The Routledge Handbook of Bodily Awareness

Chapter 15

BODILY ILLUSIONS

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Abstract

Bodily illusions are changes in immediate awareness of one's body that do not correspond to the body's veridical state. They offer a unique tool for investigating the perceptual processes and brain mechanisms that mediate the sense of our own bodies. This chapter analyzes bodily illusions from the perspectives of psychology and cognitive neuroscience. I discuss classic illusion paradigms such as the rubber hand illusion and illusory limb movements elicited by muscle-tendon vibration. Moreover, I consider both bodily illusions that involve changes in the location and movement of single limbs and more complex illusions that involve interactions between multiple limbs and body segments. Furthermore, I review illusions that involve changes in size, ownership, and number of body parts. We also highlight full-body illusions that involve changes in the perceptual aspects of one's entire body. Bodily illusions reveal how information from different sensory modalities, such as proprioception, touch, and vision, are continuously and automatically integrated to generate a coherent multisensory representation of one's body in space. This multisensory body representation is dynamic and based on information from both prior bodily experiences and bottom-up sensory signal processing.

Keywords: perceptual illusion, body representation, multisensory integration, proprioception, kinesthesia, body ownership, embodiment, bodily awareness.

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15.1 Introduction

The first time I experienced the *Pinocchio illusion*, I was blown away. My colleague Dr. Eiichi Naito, a postdoc in one of the labs where I was conducting my PhD training at the Karolinska Institutet introduced me to this muscle vibration illusion. I closed my eyes, grasped the tip of my nose with my right index finger and thumb, and relaxed the arm as much as I could (Figure 15.1). Eiichi then pressed a vibrating plastic stylus on the skin over my biceps tendon (a regular muscle massager you can buy in a shop will also do). First, I did not feel anything except the buzzing vibration on my skin. Then, it started to happen. I could vividly sense that my right forearm was passively extending at the elbow joint and slowly and continuously moving away from my face. There was no force or effort involved; the forearm was just gently "falling" down in a continuous extension movement. However, the arm movement was not the strangest thing I was experiencing; it was something astonishing that was now happening to my nose. I was still grasping my nose between my fingertips, but I could unmistakably sense how the nose was getting extremely long, unnaturally long, like tens of centimeters long! As the forearm and fingers were felt moving farther away from my face and immobile head, I perceived that the nose was continuously stretching out, like a growing Pinocchio's nose. "How in heaven's name can this be?" I remember thinking to myself. I opened my eyes, and the illusion immediately vanished.

In this chapter, I discuss bodily illusions: what they are, how to induce them, what they tell us about bodily perception, and how the body is represented in the brain. I consider bodily illusions that involve illusory limb movement and illusions where people experience changes in the shape and size of body parts, as in the example above. I also discuss illusions where rubber hands or virtual limbs in view feel like part of one's own body and full-body illusions where people experience mannequins and avatars as their own bodies. The illusions I discuss involve changes in proprioceptive and multisensory awareness of one's own body, and I will not discuss tactile illusions (Hayward 2008) or vestibular illusions (Lackner & DiZio 2005). The aim of the chapter is not to review all bodily illusions described in the literature; instead, we examine illusions that involve changes in crucial aspects of bodily awareness in terms of movement, size, numerosity, belonging to one's body, and structure as a whole. We will focus on behavioral studies but also briefly consider computational models and imaging neuroscience.

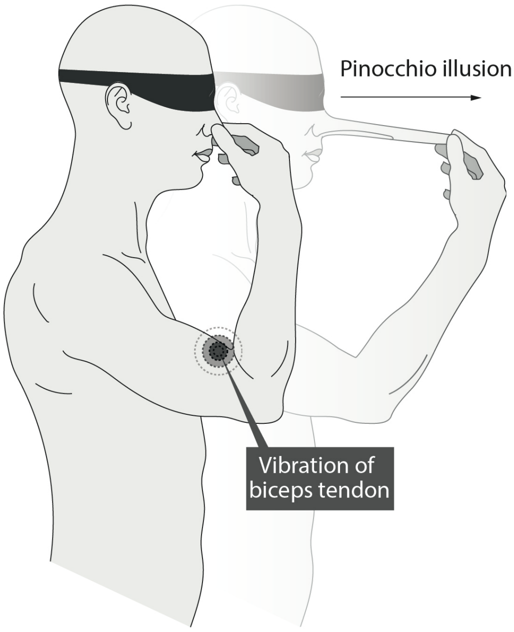

Figure 15.1 Lackner’s Pinocchio illusion. For description, see the text.

15.2 What is a bodily illusion?

Bodily illusions are sensations that do not correspond to the physical state of one’s body; thus, they are errors in perceptual awareness that deviate from reality. Even if the illusion is strong, a person might not spontaneously become aware of the mismatch. However, the error should be sufficiently large so that the person in question can notice the discrepancy if provided some other information for comparison. Tiny deviations between what we perceive and the actual state of the physical body constantly occur, as the perceptual systems do their best to describe the body as precisely as possible, given the available sensory signals and level of sensory noise. However, large errors can trigger surprise and spontaneous reactions of wonder and amazement in the person who experiences them, presumably because bodily illusions are often experienced as strange and “surreal,” as they contradict our intuitive assumptions of the trustworthiness of own-body perception.

Bodily illusions are perceptual illusions. That is, they are automatic changes in bodily perceptual awareness that occur in our minds without conscious reflection, effort, will, or intention. Thus, bodily illusions are not simply thoughts or incorrect semantic knowledge about the body but erroneous impressions of the body in immediate perceptual awareness. A bodily illusion is something you sense or feel, just like a visual illusion is something you see (Shapiro & Todorovic 2017). Thus, bodily illusions occur as a result of information processing in the perceptual systems in the brain. Bodily illusions can occur when the brain attempts to integrate sensory information from conflicting sensory modalities, when it chooses between different alternative interpretations of sensory data, or when a central body representation is updated based on afferent signals to a point where it no longer reasonably matches the body's actual state.

15.3 How to register bodily illusions?

From an experimental perspective, bodily illusions are phenomena that produce behavioral, physiological, and neural effects that can be studied via psychological and brain sciences. Subjective experiences can be quantified by having an individual rate the vividness of the illusion through questionnaires (Longo et al 2008) or visual analog scales (Naito et al 1999) or perform forced-choice discrimination or detection-like tasks (Chancel & Ehrsson 2020, Chancel et al 2022). Perceived illusory changes in the location and movement of limbs and body parts can also be registered behaviorally. For example, individuals can be asked to point to a body part or verbally report its location, and the spatial error from the body part's actual location can be used as an illusion index (Abdulkarim & Ehrsson 2016, Tsakiris & Haggard 2005). Alternatively, the participant can reproduce the illusory movement sensation they experience from one limb (e.g., the right forearm) by overtly moving another limb (e.g., the left forearm) (Proske & Gandevia 2018). Bodily illusions can also be associated with changes in tactile distance perception (de Vignemont et al 2005), tactile force perception (Kilteni & Ehrsson 2017), and visuotactile perception (Pavani et al 2000, Zopf et al 2013), and they can cause errors in goal-directed movements that can be used as an indirect proxy (Fang et al 2019, Heed et al 2011, Kammers et al 2010). Bodily illusions can also be physiologically assessed, for example, by applying a physical threat (e.g., a syringe) toward a fake or real limb and registering the fear-evoked increase in autonomous nervous system reactivity by measuring the so-called skin conductance response (Armel & Ramachandran 2003, Petkova & Ehrsson 2009). When a limb in view feels like one's own, greater skin conductance responses are recorded compared to when it does not. Bodily illusions are also associated with changes in brain activation that can be registered with modern brain imaging techniques, as will be discussed further below. Thus, bodily illusions are perceptual phenomena that can be studied and quantified in scientific experiments to teach us more about how bodily perception works and how the body is represented in the brain.

15.4 How should bodily illusions be classified?

The question of how to classify perceptual illusions and create taxonomies has been debated since the late nineteenth century, with a focus on visual illusions, and without reaching a consensus (Shapiro & Todorovic 2017). I will adopt a descriptive approach and classify the illusions according to the "object of study" (Thiéry 1895). Thus, I have created sections focusing on illusory limb *movement* sensations, illusory *size and shape* changes, and illusory feelings of body parts as one's own, that they *belong* to one's physical self (*body ownership*, see further below). In addition, I will separately group and discuss full-body illusions and supernumerary limb illusions. Although there is some overlap with the three first categories (e.g., full-body illusions can involve changes in size, body ownership and movement), they differ in other important aspects such as the perceived *structure of the body as a whole* and the *numerosity* of limbs. I will also briefly discuss illusory *numbness* sensations and illusory changes in perceived *material properties* of the body, as these are perceptual phenomena that are different from the other classes of bodily illusions. Other classifications schemas are, of course, possible. For example, classifying illusions based on the primary method of inducing them (e.g., muscle vibration, self-touch, fake limbs, crossing limbs), the sensory modalities primarily involved (kinesthetic illusions, visuo-somatic, audio-somatic, etc.), or degree of complexity ("simple": involving a single limb or body part, or "complex": involving interactions between two or more body parts).

15.5 Limb-movement illusions

When discussing specific types of bodily illusions, a good starting point is to consider *illusory limb movement* triggered by muscle vibration (Goodwin et al 1972a, Goodwin et al 1972b) (Figure 15.2). The classic way of inducing such illusions is to apply a vibratory stimulus to the tendon of a limb's flexor or extensor muscle (Goodwin et al 1972b). If the vibration is delivered at 70–100 Hz (Naito et al 1999, Roll & Vedel 1982, Roll et al 1989), it will activate the muscle stretch receptors (muscle spindles) located in the (intrafusal) muscle fibers (Goodwin et al 1972a, Naito et al 1999, Roll & Vedel 1982, Roll et al 1989). A muscle spindle receptor signals muscle length and changes in length, so when the vibration activates this class of receptors in the simulated muscle, the brain interprets the signal as limb movement. For example, if the biceps muscle that flexes the forearm is vibrated, the brain interprets it as a passive extension of the forearm (Figure 15.2A, left). Conversely, if the triceps muscle is vibrated, the brain interprets it as forearm flexion (Figure 15.2A, right). Illusory movements can be elicited for virtually all limbs and movable body parts, including the wrist, arm, foot, leg, and neck, which are among the most studied (Naito et al 2016, Proske & Gandevia 2018).

