43 The Concept of Body Ownership and Its Relation to Multisensory Integration

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How do we come to feel that we own our body? What is the relationship between our body and our sense of self? Questions like these have been discussed in philosophy and psychology for centuries (Gallagher, 2000; James, 1890; Merleau-Ponty, 1962), but what advances have been made in understanding how the brain actually distinguishes between parts of one's own body and objects in the external world? In this chapter we address this issue from the perspective of cognitive neuroscience, paying particular attention to multisensory integration.

From the neurology literature we know that people with damage to their frontal and parietal lobes can sometimes fail to recognize their paralyzed limbs as belonging to themselves (Arzy, Overney, Landis, & Blanke, 2006; Berti et al., 2005; Bottini, Bisiach, Sterzi, & Vallar, 2002; Critchley, 1953). These conditions are not always accompanied by the inability to perceive somatic stimuli applied to the affected limb (hemianesthesia), indicating that they are not simply the result of impairments in basic tactile perception associated with damage to the primary somatosensory cortex. Instead, these neurological observations suggest that the frontal and parietal association cortices are responsible for generating the feeling of owning limbs, but they tell us little about the underlying perceptual processes and neuronal mechanisms.

In psychology there is a long tradition of relating self-recognition to the correlations of concurrent sensory experiences in the different modalities. Gibson (1979/1986) emphasized how correlations between the visual impressions of movement and the somatic sensations these produce contribute to self-perception of one's body. Later studies reported that perceptual correlations between vision and proprioception (sense of position and movement of limbs) could play an important role in how we identify ourselves in mirrors and on video recordings (Bahrick & Watson, 1985; Mitchell, 1997; van den Bos & Jeannerod, 2002). Developmental studies have shown that infants are able to distinguish between congruent and incongruent visual and somatic feedback of their own movements at the age of 2–3

months (Rochat, 1998). This is an important step toward developing a sense that the body is a distinct entity that can be differentiated from the environment.

Recently, body ownership has become a lively topic in cognitive neuroscience. This development has been made possible by an experimental paradigm that allows the controlled manipulation of limb ownership in the laboratory setting: the *rubber-hand illusion* (Botvinick & Cohen, 1998). In this illusion, synchronous touches, applied to a rubber hand, in full view of the participant, and the real hand, hidden behind a screen, produce the sensation that the touches felt originate from the rubber hand, and a feeling of ownership of the artificial hand rapidly develops. What sets the rubber hand illusion apart from other body illusions (e.g., Lackner, 1988; Naito, Roland, & Ehrsson, 2002) is that it involves experiencing changes in the ownership of a limb: one moment you are looking at an inanimate object, and the next moment the object "comes alive" as one experiences the rubber hand to be one's own hand. This illusion, and later versions of it, provide a unique tool for scientists to start experimenting with the "bodily self" and to clarify the processes that produce the feeling of body ownership (Botvinick, 2004).

This chapter examines the leading hypothesis that the feeling of body ownership critically depends on multisensory integration (Botvinick, 2004; Botvinick & Cohen, 1998; Ehrsson, Spence, & Passingham, 2004; Makin, Holmes, & Ehrsson, 2008). It takes, as its starting point, Botvinick and Cohen's original suggestion that the rubber hand illusion is the result of a three-way interaction among vision, touch, and proprioception (Botvinick & Cohen, 1998) and some obvious similarities between this illusion and other multisensory phenomena such as the ventriloquism effect (Woods & Recanzone, 2004). The chapter discusses recent experimental data from the fields of experimental psychology, neurophysiology, and imaging neuroscience that further advance this idea, recent experiments that have begun to investigate illusions involving the ownership of entire bodies and their relation to the rubber hand

illusion and multisensory integration, and finally, it discusses some possible clinical applications that will put the multisensory hypothesis of body ownership to the test in the real world.

THE MULTISENSORY BODY REPRESENTATION

The experience of being the owner of one's body is clearly adaptive from an evolutionary perspective, and it is probably related to the problem of localizing and correctly identifying oneself in the sensory environment (Graziano & Botvinick, 2002; Makin et al., 2008). In recent years there has been a growing consensus in the cognitive neuroscience community that the perception of one's own body in space critically depends on multisensory integration (Ernst, 2006; Graziano & Botvinick, 2002; Lackner & DiZio, 2005; Makin et al., 2008; van Beers, Sittig, & Gon, 1999). Information from afferents in joints, muscles, tendons, and skin as well as visual, vestibular, and auditory signals reach cortical convergence zones in the frontal, parietal, and temporal lobes, where the integration of these body signals occurs (Angelaki & Cullen, 2008; Avillac, Ben Hamed, & Duhamel, 2007; Graziano & Botvinick, 2002; Graziano & Cooke, 2006; Hagura, et al., 2007; Pouget, Deneve, & Duhamel, 2002). From behavioral experiments in humans, we know that the central body representation is a dynamic one that is continuously updated on the basis of the available sensory inputs from the different modalities (Botvinick & Cohen, 1998; Lackner, 1988; Lackner & DiZio, 2005; Naito et al., 2002). Thus, it appears likely that the self-identification of body parts is achieved in a similar manner, by dynamic multisensory integration processes.

In terms of anatomical circuits, projections from the early visual and somatosensory areas in the occipital and anterior parietal lobes, respectively, reach areas in and around the intraparietal sulcus and inferior parietal cortex, and the premotor cortex (Graziano & Botvinick, 2002; Graziano, Gross, Taylor, & Moore, 2004; Rizzolatti, Luppino, & Matelli, 1998). Electrophysiological studies targeting these regions have described how neurons in areas MIP, VIP, and LIP (medial, ventral, and lateral intraparietal areas), the ventral premotor cortex, and parietal area 7 respond to visual, tactile, and proprioceptive stimulation (in the form of joint manipulation and passive movements). With respect to multisensory stimulation of the hand/arm, the ventral premotor cortex in macaque monkeys has been the most thoroughly studied area of the brain. Here, Rizzolatti and co-workers identified neurons that responded to a visual stimulus only when it was presented close to the monkey (i.e., within its reach in near-personal

space) (Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981). Crucially, these neurons typically had visual receptive fields (RFs) that centered on specific body parts and that were largely overlapping with the same neurons' tactile RFs. In other words, individual neurons that responded to touches applied to the hand would also respond to a visual object approaching the hand but not to objects approaching other parts of the body.

