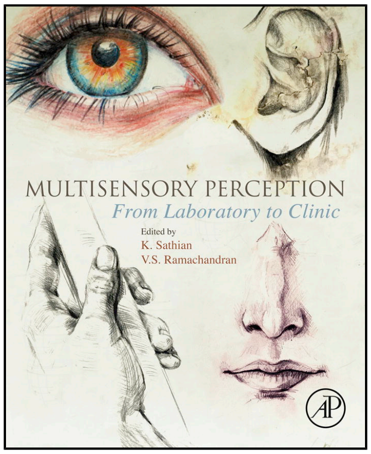

From Ehrsson HH. Multisensory processes in body ownership. In: Sathian K, Ramachandran VS, eds. Multisensory Perception: From Laboratory to Clinic. Academic Press: Elsevier; 2020:179–200.
ISBN: 9780128124925

Academic Press

CHAPTER

8

Multisensory processes in body ownership

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Introduction

On looking at one's own hands, one immediately recognizes to whom they belong. One automatically senses that these extremities are part of one's own body without the need to actively think about it. This percept of a body part or entire body as belonging to oneself is called the sense (or feeling) of *body ownership*.[1–5] The perceptual distinction between what is part of one's body and what is not is critical for survival and thus fundamentally important for human perception, action, and cognition. Moreover, the sense of one's own body is the centerpiece of human conscious experience because it is from the perspective of this bodily self that a person becomes aware of his or her surroundings. Importantly, the sense of body ownership is multisensory in nature and cannot be easily reduced to a single sensory modality. The crucial aspect seems to be how all the impressions from the different sensory modalities come together into a coherent percept of a single owned body part (or body). This includes the feeling of the skin stretching around the digits and joints, the feeling of coolness or warmth at the surface of the skin, the pressure and tension on the muscles and tendons, and perhaps an ache in the wrist from yesterday's tennis match. Thus, the various sensations originating from the body and reaching the brain through different peripheral and central pathways are effortlessly blended together into coherent percepts of one's own body parts. The way the sense of body ownership emerges from the combination of individual sensory inputs is thus somewhat similar to the way one recognizes the taste of one's favorite red wine as a distinct yet rich composite of various tastes, smells, and visual impressions. When viewed in this way, the term "*sense* of body ownership" is a misnomer, strictly speaking, because it is not referring to a single basic sense analogous to touch or olfaction, but rather a *perception* of one's own body that arises from interpretation of different kinds of afferent sensory signals. In this chapter, we will consider the problem of body ownership from the perspective of multisensory perception and integration, focusing

Multisensory Perception
https://doi.org/10.1016/B978-0-12-812492-5.00008-5

Multisensory Perception, First Edition, 2020, 179–200

on recent behavioral and neuroimaging studies in humans that have addressed this issue experimentally.

A good starting point for our discussions is a set of interesting observations published in the neurological literature. We know that people with damage to their frontal and parietal lobes can sometimes fail to recognize their paralyzed limbs as their own (asomatognosia: loss of ownership of a limb; somatoparaphrenia: denial of ownership of a limb and confabulatory attribution of this limb to another person).[6–11] This inability cannot be explained by basic sensory impairments of vision or touch, as these individuals do see that they are looking at a hand and can sometimes perceive somatic stimuli applied to the affected limb. Instead, these neurological observations suggest that nonprimary areas in the frontal and parietal association cortices that have the capacity to integrate visual and somatosensory impressions are responsible for generating the feeling of owning limbs. However, it is difficult to make inferences about the specific perceptual processes and neuronal mechanisms involved in body ownership from neuropsychological studies alone because the lesions are typically large, involving multiple areas and damaging the underlying white matter that connects different parts of the brain.

Twenty years ago, a paper was published that sparked the modern interest in experimental studies of body ownership[12] (for an earlier anecdotal observation see Ref. 13). In this article, now cited over 1500 times according to Web of Science, the authors described a fascinating perceptual illusion called the rubber hand illusion.[12] To elicit this illusion, the experimenter keeps the participant's real hand out of the field of vision (behind a screen, under the table, or under a box) while a realistic life-sized rubber hand is placed in front of the participant (Fig. 8.1A). The experimenter—or an apparatus—uses two small paintbrushes to stroke the rubber hand and the participant's hidden hand, synchronizing the timing of the brushing as accurately as possible. After a short period of repeated stroking, approximately 10 seconds on average,[14,15] the majority of people perceive that the rubber hand is their own hand and that it senses the touches of the paintbrush. The illusion can be quantified subjectively with questionnaires and visual analogue rating scales,[12,16] behaviorally as changes in reported hand location toward the location of the rubber hand ("proprioceptive drift"),[12,17]

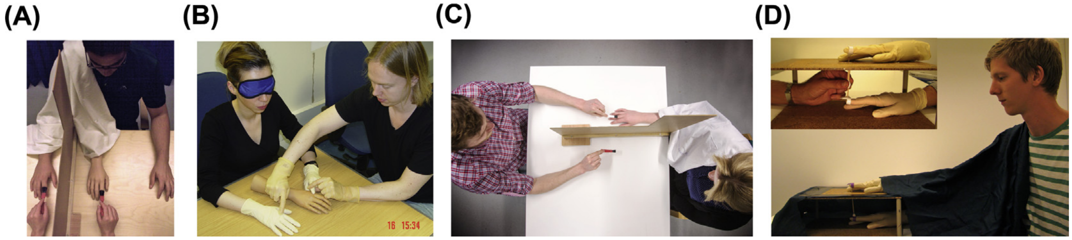

FIGURE 8.1 Induction of the classical version of the rubber hand illusion[12] with synchronous brushstrokes applied to the rubber hand, which is in view, and the participant's real hand, which is hidden (A). The somatic rubber hand illusion[70] with a blindfolded participant is elicited by having the participant touch the rubber hand with her left index finger at the same time as she receives touches on her real right hand (B). The invisible hand illusion[42] was induced by stroking "empty space" and the participant's hidden real hand with very well-matched spatiotemporal stroking patterns (C). The moving rubber hand illusion[58] was produced by congruent movements of the rubber hand's index finger and the participant's real index finger (D).

and physiologically by recording skin conductance responses when the rubber hand is physically threatened or "injured"[18] (for further discussions of these and other proposed methods, see Ref. 2,19−23). What made this illusion so popular was that it provided scientists with a model system in which to start to experiment with the sense of body ownership: one moment the participant is looking at a lifeless piece of rubber, and the next moment the rubber hand "comes alive" and becomes part of the participant's perceived body, with the subjective feelings associated with a real limb. This explicit change in the sense of ownership of the rubber hand is what sets this illusion apart from other well-known body illusions that involve stretching, moving, or dislocating limbs and body parts.[24−27] By systematically investigating the perceptual rules that govern the rubber hand illusion and similar body ownership illusions (see below) and by clarifying the associated neuronal substrates of such illusory percepts with human brain imaging experiments, a great deal can be learned about how the sense of ownership is generated under more natural conditions. In this chapter, we will consider body ownership from a multisensory perspective, focusing on the multisensory processes that underpin this perceptual phenomenon. In particular, we will review studies that show that body ownership shares many perceptual and neural similarities with fundamental principles of multisensory integration, and we will discuss the parsimonious hypothesis that body ownership can be explained as coherent multisensory perception of one's own body. We will not have time to discuss the fascinating philosophical implications of experimental body ownership research.[28] Alternative models of body ownership that are not based on multisensory perception,[29] models in which multisensory interactions are considered only at the initial stage in a more complex cognitive architecture,[3] and self-models based on predictive coding principles[30−32] are also beyond the scope of the present discussion. The overall structure of this chapter is that we will start by reviewing behavioral studies of the limb ownership and rubber hand illusions, move on to the topic of functional magnetic resonance imaging (fMRI) studies that have sought the neural correlates of limb ownership, and, finally, turn to the issue of how a person comes to experience ownership of an entire body.

Perceptual rules of body ownership

One important goal for behavioral studies of body ownership has been to work out the basic perceptual rules that determine the elicitation of ownership sensations. By clarifying the fundamental constraints on the factors that elicit body ownership illusions, we can ascertain what kinds of processes are likely to mediate this perceptual phenomenon. As will be discussed in detail below, the basic rules of body ownership bear striking similarities to the temporal and spatial congruency principles that determine multisensory integration in general,[33−35] see chapter by Stein and Rowland, this volume. These principles state that when two (or more) signals from two (or more) different sensory modalities occur at the same time (temporal principle) and in the same place (spatial principle), they will be integrated, and multisensory perceptual unity will be experienced. The congruency of other stimulus features that influence multisensory binding, such as texture, shape, and orientation,[35,36] also influences body ownership. The observation that the sense of body ownership is governed by the same principles as multisensory perception suggests that multisensory integration mechanisms play a critical role in this self-perceptual phenomenon.

Temporal rule

The feeling of ownership of a limb depends on the temporal synchrony of multisensory cues from that limb. Rubber hand illusion studies have repeatedly shown that the illusion is abolished under asynchronous control conditions in which visual and tactile stimulation have a temporal mismatch on the order of 500–1000 ms.[14,17,18,37] When the temporal delay between the visual and tactile stimulations was systematically varied, delays longer than 300 ms were found to significantly reduce the illusion[38–40] (Fig. 8.2B). Moreover, the degree of asynchrony necessary to eliminate the rubber hand illusion is related to the individual's general perceptive sensitivity to asynchrony during visuotactile stimulation.[41] Thus, there exists a systematic relationship between the temporal constraint of the rubber hand illusion and the temporal binding window of vision and touch. The importance of the temporal congruency of the somatosensory and visual events in the rubber hand illusion fits well with the temporal congruency principle in multisensory integration.[33,34]

It should be made clear that the elicitation of the rubber hand illusion requires a series of correlated synchronous (or near synchronous) visuotactile stimuli applied to the hands, usually on the order of at least five to six seen and felt strokes in participants susceptible to the illusion.[14,42] Anecdotally, an irregular pattern of simultaneous strokes gives a stronger illusion than a strictly regular pattern gives.[43] Thus, the temporal structure of the correlated signals seems to be a factor that influences the illusion over and above temporal coincidence.

