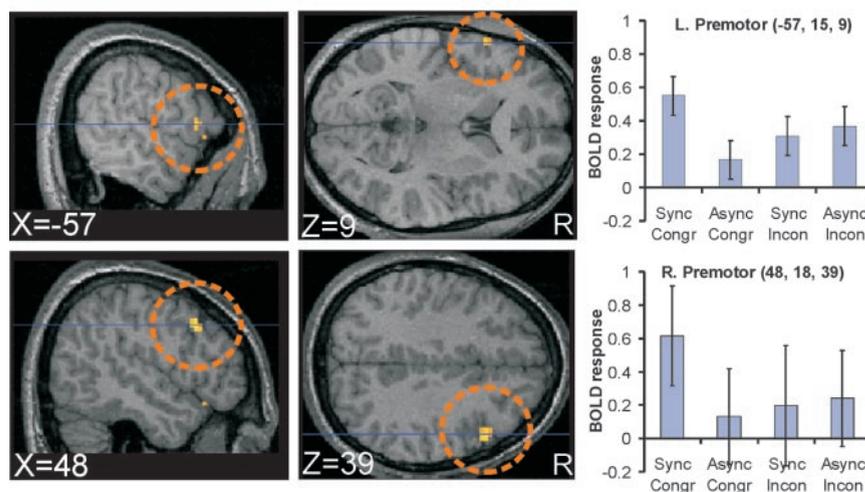


Fig. 1. Bilateral premotor activity that reflects the rubber hand illusion (interaction effect, $P < 0.005$ for display purposes). The activation peaks are located in the inferior part of the precentral sulcus. R denotes right; coordinates in standard space are indicated at lower left. The plot shows the contrast estimates; error bars denote SEs. See (8) and table S1 for details.

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showed the strongest blood oxygen level-dependent (BOLD) signal in the bilateral premotor cortex [Fig. 2; left precentral sulcus; $-48, 0, 39$ ($x, y,$ and z coordinates in standard space); $t = 3.25$; $P < 0.003$; left precentral sulcus; $-57, 15, 6$; $t = 2.62$; $P < 0.009$; right precentral sulcus; $51, 0, 48$; $t = 3.25$; $P < 0.002$]. There was thus a linear relation between the subjective rating of the illusion and the level of neural activity in premotor cortex. There was also a significant relation between activity in the right lateral cerebellum and the strength of the illusion (crus I/lobule VI; $48, -57, -27$; $t = 4.0$; $P < 0.001$).

Finally, we analyzed the temporal evolution of the premotor activity with respect to the time course of the illusion. Because it typically takes about 11 s for the illusion to start, we compared

the functional images obtained after the onset of the illusion with those collected before it commenced. The left premotor cortex showed enhanced activation after the subjects indicated that the illusion had started (left precentral sulcus; $-33, 12, 30$; $t = 4.49$; $P < 0.001$; left precentral sulcus; $-42, 12, 48$; $t = 2.94$; $P < 0.005$; see fig. S4). Also, such a response was observed in the right cerebellum (crus I; $27, -81, -27$; $t = 3.55$; $P < 0.002$).

These three observations suggest that neural activity in the premotor cortex reflects the feeling of ownership of a seen hand. Thus, activity in this area is associated with the subjective experience that the body one sees belongs to oneself. This result provides evidence for the hypothesis that self-attribution of body parts depends on multisensory integration in the pre-

motor cortex. It may do so as part of a circuit that includes the parietal cortex and the cerebellum. There were trends for an interaction effect in both areas (left parietal $P < 0.009$, left cerebellum $P < 0.003$); moreover, there was a significant relation between subjective ratings of the illusion and cerebellar activity.

The ventral premotor cortex is an ideal candidate for the multisensory representation of one's own body. It is anatomically connected to visual and somatosensory areas in the posterior parietal cortex and to frontal motor areas (17). Premotor neurons represent both the seen and felt position of the hand (12–14, 16) and discharge when the hand is touched or when a visual stimulus is presented near the hand (12–14, 18, 19). The receptive fields of the visual cells are “anchored” to the hand so that when the position of the hand changes, the receptive fields follow the hand; that is, these cells represent the space near the hand in a body-centered reference frame (12, 14). When the illusion arises, there is a change in the proprioceptive and tactile representations of the hand so that the somatic information from the hand matches the visual information. Thus, the premotor activity could reflect the matching of the visual and somatic signals, in line with the hypothesis that self-attribution is mediated by multisensory correlations (5, 9–11). Furthermore, when the illusion starts, it is likely that the hand-centered reference frame shifts from the hidden real hand to the rubber hand. Thus, the premotor activity might also reflect hand-centered cells that become active at the sight of the brush near the hand (in peripersonal space). In this, case the premotor activity would provide information about ownership by signaling that the object is close to one's own hand, thus defining the boundary zone between the body and the environment. These two interpretations are complementary and both suggest that the feeling of ownership is associated with the relocation of body space (intrapersonal and near-personal space), in this case to a nonbody object.