Further studies revealed how these cells' RFs were anchored to the upper limb so that when the arm moved, the visual RFs of the bisensory neurons moved along with it (Fogassi et al., 1996; Graziano, Hu, & Gross, 1997; Graziano, Yap, & Gross, 1994). This shift was independent of the position of the monkey's eyes, suggesting that these multisensory cells represent near-personal space in body-part-centered coordinate systems (Gentilucci, Scandolara, Pigarev, & Rizzolatti, 1983; Graziano et al., 1997). Further studies have revealed a number of frontal and parietal areas with multisensory neurons that show visual and sometimes also auditory RFs with a limited extension into the space surrounding the monkey's body. These brain areas include VIP (Avillac et al., 2007; Avillac, Deneve, Olivier, Pouget, & Duhamel, 2005; Colby, Duhamel, & Goldberg, 1993; Duhamel, Colby, & Goldberg, 1998; Ishida, Nakajima, Inase, & Murata, 2009; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005), the parietal area 7b (Duhamel, Bremmer, BenHamed, & Graf, 1997; Ishida et al., 2009), the putamen (Graziano & Gross, 1993), somatosensory cortical areas 2 and 5 (Graziano, Cooke, & Taylor, 2000; Iriki, Tanaka, & Iwamura, 1996), and the ventral premotor cortex. Most of the neurons in these studies had tactile RFs centered on the monkey's head, face, neck, torso, shoulders, hands, or arms (Avillac et al., 2005; Fogassi et al., 1996; Gentilucci et al., 1983; Graziano et al., 1997; Graziano et al., 1994; Ishida et al., 2009). Importantly, we know that these cells perform multisensory integration (Avillac et al., 2007; Graziano et al., 2000). Avillac et al. (2007), for example, showed that when visual and tactile stimuli were presented simultaneously within a VIP neuron's RF, the majority of the bisensory neurons showed neuronal evidence of multisensory integration, that is, supra-additive, subadditive, or additive effects.

Human imaging studies suggest that systems for multisensory integration in near-personal space also exist in the human brain. Functional magnetic resonance imaging (fMRI) studies have identified areas in the premotor cortex and intraparietal cortex that respond to both visual and tactile stimulation in relation to specific body parts (Bremmer et al., 2001; Ehrsson et al., 2004; Lloyd, Morrison, & Roberts, 2006; Lloyd, Shore, Spence, & Calvert, 2003; Makin, Holmes, & Zohary,

2007; Nakashita et al., 2008; Sereno & Huang, 2006). Lloyd et al. (2003) identified areas in the ventral premotor cortex and intraparietal cortex that were active when a real hand was touched in sight of the observer and showed that these activations were modulated by the position of the arm. Furthermore, Makin and colleagues (2007) reported enhanced responses in the intraparietal cortex to visual stimuli presented near the hand as opposed to far from the hand. Behavioral testing of patients suffering from "extinction" after right brain damage provides further evidence of multisensory integration in near-personal space in humans (di Pellegrino, Ladavas, & Farne, 1997; Farne, Dematte, & Ladavas, 2005; Ladavas, di Pellegrino, Farne, & Zeloni, 1998; for a recent review see Ladavas & Farne, 2006).

In summary, the system of areas that integrate multisensory information from the body and from the space surrounding the body is a good candidate for the neural substrate of limb ownership. Populations of neurons in this system could perform the multisensory integration required to bind visual, tactile, proprioceptive, and other multisensory signals to the coherent object that is one's body part as opposed to a visuotactile object that belongs to the external world.

THE RUBBER HAND ILLUSION: AN EXPERIMENTAL MODEL OF BODY OWNERSHIP

The rubber hand illusion is used as a model system for investigating the feeling of body ownership. To elicit this illusion, the participant's real hand is kept out of the field of vision (behind a screen) while a realistic life-sized rubber hand is placed in front of him or her

(figure 43.1, left panel). The experimenter uses two small paintbrushes to stroke the rubber hand and the participant's hidden hand, synchronizing the timing of the brushing. After a short period (about 10–30 sec in most cases), the majority of people have the experience that the rubber hand is their own hand and that it is the rubber hand that senses the touch of the paintbrush. The illusion is often a very vivid one, with people making spontaneous verbal comments and exhibiting reactions of amazement, excitement, or surprise.

The subjective experience of the illusion can be quantified with visual analog scales. The most commonly used questionnaire includes two or three statements about the key perceptual effects of the illusion, such as "I felt as if the rubber hand was my hand," "It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand being touched," and five to seven statements designed to control for task compliance and suggestibility (Botvinick & Cohen, 1998). Although the feeling of touch on the rubber hand is perhaps the most distinct perceptual event defining the illusion, the feeling of owning the hand can have a richer phenomenology, including experiences of expecting the rubber fingers to move when the participants intend to make a finger movement, that the real hand behind the screen has "disappeared," or that one's own hand is "in the same place" as the rubber hand (Longo, Schuur, Kammers, Tsakiris, & Haggard, 2008).

Objective Measures of the Illusion

People who experience the rubber hand illusion are not simply imagining things. Several objective tests of

FIGURE 43.1   Experimental setups used in the "classical" rubber hand illusion (left), the somatic version of this illusion (middle), and the "three-arm" version (right). For details, see the text.

the illusion have been developed, with one commonly used test registering *proprioceptive drift,* or the degree to which people experience their hand to be closer to the rubber hand than it really is. For example, having experienced the rubber hand illusion for their left hand, when asked to close their eyes and point toward their hidden left hand, subjects err in reaching, with the error being toward the location of the rubber hand (Botvinick & Cohen, 1998). Tsakiris and Haggard introduced a sensitive version of this test in which the participants verbally report the perceived location of their hand (Tsakiris & Haggard, 2005). After the illusion, people considered their hand to be closer to the rubber hand than it really was. Those people who display the greatest proprioceptive drift tend to be those who most strongly affirm that they own the rubber hand in questionnaires (Botvinick & Cohen, 1998; Longo, Schuur, et al., 2008).

Another test is to simulate an injury to the owned rubber hand to see if people flinch or display emotional reactions (Armel & Ramachandran, 2003; Petkova & Ehrsson, 2009). This emotional response can be indexed by registering changes in the conductance of the skin by placing two small electrodes on the index and middle fingers (skin conductance response, SCR). Emotional responses are associated with activation of the autonomic nervous system, which produces increased sweating and thus increases the SCR. When the finger of the rubber hand is bent backward (Armel & Ramachandran, 2003) or a needle is stabbed into it (Ehrsson et al., 2008; Petkova & Ehrsson, 2009), the SCR is significantly augmented in comparison to the appropriate control conditions (Ehrsson, 2009; Ehrsson et al., 2008; Petkova & Ehrsson, 2009). Another potentially useful autonomic measure of the illusion is to register the skin temperature on the real hand; one recent paper suggested that it drops by 0.27°C during the illusion, with the extent of the temperature drop being correlated to the subjective strength of the illusion (Moseley, Olthof, et al., 2008).

Reaction-time evidence for the rubber hand illusion can be obtained using adaptations of the cross-modal congruency task originally devised by Spence and colleagues (Spence, Nicholls, Gillespie, & Driver, 1998). This is a discrimination task in which people are required to respond as quickly as possible to tactile targets on different digits while they try to ignore irrelevant visual distractors presented to these digits, either on a congruent finger or on an incongruent one. People's tactile discriminations are slowed by the incongruent visual distractors. When the real hands are placed below an occluding screen and the visual distractors are presented near the digits of rubber hands placed in full view on top of the screen, the tactile discriminations were slowed in a similar way (Pavani, Spence, & Driver, 2000; Zopf, Savage, & Williams, 2010). This effect is absent when the rubber hands are rotated 90° (Pavani et al., 2000). Importantly, the degree of this *cross-congruency effect* is correlated to the subjective strength of owning the rubber hand (Pavani et al., 2000) and is greater following a period of synchronous stimulation on the rubber hands and the real hands than after a period of asynchronous stimulation (Zopf et al., 2010). This provides objective evidence that the multisensory integration in space surrounding artificial limbs is modulated by the feeling of ownership, as if near-personal space was being defined with respect to the rubber hands.