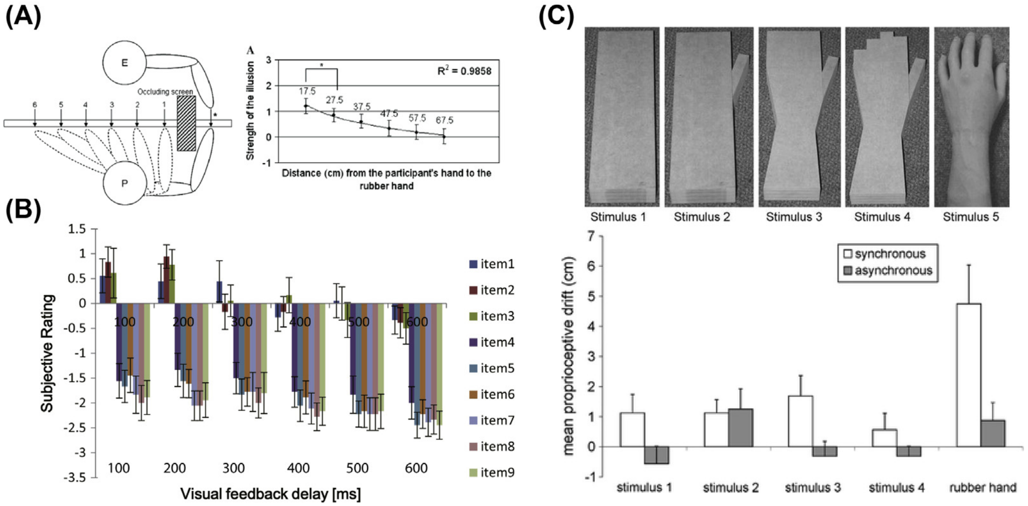

FIGURE 8.2 The distance rule of body ownership (A). The rubber hand illusion is strongest for distances less than or equal to 27.5 cm between the rubber hand and the real hand.[15] The temporal congruency rule of body ownership (B). The rubber hand illusion is reduced as the asynchrony of seen and felt strokes increases, with asynchronies of more than 300 ms breaking the illusion.[39] Items one to nine relate to the statements in a questionnaire, where statements one to three refer to the rubber hand illusion, and the others are controls for suggestibility and task compliance. The humanoid shape rule of body ownership (C). Only the realistic-looking prosthetic hand elicits the rubber hand illusion (top panel; stimulus 5, the rubber hand), and the other wooden objects with varying degrees of resemblance to a hand do not[66]; the lower panel shows a behavioral index of the illusion (proprioceptive drift) for each of the five objects tested.

This is in line with studies on audiovisual integration[44−46] that have shown that temporal correlation influences multisensory integration by strengthening the inference that the signals have a common cause. Future experiments should characterize exactly how the fine-grained patterns of temporally correlated multisensory signals influence body ownership.

Spatial rule(s)

The rubber hand illusion also depends on the spatial congruence of the various sensory signals. There are several spatial factors that influence the rubber hand illusion, such as the relative directions and locations of the tactile and visual stimulation on the seen rubber hand and the unseen real hand, the relative orientations of the two limbs, and the distance between the real hand and the rubber hand (*distance rule*), which will be discussed first. Lloyd[15] parametrically varied the distance between the rubber hand and the hidden real hand, and she found a significant decrease in the strength of the illusion for distances greater than 27.5 cm in the horizontal plane (Fig. 8.2A). Kalckert and Ehrsson[47] obtained a very similar result when examining the effect of vertical distance between the hands. These are interesting observations because the dimensions approximately match the extent of *peripersonal space* (the space immediately surrounding our bodies[48]) around the upper limb as estimated in electrophysiological[49,50] and neuropsychological[51] studies. In addition, Preston found that the strength of the illusion is affected not only by the distance between the rubber hand and the participant's real hand but also by the distance between the model hand and the participant's trunk and by whether the model hand was placed laterally or medially with respect to the participant's hand[52]; all these observations are compatible with multisensory processing in various body part−centered spatial reference frames (a combination of the hand and the trunk, for example). The fact that the limb ownership illusion can be maintained with a slowly elongating virtual arm[53] does not falsify the spatial distance rule because, in this case, peripersonal space probably gradually extends outward along with the flexible representation of the stretched arm.[25] Collectively, the above observations fit with the notion that peripersonal space is a basic constraint of body ownership illusions, which, in turn, suggests that the integration of multisensory signals in body ownership occurs in spatial reference frames centered on the body and its parts.

Another important aspect of the spatial principle is that the seen and felt brushstrokes must be in the same *direction* on the rubber hand and the real hand.[42,54,55] Importantly, "same direction" is defined with respect to a spatial reference frame centered on the hands, such that if, say, the right rubber hand is rotated 20 degrees counterclockwise (toward the body midline) while the hidden real hand is oriented straight ahead, then the strokes applied to the rubber hand must also be rotated 20 degrees counterclockwise to maintain spatial congruence with the straight strokes applied to the real hand.[54] This corresponds well with the notion that the illusion requires multisensory processing performed in body part−centered spatial coordinate systems.[50,56]

However, the rubber hand illusion is not constrained only by spatial factors relating to vision and touch. The spatial congruency between visual and proprioceptive information about the orientation of the hand and arm is also important (*orientation rule*). When the rubber hand is rotated by 90 degrees[17,57] or by 180 degrees[14,58] with respect to the real hand, the rubber hand illusion is abolished. Similarly, when the participant's real hand is rotated

90 degrees medially while the participant looks at a video image of his or her hand pointing straight ahead, i.e., 90 degrees mismatch between the seen and felt hand positions, the feeling of ownership of the seen hand is eliminated.[55] In addition to orientation congruency, the "anatomical plausibility" of the rubber hand is also important. Ide presented the rubber hand rotated by 0 degrees, 45 degrees, 90 degrees, 180 degrees, 225 degrees, 270 degrees, and 315 degrees and found significantly stronger illusions for angles that were anatomically plausible in that they were easy to mimic with the real hand (0 degrees, 45 degrees, 90 degrees, 315 degrees) than for implausible angles (180 degrees, 225 degrees, 270 degrees).[59] As expected, the strongest illusion was seen for 0 degrees, when the rubber hand was presented in the same orientation as the hidden real hand. In a similar vein, the illusion is extinguished when a left rather than right rubber hand[17] or a right rubber foot rather than a right rubber hand[60] is used in experiments involving the participant's right hand. One recent study even suggests that, with a certain set of experimental procedures, the rubber hand illusion can be elicited solely by the congruent orientation of the seen and felt hands, without any application of synchronous brush stroking[61] (however, no such effect was seen in Ref. 62). Intriguingly, one recent paper argued that a weak rubber hand illusion could be elicited when the rubber hand and the real hand were placed in different postures (palm up vs. palm down).[63] However, the questionnaire ratings of ownership were relatively low for incongruent postures, and no significant behavioral effect was observed on the proprioceptive drift test. Moreover, this study did not directly compare congruent and incongruent hand postures, meaning that the effect of postural congruency was not tested. Thus, collectively, the available data on the matter strongly suggest that the match between the seen and felt orientations of the hands is an important spatial factor in the rubber hand illusion.

Tactile congruence rule

After discussing the effects of spatiotemporal congruence, we turn to congruencies among other stimulus properties, beginning with tactile congruence between the seen and felt touches. A recent study has found that the rubber hand illusion depends on the congruency of the tools used to stroke the rubber hand and the real hand.[64] Tactile incongruence was created by touching the rubber hand with a pencil and the real hand with a paintbrush, and this led to significant reductions in the strength of the illusion. Interestingly, when more similar tools were used that differed only in terms of roughness or smoothness—a paintbrush versus a mascara brush,[64] or a piece of cotton versus a rough sponge[65]—no significant effect on the illusion was observed. It is not entirely clear why no effect was observed for these subtler incongruencies. This observation might reflect the limited sensitivity of the questionnaires and proprioceptive drift tests used to quantify limb ownership, or, more interestingly, it could suggest that there exists a "window of integration" in the dimension of tactile congruency, such that less pronounced incongruencies are tolerated but more substantial incongruencies break the illusion. The tactile congruence rule is based on the multisensory congruency between the seen and felt objects touching the hands in terms of texture and macrogeometric features; thus, similar to multisensory perception in general,[35,36] body ownership is influenced not only by spatiotemporal coincidence but also by congruencies among other stimulus properties.