Multisensory information about arm orientation and binding of synchronous visuotactile events is represented in the parietal lobe. We found activity in the same intraparietal area both when we contrasted synchronous and asynchronous brushstrokes and when we contrasted the congruent and incongruent arm position (Fig. 3) (table S2). Given that activity in this area reflects the synchrony of the visual and tactile events as well as the seen orientation of the hand, this cortical area is probably critically important for the rubber hand illusion because this illusion depends on the integration of these types of information. The active area was located in the medial wall of the intraparietal sulcus in a location that might correspond to the medial intraparietal area in nonhuman primates. This region is connected to visual, somatosen-

Fig. 2. Significant relation between the bilateral premotor activity and the subjective ratings of the illusion (left: $R^2 = 0.3969$, $P < 0.003$; right: $R^2 = 0.3982$, $P < 0.002$). See (8) for details.

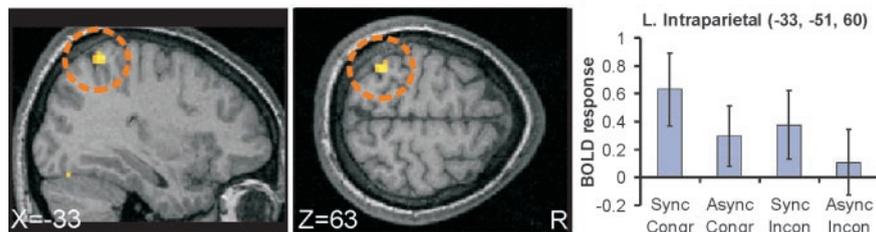
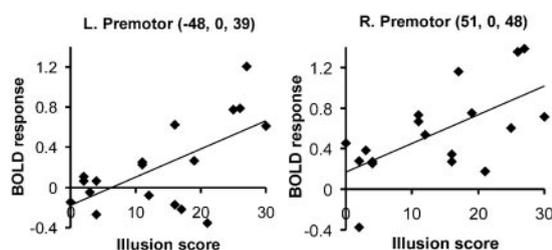
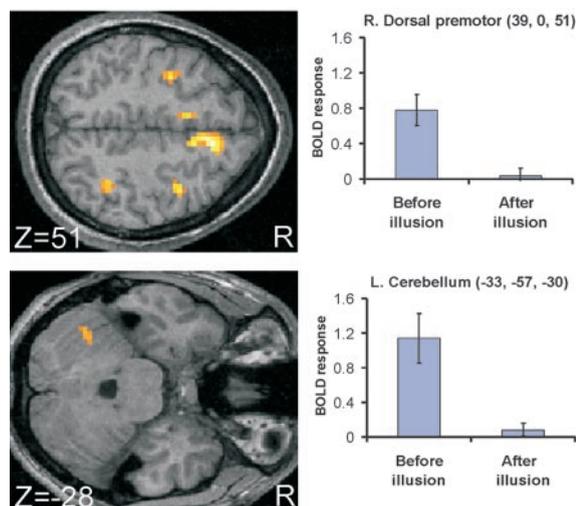


Fig. 3. Intraparietal activity that reflects the effects of both seeing the arm in a congruent position and perceiving synchronous brushstrokes [conjunction of the main effects, $P < 0.001$ in each contrast; see (8) and table S2]. As evident from the plot, the parietal cortex displayed stronger activation during the Synchronous Congruent condition relative to the control conditions, but for this peak, the activity in this condition was no greater than would be accounted for by the combination of the effects of congruent arm orientation and synchrony.

Fig. 4. Activity associated with the recalibration period before the illusion started relative to the period after the illusion onset. See table S3 and (8) for details ($P < 0.005$ for display purposes).



sory, and premotor areas (17, 20, 21), and neurons in this region integrate visual, tactile, and proprioceptive information from the hand (15, 16, 21–26). People with parietal lesions sometimes show an inability to identify their own limbs as part of the body (1). This could reflect impaired multisensory integration of body-related information. However, it is still somewhat unclear whether the activity in the intraparietal cortex reflects the feeling of ownership per se, because we only detected a trend for illusion-related activity in this region (interaction effect, $-45, -54, 57$; $P < 0.009$).