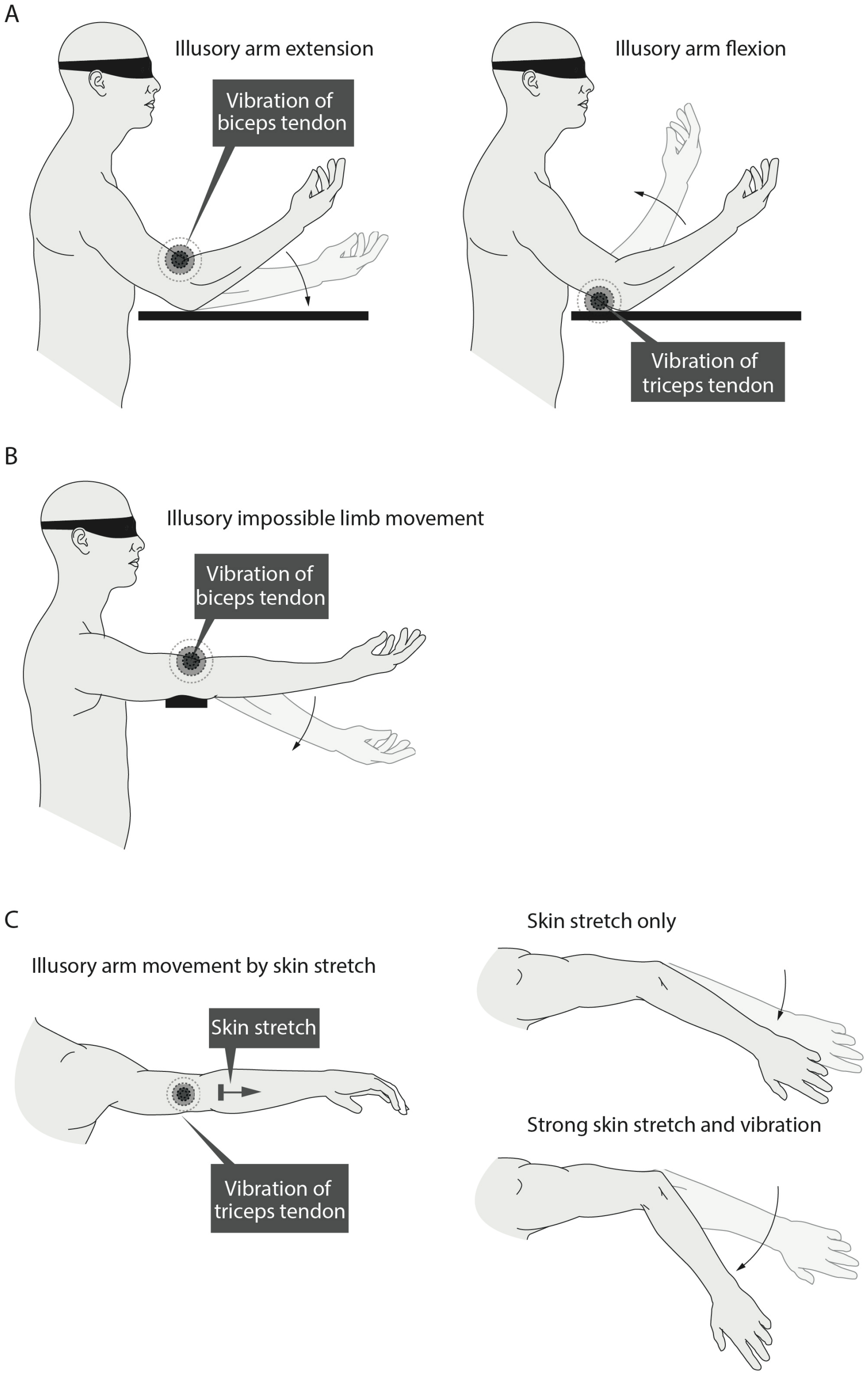

Figure 15.2 Limb-movement illusions elicited by muscle-tendon vibration. Top row slow classic induction of illusory forearm movement by biceps (extension) and triceps vibration (flexion). The middle panel shows illusory extension beyond what is anatomically possible, i.e., an impossible limb movement. The lower panel illustrates the movement illusion induced by stretching the skin with adhesive tape and how the movement effects of muscle stretch and muscle-tendon vibration combine, leading to an overall stronger illusion. *Source:* Godwin et al., 1972b, Craske 1977; Collins et al., 2005.

Importantly, limb movement illusions depend on muscle spindle signals from multiple muscles. This was demonstrated through experiments where vibration was simultaneously applied to several muscles (Gilhodes et al 1986, Roll et al 2009, Thyrion & Roll 2010, Verschueren et al 1998). For example, if the biceps and triceps are concurrently stimulated at the same optimal frequency (80 Hz), the illusions typically cancel each other out. When one of the two muscles is stimulated at the optimal frequency (e.g., 80 Hz) and the other at a suboptimal frequency (e.g., < 60 Hz or > 100 Hz), the end result is an illusion in the direction of the optimally stimulated muscle (Gilhodes et al 1986). By vibrating several synergistic antagonist and agonist muscles in the arm and shoulder simultaneously in time-varying patterns, it is even possible to create illusory 3D movements in the upper arm, such as drawing spirals or letters (Thyrion & Roll 2010).

The fact that conscious movement sensations can be evoked by muscle vibration shows that muscle spindles contribute to proprioceptive awareness, which was not known before discovering this type of illusion. However, movement illusions cannot be explained only by the moment-to-moment processing of the afferent inputs from the vibrated muscle(s) but also requires gradually updating central limb representations based on a constant accumulation of sensory information. Notably, the deviation between the limb representation and actual limb position increases over time as the vibration of a muscle continues, even reaching the point where impossible limb positions beyond what is anatomically possible can be experienced (Craske 1977) (Figure 15.2B).

Visual and cutaneous signals also contribute to illusory limb movement sensations. Seeing the vibrated limb typically cancels the movement illusions, which is consistent with the high reliability of vision as a bodily feedback signal for posture and spatial localization (Guerraz et al 2012, Hagura et al 2007, Lackner & Taublieb 1984, Seizova-Cajic & Azzi 2011). In experiments where participants receive visual feedback of the vibrated limb moving in a direction that is the same or opposite to that of the muscle vibration-induced movement illusion, interactions occur: when the visual and muscle spindle inputs are congruent, the movement illusion is enhanced, and when they are incongruent, the illusion is reduced (Guerraz et al 2012, Le Franc et al 2020, Tsuge et al 2012).

Cutaneous receptors in the skin also contribute to limb–movement illusions [slowly adapting low-threshold mechanoreceptors (Edin & Abbs 1991, Hulliger et al 1979)]. For example, it is possible to induce limb–movement illusions by stretching the skin with adhesive tape to create skin strain patterns that resemble those that occur during natural movements

(Collins & Prochazka 1996, Collins et al 2000, Collins et al 2005, Edin 2001, Edin & Johansson 1995). When such skin stretching is combined with muscle-tendon vibration, the result is an integrated estimate that reflects a combination of cutaneous and proprioceptive signals (Collins et al 2005) (Figure 15.2C). Congruent skin stretching and muscle vibration information lead to an overall stronger kinesthetic illusion than either stimulation modality alone, while incongruent skin stretching and muscle vibration reduce the illusion (Collins et al 2005).

Moving tactile stimuli and moving visual stimuli near a limb can also induce limb–movement illusions. If a participant rests with one hand palm down on a rotating textured disk or a visual pattern is rotated under the hand (vection stimuli) (Blanchard et al 2013, Chancel et al 2016a), illusory rotation movements of the hand can be experienced. Combining such rotating tactile or visual stimuli leads to even stronger illusions in line with multisensory integration principles (Blanchard et al 2013, Chancel et al 2016a). Thus, illusory limb movement is the outcome of an integration process that considers signals from different sensory modalities and not just proprioceptive afferent signals from muscles, joints, and tendons.

15.6 The rubber hand illusion and its variations

The importance of the interactions between the senses for bodily awareness is made strikingly clear in the *rubber hand illusion* (Botvinick and Cohen 1998) where a fake limb in view is misperceived as one’s own [see also (Tastevin 1937) for an early similar phenomenon with a rubber finger]. To induce the classic version of this illusion, the participant sits at a table on which a rubber hand is placed in full view in orientation and posture that matches the participant’s relaxed real hand, which is hidden behind a screen (Figure 15.3A). The experimenter then uses two small brushes to stroke the rubber hand and the real hand simultaneously and at corresponding sites (or two robots are doing the stroking). Approximately ten seconds of such repeated stroking (at 0.5-1 Hz) is typically sufficient to trigger the illusion in most cases (Chancel & Ehrsson 2020, Ehrsson et al 2004, Lloyd 2007). Subsequently, the majority of participants vividly experience the rubber hand as their own and report that they “sense” the touches of the paintbrush directly on the rubber hand (Botvinick & Cohen 1998); moreover, proprioceptive sensations are felt originating from the fake hand, and the rubber hand feels like part of one’s body (Longo et al 2008). The rubber hand illusion occurs when the brain resolves the mismatch between vision and somatosensation by updating multisensory arm representation in space so that the visual impressions from the rubber hand and somatosensory impressions from the real hand are perceptually fused and experienced as originating from a single limb (i.e., the fake hand is experienced as their own hand). The rubber hand illusion is interesting because it informs us about how visual and somatosensory signals are combined to shape our bodily awareness and how we come to experience limbs and other body parts as our own, the latter which is a perceptual experience referred to as the sense (or feeling) of body ownership (Ehrsson 2020, Kilteni et al 2015, Petkova & Ehrsson 2010, Tsakiris 2010).

Critically, eliciting this illusion depends on the temporal and spatial correspondences of visual and somatosensory stimulation. If the seen and felt strokes are out-of-sync by more than 300 ms, the illusion is not induced (Shimada et al 2009, Shimada et al 2014). In addition, applying strokes in opposite directions to the two hands breaks the illusion (Costantini & Haggard 2007, Gentile et al 2013), as does placing the rubber and real hands in significantly different orientations (Ehrsson et al 2004, Ide 2013, Pavani et al 2000, Tsakiris & Haggard 2005) or farther than approximately 30 cm apart, i.e., outside the peripersonal space of the arm (Brozzoli et al 2012, Kalckert & Ehrsson 2014b, Lloyd 2007). These temporal and spatial constraints of the illusion are highly reminiscent of the temporal and spatial congruence principles in multisensory integration (Holmes & Spence 2005, Stein & Stanford 2008), whereby two signals in two different sensory modalities tend to be combined if they occur at similar times and in close proximity. Moreover, the form and shape of the artificial hand must also match those of the participant’s real limb, and the illusion cannot be induced with a block of wood (Tsakiris et al 2010), a rubber foot (Guterstam et al 2011), or a left rubber hand if the illusion involves the participants veridical right hand (Guterstam et al 2011, Petkova & Ehrsson 2009, Tsakiris & Haggard 2005) (but see the special case of “empty space” below). Collectively, these perceptual rules indicate that multisensory integration of bodily related signals plays a critical role in the rubber hand illusion and bodily awareness more generally (Brozzoli et al 2012, Chancel & Ehrsson 2020, Ehrsson 2012, Ehrsson et al 2004, Kilteni et al 2015, Makin et al 2008, Samad et al 2015, Tsakiris & Haggard 2005). Furthermore, we know that the rubber hand illusion works well with different body parts, such as the foot (*rubber foot illusion*) (Crea et al 2015, Lenggenhager et al 2015) and the teeth and mouth (Bono & Haggard 2019), and equally well for left and right hands (Smit et al 2017), so its principles seem to generalize.