Fundamental Constraints of the Rubber Hand Illusion

We next discuss the natural constraints of the rubber hand illusion. The characterization of these constraints provides us with important information about the necessary factors for limb ownership. As we will show, the natural constraints of the illusion fit well with the temporal and spatial principles of multisensory integration (Holmes & Spence, 2005; Stein & Stanford, 2008).

TEMPORAL CONSTRAINTS   The feeling of ownership of a limb depends on the temporal synchrony of multisensory cues from that limb. Asynchronous visual and tactile stimulation involving a temporal mismatch of the order of 500 msec significantly reduces the rubber hand illusion. In one recent report the temporal delay between the visual and tactile stimulations was systematically varied in steps of 100 msec, starting with a 100-msec delay and examining delays up to 600 msec (Shimada, Fukuda, & Hiraki, 2009). The authors found that the subjective ratings of the illusion and the proprioceptive drift were significantly higher for short delays up to 300 msec. The importance of the temporal congruency of the somatic and visual events in the rubber hand illusion bears obvious similarities with the temporal congruency principle in multisensory integration (Holmes & Spence, 2005; Stein & Stanford, 2008).

SPATIAL AND ANATOMICAL CONSTRAINTS   The rubber hand illusion is also dependent on the spatial congruence of the tactile, proprioceptive, and visual information. This is akin to the spatial principle of multisensory integration (Holmes & Spence, 2005; Stein & Stanford, 2008). Lloyd (2007) found that the rubber hand illusion is limited by the distance between the rubber hand and the participant's real hand: by

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parametrically varying the distance between the two hands, she found a significant decrease in the strength of the illusion for distances greater than 27.5 cm (figure 43.2, top panels). Interestingly, she observed a nonlinear decay of the illusion: it was fairly stable for smaller distances and then exhibited a sharper decay beyond 27.5 cm. The falloff matches the extent of near-personal space as estimated in electrophysiological (Fogassi et al., 1996; Graziano et al., 1997) and neuropsychological (Ladavas et al., 1998) studies. Consistent with Lloyd's study, Armel and Ramachandran presented data demonstrating that the illusion was significantly weaker when the rubber hand was placed 0.91 m in front of the "normal" position (Armel & Ramachandran, 2003). These observations fit with the idea that the multisensory integration responsible for the illusion operates on representations of near-personal space.

As discussed above, near-personal space is defined by coordinate systems centered on body parts. Thus, an important prediction would be that rubber hand illusions operate in a hand-centered reference frame. Costantini and Haggard (2007) conducted an experiment to make a direct comparison between hand-centered coordinates and external or allocentric coordinates in the elicitation of this illusion (figure 43.2, lower panels). This was achieved by investigating the effect of variations in the position of the rubber hand, the real hand, and the direction of the brush strokes on the strength of the rubber hand illusion as indexed by verbal reports of the hand position experienced by the participant (proprioceptive drift). The rubber hand illusion was not extinguished when either the orientation of the real hand or the direction of the stroking stimulus was rotated by 10°; however, when both were rotated by this amount in opposite directions, so that the tactile stimulus was spatially aligned with the visual stimulus on the rubber hand (in external coordinates), but misaligned with respect to the hand in hand-centered coordinates, the rubber hand illusion was significantly reduced. Thus, spatial compatibility between the directions of visual and tactile stimuli seems to be defined with respect to the position of the hand, i.e., in hand-centered coordinates. This corresponds to the notion that the illusion requires multisensory integration performed by neurons that have visual and tactile RFs centered on the hand.

But the rubber hand illusion is not constrained only by spatial factors relating to visual and tactile signals. The spatial correspondences between visual and proprioceptive information about the posture of the hand and arm, and anatomical constraints, are also important. When the rubber hand is positioned in an anatomically implausible posture (e.g., rotated by 90°

(Pavani et al., 2000; Tsakiris & Haggard, 2005) or by 180° (Ehrsson et al., 2004; Lloyd, 2007), the rubber hand illusion is abolished. The illusion is also significantly diminished when a left rather than right rubber hand is used instead in an experiment involving the participant's right hand (Tsakiris & Haggard, 2005). Thus, the match between the posture of the real hand and the observed posture of the rubber hand is an important factor in the creation of the illusion. This corresponds well with the fact that many multisensory neurons in the premotor and posterior parietal cortex are sensitive to both the felt and seen positions of the arm (Graziano, 1999; Graziano et al., 2000), and the greatest discharge rates are observed when the seen and felt impressions of the hand are spatially congruent (Graziano et al., 2000) .

Given this anatomical constraint, it is hardly surprising that the illusion does not work with objects that do not resemble a human hand at all, such as a stick or wooden objects (Tsakiris, Carpenter, James, & Fotopoulou, 2010; Tsakiris & Haggard, 2005). Armel and Ramachandran (2003) famously argued that a table could be made to feel like part of oneself, but if one looks carefully at their figures, one can see that both the questionnaire ratings of the illusion and their threat-evoked SCR, which served as their objective measure, were significantly lower when a table was used rather than a rubber hand (Armel & Ramachandran, 2003, p. 1503).

In summary, the natural constraints of the rubber hand illusion fit nicely with the multisensory integration hypothesis. Thus, the illusion is best explained in terms of the integration of all available temporally and spatially congruent visual, tactile, and proprioceptive information operating in spatial coordinates that are centered on the limb.