The elicitation of the rubber hand illusion depends on the integration of visual and tactile information and the resolution of differences between the visual and position sense representations. The period before the illusion develops is critical in this respect, and it probably involves a recalibration of position sense for the hand (5). Before the illusion started, we found increased levels of activity in the bilateral intraparietal cortex, bilateral dorsal premotor cortex, and supplementary motor area, as well as the left cerebellum, left putamen, and left ventral thalamus (Fig. 4) (table S3). Several of these areas are known to be involved in the processing of proprioceptive signals as revealed by tendon vibration experiments (27). Likewise, some of the areas are involved in arm reaching in humans and nonhuman primates (20, 28–30). Thus, the recalibration of limb position in a reaching circuit might be a key mechanism for the elicitation of the illusion, and indeed experiencing the illusion has behavioral consequences for arm movements. After having experienced the rubber hand illusion of their left hand, subjects make a reaching error (toward the location of the rubber hand) when asked to point toward their hidden left hand (5, 31).

In summary, the rubber hand illusion depends on three neural mechanisms: multisensory integration in parietocerebellar regions, recalibration of proprioceptive representations of the upper limb in a reaching circuit, and self-attribution in the premotor cortex (8). Our results associate activity in the premotor cortex with the feeling of ownership of a seen limb, and we suggest that multisensory integration in a body-centered reference frame is the underlying mechanism of self-attribution.

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Supporting Online Material

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Materials and Methods

SOM Text

Figs. S1 to S4

Tables S1 to S3

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Brood Parasitic Cowbird Nestlings Use Host Young to Procure Resources

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Young brood parasites that tolerate the company of host offspring challenge the existing evolutionary view of family life. In theory, all parasitic nestlings should be ruthlessly self-interested and should kill host offspring soon after hatching. Yet many species allow host young to live, even though they are rivals for host resources. Here we show that the tolerance of host nestlings by the parasitic brown-headed cowbird *Molothrus ater* is adaptive. Host young procure the cowbird a higher provisioning rate, so it grows more rapidly. The cowbird's unexpected altruism toward host offspring simply promotes its selfish interests in exploiting host parents.

Parents provisioning young commonly balance the effort they spend on rearing their current brood with the effort they might devote to future offspring (1, 2). Members of the current brood then become rivals for limited parental resources [intra-brood conflict (3, 4)] and must also compete with future offspring to increase the total effort that parents will devote to the current breeding attempt [inter-brood conflict (5)]. In theory, the intensity of both forms of

conflict should increase as offspring relatedness declines, all else being equal (3, 6–9). We used an avian brood parasite to test the importance of relatedness in determining interactions between broodmates.

Obligate avian brood parasites lay their eggs in nests belonging to other species, leaving each of their nestlings to grow up in a family to which it is entirely unrelated (10). The host's nestlings offer formidable competition for resources (11, 12). Nonetheless, in contrast to many cuckoo and honeyguide species, the *Clamator* cuckoos, *Vidua* finches, and parasitic cowbirds tolerate the company of host young in the nest. Nestmate tolerance is unlikely to be explained by kin selection because, although multiple parasitism of individual host nests is common (10), parasite siblings

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Supplementary Online Material

Material and Methods

Eighteen right-handed healthy subjects participated in the imaging experiments (nine males and nine females). Participation was limited to subjects who felt the rubber hand illusion in preliminary testing; seven other subjects were excluded because they did not experience the illusion (see below). All subjects had given their written consent and the study was approved by the joint National Hospital for Neurology and Neurosurgery/Institute of Neurology Ethics Committee.

Experimental procedure

Prescanning testing phase

We tested potential subjects on the rubber hand illusion in a separate experiment a few days before the planned brain scan. There were four conditions (Synchronous Congruent, Asynchronous Congruent, Synchronous Incongruent, and Asynchronous Incongruent) as described in the section on scanning below. Each condition lasted for one minute and the order of the conditions was randomized across subjects. After each condition, the subject completed a questionnaire (adopted from 5) that required a description of their experience and asked them to affirm or deny the occurrence of five

specific perceptual effects. The first two questions were relevant to the illusion and the remaining three served as controls (see legend Fig. S2 for details). Eighteen subjects reported that the rubber hand appeared to be their own hand and that the rubber hand sensed the touch. The results from these eighteen subjects who also participated in the fMRI scan are highlighted in Fig. S2. Seven other subjects denied having such sensations and they were not scanned.