Humanoid shape rule

The rubber hand illusion also depends on the congruency of the shape and spatial configuration of the observed and felt limbs. When a rigid object is shown, it is clear that the object must visually resemble a human hand for the participants to be able to experience the rubber hand illusion. Objects that do not look like a human hand, such as blocks of wood or sticks, do not elicit significant limb ownership illusions.[17,42,66] One important study tested the rubber hand illusion with a series of five different objects, ranging from a plain wooden block that did not resemble a human limb to handlike wooden objects and a prosthetic hand, and found that the participants experienced a sense of ownership only for the realistic-looking prosthetic hand[66] (Fig. 8.2C). Thus, the object to be experienced as part of one's physical self must resemble a human hand in terms of its shape and structure (at least when it is a rigid physical object,[42] see further below). We know that it is the humanoid shape of the object that matters, rather than the material or color, because the illusion works well with wooden hands,[37] metallic robotic hands,[67] digital images of real hands,[55] and hands of different skin colors.[68] From a multisensory perspective, the humanoid shape rule is another example of multisensory congruency in which the shapes of the seen and felt hands are matching or nonmatching. Alternatively, this constraint could be seen as a top-down effect related to the semantic incongruency[69] between the noncorporeal object in view and the participant's real limb. A third explanation that has been put forward is that the viewed object must fit with a reference model of the body that contains structural information about body parts.[66] However, shape congruency might be the most parsimonious explanation because the rubber hand illusion can be induced in a portion of empty space. In this rather counterintuitive "invisible hand illusion,"[42] the scientist outlines the contours of an invisible hand by moving the brush in empty space straight in front of the participants while corresponding strokes are being applied to the hidden real hand (Fig. 8.1C). If these strokes are very well timed and carefully matched in terms of their spatial trajectories, then the participants will perceive that they have an invisible hand that is sensing the touches of the paintbrush. Importantly, in this case, the illusion relies entirely on the spatiotemporal correlations between vision and touch, even in the face of gross semantic incongruence between the portion of empty space and the participant's real hand. Importantly, however, the shape of the "contours" of the invisible hand and the shape of the real hand are congruent. The illusion presumably works because the brain is used to situations in which the hand cannot be seen, for example, in the dark or when it is occluded behind other objects. In summary, the basic temporal, spatial, and other stimulus property constraints of the rubber hand illusion fit well with the notion that it is a genuine multisensory illusion and that body ownership can be viewed as multisensory perception.

Multisensory congruency matters, not the particular modality

It appears that no single modality plays the all-decisive role in the elicitation of the rubber hand illusion. Rather, it is the congruent patterns of available multisensory signals that drive this perceptual phenomenon. Thus far, we have mainly considered the classic rubber hand illusion, in which the rubber hand is observed visually while tactile stimulation is applied to the model hand and the participant's real hand. Importantly, however, various versions of the rubber hand illusion have been described that depend on different combinations of sensory modalities. For example, the illusion can be elicited without vision, as in the case of the "somatic rubber hand illusion."[70–73] In this nonvisual version, the participant is blindfolded, and the researcher moves the participant's left index finger so that it is touching a right rubber hand placed in front of him or her (Fig. 8.1B). Simultaneously, the researcher is touching the corresponding part of the participant's right hand, which is placed 15 cm to the left of the rubber hand; after a short period of repeated synchronized tapping, this stimulation triggers the illusion that the participant is directly touching his or her own right hand.[70,71] Thus, in this case, it is the correlated tactile and proprioceptive signals from the two hands that are driving the illusion, without any contribution by vision. Similarly, the illusion can be elicited without touches being applied to the skin, as is the case with the "moving rubber hand illusion,"[58] in which a wooden model hand moves its index finger in synchrony with movements made actively or passively by the participant's own hidden index finger (Fig. 8.1D) (see also Ref. 37,74–76). In this situation, it is the congruency of the seen and felt finger movements that elicits the illusion, without dynamic tactile stimulation by an external object in peripersonal space. The illusion seems to be similarly strong for active and passive movements,[37] which suggests that the ownership effect is driven by visuokinesthetic integration. Moreover, this illusion can be elicited when the skin of the moving finger is anesthetized to eliminate tactile feedback from the stretching skin, which suggests that congruent visual and proprioceptive information is sufficient.[77] Importantly, the moving rubber hand illusion and the somatic rubber hand illusion both obey the basic temporal and spatial rules of the classical illusion.[47,58,70,73] Other sensory modalities can also contribute to the sense of limb ownership, as visuointeroceptive stimulation[78–80] and auditory feedback[81,82] can modulate the strength of illusory ownership, and congruent visual and thermal stimulation can elicit the rubber hand illusion.[83] Thus, body ownership seems to be shaped by the meaningful combination of all available sensory information from the different sensory modalities rather than being predominantly determined by a particular sensory domain, be it vision, touch, or proprioception.

Multisensory integration of body signals in the cortex: nonhuman primates

Before turning to the recent human neuroimaging studies that have investigated the neural substrate of body ownership, we will first consider the neurophysiological literature on nonhuman primates and discuss some key regions that contain cells with receptive field (RF) properties that makes them particularly good candidates to implement the underlying neuronal mechanisms. Specifically, we will focus on multisensory areas in the frontal and parietal association cortices, particularly the premotor cortex, the cortices lining the intraparietal sulcus (the medial, ventral, and lateral intraparietal areas, also known as the MIP, VIP, and LIP), and the inferior parietal cortex (area 7), where electrophysiological studies in macaque monkeys have described single neurons that respond to visual, tactile, and proprioceptive stimulation.[84] Interestingly, many neurons in the ventral premotor cortex respond to a visual stimulus only when it is presented close to the monkey, i.e., within peripersonal space, which extends approximately 30 cm from the body,[85] and these cells typically have overlapping visual and tactile RFs. Further studies showed that these multisensory cells in the premotor cortex encode peripersonal space in body part–centered coordinate systems[50] because these neurons' RFs were anchored to the arm, such that when the arm moved, the visual RFs of the multisensory neurons moved along with it,[49,50,86] and because the RFs were independent of the position of the monkey's gaze.[50,87] Further studies have revealed a number of frontal and parietal areas with multisensory neurons that show visual and sometimes also auditory RFs with extension limited to the space surrounding the monkey's body; these areas include the VIP,[88–93] parietal area 7b,[88,94] the putamen,[95] the secondary somatosensory cortex,[96] and parietal areas 2 and 5,[97,98] in addition to the abovementioned ventral premotor cortex. Importantly, we know that these kinds of cells can perform multisensory integration[89,97] and that they seem to do so according to the temporal and spatial congruency rules.[89] Moreover, neurons in the premotor cortex and the medial intraparietal area not only respond to dynamic tactile stimuli applied to the body but also show sensitivity to the orientation congruency of seen and felt postures of the upper limb.[97,99] Thus, areas in the frontal and parietal association cortices contain multisensory neurons that obey the temporal and spatial congruency principles of multisensory integration, which makes them good candidates to implement the perceptual rules of body ownership.

Multisensory integration of body signals in the cortex: human neuroimaging

Accumulating neuroimaging studies on healthy volunteers suggests that circuits for multisensory integration of body-related signals in peripersonal space also exist in the human brain. 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[14,55,100–104] and to visual stimulation near the hand in peripersonal space.[56,100,105] In two fMRI experiments,[55,104] Gentile and colleagues consistently observed strengthened activation in the ventral premotor cortex, intraparietal cortex, inferior parietal cortex (supramarginal gyrus), and cerebellum in a condition in which the real right index finger was stroked with a small soft ball attached to a stick in the participant's sight (congruent visuotactile condition), compared with (i) when the participants closed their eyes during the application of the strokes (unimodal tactile stimulation) (Fig. 8.3A), (ii) when the small ball was moved 2 cm above the index finger without touching it (unimodal visual stimulation) (Fig. 8.3A), or (iii) when temporally or spatially incongruent visuotactile stimulation was applied (Fig. 8.3A and B). Thus, these regions integrate visual and tactile signals from the upper limb. Moreover, multisensory neuronal populations in several of these areas show selectivity in their response profiles for visual stimuli presented near the hand, consistent with the notion that these groups of cells have RFs restricted to peripersonal space near the hand ("perihand space"). Brozzoli and colleagues used the blood oxygenation level-dependent (BOLD) adaptation technique (i.e., the suppression of BOLD signal related to the repetition of the same stimulus, which reveals neuronal stimulus selectivity at the population level[106]) to show that the active areas in the ventral and dorsal premotor cortex, intraparietal cortex, and inferior parietal cortex (supramarginal cortex) show neural selectivity for visual stimuli presented near the hand[105] and that the premotor and intraparietal responses appeared to be anchored to the hand such that when the hand was placed in a new location, the selective neural responses shifted along with the hand[56] (Fig. 8.3C). Thus, the human premotor and

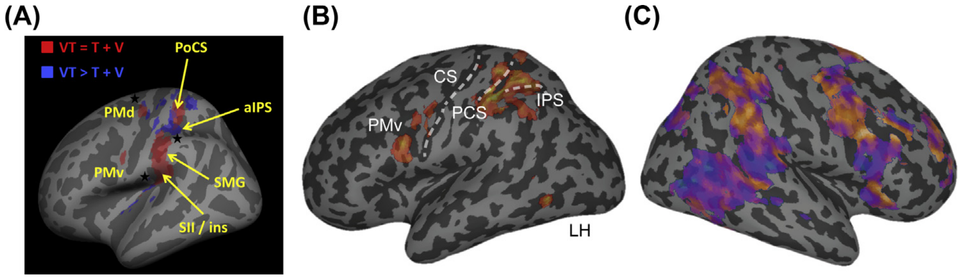

FIGURE 8.3 Areas of the premotor cortex and posterior parietal cortex that show greater fMRI activation during congruent visuotactile stimulation applied to the right hand than during unimodal visual or unimodal tactile stimulation[104] (A). The ventral premotor cortex (PMv) and the cortices lining the intraparietal sulcus (IPS) show greater activation for congruent visuotactile stimulation of the right hand than for temporally and spatially incongruent visuotactile stimulation[55] (B). Areas that show (fMRI BOLD adaptation) selectivity for visual stimulation in space near the hand (yellow) compared with areas that display a lack of such a hand-centered response profile (blue)[56] (C).

intraparietal cortices (and other regions) respond to spatially and temporally congruent multisensory stimulation from the body and the space near the body, in line with the single-cell data from nonhuman primates. In the next section, we will consider how activity in these areas relates to body ownership.