Like other bodily illusions, the rubber hand illusion depends on an interplay between the processing of bottom-up multisensory signals and updating of the central body representation. The rubber hand illusion requires a period of sensory evidence accumulation from a time series of multisensory correlations (Parise & Ernst 2016, Parise et al 2012) before the illusion is elicited. As described above, this period lasts at least 10 seconds in most people and involves approximately 6 to 10 synchronous visuotactile touch events (Chancel & Ehrsson 2020, Ehrsson et al 2004, Guterstam et al 2013, Lloyd 2007). During this phase, visuoproprioceptive recalibration and updating of peripersonal space toward the rubber hand occurs to minimize the multisensory conflict (Brozzoli et al 2012, Ehrsson et al 2004) until the automatic perceptual decision is made to start to bind visual and somatosensory signals into a single coherent multisensory representation of one's hand and the subjective illusion is experienced (Ehrsson 2012, Ehrsson et al 2004). Consequently, visual stimuli approaching the rubber hand trigger tactile expectations (Chancel et al 2021), and physical threats directed toward the rubber hand evoke emotional threat responses in an anticipatory manner (Ehrsson et al 2007, Gentile et al 2013). Notably, when the illusion was first elicited with correlated brush strokes and then stroking stopped, the illusion was maintained for at least 20 seconds (Abdulkarim et al 2021), illustrating a sustained residual effect due to the updated multisensory arm representation. There is then a gradual "re-updating" back to the veridical perpetual state, presumably driven by the spatial disparity in visual and proprioceptive signals from the rubber hand and real hand until the illusion is completely lost.

Several different versions of the rubber hand illusion have been described. In the *moving rubber hand illusion* [(Dummer et al 2009, Kalckert & Ehrsson 2012, Walsh et al 2011); see also (Tsakiris et al 2006)], the illusion is triggered by synchronized passive or active finger movements of both the model hand in view and the participant's own hidden hand (Figure 15.3D). That the illusion can be induced in this way shows that integration of visual and proprioceptive signals plays an essential role in body ownership and multisensory body representation and that tactile stimulation by an external object moving in peripersonal space is not a necessary condition to elicit the rubber hand illusion.

In the *somatic rubber hand illusion* (Ehrsson et al 2005a), a blindfolded participant passively touches a right rubber hand with their left index finger, while the experimenter applies synchronous touches to the participant's real contralateral hand on the corresponding site (Figure 15.3B). After a brief period of repeated correlated touches, most participants feel that they are touching their own hand directly even though they report that it feels harder and colder than usual. Thus, the spatiotemporal correlations of tactile and proprioceptive signals from the two hands lead to tactile-proprioceptive integration sufficient to elicit the illusion. Thus, the rubber hand does not have to be seen for the rubber hand illusion to work.

The *invisible hand illusion* is perhaps particularly astonishing and strange (Guterstam et al 2013). The experimenter brushes a portion of empty space over the table in full view of the participant (without a rubber hand), while the participant's hidden real hand is touched in a corresponding way (Figure 15.3C). The spatiotemporal patterns must be very well matched so that the brush movements precisely follow the shape of the "invisible hand" and closely match the strokes on the participant's real hand. The illusion feels like having an invisible hand lying on the table that senses the brush strokes that one observes. The invisible hand illusion underscores the importance of visuotactile correlations for updating multisensory body representation, and it shows that the brain is willing to accept ownership of hands it cannot see. Unlike the case with a woodblock, there is no mismatch between the seen shape of the wooden object and the real hand, and there is no violation of the prior knowledge that two different rigid objects cannot occupy the same space. Empty space is a place where one's hand could move, and we are used to sensing limbs we temporarily cannot see, such as in the dark or in poor viewing conditions. Thus, according to the probabilistic logic that seems to govern bodily illusions, an invisible hand is the most likely explanation for the unusual pattern of sensory stimulation that the brain is being exposed to.

The invisible, somatic, and moving rubber hand illusions all follow the same spatial and temporal congruence rules as the classic rubber hand illusion, require a similar period for elicitation (approximately 10–20 seconds in the majority of cases), and show similar effects on behavioral, skin conductance and neuroimaging measures (Ehrsson et al 2005a, Ehrsson et al 2004, Guterstam et al 2013, Kalckert & Ehrsson 2014a, Kalckert & Ehrsson 2014b, Kalckert & Ehrsson 2017, White et al 2015). These observations suggest that the various illusions are different manifestations of essentially the same multisensory perceptual phenomenon. In addition, we know that the rubber hand illusion can be influenced by the congruence of sensory signals from other sensory modalities, such as audition (Radziun & Ehrsson 2018), pain (Cordier et al 2020), pleasant touch (Crucianelli et al 2013, van Stralen et al 2014), and thermosensation (Cordier et al 2020, Trojan et al 2018). Thus, the rubber hand illusion and its many variations suggest that sensory information from many different sensory modalities contributes to bodily awareness and the sense of body ownership.

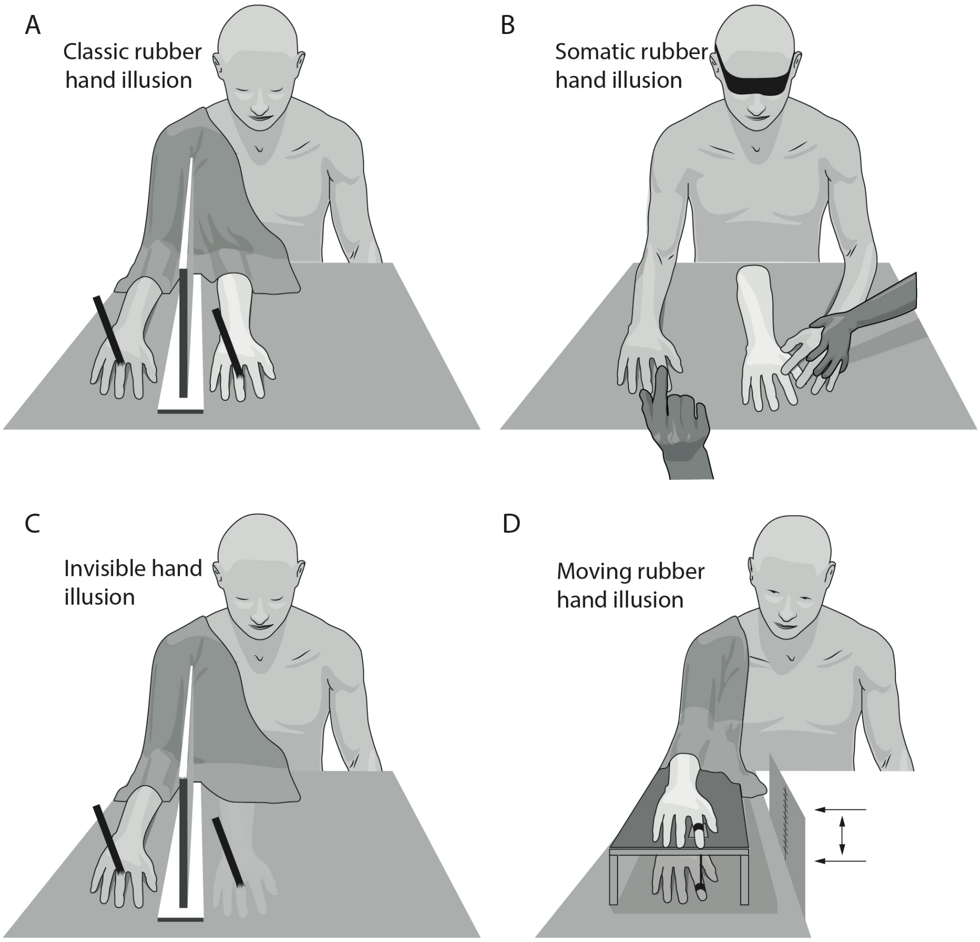

Figure 15.3 Different versions of the rubber hand illusion. The classic version of the rubber hand illusion (top left) is induced by synchronous brush stroking (black instruments) of the real hand (darker; to the left of the occluding screen) and the rubber hand in full view (lighter; to the right of the screen). In the somatic rubber hand illusion (top right), the experimenter (dark hands) touches the blindfolded participant's right hand while moving the participant's left index finger to synchronously touch the rubber hand. In the invisible hand illusion, synchronous brush strokes are applied to a portion of empty space in full view and to the participant's hidden real hand, triggering an illusory invisible hand sensing the touches (semitransparent for illustrative purposes). The moving rubber hand illusion (lower right) is elicited by the model hand (on top of the platform) and the hidden real hand (below the platform) making synchronized index finger tapping movements. *Source:* Botvinick & Cohen, 1998; Ehrsson et al., 2005a; Guterstam et al., 2013; Kalckert & Ehrsson, 2012.

15.7 Mirror illusion, real-time video illusions and virtual hand illusion

Bodily illusions similar to the rubber hand illusion can be induced using mirrors, video image-based systems, and virtual reality techniques that can manipulate visual feedback from a person's body. In the typical mirror illusion setup, a participant sits with both hands resting on a table. A mirror is placed at a 90-degree angle from the body in the sagittal plane. One hand is placed behind the mirror, for example, the right hand, so when the participants look into the mirror, they see the mirror reflection of the left hand in a similar location as the right hand behind the mirror. If the two hands are placed in the same posture, make the same movements, or an experimenter synchronously touches the two hands at the corresponding sites, the participant experiences an illusion of looking directly at their right hand – as if the mind "forgets the mirror" (Holmes et al 2004, Ramachandran & Rogers-Ramachandran 1996, Schmalzl et al 2013). The mirror illusion is a multisensory illusion that depends on the match between vision and somatosensation, similar to the rubber hand illusion, and incongruent movements or incongruent sensory stimulation will break it (Chancel et al 2016b, Fink et al 1999, Metral et al 2015).

In 'real-time video hand boxes' (e.g., Roger Newport's MIRAGE box[1]), participants place one hand inside a box and see the hand on a screen that is placed on top of the box from a natural point of view. Two cameras inside the box film the participant's hand, and the recorded video image is presented live on the screen so that it appears to the participant as if he or she is directly looking at his or her hand. If the video image is presented in good spatial alignment with the proprioceptively felt hand inside the box, a feeling of ownership of the viewed hand is triggered by visuoproprioceptive integration. In contrast, a significant spatial disparity or a delayed video feed during finger movement or brush stroking breaks or reduces the illusion by introducing multisensory incongruence that can trigger a sense of "disownership" of the hand in view (Newport & Gilpin 2011, Reader & Ehrsson 2019) [see also (Gentile et al 2013)]. Real-time video-based hand boxes have been used to induce various other types of bodily illusions (Abdulkarim & Ehrsson 2018, Newport & Gilpin 2011, Newport et al 2010, Newport & Preston 2010, Reader & Ehrsson 2019, Stone et al 2018), for example, the "*disappearing hand trick*" (Newport & Gilpin 2011). An illusory experience of looking at one's hand can also be triggered by filming the participant's hand from the first-person point of view and displaying the images in a head-mounted display (HMD) worn by the participant as he or she directs his or her head and gaze toward the hand (Gentile et al 2013, Kannape et al 2019, Roel Lesur et al 2020). Finally, the *virtual arm illusion* (Slater et al 2008) is a version of the rubber hand illusion conducted in immersive virtual reality; here, the hand, the object touching the hand, and the environment are all computer-generated graphics. Many different versions of virtual arm illusions have been described (Kilteni et al 2015), and they are effectively induced by congruent movement (Sanchez-Vives et al 2010), visuoproprioceptive congruence (Perez-Marcos et al 2012, Tieri et al 2015), and visuotactile congruence (Slater et al 2008).