Scanning phase

Whilst the brain scans were being performed, the subjects rested comfortably in a supine position on the bed in the MRI scanner. All subjects wore headphones to reduce noise and to receive auditory cues. The right arm was extended and placed on a support so that the right hand was positioned in a relaxed position (just below the table, see below).

In this experiment it was necessary that the subjects could see the rubber hand in a position where their real hand could be placed. We avoided using a mirror because looking at the hand in a mirror is not the natural way to look at our hand. Indeed, pilot experiments showed that seeing the rubber hand in a mirror could reduce or eliminate the illusion in some subjects and we were concerned that different neural networks might be engaged when looking at oneself in a mirror compared to when one looks at oneself directly. Therefore, within the cylindrical head coil the head was tilted approximately 20-30 degrees by placing foam wedges underneath. Thus the natural direction of the gaze was oblique so that the subjects could see the rubber hand by direct vision without any discomfort (this approach has been used before, see ref. S1).

We used a life size rubber prosthesis of a male or female right hand (gender matched). This rubber arm was placed on a tilted (30-45°) plastic table that was positioned over the stomach of the subject. The rubber hand was orientated in an anatomically plausible position on the table pointing slightly left, toward the bodily midline (approx. 20-30°). The table was covered with a soft black material and the subject's own right hand was placed on a plastic support (30 x 30 cm) covered with the same soft material below the table (about 40 cm from the seen rubber hand). Finally, to reduce potential head movements, we fixed the position of the head using foam pads.

In the brain imaging experiment there were four experimental conditions, corresponding to a two-by-two factorial design (see Fig. S1), and one rest condition serving as the baseline. In the factorial design, we manipulated the *position* of the rubber hand relative to the subject's hidden arm and the *timing* of the brushstrokes on the two hands. Thus the four conditions were: (1) Synchronous Congruent - the rubber hand was aligned to the subject's own hand and the experimenter brushed the fake hand and the subject's hidden hand as synchronously as possible with two small paintbrushes. (2) Asynchronous Congruent - the rubber hand was aligned to the subject's own hand but alternating brushstrokes were applied to the two hands. (3) Synchronous Incongruent - synchronous brushstrokes were applied to the real hand and the rubber hand but the rubber hand was positioned so that it was pointing toward the subject (i.e., rotated 180° relative the subject's own hand). (4) Asynchronous Incongruent - the rubber hand was positioned so that it pointed toward the subject (180° rotated) and alternating brushstrokes were applied. The brushstrokes were small (1 cm) and brisk (<400ms) and

applied to the upper parts of the index finger and middle finger at a frequency of 1 Hz in all conditions. To help the experimenter apply the same number of brushstrokes in the different conditions he listened to an auditory metronome at 1 Hz over earphones. Thus, we matched the number of seen and felt brushstrokes in each experimental condition to eliminate effects related to the visual or tactile signals caused by the brushstrokes.

Each condition lasted 42 seconds. To indicate the onset of the illusion in the Synchronous Congruent condition, the subject was instructed to press a key-pad with their left foot in a relaxed manner when they first started to feel that the rubber hand was their own. When they pressed the key they heard a brief tone in the earphones to match the tone presented in the other conditions (see below). After having made the keypress response, subjects were instructed to relax completely and to continue maintaining their gaze on the part of the rubber hand that was being brushed. The illusion started after 11.3 ± 7.0 seconds (mean \pm SD).

To control for the foot response in the Synchronous Congruent condition, subjects were instructed to press the response-key with their foot in the three other conditions as well when they heard a tone (in the rest condition there was no tone or keypress response). The timing of the presentation of these tones was yoked to the recorded times of the key response during the preceding illusion condition (Cogent 2000 software; Wellcome Department of Imaging Neuroscience, London, UK). After having made the key press the participants relaxed and looked at the rubber hand.

To investigate the neural correlates of the rubber hand illusion it is only relevant to analyze the functional images from the period when the subjects actually feel the

illusion, i.e. the period after they had pressed the key pad with their foot. Therefore we defined sub-conditions corresponding to the periods before and after the key press for each of the four main conditions, e.g., the Synchronous Congruent condition was divided into Synchronous Congruent^{Before Key Press} and Synchronous Congruent^{After Key Press}, and we only used the latter condition in the analyses searching for illusion-related activity (see below). During the periods after the key press the participants relaxed and looked at the rubber and performed no active task. Thus, the results from this period were not confounded by any task-related processes.