Neuroimaging Studies

Neuroimaging experiments have provided direct evidence that the rubber hand illusion is associated with activation of multisensory areas in the frontal and parietal lobes. We used fMRI to register the blood oxygenation level–dependent (BOLD) signal in the premotor cortex and intraparietal cortex during the rubber hand illusion (Fig. 43.3 [plate 41]) (Ehrsson et al., 2004). The experimental design consisted of independent manipulation of the temporal congruency of the tactile and visual stimuli and the spatial congruency in orientation between the real and the rubber hands (four conditions in a 2×2 factorial design). We observed greater activity bilaterally in the ventral premotor cortex and in the left (contralateral) intraparietal cortex in the
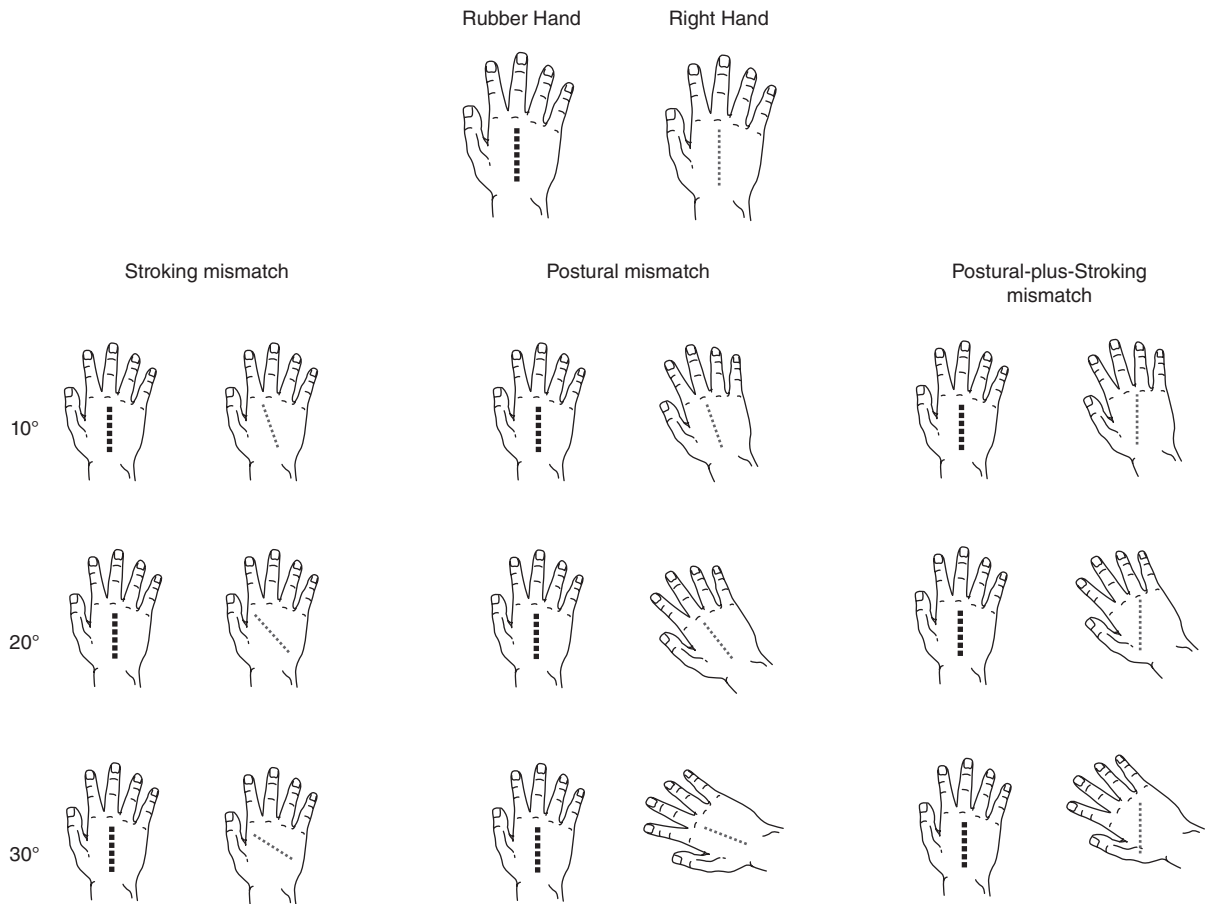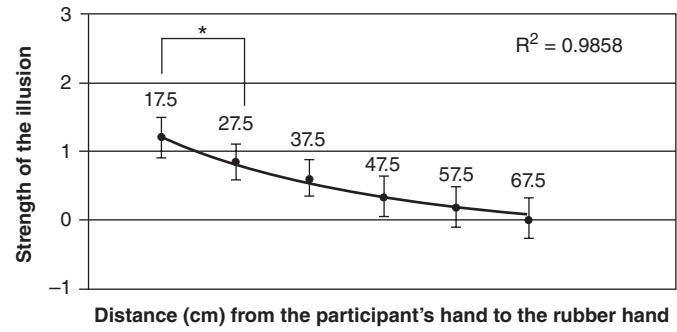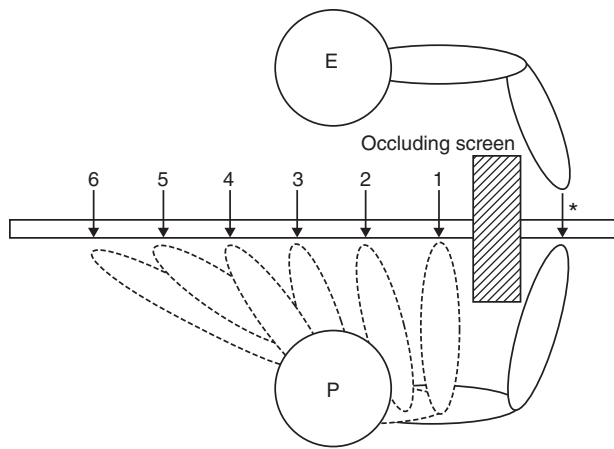
FIGURE 43.2   Behavioral evidence for spatial constraints and hand-centered reference frames in the rubber hand illusion. The top panel illustrates Lloyd's experiment (Lloyd 2007) demonstrating that the illusion is strongest when the rubber hand is placed within 30 cm of the real hand (near-personal space). The lower panel illustrates the experimental manipulation used by Costantini and Haggard (2007) to dissociate hand-centered and external coordinate systems. These authors independently and systematically varied the orientation of the hand and the direction of the brushstrokes on the hand (right hand, dotted lines). The illusion was maintained as long as the hand and the direction of the brushstrokes were rotated the same way (middle column). In these conditions the brushstrokes are isodirectional in hand-centered coordinates but not in external coordinates. In contrast, when only the hand was rotated (right column) or only the brushstrokes rotated (left column) the illusion was reduced, even though in the former case the brushstrokes were isodirectional in external coordinates. See text for further details.

condition with both spatial and temporal congruency than in any of the three control conditions in which temporal asynchrony or spatial incongruency was introduced (figure 43.3, plate 41). The intraparietal cortex was sensitive to both the orientation of the rubber hand and the synchrony of the visual and tactile stimuli. The level of activity in this area during the illusion condition seemed to reflect a summation of the effects of temporal and spatial congruency. The premotor cortex, on the other hand, showed an activation response that was even more specific to the illusion condition. This premotor activity was greater than would be expected from a linear summation of the effects of temporal congruency and spatial congruency; that is, the premotor activation reflected a *supra-additive effect*. In technical terms, this activation was revealed as a significant interaction effect in our factorial design. In a separate analysis, we found that the degree of activity in the ventral premotor cortex seemed to correlate with the subjectively rated strength of the illusion across individuals. The location of these activations in the premotor and intraparietal cortex, and how they are affected by the degree of visuotactile and visuoproprioceptive congruence is highly consistent with the multisensory hypothesis of body ownership (Makin et al., 2008). These brain imaging findings have been replicated with fMRI (Ehrsson, Holmes, & Passingham, 2005; Ehrsson, Weich, Weiskopf, Dolan, & Passingham, 2007), although a recent positron emission tomography (PET) study failed to do so (Tsakiris, Hesse, Boy, Haggard, & Fink, 2007), possibly because of the much poorer sensitivity of PET.
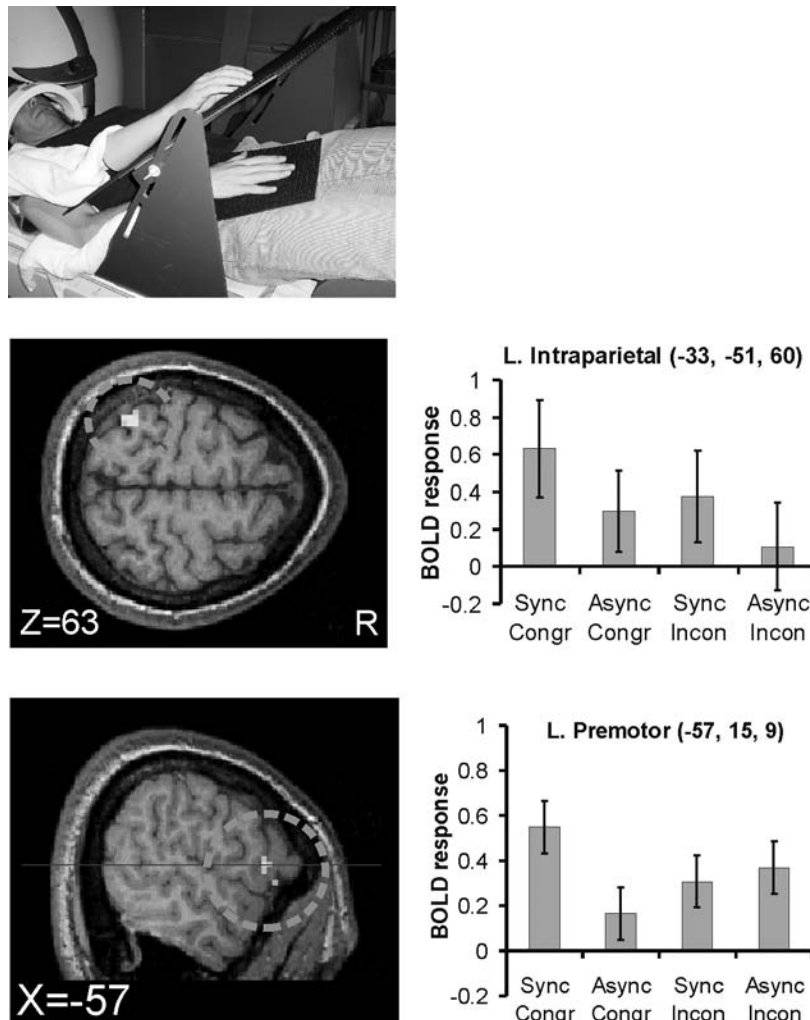

