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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

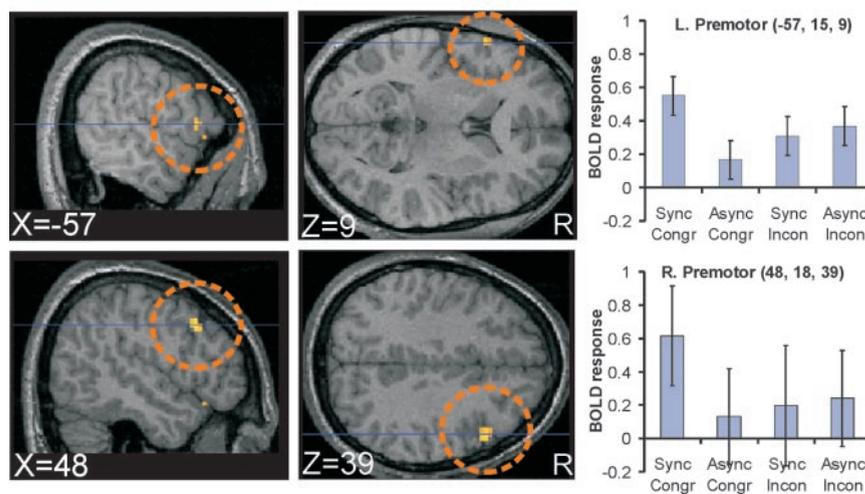


Fig. 1. Bilateral premotor activity that reflects the rubber hand illusion (interaction effect, $P < 0.005$ for display purposes). The activation peaks are located in the inferior part of the precentral sulcus. R denotes right; coordinates in standard space are indicated at lower left. The plot shows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

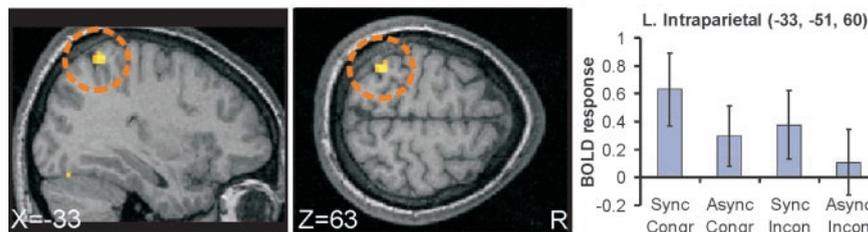
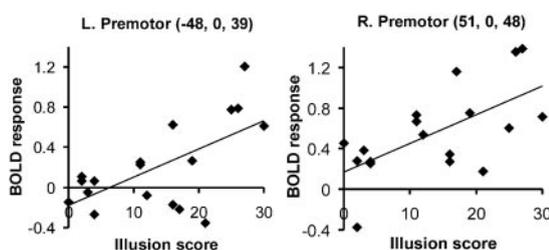
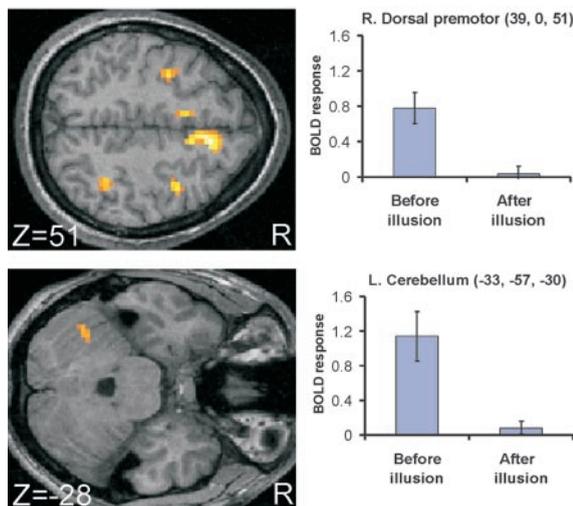


Fig. 3. Intraparietal activity that reflects the effects of both seeing the arm in a congruent position and perceiving synchronous brushstrokes [conjunction of the main effects, $P < 0.001$ in each contrast; see (8) and table S2]. As evident from the plot, the parietal cortex displayed stronger activation 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

References

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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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