15.8 The Pinocchio illusion and body-size illusions

The perceived size and shape of body parts can also change during bodily illusions. Such body-size illusions are fascinating because there are no specialized peripheral receptors in the skin, muscles, and joints that provide afferent information about the size or shape of body parts. Therefore, these illusory perceptions must stem from central processing in the brain and arise from the integration of different sensory sources.

The reader is already familiar with the author's recollection of experiencing the Pinocchio illusion for the first time (Lackner 1988). This illusion arises when the central perceptual systems overcome the conflict between arm movement, driven by the forearm's vibrated flexor muscle, and the immobile position of the head, when the fingertips create a contact point at the nose tip (Figure 15.1). To resolve the conflict, the nose representation is updated so that it feels as if the nose is stretching and becoming longer. In his 1988 paper, Lackner described many different versions of this illusion involving spatial distortions of length, width, and shape of various body parts. The nose can shrink when the triceps is vibrated instead of the biceps, for example. If one puts the hand on top of one's head, one can experience an "egghead illusion" (Figure 15.4A) or "shrinking head illusion" depending on whether the flexor or the extensor muscle is being stimulated. Similarly, if both hands are placed on the waist, palm-to-waist, and wrist extensor or flexor muscles are vibrated, it is possible to elicit shrinking or expanding waist illusions (Ehrsson et al 2005b, Lackner 1988) (Figure 15.4B). The illusion also works well on the index finger, leading to illusory finger elongation or shrinkage (de Vignemont et al 2005).

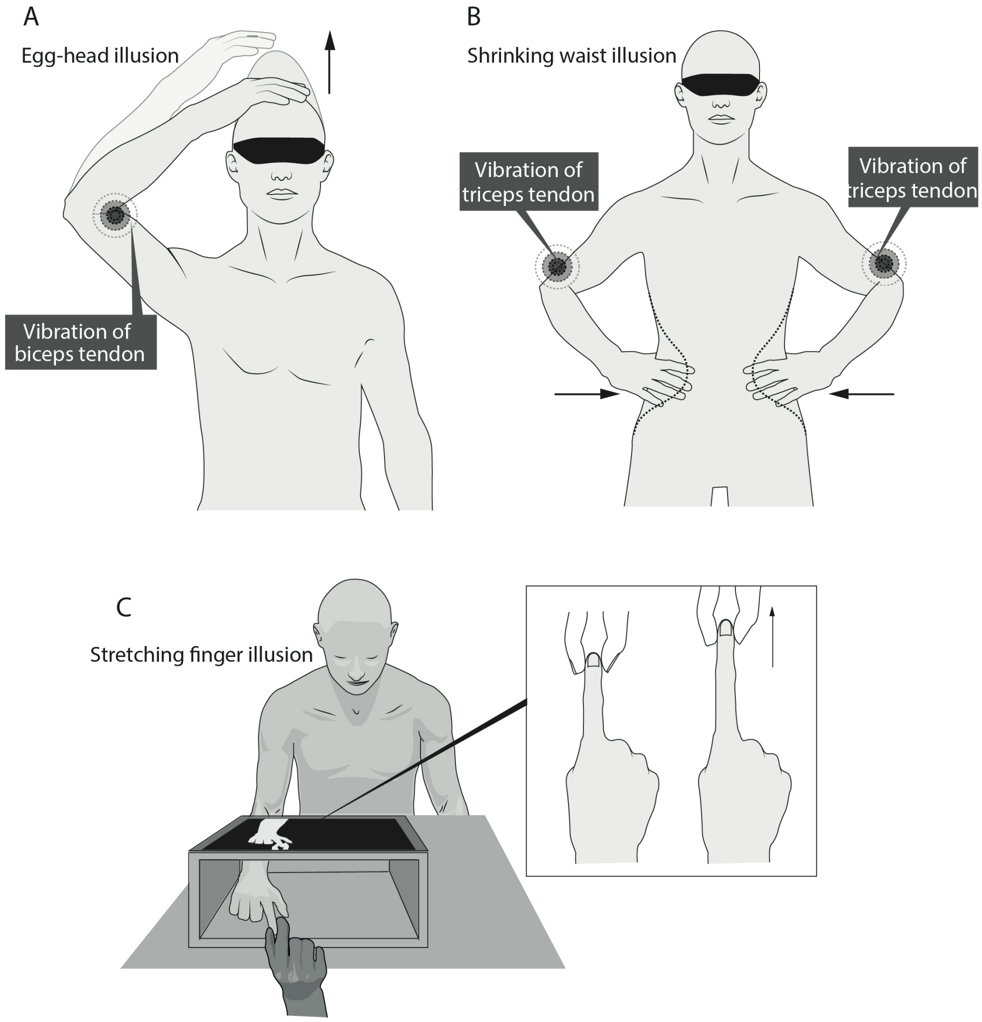

Figure 15.4 Illusions of body size. Illusory expansion of the head (top left panel) or shrinkage of the waist (top right panel) during two versions of Lackner's muscle-tendon vibration illusions. Illusory finger stretching in a 'real-time video hand box' setup is illustrated in the lower panel. For details, see the text. *Source:* Lackner 1988; Ehrsson et al., 2005b; Newport & Preston, 2010.

In Lackner's paradigm, the participants are blindfolded, but illusory body-part size changes can also be induced with visual feedback from the body using rubber hands or virtual hands (Byrne & Preston 2019, Kilteni et al 2012, Newport & Preston 2010)(Figure 15.4C). In virtual reality experiments or real-time video hand boxes, participants see their limb gradually expanding while congruent multisensory stimulation is provided, such as in the *very-long-arm illusion* (Kilteni et al 2012). Similar effects can also be achieved in the invisible hand illusion paradigm by slowly "pulling out" a very long invisible finger with visible synchronous strokes that become increasingly longer (Byrne & Preston 2019). Furthermore, by using different rubber hand sizes (Bruno & Bertamini 2010, Haggard & Jundi 2009, Heed et al 2011) or magnifying and minifying mirrors (Perera et al 2021), it is also possible to induce illusions of ownership of hands of different sizes. Moreover, synchronized finger taps and tactile feedback from another body part can also be used to induce illusory changes in body-part size without visual feedback (Craske et al 1984, Ramachandran & Hirstein 1997). Additionally, sound feedback can modify perceived limb length, as in the so-called "auditory Pinocchio illusion," where participants feel their finger to be longer when the action of pulling their finger is paired with a rising pitch (Tajadura-Jimenez et al 2017). Finally, changes in the size and shape of body parts have also been introduced in full-body illusions (see next paragraph) when normal-sized individuals experience obese or slim bodies as their own (Preston & Ehrsson 2014, Preston & Ehrsson 2016, Preston & Ehrsson 2018). The above illusions inform us how the relative sizes of limbs and body parts are centrally represented and reveal the importance of perceptual interactions between various body parts for multisensory conflict resolution and coherent bodily awareness.

15.9 Full-body illusions

Bodily illusions can also involve the entire body, and full-body versions of the rubber hand illusion have been described where people experience artificial bodies, virtual bodies, or other people's bodies as their own. These *full-body ownership illusions* (or *body-swap* or *body-transfer illusions* as they are also referred to) generalize the multisensory principles of bodily illusions from single limbs to the case of the entire body and raise fundamental questions of how coherent whole-body perception is constructed and if the perception of the whole body is more than the sum of its parts.

In 2008, my PhD student Valeria Petkova and I described an illusion where participants experienced a mannequin as their own body (Petkova & Ehrsson 2008). In this paradigm, the participants viewed a mannequin's body from the point of view of the mannequin's head, where two cameras were placed that transmitted video signals to an HMD worn by the participant (Figure 15.5A). The participant bent his or her head forward as if to look down on his or her body but saw the mannequin's body in a similar location where he or she would expect to see their own. The researcher then repeatedly touched the mannequin and the participant's unseen real body at the same time and in corresponding places on the abdomen. After a short period of such repeated stimulation, most participants started to perceive the touches directly on the mannequin's body and sense the mannequin as their own body. It is as if the visual impressions of the mannequin and the proprioceptive impressions of one's real body fused into a single coherent multisensory object that is oneself. This illusion follows similar temporal, spatial, and humanoid congruence rules as the rubber hand illusion (Petkova et al 2011a, Petkova & Ehrsson

2008, Petkova et al 2011b, van der Hoort et al 2011), which suggests that the illusion of owning the mannequin's body is based on similar multisensory integration mechanisms. Furthermore, the first-person point of view and peripersonal space are critical factors because if the artificial body is viewed from a distance outside of peripersonal space, from a third-person perspective, the bodily illusion substantially weakens (Gorisse et al 2017, Maselli & Slater 2013, Maselli & Slater 2014, Petkova et al 2011b).