FIGURE 43.3 (PLATE 41) fMRI activations in multisensory areas during the rubber hand illusion (Ehrsson et al., 2004). The top panel shows the position of the participant in the scanner. Activity is seen in both the intraparietal sulcus (middle panel) and the ventral part of the premotor cortex (lower panel). The results of these experiments are summarized in the text.

Summary: A Multisensory Model of Limb Ownership

The behavioral and neuroimaging work discussed so far provide a strong case for the multisensory integrative hypothesis of limb ownership. Botvinick and Cohen's simple suggestion (Botvinick & Cohen, 1998) that the rubber hand illusion happens as a result of a three-way interaction among vision, touch, and proprioception is still consistent with the data. But from the new studies we have learned much more about the nature and details of these intermodal interactions. A substantial body of objective data now exists validating the rubber hand illusion as a good model system for limb ownership in normal individuals. We have learned that the mechanisms responsible for the elicitation of the illusion operate in near-personal space and use coordinates that are centered on the hand. We also know that the illusion is associated with activity in specific frontal and parietal multisensory areas, probably reflecting the underlying multisensory integrative processes. Thus, one possible scenario is that ownership of a hand corresponds to the perceptual fusion of visual, tactile, and proprioceptive inputs into one multisensory object that is one's hand. This perceptual fusion could be mediated by neuronal populations in the ventral premotor cortex, the intraparietal cortex, and other key multisensory sites that integrate visual, tactile, and proprioceptive information in common reference frames centered on the hand and arm. This thus represents a genuinely multisensory account of limb ownership in which the key causal mechanisms are considered to be implemented in the brain's multisensory perceptual systems. Further cognitive and emotional effects of the illusion are considered to be *consequences* of the causal multisensory mechanisms such as the fear experienced when an owned artificial limb is physically "hurt" or the participant's verbal reflections on the identity of the seen limb.

ALTERNATIVE EXPLANATIONS OF LIMB OWNERSHIP

Is Ownership the Same Thing as Visual Referral of Touch onto an External Object?

So far we have discussed a multisensory model of ownership that involves interactions among vision, touch, and proprioception. At this point a reader might ask if any alternative hypotheses exist? Let us first consider the possibility that the rubber hand illusion relies solely on visual and tactile signals. One possibility would be that the rubber hand illusion is produced by the bisensory visuotactile cells in the intraparietal cortex (Iriki et al.,

1996) that have been put forward as mediators of the referral of touch to the tips of hand-held tools (Paillard, 1993; Yamamoto, Moizumi, & Kitazawa, 2005). In this schema the visual capture of touch, purely driven by the visuotactile correlations, would explain ownership. However, this explanation does not explain why a match between the felt and seen posture of the hand is a fundamental constraint on the illusion. Furthermore, the tactile sensations sensed in hand-held tools are attributed to the external object being touched by the tips of the tool, in the same way as somatic sensations are attributed to external objects during manual exploration. Finally, phenomenologically, we do not experience tools as being part of our own body, and few of us would mistake a hammer for his/her own hand or be anxious if the hammer were to be threatened by a sharp object.

A purely visuotactile explanation for ownership is also unlikely, given that the rubber hand illusion can be produced without the hand being seen. Ehrsson et al. (2005) demonstrated that changes in hand ownership can occur in blindfolded participants in a somatic version of the rubber hand illusion (figure 43.1, central panel). In this experiment, the investigator moved each blindfolded participant's left index finger so that it touched the knuckle of a right rubber hand; at the same time the investigator touched the participant's right hand on the knuckle on the corresponding site. After 10–15 sec, most participants started to have the experience that they were touching their right hand directly with their left one. This effect depended on synchronization of the touches applied by the left finger and those perceived on the right hand; an asynchronous mode of stimulation abolished the illusion. Likewise, the illusion was significantly reduced when the rubber hand was replaced with an object that did not feel like a hand at all (in this instance, a small dish brush). Thus, it is the integration of functionally meaningful correlations among all available sensory data that seems to be crucial for ownership, and not vision per se.

Is Ownership the Same as Proprioceptive Recalibration?

Another seductively simple explanation would be to say that the feeling of ownership is really the same thing as a recalibration of the sense of hand position. However, we know that recalibration of the *felt* hand position can occur independently of the illusion of ownership (Holmes, Snijders, & Spence, 2006). Furthermore, the proprioceptive drift is never absolute; subjects report a drift of only about 15–30% of the full distance between the real hand and the dummy hand (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005). Further-

more, the time courses of ownership and propriocep-tive drift are different: the illusion of owning the hand can occur as early as 6 to 11 sec after the onset of simul-taneous stroking (Ehrsson et al., 2004; Lloyd, 2007), but the proprioceptive drift continues to increase after the illusion has begun, sometimes for several minutes (Tsakiris & Haggard, 2005; Tsakiris et al., 2007). For similar reasons, it is unlikely that the feeling of owner-ship is the same thing as the visuoproprioceptive recali-bration that occurs during prism adaptation (Welch, 1986). Massive adaptation to wearing a displacing prism can occur without any noticeable changes in ownership. Similarly, a match between the seen and felt orientation of the hand is not sufficient; just looking at the rubber hand, with no simultaneous brushing or other dynamic somatic cues, does not produce a strong illusion (Longo, Cardozo, & Haggard, 2008).

Is Ownership an "Interoceptive" Sensation Produced by the Posterior Insula?