Three experimental runs, each lasting 17 minutes, were performed for each subject. The five conditions were repeated three times in a pseudorandomized order. The duration of each epoch was set at 42 seconds. Thus, the period when they felt the illusion after they had pressed the key pad lasted 30.7 ± 7.0 (mean \pm SD) seconds. Between the experimental epochs there was a period of 8 seconds when the experimenter changed the position of the rubber hand. During this period the subjects were instructed, with a brief verbal cue presented over the headphones, to close their eyes so as not to see the rubber arm being manipulated between tests and to relax their eyes.

After the scans, each subject was requested to rate the vividness and prevalence of the feeling that the rubber hand was their own hand using a visual analogue scale (0-9). The vividness was defined as how life-like and realistic the illusion was when it was experienced. The prevalence score reflected the continuance of the illusion (equivalent to the percentage of time that the illusion was experienced). Subjects were asked to rate the average sensation across the whole experiment for each of the four conditions. To get one

value per subject that reflected the overall strength of illusion experienced during the approximately 31 second periods, we multiplied the vividness and prevalence scores. We used these values in a linear regression analysis to relate the subjective rating of the illusion to the BOLD signal (see below and Fig. 2).

Acquisition and analysis of functional imaging data

The functional imaging was conducted by using a Siemens Sonata 1.5T Scanner to acquire gradient echo T2*-weighted echo-planar images with blood oxygenation level-dependent contrast (BOLD) as an index of local increases in synaptic activity (S2). A functional image volume comprised 48 continuous slices of 2.5 mm thickness (with a 1.25 mm interslice gap) which ensured that the whole brain was within the field of view (64 by 64 matrix, 3.0 mm by 3.0 mm, TE = 40 ms). One functional image volume of the brain was collected every 3.6 seconds (TR=3600 ms). Thus, during the three experimental runs performed for each subject a total of 540 image volumes were collected. The fMRI data was analysed using the Statistical Parametric Mapping Software 2 (SPM2; <http://www.fil.ion.ucl.ac.uk/spm>; Wellcome Department of Cognitive Neurology, London; see also S3). The functional images were realigned and unwarped to correct for head movements, co-registered with each subject's anatomical MRI and transformed (linear and non-linear transformation) to the format of the Montréal Neurological Institute (MNI) standard brain. The functional images were scaled to 100

and spatially smoothed with a 10 mm full width at half maximum (FWHM) isotropic Gaussian kernel, and smoothed in time by a 4 s FWHM Gaussian kernel.

For each individual subject, we fitted a linear regression model (general linear model) to the data (first level analysis). For each of the four experimental conditions described above we defined one regressor for the period before the key press and one regressor for the periods after the key press. We also defined conditions of no interest corresponding to the 8 second periods between the experimental conditions where we changed the position of the rubber hand, and the key response in the illusion condition and the control conditions (event-related responses). Each condition was modelled with a boxcar function delayed by 4 s and convoluted with the standard SPM2 hemodynamic response function. We defined linear contrasts in the general linear model (see below). The result from this analysis was contrast estimates for each condition from each of the 18 subjects (contrast images). To accommodate inter-subject variability, the contrast images from all subjects were entered into a random effect group analysis (second level analysis). One-sample t-tests were used (17 degrees of freedom). In the factorial design, we only report peaks of activation corresponding to the statistical threshold of $p < 0.001$ (uncorrected). In addition, in the intraparietal sulcus and the ventral premotor cortex for which we had an *a priori* hypothesis we used the significance level that corresponded to $p < 0.05$ corrected for multiple comparisons using a small volume correction (the peak coordinates taken from a previous study; ref. S4). In the other analyses we use the threshold $p < 0.001$ (uncorrected) unless otherwise specified. We also used a conjunction analysis to detect areas that were associated with both main effects at $p < 0.001$

uncorrected, respectively. Finally, areas that showed a deactivation, i.e., less activity in the Synchronous Congruent condition as compared to the resting baseline, are not reported ($p < 0.05$ uncorrected).

Five statistical analyses were performed. We analysed the relationship between brain activity in the illusion of ownership of the seen hand in three ways. First we analyzed the areas in which there was activity in the illusion condition that could not be accounted for by the summation of the effects of seeing the arm in a congruent position and feeling the synchronous brushstrokes (Fig. S1). In more technical terms, we analysed the interaction term in the factorial design using the contrast (Synchronous Congruent^{After Key Press} – Asynchronous Congruent^{After Key Press}) – (Synchronous Incongruent^{After Key Press} – Asynchronous Incongruent^{After Key Press}).