Neuroimaging studies of limb ownership

Neuroimaging experiments conducted in different laboratories over the last 5 years have provided accumulating evidence that the sense of ownership of a limb is associated with activation of multisensory areas in the frontal and parietal lobes.[40,42,55,107–109] Ehrsson and colleagues conducted the first fMRI study of the rubber hand illusion, and these authors found increased BOLD signal in the premotor cortex and intraparietal cortex during the rubber hand illusion compared with relevant control conditions with visuotactile asynchrony and/or spatial incongruency in terms of seen and felt hand orientation[14] (Fig. 8.4A). Moreover, the subjectively rated strength of the illusion across individuals predicted the degree of activity in the bilateral ventral premotor cortex. The activation of the ventral premotor cortex[40,42,55,56,107,108,110] and intraparietal cortex[42,55,56,107,108] has been reproduced in fMRI studies involving various versions of the rubber hand illusion (Fig. 8.4C and D) including the invisible rubber hand illusion[42] and the somatic rubber hand illusion.[70] Interestingly, activity in the bilateral ventral premotor cortex and the bilateral intraparietal cortex, as well as the bilateral inferior parietal cortex (supramarginal gyrus) and the right cerebellum, also reflects the default sense of ownership when participants look at their real hand being stroked, and this activity is reduced when spatial and temporal incongruencies between the visual and tactile stimuli are introduced, which also causes the participants to lose the sense of ownership of their hand[55] (Fig. 8.4B). The stronger this "hand disownership" effect, the greater the reduction in the fMRI signal in the left ventral premotor cortex and right intraparietal cortex. Thus, the activity in the premotor cortex and the intraparietal cortex is not restricted to the cases of illusory ownership of rubber hands but also reflects ownership of real hands.

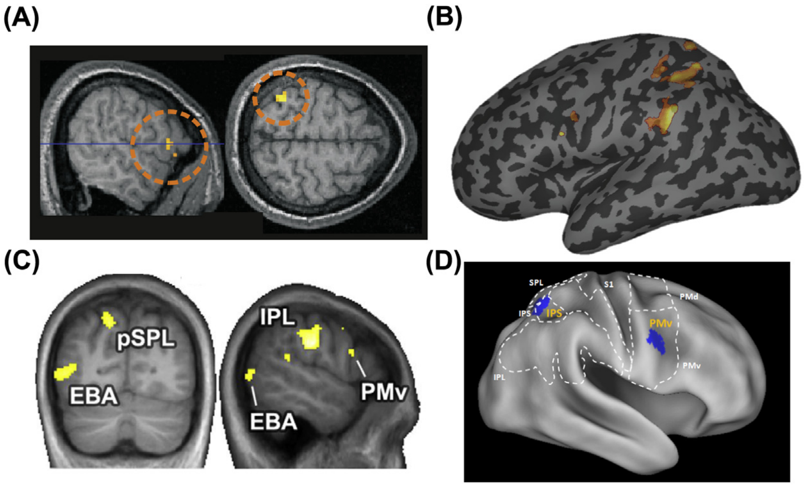

FIGURE 8.4 fMRI activity in the ventral premotor cortex (left) and intraparietal cortex (right) that reflects the sense of ownership of a rubber hand[14] (A). Activation in the ventral premotor cortex, intraparietal cortex, and inferior parietal cortex that reflects the default sense of ownership of one's real hand[55] (B). Ownership of the upper limb driven by orientation congruency of the observed and felt hand is associated with activation in the ventral premotor cortex (PMv), the inferior parietal lobule (IPL), the extrastriate body area (EBA), and the medial aspect of the posterior part of the intraparietal sulcus (here termed the posterior superior parietal lobe, pSPL)[107] (C). Metaanalysis of neuroimaging studies that associate activation (blue) in the ventral premotor cortex (PMv) and intraparietal cortex (IPS) with body ownership in various illusion-based paradigms[109] (D).

fMRI has also been used to investigate whether the rubber hand illusion is associated with a dynamic shift in peripersonal space—from the hidden real hand toward the model hand in view, which is indicated by changes in the visual RFs of a small number of neurons recorded from the posterior parietal cortex when monkeys observed a stuffed monkey arm being stroked in synchrony with strokes applied to the monkey's hidden real arm.[97] In a study by Brozzoli and colleagues,[56] a small ball was repeatedly presented close to the illusorily owned rubber hand, and the BOLD adaptation responses selective to this visual stimulus in perihand space around the upper limb were quantified and compared with a control condition without illusory ownership. The responses indicative of a selective near-hand response in the bilateral ventral premotor cortex, bilateral putamen, and right intraparietal cortex were greater during the rubber hand illusion than without the illusion,[56] an observation that is well in line with the notion that, when the rubber hand is owned, the multisensory neurons encode peripersonal space around the model hand just as they do around the real hand under natural conditions.[56,97,105] Furthermore, the greater the subjective strength of the illusion, the stronger this neuronal shift in perihand space in the ventral premotor cortex,[56] linking the subjective illusion phenomenon to dynamic shifts in the RF properties of multisensory neurons in this area.

In addition to the premotor cortex and the intraparietal cortex as discussed above, recent neuroimaging studies of limb ownership have also consistently found activation in an area tentatively identified as the extrastriate body area (EBA), as well as in the cerebellum. The

EBA is a region located in the lateral occipital cortices (LOCs) that is specialized for the visual processing of body parts.[111] Earlier studies suggested that the visual processing in this region might be influenced by somatosensory information because modulations of LOC activity have been seen during tactile[112−114] and proprioceptive[115,116] stimulation procedures. These crossmodal influences likely stem from sources in the posterior parietal cortex,[117] which is functionally connected to the LOC.[118] In terms of body ownership, several studies have reported significant increases in activation in the LOC during versions of the rubber hand illusion paradigm[42,55,107,108,119] (Fig. 8.4C), and the stronger the subjective ownership illusion, the stronger the LOC activation.[55,107] The 2014 study by Limanowski and Blankenburg[119] is important in this respect because they used a well-established functional localizer procedure to identify the EBA in their particular group of participants, which enabled them to demonstrate that the activity associated with the rubber hand illusion was indeed located in the EBA. One interpretation of this EBA activity is that it reflects crossmodal interplay,[120] whereby congruent tactile and proprioceptive signals influence the visual processing of hand signals via top-down modulations from posterior parietal regions in a way that potentially aids visual self-recognition of the hand. This notion is consistent with the increased effective connectivity found between the intraparietal cortex and the LOC when participants experience ownership of a limb in view.[55,108]

There are also compelling indications that the cerebellum is involved in the rubber hand illusion (not shown in the figures). Several experiments have found activation of the lateral cerebellar hemispheres in the integration of spatially and temporally congruent multisensory signals from the hand in various versions of the rubber hand illusion paradigm.[14,42,55,70,108] This part of the cerebellum receives proprioceptive,[121] visual,[122] and tactile[123] inputs and is responsive to congruent multisensory stimulation of the right upper limb.[104,124] Interestingly, there is increased effective connectivity between this cerebellar region and the intraparietal cortex when people experience ownership of a limb,[55] an observation that is consistent with known anatomical connections between these areas.[122,125] Thus, given the important role of the cerebellum in generating sensory predictions,[126] it can be speculated that the cerebellum is involved in the detection of synchronous multisensory signals and the formation of crossmodal temporal predictions that support the multisensory processing in frontoparietal cortical areas.[55]

Full-body ownership

Thus far, we have considered the sense of ownership of a single limb only. However, the rubber hand illusion can be extended to the entire body, and such studies provide additional information about the relationship between body ownership and multisensory processing. Petkova and Ehrsson described how a full-body ownership illusion could be elicited with the body of a mannequin.[127] To observe the mannequin's body from the natural first-person perspective, the participants wore head-mounted displays (HMDs) connected to two cameras placed side by side to provide a 3D video image feed to the HMDs (Fig. 8.5A). The two cameras were positioned on the head of a mannequin so that the participants were looking down on the mannequin's body with stereoscopic vision.[127] Thus, when the participants wore the HMDs connected to these cameras and looked down, they saw the mannequin's body in the location to that where they would expect to see their own real body

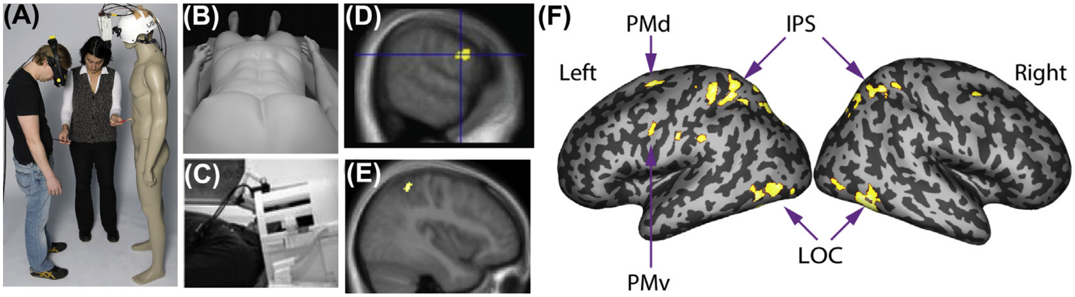

FIGURE 8.5 Elicitation of the full-body ownership illusion with a mannequin, head-mounted displays (HMDs), and synchronized touches[127] (A). In the HMDs, the participants observed the mannequin from the first-person perspective (B), as shown here from an fMRI experiment that associated activation in the ventral premotor cortex (D) and intraparietal cortex (E) with the full-body ownership illusion.[136] The arrangement of the HMDs, the tilted head coil, and the participant's head that is tilted inside the head coil to simulate a natural view of the body during the fMRI experiments (C). Activation associated with illusory full-body ownership of a stranger's body is shown projected onto a "flattened" 3D image of a standard brain[109] (F). *IPS*, Intraparietal sulcus; *PMv*: Ventral premotor cortex; *PMd*, Dorsal premotor cortex; *LOC*, Lateral occipital cortex.