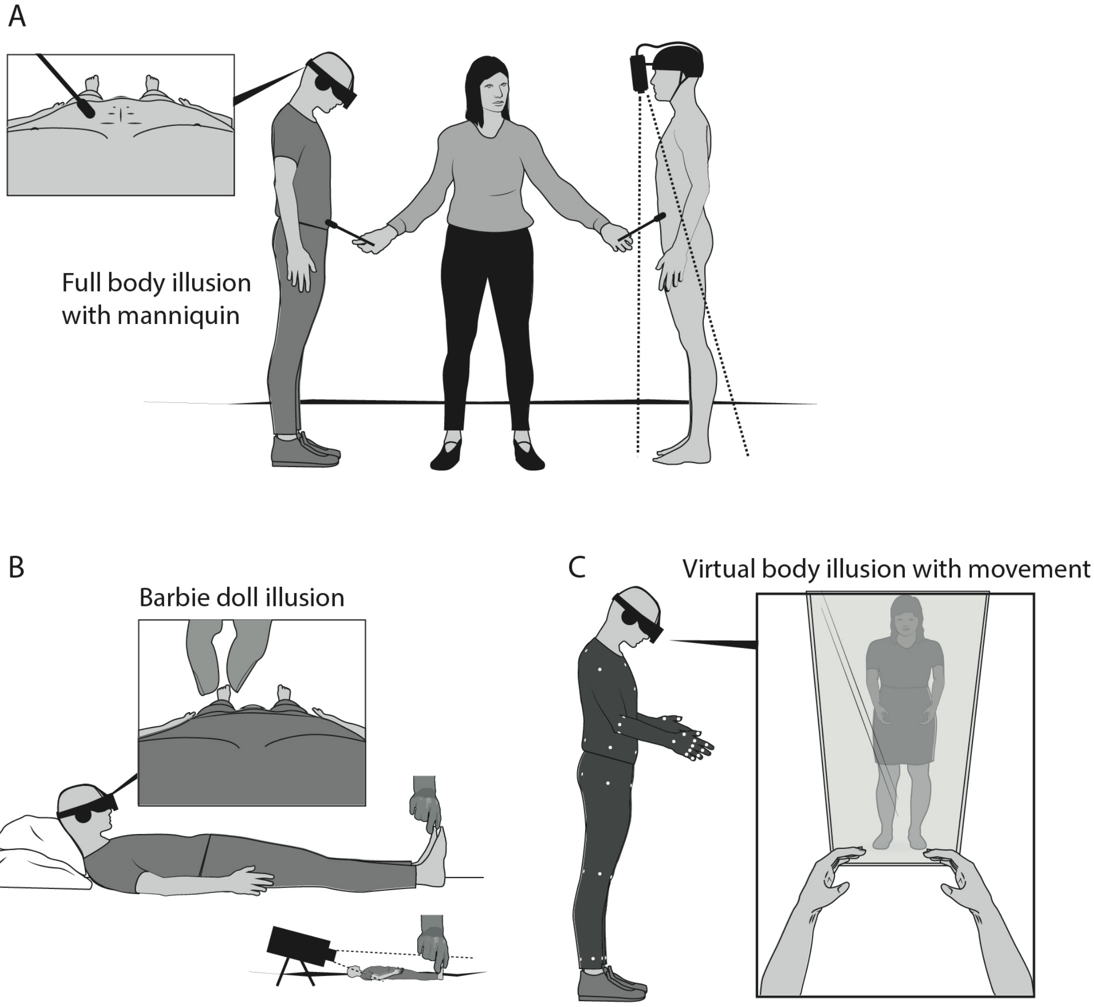

Figure 15.5 Full-body illusions of perceiving artificial and virtual bodies as one's own. A mannequin (top panel), a small doll (lower left panel) or a computer-generated body (avatar) in virtual reality (lower right) viewed from the first-person perspective are experienced as one's own when combined with visuotactile (mannequin and doll) or visuomotor correlations (avatar; note that a virtual mirror has been placed in front of the avatar so that then the participants look down they see the avatar from the first-person perspective and when they look up the see the avatar's mirror reflection); adopted from a video provided by Mel Slater (The Event Lab, University of Barcelona). For details, see the text. *Source:* Petkova & Ehrsson, 2008; van der Hoort et al., 2011; Slater et al., 2009.

In virtual reality (VR), where it is easier to implement moving avatars through motion tracking, the full-body ownership illusion can be induced by congruent limb movements

(Maselli & Slater 2013, Petkova & Ehrsson 2008, Slater et al 2009) or congruent head movements and visual feedback in the HMD (through head tracking) (Maselli & Slater 2013, Slater et al 2009)(Figure 15.5C). Congruent vestibular feedback and visual information about bodily rotation signals can also elicit full-body illusions without tactile stimulation or voluntary movements (Preuss & Ehrsson 2019), and therefore, the vestibular sense also contributes. Furthermore, just looking at a stationary artificial body can elicit the full-body illusion through visuoproprioceptive integration if the spatial disparity between the seen artificial body and the sensed unseen real body is small (Carey et al 2019, Maselli & Slater 2013). The illusion of owning an artificial body can also be induced without the use of HMD, video technology, or VR by simply placing the front half of a mannequin on top of the participant's real body like a suit of armor and applying synchronous stroking (Petkova et al 2011b).

As long as the multisensory spatial and temporal congruence rules are obeyed in the appropriate sensory modalities, the illusion works well with many types of bodies: strangers (Petkova & Ehrsson 2008, Preston & Ehrsson 2018, Tacikowski et al 2020b), friends (Tacikowski et al 2020b), people of the opposite sex (Tacikowski et al 2020a), people with a different skin tone (Peck et al 2013), androids (Nishio et al 2012), and, as mentioned above, computer-generated avatars in immersive virtual reality (Kilteni et al 2015, Slater et al 2009). A block of wood eliminates the illusion (Petkova & Ehrsson 2008), although an invisible full-body illusion can be elicited if the experimenter strokes five body parts of a participant with a large paintbrush, while synchronously, in the corresponding position, moving another paintbrush in the empty space in view in the HMDs (D'Angelo et al 2017, Guterstam et al 2015a). Similarly, body-size illusions have been induced where the perceived size of one's entire body changes with respect to the spatial perception of the external environment so that one has illusory ownership of tiny (30 cm; *Barbie-doll illusion*)(Figure 15.5B), small (80 cm), or huge (300 cm) dolls (van der Hoort et al 2011) or child-sized avatars (Banakou et al 2013).

An important difference from the illusions that involve a single limb or a couple of body segments is that the participants experience ownership over the *entire* body in full-body illusions – not just the body part that moves or receives dynamic multisensory stimuli (Gentile et al 2015, O'Kane & Ehrsson 2021, Petkova et al 2011a, Petkova & Ehrsson 2008). The illusion "spreads" from a stimulated body part to encompass the entire mannequin (Petkova & Ehrsson 2008), and a similarly strong full-body illusion can be elicited by stimulating different parts of the body, such as the abdomen, right hand or right foot (Gentile et al 2015). Moreover, the perception of owning the entire body is unlikely to correspond to a simple summation of body-part ownership (O'Kane & Ehrsson 2021, Petkova et al 2011a) but requires perceptually connecting the parts into an overall perceptual structure. The structure of the body is essential; presenting a “scrambled body” eliminates the full-body ownership experience (Kondo et al 2020). Thus, the full-body ownership illusion requires integrating multisensory information across multiple body parts and perceiving a single whole bodily "gestalt."

The basic illusion of owning an entire body viewed from the first-person perspective has been used in more complex illusion paradigms. For example, in the *out-of-body illusion* (Ehrsson 2007), a participant experiences his or her bodily self being located in a different place from the real body, the latter which is viewed from a distance and feels “disembodied” as if looking at a stranger (Bergouignan et al 2014, Guterstam et al 2015b, Guterstam et al 2015c, Guterstam & Ehrsson 2012) [for a VR-version see (Bourdin et al 2017) and for a version when shaking hands with the disowned real body see (Petkova & Ehrsson 2008)]. However, the out-of-body illusion involves illusory changes in perceived self-location in the local environment (spatial cognition) beyond the topic of the current chapter. In the paradigm by Lenggenhager and Blanke (Lenggenhager et al 2007), participants self-identify with a virtual body that stands with its back toward the participant two meters in front of them while simultaneous visual and tactile stimuli are applied to the participant's back and the virtual body's back [for review see (Blanke et al 2015)]. However, in this paradigm, the sensory conflict between the real unseen body sensed from the first-person perspective and the distal virtual body viewed from the third-person perspective is not resolved. Thus, vision and proprioception are not combined into a unified multisensory representation of one’s body as in full-body illusions when the body is viewed from the first-person perspective.

15.10 Supernumerary limb illusions

Supernumerary limb illusions fascinate many of us because they seem to violate the human body plan, and I have grouped them in a separate category because they differ from the other illusions in one specific aspect: changes in perceived *numerosity* of one’s limbs. In the *supernumerary rubber hand illusion* (Figure 15.6A), two identical right rubber hands are presented to the participants at similar distances (within peripersonal space) from the real hand, which is hidden on a lower platform (Ehrsson 2009, Fan et al 2021). In another version (Figure 15.6B), a single right rubber hand is placed next to the participant's fully visible real right hand (Guterstam et al 2011) [see (Rosa et al 2019) for an augmented reality version]. The two rubber hands or the single rubber hand are then brushed synchronously with the real hand at corresponding locations, triggering the illusions that both the right rubber hands feel like one’s own simultaneously (Fan et al 2021) or that the single rubber hand and the real hand are both perceived as part of one's body (Guterstam et al 2011). The feeling of touch is also duplicated in these instances; the participants perceive two separate visuotactile brush events on the two 'owned' hands in view. Illusions of having extra hands can also be induced by congruent movements, as experiments using real-time video images of hands have shown (Newport et al 2010)(Figure 15.6C). In these experiments, participants reported that the two virtual hands in view felt like their own when executing synchronous finger movements and when the virtual hands copied the same movements. Furthermore, in the *Anne Boleyn illusion* (Newport et al 2016), people sense an invisible sixth finger in a version of the mirror illusion. Recent work has demonstrated that this illusion can be modified to produce a continuous illusion of a sixth finger (Cadete & Longo 2020), rather than the momentary experience probed in Newport's original study. Finally, the principles from supernumerary limb illusions have been extended to the case of whole bodies in the *supernumerary body illusion* (or "two-body illusion"), where people experience two strangers' bodies viewed from the first-person perspective as their own (Guterstam et al 2020).

Supernumerary hand illusions arise when there is equally strong sensory evidence that two rubber hands or virtual hands are one's own. Instead of "randomly choosing" one of the two hands or switching back and forth between two competing percepts (as in binocular rivalry), the brain is willing to accept the scenario in which both fake hands are one's own at the same time. Evidently, this is the solution that best minimizes the multisensory conflict between vision and somatosensation. Thus, tactile and proprioceptive signals from the single real hand are simultaneously integrated with the visual signals from the two fake hands in view, leading to an experienced "duplication" of the own hand and brush stroke events (Fan et al 2021). Supernumerary limb illusions suggest that the singleness of limb representation, i.e., that we have only one right hand, one left foot, etc., is not a fundamental constraint of body representation and that multisensory binding in bodily awareness is flexible enough to combine somatosensory information and visual information at multiple locations simultaneously.

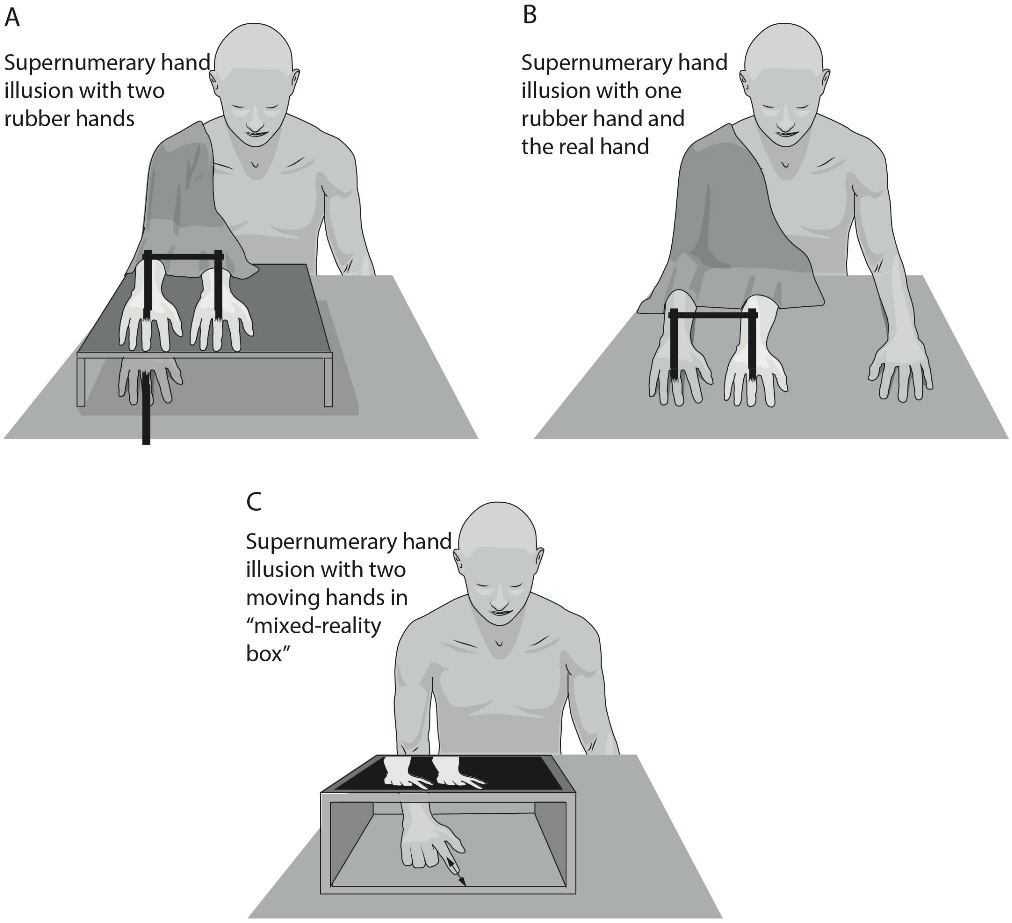

Figure 15.6 Supernumerary limb illusions. Supernumerary rubber hand illusions induced by synchronized brush stroking where the participants experience two fake hands as their own (top left panel) (Fan et al 2021) or a fake hand as their own lying next to the real hand that still feels like their own (top right panel) (Guterstam et al 2011). The lower panel shows supernumerary virtual hand illusion induced by synchronized finger movements and video images of the hands presented on a screen (Newport et al 2010). *Source:* Fan et al., 2021; Guterstam et al., 2011; Newport et al., 2010.