Second, we used a linear regression analysis to look for areas in which the activity was related to the strength of the illusion as rated by the subjects just after the scan (Fig 2; see above for details about the subjective ratings). In this analysis, we used the SPM2 simple regression model with the illusion ratings as the covariate and the contrast images from the interaction analysis.

The final way in which we investigated activity related to the experience of the illusion was by analyzing the temporal evolution of the premotor activity with respect to the time course of the illusion. Because it typically takes about 11 seconds for the illusion to start we were able to compare the functional images obtained after the onset of the illusion with those collected before it commenced (Fig S4). To eliminate nonspecific time effects we used the data from the Asynchronous Incongruent as a control. Thus the

contrast used was: (Synchronous Congruent^{After Key Press} – Asynchronous Incongruent^{After Key Press}) - (Synchronous Congruent^{Before Key Press} – Asynchronous Incongruent^{Before Key Press}).

The two last analyses were performed to further investigate the mechanism of the illusion. First, we wanted to investigate how visual information regarding arm orientation and information about synchronous tactile and visual stimuli are integrated in multisensory brain areas. Thus, to detect areas that were associated with *both* the factors of congruent arm position and synchrony we analyzed the conjunction of the main effects (Fig. 3 and Table S2). In this conjunction analysis we used the two contrasts (Synchronous Congruent^{After Key Press} + Synchronous Incongruent^{After Key Press} - Asynchronous Congruent^{After Key Press} - Asynchronous Incongruent^{After Key Press}) and (Synchronous Congruent^{After Key Press} + Asynchronous Congruent^{After Key Press} - Synchronous Incongruent^{After Key Press} - Asynchronous Incongruent^{After Key Press}).

Second, we analyzed activity during the period while the hands were being brushed but before the subjects reported the illusion. During this period, the inter-sensory conflict is presumably being resolved by means of a re-calibration of the somatosensory representation of the hand (5). We compared the imaging data acquired before the onset of the illusion, in the Synchronous Congruent condition, with the data obtained after the illusion had started (Fig. 4 and Table S3). We used the data from the Asynchronous Incongruent condition to control for the key press and unspecific time effects. Thus, the contrast used was: (Synchronous Congruent^{Before Key Press} – Asynchronous Incongruent

Before Key press) – (Synchronous Congruent^{After Key Press} – Asynchronous Incongruent^{After Key press}).

In some of the figures we display the effect size using histogram-plots (Figs 1, 3, 4 and S4). The values on the y-axis correspond to the contrast estimates from each of the four stimulation conditions minus rest (in Figs 1, 3 and S4), or the contrast between Synchronous Congruent and Asynchronous Incongruent (in Fig. 4). The error bars reflect the standard error.

The anatomical localization of the activations was related to the major sulci and gyri (S5), distinguishable on a mean MRI generated from the standardized anatomical MRIs from the eighteen subjects. For the cerebellum we use the terminology of the Schmahmann Atlas (S6).

Supporting text

Psychophysical Results

We tested potential subjects on the rubber hand illusion in a separate experiment a few days before the planned brain scan (see Material and Methods). These tests confirmed that the subjects experienced the rubber hand illusion, and that they reported stronger illusory sensations in the Synchronous Congruent condition as compared to the three control conditions (see text below and Fig. S2). We carried out two analyses. First, we compared the ratings on the two questions concerning the illusion with the ratings on the three control questions (see Fig. S2). During the Synchronous Congruent condition, the subjects were more likely to report that the rubber hand was their own hand and that they felt the touch on the rubber hand (paired t-tests $p < 0.001$; see Fig S2). Second, we compared the ratings for these two illusion relevant questions across the four conditions in the factorial design. During the Synchronous Congruent condition, the subjects felt more strongly that the rubber hand was their own hand (interaction position x timing = $F(1, 17) = 14.22$; $p < 0.005$) and that touch sensations were located on the fake hand (interaction position x timing = $F(1, 17) = 31.77$; $p < 0.05$). Thus, the rubber hand illusion corresponds to the interaction between hand orientation and the timing of the brushstrokes. Indeed, a similar interaction effect between brushstroke timing and position of the hand have been recently been observed in another laboratory (S7)

After the scans we asked subjects to rate the vividness and prevalence of the illusion during the experiments (see Fig. S3). The subjects reported stronger vividness

and prevalence during Synchronous Congruent than during the three control conditions ($p < 0.001$; paired t-tests). Furthermore, they reported that the illusion was stronger during Synchronous Congruent as compared to the sum of the responses during the control conditions (interaction position \times timing = $F(1, 17)=31.77$; $p < 0.001$, for both the vividness and continuance ratings, respectively).