(Fig. 8.5B). When the experimenter used a pair of rods to touch the mannequin's abdomen and the person's real abdomen simultaneously at corresponding sites for 1 minute, this elicited in participants the illusion that the mannequin's body was their own.[127] 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.[127] The illusion is robust and works just as well with real human bodies[128–130] and computer-generated avatars[131,132] as with mannequins.

The full-body ownership illusion seems to depend on the same perceptual rules as the rubber hand illusion. Asynchronous stroking of the mannequin body and the participant's real body significantly reduces the illusion, and anecdotal observations suggest that this reducing effect of asynchrony is strengthened when combined with stroking noncorresponding body parts.[133] Furthermore, the mannequin viewed from the first-person point of view needs to be presented in the same orientation in peripersonal space as the real body, so that the body one sees matches the body one senses through proprioception. Presenting the mannequin's body several meters away from the person's real body viewed from the third-person perspective (as one sees another individual[134,135]; see also Ref. 132) or presenting the mannequin in peripersonal space but rotating it so that the head is placed near participants' unseen feet[136] significantly reduces the illusion. This orientation congruency effect is so strong that the illusion can be elicited even without the applications of synchronous touches, especially if the spatial match is so close that the artificial body is "substituted" for the real body.[132] Moreover, the illusion is eliminated when a large block of wood is presented instead of a mannequin,[127,136] in line with the humanoid shape rule; however, as with the invisible hand illusion described above, it is possible to elicit an "invisible-body illusion" if the experimenter very carefully outlines the "contours" of an invisible body by systematically stroking different body parts.[137] Furthermore, as with the rubber hand illusion, the full-body ownership illusion can be elicited by congruent seen and felt movements instead of touches applied with probes or brushes.[127,132,138,139] Thus, the full-body ownership illusion depends on the same temporal, spatial, and humanoid shape congruency principles as the rubber hand illusion described earlier, suggesting the involvement of similar multisensory processes.

This conclusion is further supported by fMRI studies describing how the full-body ownership illusion is associated with activity increases in the ventral premotor cortex[128,136,140] (Fig. 8.5D and F), the intraparietal cortex[128,136,140] (Fig. 8.5E and F), the LOC[128,140] (Fig. 8.5F), the lateral cerebellar hemispheres,[128,136] and the putamen[128,136] compared with various control conditions with temporally and spatially incongruent visuotactile stimulation or with the mannequin replaced by a block of wood or with the mannequin presented from a third-person perspective. Moreover, the degree of activation in the ventral premotor cortex correlates with the strength of the full-body ownership illusion as rated in questionnaires.[128,136,140] Thus, both the perceptual rules and the patterns of brain activation support the notion that similar multisensory processes are involved in limb and full-body ownership.

Still, how are the parts integrated into the whole in own-body perception? One experiences a single coherent body, not a set of disconnected parts, as one's own physical self. The full-body ownership paradigm has been used to address this question. A striking feature of the full-body illusion is that one experiences the *entire* body in view as one's own, not merely the particular part that receives the dynamic visuotactile stimulation.[127,141] This effect can be studied by stimulating one body part (e.g., the right hand) and then probing ownership of specific other body parts (e.g., the abdomen) by using questionnaire ratings or threat-evoked skin conductance responses. The results show how ownership "spreads" from the body part that is stroked to also encompass the others, in line with the entire mannequin's body being experienced as one's own.[127,141] This unitary experience probably requires multisensory perceptual binding of the different limbs and body segments into a single perceptual whole.

In terms of a possible brain mechanism for such full-body perceptual binding, neuronal populations with the capacity to integrate visual, tactile, and proprioceptive signals across body segments might play a key role. Multisensory neurons with RFs that cover two or more body segments have been described in the ventral premotor cortex,[49,85,142] the cortices lining the intraparietal sulcus,[92,143] and the inferior parietal cortex[144]; even neurons that respond to the entire body have been reported.[92,142,144,145] fMRI has been used to search for neural correlates of whole-body perceptual binding effects.[136,141] One approach is to compare the synchronous versus asynchronous stroking of the mannequin's hand in two contexts: either the mannequin's hand was visibly attached to the rest of the mannequin, which triggers the full-body ownership illusion when synchronous stroking is added, or the artificial hand was detached from the mannequin and simply displayed in isolation without any mannequin next to it, which is a condition that does not elicit a full-body ownership illusion even with synchronous visuotactile stimulation.[136] The former condition, with the artificial hand attached to the mannequin's body and the experience of illusory full-body ownership, was associated with increased activation in sections of the dorsal and ventral premotor cortices, the intraparietal cortex, the secondary somatosensory cortex, and the lateral cerebellum. This finding suggests that whole-body multisensory binding requires additional neural processing in these regions over and above the multisensory processing related to the "detached" hand. A multivariate pattern recognition technique called "multivoxel pattern analysis" has been used to further examine how neuronal population responses relate to full-body perceptual binding.[136,141] In these experiments, classifiers were trained to identify fine-grained patterns of activity that were similar regardless of whether the full-body ownership illusion with a mannequin was elicited by synchronously stimulating the abdomen or the right hand,[136] or by stimulating the abdomen, the right hand, or the right foot[141] (compared with control conditions with asynchronous stimulation of the corresponding body parts). Patterns of active voxels that contained information about full-body ownership irrespective of which body part was used to elicit the illusion were identified in the ventral premotor cortex,[136,141] which supports the idea that whole-body ownership percepts are associated with the integration of multisensory signals originating from multiple segments of the body.

Self-identification, mirrors, and the third-person visual perspective

In this chapter, we have focused on the rubber hand illusion and the full-body ownership illusion when the mannequin body is viewed from the first-person perspective. In these cases, vivid and explicit body ownership is experienced, and the initial conflict between the senses is resolved by the formation of a coherent illusory percept of the artificial hand or plastic body in view as one's own. However, multisensory interactions can also influence self-recognition of faces and bodies observed at a distance. When participants are stroked on their face while they are looking at a morphed face on a computer screen[146] or another person's face[147] being touched in synchrony, this visuotactile stimulation promotes recognition of the face as their own compared with asynchronous conditions ("enfacement illusion"). Similarly, synchronous stimulation of the participant's real back and the back of a virtual body presented several meters in front of the participant through an HMD makes the participant self-identify with the virtual body,[148] and this is accompanied by behavioral changes in indices of body representation and peripersonal space.[149−152] These "enfacement illusions" and "full-body illusions" for bodies viewed at a distance from a third-person perspective are very interesting in their own right and have been used to address a wide range of issues related to self-identification (or self-recognition), bodily self-consciousness, and sense of self.[30,153] However, these findings do not contradict the spatial constraints of body ownership that we have discussed in this chapter because even if illusory self-recognition is boosted by visuotactile correlations, the participants still sense the spatial discrepancy between their own body as sensed from the first-person perspective and the artificial body or other person's face they observe at a distance, that is, the perceived spatial conflict is not eliminated[154] and a full-blown body ownership illusion is not experienced as in the rubber hand illusion and full-body ownership illusions from the first-person perspective.[132,134] Interestingly, the rubber hand illusion and the full-body ownership illusion work when the participant sees the rubber hand,[155] the mannequin,[135] or a virtual body[139,156,157] in a mirror placed straight in front of him or her. However, these observations do not falsify the spatial constraints of body ownership, as, in these cases, the visual information from the mirror reflection is automatically projected back to the participant's own body standing in front of the mirror. Importantly, if the mirror is removed and replaced by a rubber hand or mannequin facing the participant, the ownership illusion is significantly reduced, which demonstrates that the mirror transformation plays a critical role in perceived ownership of the body reflected in the mirror.[135,155]

Summary

This chapter has discussed multisensory processes in body ownership. A large body of behavioral and neuroimaging data supports a close relationship between multisensory perception and the sense of ownership of limbs and entire bodies. From behavioral experiments, we have learned that the rubber hand illusion and other limb ownership illusions obey temporal, spatial, and other congruency rules that are related to the properties of the stimuli, which fits well with the congruency principles of multisensory integration. Moreover, illusory changes in body ownership do not seem to depend on, or to be dominated by, a single particular modality; rather, such illusions are the outcome of a flexible integration process in which all available information from the different sensory modalities is used. This is illustrated, for example, by the many different versions of the rubber hand illusion that are based on different combinations of multisensory stimuli. In terms of the human brain, fMRI studies associate changes in the sense of body ownership with increases in activity in multisensory cortical areas such as the premotor cortex and posterior parietal cortex. Importantly, the degree of activity in these areas mirrors the perceptual rules of the rubber hand illusion and shows a systematic relationship with the subjective strength of experienced ownership. The behavioral and neural principles of body ownership have also been extended to the case of the entire body with full-body ownership illusions in which people experience the bodies of mannequins, strangers, and simulated avatars as their own. Collectively, the reviewed studies not only show that multisensory processes play an important role in how we come to experience our body as our own but also suggest that body ownership can be explained as the formation of a coherent multisensory percept of one's body by multisensory integration mechanisms.