Recent advances in research on supernumerary limb illusions are relevant for the over 2000-year-old tactile illusion described by the Greek philosopher Aristotle (384–322 BC) (in Metaphysica IV, 6 and De Somniis 2). In one version of *Aristotle's illusion*, the participant crosses his or her index finger and middle finger and touches the tip of the nose between the crossed index and middle fingers, which triggers an illusion of touching two noses. *Aristotle's illusion* presumably occurs because the brain is unused to crossed-finger postures and therefore interprets the tactile stimuli as if the fingers were uncrossed (Benedetti 1985, Benedetti 1988), and simultaneous touches on the lateral side of the index finger and the medial side of the middle finger – the parts of the digits contacting the nose – are perceived as originating from different objects (Benedetti 1986). However, Aristotle's illusion has been experimentally studied with only small external objects such as a small rod or point-like touch stimuli

(Benedetti 1985, Benedetti 1988, Fiorio et al 2014, Nava et al 2014, Tinazzi et al 2013), which was also Aristotle's primary interest. To the best of my knowledge, the effects on nose representation have never been investigated. However, the supernumerary rubber hand illusion and similar phenomena discussed above suggest that a genuine nose duplication may occur in Aristotle's illusion performed on the nose.

15.11 Illusions of material properties, numbness, and right-left hand reversal

Three other bodily illusions deserve brief mention before we conclude, as they concern aspects of body representation we have not discussed thus far. First, in the *marble-hand illusion*, the hand is perceived as made out of hard rock (Senna et al 2014). To induce this illusion, the experimenter repeatedly and gently hits the participant's hand with a small hammer, while the hammer's natural sound against the skin is slowly and steadily replaced with the sound of a hammer hitting a piece of marble. According to the participant's reports, the hand started feeling stiffer, heavier, harder, and less sensitive after five minutes of such auditory stimulation. The marble hand illusion is interesting because it involves changes in the body's perceived material properties, an understudied aspect of body representation. Anecdotally, similar effects occur in the somatic rubber hand illusion where the embodied fake hand one perceives touching feels colder and harder than usual.

Second, *numbness illusions* are elicited when tactile expectations on limbs that are felt as one's own are not met. Numbness sensations can arise during the rubber hand illusion if the illusion is first induced, and then only the rubber hand is stroked in view without touches being delivered to the hidden real hand (Aymerich-Franch et al 2016, Gentile 2013). In this situation, the rubber hand illusion is not immediately eliminated, but ownership of the rubber hand is maintained for a couple of strokes during which the fake hand appears to have gone numb or feels "anesthetized". A numbness illusion can also arise when one person holds the palm of one hand against another person's opposite palm and strokes the two joined index fingers with his or her other hand (Arnold 1952, Dieguez et al 2009). The participant experiences an illusion of stroking a single (thicker) own finger but with one side gone numb, but this occurs only during self-touch with synchronous tactile feedback (Dieguez et al 2009).

Finally, in the *Japanese illusion* (Burnett 1904, Schilder 1950, van Riper 1935), the participant crosses his or her straight arms so that the wrists are crossed, clasping the hands with thumbs down, and then turns the hands and lower arms inward toward the body (in a 270-

degree rotation) until fingers point upwards. At this unusual posture, the clasped hands have changed sides so that the hand seen to the right is actually the left hand and vice versa. Critically, when the experimenter points to a particular finger in view and the participant's task is to move this finger, the participants are often unable to move the correct finger and instead move the corresponding finger on the other hand. The brain has little experience with the unusual postures of arms and hands and interprets the visual feedback from the clasped hands as if they were held in a normal uncrossed posture. The illusion depends on vision because if the participants close their eyes and the experimenter touches the finger to be moved, there are typically no errors (van Riper 1935). However, the left-right reversal of hands' positions in extrapersonal space itself also contributes as delayed reaction times are observed in the absence of visual feedback (Hong et al 2012). The importance of visual feedback and incorrect binding of vision and proprioception is further underscored in the *two-person Japanese illusion* (Boulware 1951), where two individuals are jointly clasping their hands in the same way as in the original illusion, using the right hand one of person and the left hand of the other. If one person is asked to use their free hand to touch the finger of the other individual, they sometimes report that the finger they touch has gone numb (Boulware 1951). Thus, the sight of the other person's left hand in a location and orientation where one could expect to see one's own right hand during natural hand clasping, combined with the unusual left-right reversed hand posture itself, seems to lead to some degree of illusory ownership of the other person's hand and numbness felt in the other person's finger.

15.12 Imaging bodily illusions in the human brain

Thus far, we have mainly been discussing behavior and subjective experiences, but imaging neuroscience using functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) to register brain activity also contributes to our understanding of bodily illusions. An important general observation is that the brain activation detected during a particular bodily illusion fits well with the activation that occurs during the corresponding real stimulation conditions, which supports the view that bodily illusions involve the same neural mechanisms as veridical bodily perception. For example, limb-movement illusions (Naito et al 1999, Naito et al 2007, Naito et al 2005, Romaiguere et al 2003) activate a set of sensorimotor-related frontoparietal and subcortical brain regions that are also active during real movements of the corresponding limb (Ehrsson et al 2000, Rijntjes et al 1999, Weiller et al 1996). These regions include the primary somatosensory cortex (area 3), primary motor cortex, supplementary motor area, dorsal premotor cortex, inferior parietal cortex, lateral cerebellum, basal ganglia, thalamus and anterior insular cortex (Naito et al 1999, Naito et al 2007, Naito et al 2002, Naito et al 2005, Romaiguere et al 2003). Similarly, the rubber hand illusion (Ehrsson et al 2004) is associated with increases in activity in multisensory brain regions that also activate when the real hand is touched in direct view of the participant (Gentile et al 2013, Gentile et al 2011). This illusion is associated with replicable activations of the premotor cortex (Bekrater-Bodmann et al 2012, Brozzoli et al 2012, Ehrsson et al 2004, Gentile et al 2013, Guterstam et al 2013, Limanowski & Blankenburg 2016), posterior parietal cortex (intraparietal sulcus and supramarginal gyrus) (Ehrsson et al 2005a, Ehrsson et al 2004, Gentile et al 2013, Guterstam et al 2013, Limanowski & Blankenburg 2016), lateral occipital cortex, cerebellum, putamen, and anterior insular cortex (Brozzoli et al 2012, Gentile et al 2013, Guterstam et al 2013, Limanowski & Blankenburg 2016). The premotor cortex and intraparietal cortex possess the anatomical and neurophysiological properties required to form a multisensory representation of the upper arm (Fang et al 2019, Gentile et al 2011, Graziano 1999, Graziano et al 2000, Graziano et al 1997, Guterstam et al 2019, Lloyd 2003). Moreover, the activity in these areas correlates with the subjective strength of the rubber hand illusion (Brozzoli et al 2012, Ehrsson et al 2005a, Ehrsson et al 2004, Gentile et al 2013), the illusion-related proprioceptive drift toward the rubber hand (Brozzoli et al 2012, Fang et al 2019) and the illusion-related increase in threat-evoked SCR (Gentile et al 2013). Thus, active neuronal populations in these premotor and posterior parietal areas could implement the key multisensory integration processes that produce the rubber hand illusion.

Interestingly, the full-body ownership illusion that occurs when an artificial or stranger's body is viewed from the first-person perspective is also associated with activity patterns in the premotor cortex, posterior parietal cortex, cerebellum, and putamen (Guterstam et al 2015c, Petkova et al 2011a, Preston & Ehrsson 2016), i.e., a similar set of areas as is active during the rubber hand illusion, which suggests the engagement of similar multisensory processes. However, a critical difference is that the full-body illusion is associated with premotor activity patterns that generalize across stimulated body parts in experiments where the illusion is elicited by visuotactile stimulation applied to the mannequin's hand, trunk, or foot (Gentile et al 2015, Petkova et al 2011a). These activity patterns might thus reflect the integration of multisensory signals across multiple body segments required for unified whole-body perception. Furthermore, the mannequin illusion is associated with stronger and more extensive activations in the premotor cortex and posterior parietal cortex compared to synchronous visuotactile stimulation delivered to an isolated and detached mannequin's arm

(Petkova et al 2011a), which is consistent with multisensory processing involving more, or all, body parts in the former case.

The posterior parietal cortex seems to be a key region for body-size perception. An fMRI study investigating Lackner's *shrinking-waist illusion* (Ehrsson et al 2005b) found that the perceived changes in waist size were specifically associated with activity in a particular section of the posterior parietal cortex located at the junction of the anterior intraparietal sulcus and postcentral sulcus, probably area 5. Moreover, the activity in this area correlated with the strength of the subjective illusion. This part of the parietal lobe is a somatosensory association area that has the capacity to integrate cutaneous and proprioceptive signals across body segments (Iwamura 1998); thus, activity in this area could reflect either the updating of the waist representation in terms of size and shape or the integration of cutaneous and proprioceptive signals from the waist and hands that drives this illusory effect. As we can see from these examples, neuroimaging studies do not only inform us about which areas that are active during bodily illusions, but also gives us information about possible neuronal mechanisms and provide support for multisensory and perceptual models of bodily illusions.