It has been proposed that the subjective experience of body ownership is underpinned by activity in the poste-rior insular cortex (Tsakiris, 2009). This is an interest-ing hypothesis, as lesions involving this region can cause denial of ownership in stroke patients (Baier & Karnath, 2008; Karnath, Baier, & Nagele, 2005), and a PET study found a correlation between the proprioceptive drift and the activity in this region across scans (Tsakiris et al., 2007). The posterior insula is the cortical target of C-fiber-mediated afferent input from the body signaling pain, temperature, pleasant touch, and muscle fatigue and part of a system that, together with the anterior insula and the anterior cingulate cortex (ACC), medi-ates homeostatic emotions and bodily interoceptive sensations (Craig, 2002). Activation of this system (in the anterior insula and ACC) is seen when *owned* body parts are under physical threat (Ehrsson et al., 2007). However, it is unclear if the engagement of this system represents a causal mechanism of ownership or is simply a consequence of ownership in the multisensory areas. A limitation of the insula/interoceptive account of own-ership is that it does not explain the temporal and spatial constraints or the illusion.

UNRESOLVED ISSUES AND DIRECTIONS FOR FUTURE RESEARCH

Owned Rubber Hands in Action

Humans use their hands to interact with objects and tools, making it important to understand the relation-ship between ownership and action. The rubber hand

illusion can be induced in passive participants, so active formation of motor commands does not seem to be a necessary condition for changes in ownership to occur. However, information about motor commands and the sensory predictions they produce could still provide information that could be used in the self-attribution process. We know that the rubber hand illusion can be elicited with active and passive movements instead of brushstrokes or touches applied by the experimenter (Dummer, Picot-Annand, Neal, & Moore, 2009; Kalck-ert & Ehrsson, unpublished data; Tsakiris, Prabhu, & Haggard, 2006). This demonstrates that the dynamic somatic input from a moving digit can act as a substitute for the dynamic tactile input from the brush strokes in the classical rubber hand illusion. More importantly, if information about the motor commands is used in the self-attribution process, then the illusion should be stronger when the movements are produced actively, but we have no conclusive evidence of this (Dummer, et al., 2009; Tsakiris, et al., 2006). We also need to figure out if the feeling of ownership is modulating the experi-ence of being in control of bodily movements (the sense of agency) (Farrer et al., 2003; van den Bos & Jeannerod, 2002), and vice versa. Indeed, such a link might seem plausible given that the multisensory responses related to ownership occur in the premotor cortex, which traditionally is considered to be a motor area (Rizzolatti, Fogassi, & Gallese, 2002).

Individual Differences

If we return to the traditional rubber hand illusion, it is a striking observation that not all people experience it, and we do not know why. Approximately 30% of the population seems to be "immune" to its induction (Ehrsson et al., 2004; Lloyd, 2007). We need to know more about individual differences in the flexibility of inducing changes in ownership. A multisensory account of the illusion would predict that differences in the susceptibility of the illusion should relate to how differ-ent brains put different weighting on visual, tactile, and proprioceptive information in the integration process (van Beers et al., 1999). In this view, people who have refined the usage of their body (such as dancers, gym-nasts, and guitarists), and are therefore better at relying on proprioceptive information, should be more resis-tant to the illusion than the average person.

Ownership and Multisensory Predictions

We also need to know more about the relationship between ownership and the generation of multisensory predictions (Friston, 2005; von Kriegstein et al., 2008).

Anecdotally, people say that they expect to feel the touch of the paintbrush when it is approaching the hand. Possibly, such sensory predictions could explain why repeatedly stroking a rubber hand with the bright beam of a laser pointer produces tactile and thermal sensations without any somatic stimulation of the hidden real hand (Durgin, Evans, Dunphy, Klostermann, & Simmons, 2007).

Probabilistic Models of Ownership

In a similar way more modeling work is required to relate the rubber hand illusion to probabilistic models of multisensory integration (Angelaki, Gu, & DeAngelis, 2009; Ernst, 2006; Kording et al., 2007; Pouget et al., 2002). This might help to explain why some people can experience a *three-arm illusion* (Ehrsson, 2009) (figure 43.1, right panel). In this experiment, two rubber hands were placed side by side and both were brushed simultaneously with a "twin-brush" in synchrony with brushing being applied to the hidden real hand. This produces an illusion of owning both hands and the sensation of feeling two touches, one on each rubber hand. Speculatively, this could indicate that the brain is capable of representing the hand in two equally probable locations simultaneously, maybe as a biphasic probability distribution of hand location.

OWNERSHIP OF ENTIRE BODIES

So far in this chapter, we have only considered cases in which people experience changes in the ownership of a single limb. Is it possible, though, to change ownership of an entire body by manipulating multisensory correlations? New experiments suggest that it is. We had participants wearing head-mounted displays (HMDs, computer display devices that are worn on the head in front of their eyes) that were connected to two closed-circuit television cameras (figure 43.4A) (Petkova & Ehrsson, 2008). The two cameras were attached to a helmet worn by a life-size mannequin and positioned so that they were looking down on the mannequin's body with stereoscopic vision. Thus, when the participants wore the HMDs connected to these cameras and looked down, they saw the mannequin's body in a similar location to that where they would expect to see their own real body. When the experimenter used a couple of rods to touch the mannequin's belly and the person's belly simultaneously at corresponding sites for a minute, the majority of the participants began to have the experience that the mannequin's body was their own. This effect was quantified with questionnaires and by registering the skin conductance responses when the participants observed a knife cutting the belly of the mannequin. The responses observed after the illusion condition were greater than those after various appropriate control conditions. Importantly, this illusion, just like the rubber hand illusion, seems to obey the spatial and temporal congruency principles. Asynchronous visual and somatic stimulation, replacement of the mannequin by a block of wood, or presentation of the mannequin 2 m in front of the participant, which is outside the person's near-personal space, were all conditions that eliminated or strongly reduced the illusion (Petkova & Ehrsson, 2008; Petkova, Khoshnevis, & Ehrsson, 2011). Thus, temporally and spatially matching visual, tactile, and proprioceptive information in coordinates centered on an artificial body is sufficient to produce a sense of ownership of an entire body.

Interestingly, this full-body illusion does not break down even if one sees the real body. In a recent manuscript we showed that correlated visual and tactile stimulation can produce an "out-of-body illusion" in which people experienced being in a different place in the room and looking at themselves from the perspective of another individual (figure 43.4B) (Ehrsson, 2007). The participants in this study wore head-mounted displays that were connected to two closed-circuit television cameras placed about 1.5 m behind them. The two cameras provided a stereoscopic image, enabling the participants to see themselves from the point of view of the cameras, that is, from behind. The experimenter then jabbed a rod toward a location just below the cameras while simultaneously touching the participant's chest, which was out of view. The visual impressions of a hand approaching a point below the cameras and the touch felt on the chest led the participants to experience the illusion of being located 1.5 m behind their real body. Interestingly, many individuals reported having the feeling that their real body, which they observed from the back, belonged to someone else; that is, they seemed to experience a partial loss of self-identification with their own body. Similar to the rubber hand illusion, physical threats to the "illusory body" below the cameras produced enhanced SCRs.