Summary

Based on our results we propose a neurophysiological explanation for the rubber hand illusion. When the experimenter starts to brush the rubber hand and the hidden real hand, the contralateral extrastriate cortex, the contralateral intraparietal cortex, and the left and medial cerebellum receive visual information about the position of the seen hand and detect the strongly correlated visual and tactile brushstrokes (Table S2). The parieto-cerebellar regions probably play an important role in the integration of these types of multisensory information. During the initial period before the illusions starts, the subjects are aware of the position of their real hand hidden under the table. In other words, there is a conflict between the felt position of the hand and the seen position. During this period the inter-sensory conflict is probably resolved by a re-calibration of a proprioceptive representation of the arm in a reaching circuit involving the intraparietal cortex, the dorsal premotor cortex, the supplementary motor area, and the lateral cerebellum (Table S1). This change in the proprioceptive representations probably leads to changes in the body-centered reference frames, most notably in the premotor cortex. Finally, when the illusion arises and the premotor cortex plays a key role in the self attribution of the seen

hand (Table S1). The premotor cortex might do so by integrating visual and somatosensory signals in a body centered reference frame. Thus, the subjects experience that the rubber hand is part of their own body and that it senses the touch.

Supporting References and Notes

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Supporting Figures

		Timing of brushstrokes	
		<i>Asynchronous</i>	<i>Synchronous</i>
Arm orientation	<i>Incongruent</i>	Asynch. Incongr.	Synch. Incongr.
	<i>Congruent</i>	Asynch. Congr.	Synch. Congr.

Fig. S1 Factorial design of the experiment. The illusion-related activity is revealed by examining the interaction between arm orientation and the timing of the brushstrokes.

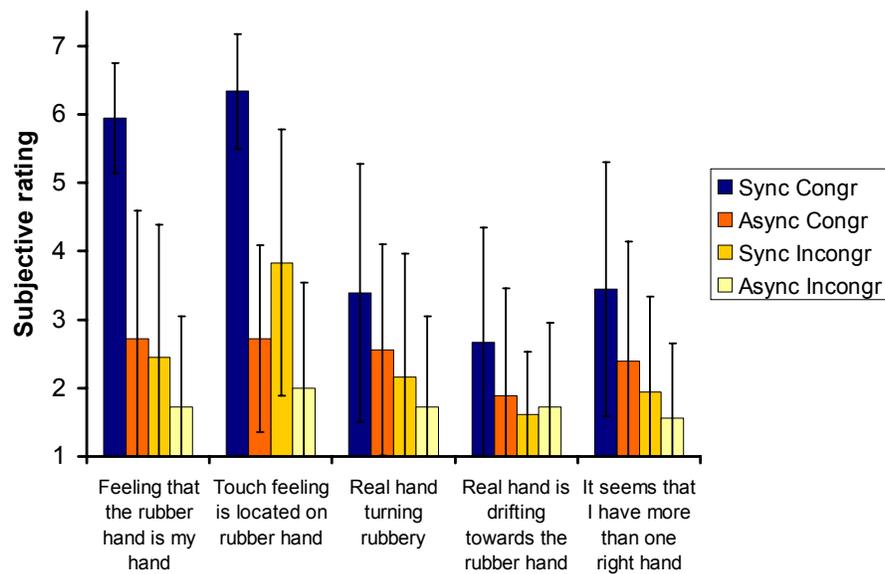


Fig. S2 The result of the rubber hand illusion questionnaire. The 18 subjects who participated in the study were asked to complete a questionnaire (adapted from ref 5) that required a description of their experiences during the four conditions. After being tested on the four experimental conditions, the subjects had to affirm or deny five perceptual effects (reporting ---, --, -, 0, +, ++, +++; in this table these reports are represented with values from 1 to 7). The five statements that the subjects had to deny (score 1-3), affirm (score 5-7) or report that they neither could confirm nor deny (score 4), are given. Error bars correspond to the standard deviation (SD). The two left statements are relevant for the illusory experience and the other serve as controls. See Supporting online text for details (Psychophysical Results).