15.13 Principles

What general principles can we identify from the study of bodily illusions? First, bodily perception is dynamic and reflects "best guesses" of the body's physical state based on the currently available sensory data and prior experience. The perceptual representation of one's own body can undergo rapid dynamic changes to best fit the overall patterns of sensory inputs and minimize sensory conflicts. This process is probabilistic in nature, taking into account the relative likelihood of different sensory evidence, correlations, and prior experience of one's body. Second, multisensory integration seems to play an essential role in bodily awareness. A particular bodily illusion, such as the rubber hand illusion or illusory limb movement, can be elicited by sensory stimulation in different combinations of sensory modalities, and such illusions depend on temporal and spatial congruence principles of multisensory integration. Third, our perceptual bodily experience arises from an interplay between the central body representation and the bottom-up processing of afferent sensory signals. Bodily perception is not merely the result of moment-to-moment fluctuations in bottom-up afferent signals but also depends on changes in a persisting body representation. This internal multisensory perceptual representation of one's own body in space is flexible and ongoing, as it supports the ever-persisting experience of the bodily self while simultaneously providing information that is combined with new afferent information that is constantly reaching the brain. Thus, afferent sensory information shapes body representation, and body representation shapes the processing of afferent sensory signals from the body and space surrounding the body in an ongoing cyclical interplay. Finally, bodily illusions reveal that our perception of limbs and body parts does not occur in isolation but that there are continuous perceptual interactions between all the different segments of the body. This is clear from more complex illusions where sensory stimulation and bodily awareness of one body part influence bodily awareness of other body parts through self-touch (e.g., hand grasping nose) or spatial proximity and physical connection, as in different versions of Pinocchio's illusion and full-body illusions with mannequins, for example. We perceive limbs and body parts as components of a whole unitary body.

15.14 Models

Relatively few models for bodily illusions have been developed, and the available models tend to focus on illusory limb movements and the rubber hand illusion. A population vector model for illusory limb movements has been proposed where the muscle spindle inputs from multiple muscles are integrated (Roll et al 2009, Thyrion & Roll 2010). These population vectors represent the weighted contribution of each receptor population to the coding of the ongoing movement. Multisensory integration models of limb movement illusions based on the concept of optimal integration of vision and proprioception information (Reuschel et al 2010, van Beers et al 1999, van Beers et al 2002) have also been proposed and tested (Blanchard et al 2013, Chancel et al 2016a).

The rubber hand illusion models also emphasize multisensory integration. Earlier models focused on the integration of visual, tactile, and proprioceptive signals from the body and peripersonal space based on temporal and spatial congruence rules (Ehrsson 2012, Ehrsson 2020, Ehrsson et al 2004, Makin et al 2008). According to these models, the sensory conflict between vision and proprioception is resolved by visuoproprioceptive recalibration (Ehrsson et al 2004), updating of the body representation with a shift in peripersonal space toward the fake hand (Brozzoli et al 2012, Makin et al 2008), and the formation of coherent multisensory representation of the upper arm centered on the rubber hand in view (Ehrsson 2012, Ehrsson et al 2004). Similarly, in the model developed by Tsakiris (Tsakiris 2010), the rubber hand illusion arises as an interaction between the current multisensory input and internal body models through a series of "categorical comparisons" with a particular emphasis on comparing the visual form of the object with an internal model of body structure.

More recent multisensory models explain the rubber hand illusion in a probabilistic computational framework rather than “fixed” rules (Chancel et al 2022, Ehrsson 2020, Ehrsson & Chancel 2019, Fang et al 2019, Kilteni et al 2015, Litwin 2019, Samad et al 2015). According to these models, the rubber hand illusion results from the automatic perceptual decision to combine, as opposed to segregate, the visual signals from the rubber hand and somatosensory signals from the real hand. The perceptual decision is based on the probability that these signals are caused by the same object (one’s hand), and this probability is estimated from the sensory signals themselves (e.g., spatiotemporal patterns and sensory uncertainty) and top-down factors (e.g., prior bodily experiences). A difference from multisensory models based on fixed rules is that the illusion is not an all-or-nothing phenomenon (Kalckert & Ehrsson 2014a) but a matter of degree where all evidence is taken into account in a flexible probabilistic process based on their reliability (Chancel & Ehrsson 2020, Chancel et al 2022, Samad et al 2015).

Finally, predictive coding models (Friston 2010, Friston et al 2006, Rao & Ballard 1999) emphasize top-down processing and minimization of prediction error as the chief reasons behind the resolution of sensory conflicts and elicitation of bodily illusions (Apps & Tsakiris 2014, Hohwy & Paton 2010, Limanowski & Blankenburg 2013, Zeller et al 2015). According to these models, higher-level neural representations try to “explain away” bottom-up "surprise" signals from lower-level neural representations through top-down processes that minimize the total surprise value across all levels and systems in the brain. An attractive aspect of predictive coding models is that they combine theories of perception and learning and thus provide a framework to explain multisensory conflict resolution and multisensory plasticity by minimizing prediction errors.

15.15 Individual differences

Not all people experience all bodily illusions, and there are individual differences in how a particular illusion is experienced. This is not unique for bodily illusions; not everyone sees certain visual illusions, and there are individual differences in how the viewer perceives them. Nevertheless, the issue of individual differences in bodily illusions has attracted particular interest. It is fascinating to consider why some individuals experience vivid changes in their own-body perception, while others appear immune to the same illusion when exposed to identical sensory stimulation.

For example, the rubber hand illusion and its variants are typically affirmed by approximately 60–80 percent of participants based on subjective ratings (Ehrsson et al 2005a, Ehrsson et al 2004, Guterstam et al 2013, Kalckert & Ehrsson 2014a, Reader et al 2021). Not all people are susceptible to the Japanese illusion (van Riper 1935), and even if the vast majority of individuals experience illusory movements when muscle vibration is applied at optimal frequency and amplitude by a skilled experimenter, there are individual differences in the vividness and amplitude of such illusions (Burrack & Brugger 2005, Goodwin et al 1972b, Naito et al 1999). Lackner (1988) described individual differences in the Pinocchio illusion and its variants; instead of experiencing nose elongation, some individuals described how the fingers grasping the tip of their nose grew longer instead, or a combination of nose and digit elongation [see also (Burrack & Brugger 2005)]. The observation that perceptual systems – when faced with conflicting sensory information – can end up choosing different solutions is probably not very surprising. Similarly, that some brains make the veridically correct interpretation of the sensory information in the rubber hand illusion and segregate, rather than combine, the visual and somatosensory impressions, is also perhaps not surprising. The interesting question is why different minds choose different interpretations of the sensory data in illusions paradigms.

At the perceptual level, individual differences in bodily illusions can be explained as variability in how different brains interpret and integrate multiple sources of sensory signals (i.e., multisensory integration), balance between bottom-up and top-down processing, and flexibly update one's body representation. From this perspective, individual differences in the rubber hand illusion have been linked to individual differences in the temporal congruence principle (i.e., variations in the width of the temporal window that determines integration; (Costantini et al 2016), the relationship between the degree of asynchrony and causal inference (Chancel et al 2022), and the relative weighting of visual versus proprioceptive signals in the underlying multisensory integration process (Horváth et al 2020). Further, bodily illusion reports are influenced by individual differences in metacognition, which can impact how illusory sensations are rated, judged, or compared with previous experiences, post-perceptually, at a cognitive level. A growing body of work has investigated how various cognitive factors (Haans et al 2012, Marotta et al 2016), personality factors (Romano et al 2021), and risk factors for psychiatric disorders (Eshkevari et al 2012, Germine et al 2013, Louzolo et al 2015) can modulate rubber hand illusion measures.

15.16 Conclusions

Bodily illusions are perceptions of one’s own body that are inconsistent with the body's actual physical state. Many different kinds of bodily illusions exist, and they involve changes in various aspects of perceptual bodily awareness of limbs, other body parts and even the whole body, including illusory changes in movement, ownership, size, and numerosity. By studying such illusions, we have learned that bodily perceptual awareness is flexible and depends on multisensory integration and dynamic interactions between bottom-up processing of afferent sensory signals and updating of the central body representation. Moreover, these dynamic processes are probabilistic, taking into account multiple sources of sensory evidence to infer the most likely perceptual configuration of one’s own body in space at any given time. Finally, neuroimaging studies have associated specific bodily illusion experiences with particular sets of active neuronal populations in multisensory frontal, parietal and subcortical brain regions. In conclusion, bodily illusions are tools that help us understand the relationship between sensory stimulation, brain activity, and bodily awareness.

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Note

1 See http://miragemultisensoryillusions.blogspot.com/p/about-mirage.html

References

Abdulkarim Z, Ehrsson HH. 2016. No causal link between changes in hand position sense and feeling of limb ownership in the rubber hand illusion. *Attention, Perception & Psychophysics* 78: 707-20

Abdulkarim Z, Ehrsson HH. 2018. Recalibration of hand position sense during unconscious active and passive movement. *Experimental Brain Research* 236: 551-61

Abdulkarim Z, Hayatou Z, Ehrsson HH. 2021. Sustained rubber hand illusion after the end of visuotactile stimulation with a similar time course for the reduction of subjective ownership and proprioceptive drift. *Experimental Brain Research* 239: 3471-86

Apps MA, Tsakiris M. 2014. The free-energy self: a predictive coding account of self-recognition. *Neuroscience & Biobehavioral Review* 41: 85-97

Armel KC, Ramachandran VS. 2003. Projecting sensations to external objects: evidence from skin conductance response. *Proceedings of the Royal Society of London B* 270: 1499-506

Arnold HL, Jr. 1952. Japanese Illusion. *Science* 115: 577

Aymerich-Franch L, Petit D, Kheddar A, Ganesh G. 2016. Forward modelling the rubber hand: illusion of ownership modifies motor-sensory predictions by the brain. *Royal Society Open Science* 3: 160407

Banakou D, Groten R, Slater M. 2013. Illusory ownership of a virtual child body causes overestimation of object sizes and implicit attitude changes. *Proceedings of the National Academy of Sciences U S A* 110: 12846-51

Bekrater-Bodmann R, Foell J, Diers M, Flor H. 2012. The perceptual and neuronal stability of the rubber hand illusion across contexts and over time. *Brain Research* 1452: 130-9

Benedetti F. 1985. Processing of tactile spatial information with crossed fingers. *Journal of Experimental Psychology: Human Perception and Performance* 11: 517-25

Benedetti F. 1986. Spatial organization of the diplesthetic and nondiplesthetic areas of the fingers. *Perception* 15: 285-301

Benedetti F. 1988. Exploration of a rod with crossed fingers. *Perception & Psychophysics* 44: 281-4

Bergouignan L, Nyberg L, Ehrsson HH. 2014. Out-of-body-induced hippocampal amnesia. *Proceedings of the National Academy of Sciences U S A* 111: 4421-6

Blanchard C, Roll R, Roll JP, Kavounoudias A. 2013. Differential contributions of vision, touch and muscle proprioception to the coding of hand movements. *PLoS One* 8: e62475

Blanke O, Slater M, Serino A. 2015. Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness. *Neuron* 88: 145-66

Bono D, Haggard P. 2019. Where is my mouth? Rapid experience-dependent plasticity of perceived mouth position in humans. *European Journal of Neuroscience* 50: 3814-30

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

Boulware JT. 1951. Numbness, body-image, and the Japanese illusion. *Science* 114: 584-5

Bourdin P, Barberia I, Oliva R, Slater M. 2017. A Virtual Out-of-Body Experience Reduces Fear of Death. *PLoS One* 12: e0169343

Brozzoli C, Gentile G, Ehrsson HH. 2012. That's near my hand! Parietal and premotor coding of hand-centered space contributes to localization and self-attribution of the hand. *Journal of Neuroscience* 32: 14573-82