Acknowledgments

Henrik Ehrsson is supported by the Swedish Research Council, Hjärnfonden, and Torsten Söderbergs Stiftelse.

References

1. Botvinick M. Neuroscience. Probing the neural basis of body ownership. *Science*. 2004;305(5685):782–783.
2. Ehrsson HH. The concept of body ownership and its relation to multisensory integration. In: Stein BE, ed. *The Handbook of Multisensory Processes*. Cambridge, Massachusetts: MIT Press; 2012:775–792.
3. Tsakiris M. My body in the brain: a neurocognitive model of body-ownership. *Neuropsychologia*. 2010;48(3):703–712.
4. Jeannerod M. The mechanism of self-recognition in humans. *Behav Brain Res*. 2003;142(1–2):1–15.
5. Gallagher II . Philosophical conceptions of the self: implications for cognitive science. *Trends Cogn Sci*. 2000;4(1):14–21.
6. Jenkinson PM, Moro V, Fotopoulou A. Definition: asomatognosia. *Cortex*. 2018;101:300–301.
7. Critchley M. *The Parietal Lobes*. 1953. London.
8. Arzy S, Overney LS, Landis T, Blanke O. Neural mechanisms of embodiment: asomatognosia due to premotor cortex damage. *Arch Neurol*. 2006;63(7):1022–1025.
9. Bottini G, Bisiach E, Sterzi R, Vallar G. Feeling touches in someone else's hand. *Neuroreport*. 2002;13(2):249–252.
10. Feinberg TE, Venneri A, Simone AM, Fan Y, Northoff G. The neuroanatomy of asomatognosia and somatoparaphrenia. *J Neurol Neurosurg Psychiatry*. 2010;81(3):276–281.
11. Feinberg TE, Venneri A. Somatoparaphrenia: evolving theories and concepts. *Cortex*. 2014;61:74–80.

12. Botvinick M, Cohen J. Rubber hands ’feel’ touch that eyes see. *Nature*. 1998;391(6669):756.
13. Tastevin J. En partant de l’experience d’Aristotle [Starting from Aristotle’s experience]. *L’Encephale*. 1937;1(57−84):140−158.
14. Ehrsson HH, Spence C, Passingham RE. That’s my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science*. 2004;305(5685):875−877.
15. Lloyd DM. Spatial limits on referred touch to an alien limb may reflect boundaries of visuo-tactile peripersonal space surrounding the hand. *Brain Cogn*. 2007;64(1):104−109.
16. Longo MR, Schuur F, Kammers MP, Tsakiris M, Haggard P. What is embodiment? A psychometric approach. *Cognition*. 2008;107(3):978−998.
17. Tsakiris M, Haggard P. The rubber hand illusion revisited: visuotactile integration and self-attribution. *J Exp Psychol Hum Percept Perform*. 2005;31(1):80−91.
18. Armel KC, Ramachandran VS. Projecting sensations to external objects: evidence from skin conductance response. *Proc Biol Sci*. 2003;270(1523):1499−1506.
19. Abdulkarim Z, Ehrsson HH. No causal link between changes in hand position sense and feeling of limb ownership in the rubber hand illusion. *Atten Percept Psychophys*. 2016;78(2):707−720.
20. Rohde M, Wold A, Karnath HO, Ernst MO. The human touch: skin temperature during the rubber hand illusion in manual and automated stroking procedures. *PLoS One*. 2013;8(11):e80688.
21. Rohde M, Di Luca M, Ernst MO. The rubber hand illusion: feeling of ownership and proprioceptive drift do not go hand in hand. *PLoS One*. 2011;6(6):e21659.
22. Zopf R, Savage G, Williams MA. The crossmodal congruency task as a means to obtain an objective behavioral measure in the rubber hand illusion paradigm. *J Vis Exp*. 2013;77.
23. de Haan AM, Van Stralen HE, Smit M, Keizer A, Van der Stigchel S, Dijkerman HC. No consistent cooling of the real hand in the rubber hand illusion. *Acta Psychol (Amst)*. 2017;179:68−77.
24. Craske B. Perception of impossible limb positions induced by tendon vibration. *Science*. 1977;196(4285):71−73.
25. Lackner JR. Some proprioceptive influences on the perceptual representation of body shape and orientation. *Brain*. 1988;111(Pt 2):281−297.
26. Ramachandran VS, Hirstein W. Three laws of qualia: clues from neurology about the biological functions of consciousness and qualia. *J Conscious Stud*. 1997;4:28.
27. Naito E, Roland PE, Ehrsson HH. I feel my hand moving: a new role of the primary motor cortex in somatic perception of limb movement. *Neuron*. 2002;36(5):979−988.
28. de Vignemont F. Embodiment, ownership and disownership. *Conscious Cognit*. 2011;20(1):82−93.
29. de Vignemont F. Agency and bodily ownership: the bodyguard hypothesis. In: de Vignemont F, Alsmith A, eds. *The Subject’s Matter: The Body and Self-Consciousness*. Cambridge, Massachusetts, USA: MIT Press; 2017.
30. Tsakiris M. The multisensory basis of the self: from body to identity to others. *Q J Exp Psychol (Hove)*. 2017;70(4):597−609.
31. Limanowski J, Blankenburg F. Minimal self-models and the free energy principle. *Front Hum Neurosci*. 2013;7:547.
32. Apps MA, Tsakiris M. The free-energy self: a predictive coding account of self-recognition. *Neurosci Biobehav Rev*. 2014;41:85−97.
33. Holmes NP, Spence C. Multisensory integration: space, time and superadditivity. *Curr Biol*. 2005;15(18):R762−R764.
34. Stein BE, Stanford TR. Multisensory integration: current issues from the perspective of the single neuron. *Nat Rev Neurosci*. 2008;9(4):255−266.
35. *The New Handbook of Multisensory Processing*. Cambridge, Massachusetts: The MIT Press; 2012.
36. Chen YC, Spence C. Assessing the role of the ’unity assumption’ on multisensory integration: a review. *Front Psychol*. 2017;8:445.
37. Kalkert A, Ehrsson HH. The moving rubber hand illusion revisited: comparing movements and visuotactile stimulation to induce illusory ownership. *Conscious Cognit*. 2017;26:117−132.
38. Shimada S, Fukuda K, Hiraki K. Rubber hand illusion under delayed visual feedback. *PLoS One*. 2009;4(7):e6185.
39. Shimada S, Suzuki T, Yoda N, Hayashi T. Relationship between sensitivity to visuotactile temporal discrepancy and the rubber hand illusion. *Neurosci Res*. 2014;85:33−38.
40. Bekrater-Bodmann R, Foell J, Diers M, et al. The importance of synchrony and temporal order of visual and tactile input for illusory limb ownership experiences - an FMRI study applying virtual reality. *PLoS One*. 2014;9(1):e87013.