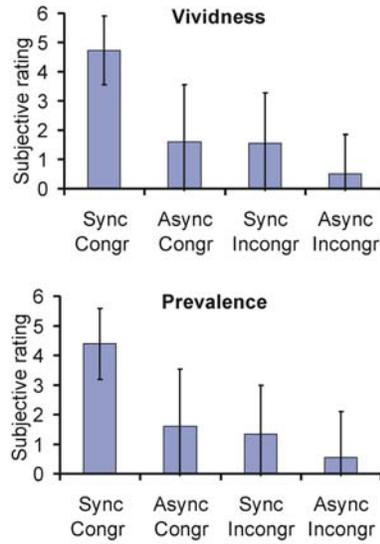


Fig. S3 The subjective ratings of the vividness and prevalence of the illusion in the four experimental conditions during the fMRI scans. Error bars correspond to the standard deviation (SD). See Supporting online text for details (Psychophysical Results).

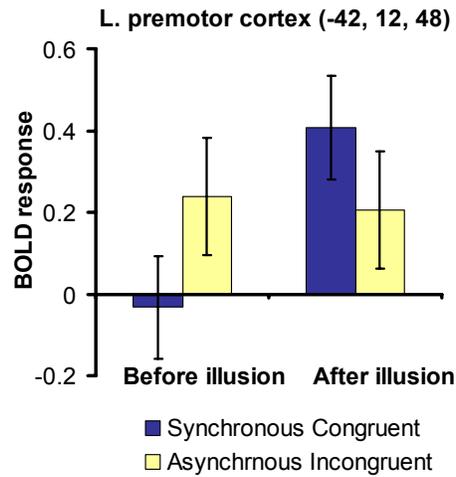


Fig. S4 Activity in the premotor cortex during the Synchronous Congruent condition before and after the subjects reported that the illusion had started. The activity during a control condition is also displayed (Asynchronous Incongruent). The BOLD response corresponds to the contrast estimates for the conditions minus rest. Error bars reflect the standard error. Importantly, there was an increased response after the subjects reported that the illusion started (interaction task x period, $p < 0.001$).

Supporting Tables

TABLE S1. Activity reflecting the rubber arm illusion *per se* (interaction effect)

Anatomical region	Talairach coordinates			Peak T-value ^(†)
	X	Y	Z	
L. frontal operculum	-48	24	-12	5.76
R. ventral premotor cortex (inf. precentral s.)	48	18	39	4.03 ^(‡)
R. frontal operculum	54	18	-12	3.67
L. anterior insula ^(*)	-36	18	0	3.66
Posterior cingulate cortex	0	-33	33	3.65
L. ventral premotor cortex (inf. precentral s.)	-57	15	9	3.53 ^(‡)

(*) Deactivated in Synchronous Congruent as compared to the Rest

(†) $p < 0.001$ uncorrected

(‡) $p < 0.05$ corrected after a small volume correction based on a *a priori* hypothesis

TABLE S2. Areas associated with both the seen orientation of the arm and synchrony of the brushstrokes (conjunction of main effect)

Anatomical region	Talairach coordinates			Peak minimum T-value ^(*)
	X	Y	Z	
L. extrastriate cortex	-45	-72	0	5.32
L. extrastriate cortex	-42	-66	-18	3.77
Left cerebellar hemisphere (lobule IV)	-30	-72	-18	3.60
L. Intraparietal	-33	-51	63	3.60
Medial cerebellum (lobule IV/ Crus I)	-3	-84	-18	3.19

(*) $p < 0.001$ uncorrected in both contrasts (this correspond to $p < 0.05$ corrected)

TABLE S3. Activity reflecting the re-calibration period before the illusion starts

Anatomical region	Talairach coordinates			Peak T-value ⁽¹⁾
	X	Y	Z	
Anterior cingulate cortex	6	33	30	6.34
R. Pre-SMA	9	21	51	6.04
SMA	15	3	69	4.65
L. dorsal premotor cortex (precentral s.)	-33	-6	51	4.43
R. dorsal premotor cortex (precentral s.)	39	0	51	4.40
R. prefrontal cortex (Med Front g.)	33	45	27	4.28
L putamen	-18	6	12	4.22
R. ventral thalamus	15	-12	6	4.18
L. cerebellar hemisphere (Lobule IV)	-33	-57	-30	3.82
Left insula	-33	15	9	3.83
Left frontal operculum	-45	15	9	3.80
R. intraparietal cortex	33	-45	51	3.78
L. ventral thalamus	-15	-9	6	3.74
L. intreaparietal cortex	-36	-42	51	3.09 ⁽²⁾

⁽¹⁾ p<0.001 uncorrected

⁽²⁾ p<0.003 uncorrected