We have recently taken this illusion one step further and demonstrated that it can be maintained even when the participants are shaking hands with their real body (Petkova & Ehrsson, 2008). In this experiment, the two CCTV cameras were mounted on the investigator's head and connected to the HMDs worn by the participants, who then looked at themselves from the investigator's perspective (figure 43.4C). When the investigator and the participant repeatedly squeezed their hands in
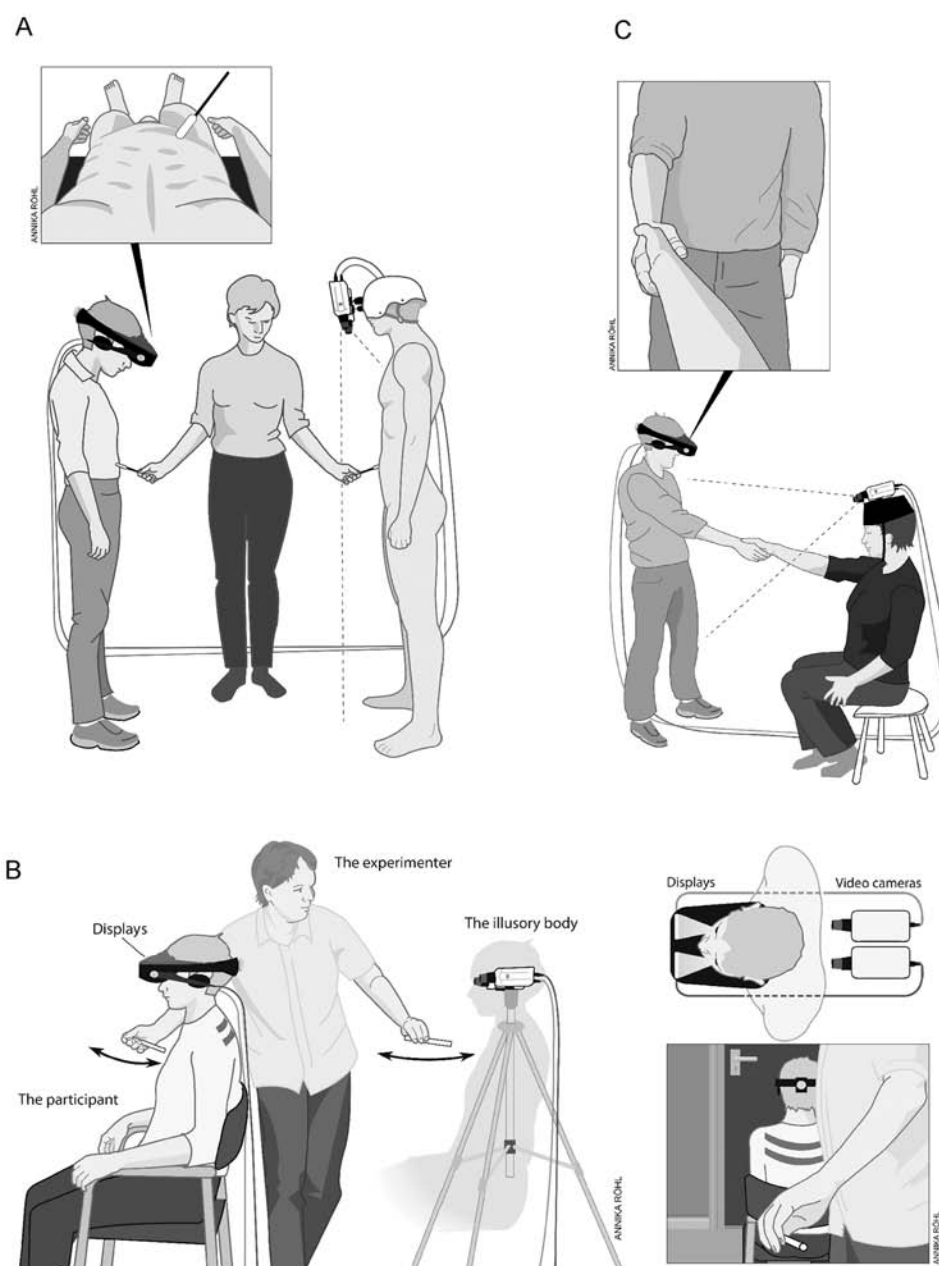
FIGURE 43.4   Eliciting illusions of entire bodies. (A) The *mannequin illusion* (Petkova & Ehrsson, 2008) and the participant's perspective in this illusion. (B) The *out-of-body-illusion* (Ehrsson, 2007) and what the participants see. (C) The 'body-swap illusion' and the participant's perspective (Petkova & Ehrsson 2008). In all experiments the participants are wearing a set of head-mounted displays connected to two video cameras placed on the mannequin's head (A), a tripod 1.5 m behind the participant (B), or on the head of the investigator (C). Synchronous somatic and visual events are provided by touches applied to the mannequin's belly and the participant's belly (A), the participant's chest and the "chest" of the "illusory body" (B), or by the repetitive squeezing of the hands (C). For further details, see text.

a synchronized fashion, most participants experienced an illusion of being "inside" the investigator's body and owning the investigator's hand. Strikingly, people were more scared when they saw a knife threatening the investigator's arm than when the knife threatened their real hand during the illusion, as indexed by the SCRs. These "out-of-body" illusions corroborate the importance of multisensory correlations in body-centered reference frames for ownership. Furthermore, they show that the sense of where one is located in the

environment can be determined by the multisensory correlations and the first-person visual perspective, hence the experience of being outside the seen veridical location of the body.

THE ROLE OF THE VISUAL FIRST-PERSON PERSPECTIVE

The importance of near-personal space and the visual first-person perspective for body ownership seems to be contradicted by the results presented in a set of experiments on full-body ownership from Blanke's research team (Aspell, Lenggenhager, & Blanke, 2009; Lenggenhager, Mouthon, & Blanke, 2009; Lenggenhager, Tadi, Metzinger, & Blanke, 2007). In their approach, the participants looked at a mannequin's body presented a few meters in front of them with a head-mounted display set (Lenggenhager et al., 2007). Thus, the participants saw the back of the plastic body as it was touched in synchrony with their own back. This resulted in self-identification with the "virtual" body and the reported experience that the touches they saw being applied to the mannequin were being applied directly to them (Lenggenhager et al., 2007). This result apparently suggests that ownership and the sense of touch can be projected to a body in far extrapersonal space observed from a third-person perspective, directly contradicting the spatial constraints of the rubber hand illusion (Ehrsson & Petkova, 2008).

One possibility is that the reported self-identification with the mannequin in the setup used by Blanke and colleagues is akin to self-recognition in mirrors or on TV screens. It is well known that correlations between visual and somatic information are used when we recognize ourselves on TV screens or in mirrors. But this type of self-recognition does not involve an explicit body illusion like the rubber hand one. Instead one's perceptual system has learned the spatial transformation of the mirror or the video system so that one can associate somatic events on one's own body with visual events on the body in far extrapersonal space or in the mirror. Interestingly, Altschuler and Ramachandran have recently reported how the recognition of oneself in mirrors could be manipulated by discrepancies between visual and tactile impressions (Altschuler & Ramachandran, 2007). Thus, in Blanke's group's experiments, people might develop a feeling that they are looking at their own back being filmed from behind. This probably would require cognitive spatial transformations, possibly involving the temporoparietal junction, as this region seems to be engaged when people imagine mental rotations of a body in space (Arzy, Thut, Mohr, Michel, & Blanke, 2006; Blanke et al., 2005).