41. Costantini M, Robinson J, Migliorati D, Donno B, Ferri F, Northoff G. Temporal limits on rubber hand illusion reflect individuals' temporal resolution in multisensory perception. *Cognition*. 2016;157:39−48.
42. Guterstam A, Gentile G, Ehrsson HH. The invisible hand illusion: multisensory integration leads to the embodiment of a discrete volume of empty space. *J Cogn Neurosci*. 2013;25(7):1078−1099.
43. Petkova VI, Ehrsson HH. When right feels left: referral of touch and ownership between the hands. *PLoS One*. 2009;4(9):e6933.
44. Parise CV, Ernst MO. Correlation detection as a general mechanism for multisensory integration. *Nat Commun*. 2016;7.
45. Parise CV, Spence C, Ernst MO. When correlation implies causation in multisensory integration. *Curr Biol*. 2012;22(1):46−49.
46. Burr D, Silva O, Cicchini GM, Banks MS, Morrone MC. Temporal mechanisms of multimodal binding. *Proc R Soc B Biol Sci*. 2009;276(1663):1761−1769.
47. Kalckert A, Ehrsson HH. The spatial distance rule in the moving and classical rubber hand illusions. *Conscious Cognit*. 2014;30:118−132.
48. Rizzolatti G, Fadiga L, Fogassi L, Gallese V. The space around us. *Science*. 1997;277(5323):190−191.
49. Fogassi L, Gallese V, Fadiga L, Luppino G, Matelli M, Rizzolatti G. Coding of peripersonal space in inferior premotor cortex (area F4). *J Neurophysiol*. 1996;76(1):141−157.
50. Graziano MS, Hu XT, Gross CG. Visuospatial properties of ventral premotor cortex. *J Neurophysiol*. 1997;77(5):2268−2292.
51. Ladavas E, di Pellegrino G, Farne A, Zeloni G. Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *J Cogn Neurosci*. 1998;10(5):581−589.
52. Preston C. The role of distance from the body and distance from the real hand in ownership and disownership during the rubber hand illusion. *Acta Psychol (Amst)*. 2013;142(2):177−183.
53. Kilteni K, Normand JM, Sanchez-Vives MV, Slater M. Extending body space in immersive virtual reality: a very long arm illusion. *PLoS One*. 2012;7(7):e40867.
54. Costantini M, Haggard P. The rubber hand illusion: sensitivity and reference frame for body ownership. *Conscious Cognit*. 2007;16(2):229−240.
55. Gentile G, Guterstam A, Brozzoli C, Ehrsson HH. Disintegration of multisensory signals from the real hand reduces default limb self-attribution: an fMRI study. *J Neurosci*. 2013;33(33):13350−13366.
56. Brozzoli C, Gentile G, Ehrsson HH. That's near my hand! Parietal and premotor coding of hand-centered space contributes to localization and self-attribution of the hand. *J Neurosci*. 2012;32(42):14573−14582.
57. Pavani F, Spence C, Driver J. Visual capture of touch: out-of-the-body experiences with rubber gloves. *Psychol Sci*. 2000;11(5):353−359.
58. Kalckert A, Ehrsson HH. Moving a rubber hand that feels like your own: a dissociation of ownership and agency. *Front Hum Neurosci*. 2012;6:40.
59. Ide M. The effect of "anatomical plausibility" of hand angle on the rubber-hand illusion. *Perception*. 2013;42(1):103−111.
60. Guterstam A, Petkova VI, Ehrsson HH. The illusion of owning a third arm. *PLoS One*. 2011;6(2):e17208.
61. Samad M, Chung AJ, Shams L. Perception of body ownership is driven by Bayesian sensory inference. *PLoS One*. 2015;10(2):e0117178.
62. Guterstam A, Zeberg H, Ozciftci VM, Ehrsson HH. The magnetic touch illusion: a perceptual correlate of visuo-tactile integration in peripersonal space. *Cognition*. 2016;155:44−56.
63. Ionta S, Sforza A, Funato M, Blanke O. Anatomically plausible illusory posture affects mental rotation of body parts. *Cognit Affect Behav Neurosci*. 2013;13(1):197−209.
64. Ward J, Mensah A, Junemann K. The rubber hand illusion depends on the tactile congruency of the observed and felt touch. *J Exp Psychol Hum Percept Perform*. 2015;41(5):1203−1208.
65. Schutz-Bosbach S, Tausche P, Weiss C. Roughness perception during the rubber hand illusion. *Brain Cogn*. 2009;70(1):136−144.
66. Tsakiris M, Carpenter L, James D, Fotopoulou A. Hands only illusion: multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. *Exp Brain Res*. 2010;204(3):343−352.
67. Rosen B, Ehrsson HH, Antfolk C, Cipriani C, Sebelius F, Lundborg G. Referral of sensation to an advanced humanoid robotic hand prosthesis. *Scand J Plast Reconstr Surg Hand Surg*. 2009;43(5):260−266.

68. Farmer H, Tajadura-Jimenez A, Tsakiris M. Beyond the colour of my skin: how skin colour affects the sense of body-ownership. *Conscious Cognit*. 2012;21(3):1242−1256.
69. Hein G, Doehrmann O, Muller NG, Kaiser J, Muckli L, Naumer MJ. Object familiarity and semantic congruency modulate responses in cortical audiovisual integration areas. *J Neurosci*. 2007;27(30):7881−7887.
70. Ehrsson HH, Holmes NP, Passingham RE. Touching a rubber hand: feeling of body ownership is associated with activity in multisensory brain areas. *J Neurosci*. 2005;25(45):10564−10573.
71. Petkova VI, Zetterberg H, Ehrsson HH. Rubber hands feel touch, but not in blind individuals. *PLoS One*. 2012;7(4):e35912.
72. White RC, Aimola Davies AM, Halleen TJ, Davies M. Tactile expectations and the perception of self-touch: an investigation using the rubber hand paradigm. *Conscious Cognit*. 2010;19(2):505−519.
73. Aimola Davies AM, White RC, Davies M. Spatial limits on the nonvisual self-touch illusion and the visual rubber hand illusion: subjective experience of the illusion and proprioceptive drift. *Conscious Cognit*. 2013;22(2):613−636.
74. Dummer T, Picot-Annand A, Neal T, Moore C. Movement and the rubber hand illusion. *Perception*. 2009;38(2):271−280.
75. Tsakiris M, Prabhu G, Haggard P. Having a body versus moving your body: how agency structures body-ownership. *Conscious Cognit*. 2006;15(2):423−432.
76. Sanchez-Vives MV, Spanlang B, Frisoli A, Bergamasco M, Slater M. Virtual hand illusion induced by visuomotor correlations. *PLoS One*. 2010;5(4):e10381.
77. Walsh LD, Moseley GL, Taylor JL, Gandevia SC. Proprioceptive signals contribute to the sense of body ownership. *J Physiol*. 2011;589(Pt 12):3009−3021.
78. Suzuki K, Garfinkel SN, Critchley HD, Seth AK. Multisensory integration across exteroceptive and interoceptive domains modulates self-experience in the rubber-hand illusion. *Neuropsychologia*. 2013;51(13):2909−2917.
79. van Stralen HE, van Zandvoort MJ, Hoppenbrouwers SS, Vissers LM, Kappelle LJ, Dijkerman HC. Affective touch modulates the rubber hand illusion. *Cognition*. 2014;131(1):147−158.
80. Crucianelli L, Metcalf NK, Fotopoulou AK, Jenkinson PM. Bodily pleasure matters: velocity of touch modulates body ownership during the rubber hand illusion. *Front Psychol*. 2013;4:703.
81. Radziun D, Ehrsson HH. Auditory cues influence the rubber hand illusion. *J Exp Psychol Hum Percept Perform*. 2017 (in press).
82. Darnai G, Szolcsanyi T, Hegedus G, et al. Hearing visuo-tactile synchrony - sound-induced proprioceptive drift in the invisible hand illusion. *Br J Psychol*. 2017;108(1):91−106.
83. Trojan J, Fuchs X, Speth SL, Diers M. The rubber hand illusion induced by visual-thermal stimulation. *Sci Rep*. 2018;8(1):12417.
84. Graziano MS, Gross CG, Taylor CSR, Moore T. A system of multimodal areas in the primate brain. In: Spence C, Driver J, eds. *Crossmodal Space and Crossmodal Attention*. Oxford, UK: Oxford University Press; 2004:51−67.
85. Rizzolatti G, Scandolara C, Matelli M, Gentilucci M. Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses. *Behav Brain Res*. 1981;2(2):147−163.
86. Graziano MS, Yap GS, Gross CG. Coding of visual space by premotor neurons. *Science*. 1994;266(5187):1054−1057.
87. Gentilucci M, Scandolara C, Pigarev IN, Rizzolatti G. Visual responses in the postarcuate cortex (area 6) of the monkey that are independent of eye position. *Exp Brain Res*. 1983;50(2−3):464−468.
88. Ishida H, Nakajima K, Inase M, Murata A. Shared mapping of own and others' bodies in visuotactile bimodal area of monkey parietal cortex. *J Cogn Neurosci*. 2010;22(1):83−96.
89. Avillac M, Ben Hamed S, Duhamel JR. Multisensory integration in the ventral intraparietal area of the macaque monkey. *J Neurosci*. 2007;27(8):1922−1932.
90. Avillac M, Deneve S, Olivier E, Pouget A, Duhamel JR. Reference frames for representing visual and tactile locations in parietal cortex. *Nat Neurosci*. 2005;8(7):941−949.
91. Colby CL, Duhamel JR, Goldberg ME. Ventral intraparietal area of the macaque: anatomic location and visual response properties. *J Neurophysiol*. 1993;69(3):902−914.
92. Duhamel JR, Colby CL, Goldberg ME. Ventral intraparietal area of the macaque: congruent visual and somatic response properties. *J Neurophysiol*. 1998;79(1):126−136.
93. Schlack A, Sterbing-D'Angelo SJ, Hartung K, Hoffmann KP, Bremmer F. Multisensory space representations in the macaque ventral intraparietal area. *J Neurosci*. 2005;25(18):4616−4625.