FULL-BODY OWNERSHIP VERSUS OWNERSHIP OF INDIVIDUAL BODY PARTS

An important question is whether owning an entire body is just the sum of ownership of all body parts, or if full-body ownership requires fundamentally different cognitive processes (Blanke & Metzinger, 2009). As of this date we have no data that directly support the latter claim; however, it is reasonable to assume that ownership of entire bodies might activate more neurons with large RFs covering multiple body parts. In higher-order somatosensory areas, area 5 neurons have large RFs often involving multiple limbs and body parts (Iwamura, 1998), and in the premotor cortex, Graziano described bisensory neurons with RFs involving multiple body parts and even the entire body (Graziano & Gandhi, 2000). Another possible difference is that ownership of entire bodies might involve changes in allocentric representations of where one is located with respect to environmental landmarks (allocentric coordinates). Thus, full-body illusions could involve a spatial *place* illusion, in addition to the body ownership illusion, which could then be expected to involve neural processing in the hippocampus, retrosplenial cortex, precuneus, and inferior parietal cortex (Burgess, 2006; Maguire et al., 1998).

CLINICAL APPLICATIONS

Manipulation of Pain Perception via Manipulation of Body Ownership

We know that being able to see a limb improves the tactile perception from that limb (Kennett, Taylor-Clarke, & Haggard, 2001; Taylor-Clarke, Kennett, & Haggard, 2002; Tipper et al., 1998). One recent study suggests that visual input from a hand also reduces the perceived intensity of pain (Longo, Betti, Aglioti, & Haggard, 2009). Does the feeling of ownership of the rubber hand similarly cause changes in tactile and pain perception of the real hand? Clinically, the latter is a very interesting question, as it has the potential to enable "rubber hand illusion therapy" to treat neurological pain syndromes. This could complement mirror-box treatment of phantom limb pain (Ramachandran & Rogers-Ramachandran, 1996), in which visual impressions of the lost limb are considered to produce a reduction in pain (Chan et al., 2007; Moseley, Gallace, & Spence, 2008; Ramachandran & Altschuler, 2009). A potential link between pain perception and ownership is encouraged by the fact that there is a slowing down of tactile perception on the hidden real hand during the rubber hand illusion (Folegatti, de Vignemont,

Pavani, Rossetti, & Farne, 2009; Moseley, Olthof, et al., 2008), suggesting that ownership might modulate somatic perception. Whether ownership also modulates pain perception is still an open question.

Projection of Ownership onto Advanced Hand Prostheses

The projection of ownership and sense of touch to advanced hand prostheses represents another interesting clinical direction of body ownership research. In principle, by connecting sensors in the artificial limbs to electrodes in the primary somatosensory cortex (London, Jordan, Jackson, & Miller, 2008) or peripheral nerves (Kuiken et al., 2007; Navarro et al., 2005), one could effectively create tactile sensibility and ownership in the prosthetic limb. However, these emerging approaches are invasive and associated with major technical challenges. A simpler approach would be to use the rubber hand illusion to project ownership and somatic sensations onto the prosthesis by tricking the brain. A first pilot study suggests that synchronized brushing of the participant's stump and the finger of a prosthetic hand does indeed produce the rubber hand illusion in some amputees (figure 43.5) (Ehrsson et al., 2008). Before these experiments were conducted, the presence of a "map" of referred phantom sensations on the stump was carefully established for each participant (figure 43.5, left panel). If the person had such a map including the index finger, that very spot could be touched. Six of the 18 participants reported strong sensations of touch from the prosthesis when the relevant part of their stump was touched and reported developing a sense of ownership of the artificial hand. This effect was supported by a version of the proprioceptive drift measure and SCR registration when the prosthesis was stabbed. With respect to the mechanism, it could be that the brushstrokes applied to the stump elicit referred tactile sensations in the phantom index finger and that the sight of the brush touching the rubber hand produced the rubber hand illusion using the same multisensory processes involved in the rubber hand illusion in normal individuals (as outlined above). These observations suggest that, in principle, it should be possible to design prostheses equipped with tactile sensors in the fingertips that can be connected to an array of tactile simulators on the stump that would reproduce the illusion recounted here during everyday usage (Rosén et al., 2009). This method could provide a relatively easy way to restore rudimentary tactile sensibility in the prostheses, which would complement existing approaches to the provision of sensory feedback from prosthetic limb devices (Lundborg & Rosen, 2001).

Projection of Ownership to Simulated Bodies in Virtual Reality

A new direction in virtual reality research is to use body illusions to project ownership onto virtual limbs and bodies in simulated environments (Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2009) (figure 43.6). This could improve present-day applications in education, communication, medicine, and entertainment. The first crucial step has already been taken in a replication of the rubber hand illusion with an entirely virtual three-dimensional arm and hand—not only was the arm virtual, but the object seen to be touching it was virtual too (Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2008) (figure 43.6, top panels). More recent experiments have shown that people can maintain

FIGURE 43.5   Inducing the rubber hand illusion in amputees. (Left) The maps of referred tactile sensations to the phantom in one upper limb amputee. (Middle) Simultaneous brushing of the index finger of the cosmetic prosthesis and the finger zone of referred sensations in the stump (Ehrsson et al., 2008). (Right) This illusion can also be induced in a more advanced humanoid robotic hand prosthesis using the same procedure (SMARTHAND) (Rosén et al., 2009). These experiments are discussed more fully in the text.

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FIGURE 43.6 Replication of the rubber hand illusion with simulated hand and object (top two panels) and ownership of an entire simulated body in virtual reality (lower panel). The participants see a simulated ball touching a simulated arm (top panels). The movement of the virtual ball is controlled by the wand used by the experimenter to touch the participant's real hand, thus producing synchronous visuotactile stimulation. (From Slater et al., 2008). See the text for details.)

ownership of a virtual hand as long as its movements are temporally and spatially congruent with movements of the real hand (Slater et al., 2009). Further experiments have begun to reproduce the full-body illusion of Petkova and Ehrsson (2008) using simulated bodies (Slater et al., 2009) (figure 43.6, lower panel). An interesting development of this line of research would be to investigate the degree to which an owned virtual limb could be controlled directly via the participant's brain activity through a brain-computer interface (BCI) (Perez-Marcos, Slater, & Sanchez-Vives, 2009). In principle, this could be used to allow paralyzed people to own a virtual limb and use it as a real one in various virtual and mixed-reality applications.

CONCLUSIONS

This chapter has reviewed the multisensory hypothesis of body ownership. A large body of behavioral and neuroimaging data supports the hypothesis that self-attribution of limbs and other body parts depends on the integration of multisensory signals operating in body part-centered coordinate systems. The strength of tackling this problem from a multisensory perceptive is that it provides a parsimonious explanation of body ownership that does not require the inclusion of higher cognitive functions, which are often hard to define and even harder to relate to neuronal mechanisms. The perceptual distinction between one's own body and the environment could create the necessary foundation for higher cognitive functions related to self-consciousness to emerge, such as reflective self-awareness and the autobiographical self.

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