94. Duhamel JR, Bremmer F, BenHamed S, Graf W. Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature*. 1997;389(6653):845−848.
95. Graziano MS, Gross CG. A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields. *Exp Brain Res*. 1993;97(1):96−109.
96. Hihara S, Taoka M, Tanaka M, Iriki A. Visual responsiveness of neurons in the secondary somatosensory area and its surrounding parietal operculum regions in awake macaque monkeys. *Cerebr Cortex*. 2015;25(11):4535−4550.
97. Graziano MS, Cooke DF, Taylor CS. Coding the location of the arm by sight. *Science*. 2000;290(5497):1782−1786.
98. Iriki A, Tanaka M, Iwamura Y. Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport*. 1996;7(14):2325−2330.
99. Graziano MS. Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proc Natl Acad Sci U S A*. 1999;96(18):10418−10421.
100. Makin TR, Holmes NP, Zohary E. Is that near my hand? Multisensory representation of peripersonal space in human intraparietal sulcus. *J Neurosci*. 2007;27:731−740.
101. Sereno MI, Huang RS. A human parietal face area contains aligned head-centered visual and tactile maps. *Nat Neurosci*. 2006;9(10):1337−1343.
102. Nakashita S, Saito DN, Kochiyama T, Honda M, Tanabe HC, Sadato N. Tactile-visual integration in the posterior parietal cortex: a functional magnetic resonance imaging study. *Brain Res Bull*. 2008;75(5):513−525.
103. Lloyd DM, Shore DI, Spence C, Calvert GA. Multisensory representation of limb position in human premotor cortex. *Nat Neurosci*. 2003;6:17−18.
104. Gentile G, Petkova VI, Ehrsson HH. Integration of visual and tactile signals from the hand in the human brain: an FMRI study. *J Neurophysiol*. 2011;105(2):910−922.
105. Brozzoli C, Gentile G, Petkova VI, Ehrsson HH. FMRI adaptation reveals a cortical mechanism for the coding of space near the hand. *J Neurosci*. 2011;31(24):9023−9031.
106. Grill-Spector K, Henson R, Martin A. Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn Sci*. 2006;10(1):14−23.
107. Limanowski J, Blankenburg F. Integration of visual and proprioceptive limb position information in human posterior parietal, premotor, and extrastriate cortex. *J Neurosci*. 2016;36(9):2582−2589.
108. Limanowski J, Blankenburg F. Network activity underlying the illusory self-attribution of a dummy arm. *Hum Brain Mapp*. 2015;36(6):2284−2304.
109. Grivaz P, Blanke O, Serino A. Common and distinct brain regions processing multisensory bodily signals for peripersonal space and body ownership. *Neuroimage*. 2016;147:602−618.
110. Bekrater-Bodmann R, Foell J, Diers M, Flor H. The perceptual and neuronal stability of the rubber hand illusion across contexts and over time. *Brain Res*. 2012;1452:130−139.
111. Downing PE, Jiang Y, Shuman M, Kanwisher N. A cortical area selective for visual processing of the human body. *Science*. 2001;293(5539):2470−2473.
112. Amedi A, Jacobson G, Hendler T, Malach R, Zohary E. Convergence of visual and tactile shape processing in the human lateral occipital complex. *Cerebr Cortex*. 2002;12(11):1202−1212.
113. Kitada R, Johnsrude IS, Kochiyama T, Lederman SJ. Functional specialization and convergence in the occipito-temporal cortex supporting haptic and visual identification of human faces and body parts: an fMRI study. *J Cogn Neurosci*. 2009;21(10):2027−2045.
114. Stilla R, Sathian K. Selective visuo-haptic processing of shape and texture. *Hum Brain Mapp*. 2008;29(10):1123−1138.
115. Astafiev SV, Stanley CM, Shulman GL, Corbetta M. Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nat Neurosci*. 2004;7(5):542−548.
116. Orlov T, Makin TR, Zohary E. Topographic representation of the human body in the occipitotemporal cortex. *Neuron*. 2010;68(3):586−600.
117. Macaluso E, Frith CD, Driver J. Modulation of human visual cortex by crossmodal spatial attention. *Science*. 2000;289(5482):1206−1208.
118. Peltier S, Stilla R, Mariola E, LaConte S, Hu X, Sathian K. Activity and effective connectivity of parietal and occipital cortical regions during haptic shape perception. *Neuropsychologia*. 2007;45(3):476−483.
119. Limanowski J, Lutti A, Blankenburg F. The extrastriate body area is involved in illusory limb ownership. *Neuroimage*. 2014;86:514−524.

120. Driver J, Noesselt T. Multisensory interplay reveals crossmodal influences on 'sensory-specific' brain regions, neural responses, and judgments. *Neuron*. 2008;57(1):11−23.
121. Murphy JT, MacKay WA, Johnson F. Responses of cerebellar cortical neurons to dynamic proprioceptive inputs from forelimb muscles. *J Neurophysiol*. 1973;36(4):711−723.
122. Glickstein M, Gerrits N, Kralj-Hans I, Mercier B, Stein J, Voogd J. Visual pontocerebellar projections in the macaque. *J Comp Neurol*. 1994;349(1):51−72.
123. Bloedel JR. Cerebellar afferent systems: a review. *Prog Neurobiol*. 1973;2(1):3−68.
124. Naumer MJ, Ratz L, Yalachkov Y, et al. Visuohaptic convergence in a corticocerebellar network. *Eur J Neurosci*. 2010;31(10):1730−1736.
125. Ramnani N. The primate cortico-cerebellar system: anatomy and function. *Nat Rev Neurosci*. 2006;7(7):511−522.
126. Blakemore SJ, Wolpert D, Frith C. Why can't you tickle yourself? *Neuroreport*. 2000;11(11):R11−R16.
127. Petkova VI, Ehrsson HH. If I were you: perceptual illusion of body swapping. *PLoS One*. 2008;3(12):e3832.
128. Preston C, Ehrsson HH. Illusory obesity triggers body dissatisfaction responses in the insula and anterior cingulate cortex. *Cerebr Cortex*. 2016;26(12):4450−4460.
129. Preston C, Ehrsson HH. Illusory changes in body size modulate body satisfaction in a way that is related to non-clinical eating disorder psychopathology. *PLoS One*. 2014;9(1):e85773.
130. Guterstam A, Bjornsdotter M, Bergouignan L, Gentile G, Li TQ, Ehrsson HH. Decoding illusory self-location from activity in the human hippocampus. *Front Hum Neurosci*. 2015;9:412.
131. Slater M, Perez-Marcos D, Ehrsson HH, Sanchez-Vives MV. Inducing illusory ownership of a virtual body. *Front Neurosci*. 2009;3(2):214−220.
132. Maselli A, Slater M. The building blocks of the full body ownership illusion. *Front Hum Neurosci*. 2013;7:83.
133. van der Hoort B, Guterstam A, Ehrsson HH. Being Barbie: the size of one's own body determines the perceived size of the world. *PLoS One*. 2011;6(5):e20195.
134. Petkova VI, Khoshnevis M, Ehrsson HH. The perspective matters! Multisensory integration in ego-centric reference frames determines full-body ownership. *Front Psychol*. 2011;2:35.
135. Preston C, Kuper-Smith BJ, Ehrsson HH. Owning the body in the mirror: the effect of visual perspective and mirror view on the full-body illusion. *Sci Rep*. 2015;5:18345.
136. Petkova VI, Bjornsdotter M, Gentile G, Jonsson T, Li TQ, Ehrsson HH. From part- to whole-body ownership in the multisensory brain. *Curr Biol*. 2011;21(13):1118−1122.
137. Guterstam A, Abdulkarim Z, Ehrsson HH. Illusory ownership of an invisible body reduces autonomic and subjective social anxiety responses. *Sci Rep*. 2015;5:9831.
138. Kilteni K, Bergstrom I, Slater M. Drumming in immersive virtual reality: the body shapes the way we play. *IEEE Trans Vis Comput Graph*. 2013;19(4):597−605.
139. Banakou D, Groten R, Slater M. Illusory ownership of a virtual child body causes overestimation of object sizes and implicit attitude changes. *Proc Natl Acad Sci U S A*. 2013;110(31):12846−12851.
140. Guterstam A, Bjornsdotter M, Gentile G, Ehrsson HH. Posterior cingulate cortex integrates the senses of self-location and body ownership. *Curr Biol*. 2015;25(11):1416−1425.
141. Gentile G, Bjornsdotter M, Petkova VI, Abdulkarim Z, Ehrsson HH. Patterns of neural activity in the human ventral premotor cortex reflect a whole-body multisensory percept. *Neuroimage*. 2015;109:328−340.
142. Graziano MS, Gandhi S. Location of the polysensory zone in the precentral gyrus of anesthetized monkeys. *Exp Brain Res*. 2000;135(2):259−266.
143. Iwamura Y. Hierarchical somatosensory processing. *Curr Opin Neurobiol*. 1998;8(4):522−528.
144. Hyvarinen J. Regional distribution of functions in parietal association area 7 of the monkey. *Brain Res*. 1981;206(2):287−303.
145. Leinonen L, Hyvarinen J, Nyman G, Linnankoski II. Functional properties of neurons in lateral part of associative area 7 in awake monkeys. *Exp Brain Res*. 1979;34(2):299−320.
146. Tsakiris M. Looking for myself: current multisensory input alters self-face recognition. *PLoS One*. 2008;3(12):e4040.
147. Sforza A, Bufalari I, Haggard P, Aglioti SM. My face in yours: visuo-tactile facial stimulation influences sense of identity. *Soc Neurosci*. 2010;5(2):148−162.
148. Lenggenhager B, Tadi T, Metzinger T, Blanke O. Video ergo sum: manipulating bodily self-consciousness. *Science*. 2007;317(5841):1096−1099.

149. Aspell JE, Lenggenhager B, Blanke O. Keeping in touch with one's self: multisensory mechanisms of self-consciousness. *PLoS One*. 2009;4(8):e6488.
150. Ionta S, Heydrich L, Lenggenhager B, et al. Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron*. 2011;70(2):363−374.
151. Canzoneri E, di Pellegrino G, Herbelin B, Blanke O, Serino A. Conceptual processing is referenced to the experienced location of the self, not to the location of the physical body. *Cognition*. 2016;154:182−192.
152. Noel JP, Pfeiffer C, Blanke O, Serino A. Peripersonal space as the space of the bodily self. *Cognition*. 2015;144:49−57.
153. Blanke O, Slater M, Serino A. Behavioral, neural, and computational principles of bodily self-consciousness. *Neuron*. 2015;88(1):145−166.
154. Pomes A, Slater M. Drift and ownership toward a distant virtual body. *Front Hum Neurosci*. 2013;7:908.
155. Bertamini M, Berselli N, Bode C, Lawson R, Wong LT. The rubber hand illusion in a mirror. *Conscious Cognit*. 2011;20(4):1108−1119.
156. Slater M, Spanlang B, Sanchez-Vives MV, Blanke O. First person experience of body transfer in virtual reality. *PLoS One*. 2010;5(5):e10564.
157. Gonzalez-Franco M, Perez-Marcos D, Spanlang B, Slater M. The contribution of real-time mirror reflections of motor actions on virtual body ownership in an immersive virtual environment. *IEEE Virtual Reality Conference (VR) (Waltham, MA: IEEE)*. 2010:111−114.

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