Bruno N, Bertamini M. 2010. Haptic perception after a change in hand size. *Neuropsychologia* 48: 1853-6

Burnett CT. 1904. Studies in influence of abnormal position on motor impulse *Psychological Review* 11: 370–94

Burrack A, Brugger P. 2005. Individual differences in susceptibility to experimentally induced phantom sensations. *Body Image* 2: 307-13

Byrne A, Preston C. 2019. Mr Fantastic Meets The Invisible Man: An Illusion of Invisible Finger Stretching. *Perception* 48: 185-88

Cadete D, Longo MR. 2020. A Continuous Illusion of Having a Sixth Finger. *Perception* 49: 807-21

Carey M, Crucianelli L, Preston C, Fotopoulou A. 2019. The Effect of Visual Capture Towards Subjective Embodiment Within the Full Body Illusion. *Scientific Reports* 9: 2889

Chancel M, Blanchard C, Guerraz M, Montagnini A, Kavounoudias A. 2016a. Optimal visuotactile integration for velocity discrimination of self-hand movements. *Journal of Neurophysiology* 116: 1522-35

Chancel M, Brun C, Kavounoudias A, Guerraz M. 2016b. The kinaesthetic mirror illusion: How much does the mirror matter? *Experimental Brain Research* 234: 1459-68

Chancel M, Ehrsson HH. 2020. Which hand is mine? Discriminating body ownership perception in a two-alternative forced-choice task. *Attention, Perception & Psychophysics* 82: 4058-83

Chancel M, Ehrsson HH, Ma WJ. 2022. Uncertainty-based inference of a common cause for body ownership. *Elife* 11: e77221

Chancel M, Hasenack B, Ehrsson HH. 2021. Integration of predictions and afferent signals in body ownership. *Cognition* 212: 104722

Collins DF, Prochazka A. 1996. Movement illusions evoked by ensemble cutaneous input from the dorsum of the human hand. *Journal of Physiology* 496: 857-71

Collins DF, Refshauge KM, Gandevia SC. 2000. Sensory integration in the perception of movements at the human metacarpophalangeal joint. *Journal of Physiology* 529: 505-15

Collins DF, Refshauge KM, Todd G, Gandevia SC. 2005. Cutaneous receptors contribute to kinesthesia at the index finger, elbow, and knee. *Journal of Neurophysiology* 94: 1699-706

Cordier L, Fuchs X, Herpertz S, Trojan J, Diers M. 2020. Synchronous Stimulation with Light and Heat Induces Body Ownership and Reduces Pain Perception. *The Journal of Pain* 21: 700-07

Costantini M, Haggard P. 2007. The rubber hand illusion: sensitivity and reference frame for body ownership. *Consciousness & Cognition* 16: 229-40

Costantini M, Robinson J, Migliorati D, Donno B, Ferri F, Northoff G. 2016. Temporal limits on rubber hand illusion reflect individuals' temporal resolution in multisensory perception. *Cognition* 157: 39-48

Craske B. 1977. Perception of impossible limb positions induced by tendon vibration. *Science* 196: 71-3

Craske B, Kenny FT, Keith D. 1984. Modifying an Underlying Component of Perceived Arm Length - Adaptation of Tactile Location Induced by Spatial Discordance. *Journal of Experimental Psychology: Human Perception and Performance* 10: 307-17

Crea S, D'Alonzo M, Vitiello N, Cipriani C. 2015. The rubber foot illusion. *Journal of Neuroengineering & Rehabilitation* 12: 77

Crucianelli L, Metcalf NK, Fotopoulou AK, Jenkinson PM. 2013. Bodily pleasure matters: velocity of touch modulates body ownership during the rubber hand illusion. *Frontiers in Psychology* 4: 703

D'Angelo M, di Pellegrino G, Frassinetti F. 2017. Invisible body illusion modulates interpersonal space. *Scientific Reports* 7: 1302

de Vignemont F, Ehrsson HH, Haggard P. 2005. Bodily illusions modulate tactile perception. *Current Biology* 15: 1286-90

Dieguez S, Mercier MR, Newby N, Blanke O. 2009. Feeling numbness for someone else's finger. *Current Biology* 19: R1108-9

Dummer T, Picot-Annand A, Neal T, Moore C. 2009. Movement and the rubber hand illusion. *Perception* 38: 271-80

Edin B. 2001. Cutaneous afferents provide information about knee joint movements in humans. *Journal of Physiology* 531: 289-97

Edin BB, Abbs JH. 1991. Finger movement responses of cutaneous mechanoreceptors in the dorsal skin of the human hand. *Journal of Neurophysiology* 65: 657-70

Edin BB, Johansson N. 1995. Skin strain patterns provide kinaesthetic information to the human central nervous system. *Journal of Physiology* 487: 243-51

Ehrsson HH. 2007. The experimental induction of out-of-body experiences. *Science* 317: 1048

Ehrsson HH. 2009. How many arms make a pair? Perceptual illusion of having an additional limb. *Perception* 38: 310-2

Ehrsson HH. 2012. The concept of body ownership and its relation to multisensory integration. In *The New handbook of multisensory processes*, ed. BE Stein, pp. 179-200. Cambridge, Massachusetts: MIT Press

Ehrsson HH. 2020. Multisensory processes in body ownership. In *Multisensory Perception: From Laboratory to Clinic*, ed. K Sathian, VS Ramachandran, pp. 775-92. San Diego: Elsevier Inc./Academic Press

Ehrsson HH, Chancel M. 2019. Premotor cortex implements causal inference in multisensory own-body perception. *Proceedings of the National Academy of Sciences U S A* 116: 19771-73

Ehrsson HH, Holmes NP, Passingham RE. 2005a. Touching a rubber hand: feeling of body ownership is associated with activity in multisensory brain areas. *Journal of Neuroscience* 25: 10564-73

Ehrsson HH, Kito T, Sadato N, Passingham RE, Naito E. 2005b. Neural substrate of body size: illusory feeling of shrinking of the waist. *PLoS Biology* 3: e412

Ehrsson HH, Naito E, Geyer S, Amunts K, Zilles K, et al. 2000. Simultaneous movements of upper and lower limbs are coordinated by motor representations that are shared by both limbs: a PET study. *European Journal of Neuroscience* 12: 3385-98

Ehrsson HH, Spence C, Passingham RE. 2004. That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science* 305: 875-7

Ehrsson HH, Wiech K, Weiskopf N, Dolan RJ, Passingham RE. 2007. Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. *Proceedings of the National Academy of Sciences U S A* 104: 9828-33

Eshkevari E, Rieger E, Longo MR, Haggard P, Treasure J. 2012. Increased plasticity of the bodily self in eating disorders. *Psychological Medicine* 42: 819-28

Fan C, Coppi S, Ehrsson HH. 2021. The supernumerary rubber hand illusion revisited: Perceived duplication of limbs and visuotactile events. *Journal of Experimental Psychology: Human Perception and Performance* 47: 810-29

Fang W, Li J, Qi G, Li S, Sigman M, Wang L. 2019. Statistical inference of body representation in the macaque brain. *Proceedings of the National Academy of Sciences U S A* 116: 20151-57

Fink GR, Marshall JC, Halligan PW, Frith CD, Driver J, et al. 1999. The neural consequences of conflict between intention and the senses. *Brain* 122: 497-512

Fiorio M, Marotta A, Ottaviani S, Pozzer L, Tinazzi M. 2014. Aristotle's illusion in Parkinson's disease: evidence for normal interdigit tactile perception. *PLoS One* 9: e88686

Friston K. 2010. The free-energy principle: a unified brain theory? *Nature Reviews Neuroscience* 11: 127-38

Friston K, Kilner J, Harrison L. 2006. A free energy principle for the brain. *Journal of Physiology Paris* 100: 70-87

Gentile G. 2013. Investigating the multisensory reporesentation of the hand and space around it using fMRI. PhD thesis. Karolinska Institutet, Stockholm

Gentile G, Bjornsdotter M, Petkova VI, Abdulkarim Z, Ehrsson HH. 2015. Patterns of neural activity in the human ventral premotor cortex reflect a whole-body multisensory percept. *Neuroimage* 109: 328-40

Gentile G, Guterstam A, Brozzoli C, Ehrsson HH. 2013. Disintegration of multisensory signals from the real hand reduces default limb self-attribution: an fMRI study. *Journal of Neuroscience* 33: 13350-66

Gentile G, Petkova VI, Ehrsson HH. 2011. Integration of visual and tactile signals from the hand in the human brain: an FMRI study. *Journal of Neurophysiology* 105: 910-22

Germine L, Benson TL, Cohen F, Hooker CI. 2013. Psychosis-proneness and the rubber hand illusion of body ownership. *Psychiatry Research* 207: 45-52

Gilhodes JC, Roll JP, Tardy-Gervet MF. 1986. Perceptual and motor effects of agonist-antagonist muscle vibration in man. *Experimental Brain Research* 61: 395-402

Goodwin GM, McCloskey DI, Matthews PB. 1972a. The contribution of muscle afferents to kinaesthesia shown by vibration induced illusions of movement and by the effects of paralysing joint afferents. *Brain* 95: 705-48

Goodwin GM, McCloskey DI, Matthews PB. 1972b. Proprioceptive illusions induced by muscle vibration: contribution by muscle spindles to perception? *Science* 175: 1382-4

Gorisse G, Christmann O, Amato EA, Richir S. 2017. First- and Third-Person Perspectives in Immersive Virtual Environments: Presence and Performance Analysis of Embodied Users. *Frontiers in Robotics and AI* 4:33

Graziano MS. 1999. Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proceedings of the National Academy of Sciences U S A* 96: 10418-21

Graziano MS, Cooke DF, Taylor CS. 2000. Coding the location of the arm by sight. *Science* 290: 1782-6

Graziano MS, Hu XT, Gross CG. 1997. Visuospatial properties of ventral premotor cortex. *Journal of Neurophysiology* 77: 2268-92

Guerraz M, Provost S, Narison R, Brugnon A, Virolle S, Bresciani JP. 2012. Integration of visual and proprioceptive afferents in kinesthesia. *Neuroscience* 223: 258-68

Guterstam A, Abdulkarim Z, Ehrsson HH. 2015a. Illusory ownership of an invisible body reduces autonomic and subjective social anxiety responses. *Scientific Reports* 5: 9831

Guterstam A, Bjornsdotter M, Bergouignan L, Gentile G, Li TQ, Ehrsson HH. 2015b. Decoding illusory self-location from activity in the human hippocampus. *Frontiers in Human Neuroscience* 9: 412

Guterstam A, Bjornsdotter M, Gentile G, Ehrsson HH. 2015c. Posterior cingulate cortex integrates the senses of self-location and body ownership. *Current Biology* 25: 1416-25

Guterstam A, Collins KL, Cronin JA, Zeberg H, Darvas F, et al. 2019. Direct Electrophysiological Correlates of Body Ownership in Human Cerebral Cortex. *Cerebral Cortex* 29: 1328-41

Guterstam A, Ehrsson HH. 2012. Disowning one's seen real body during an out-of-body illusion. *Consciousness & Cognition* 21: 1037-42

Guterstam A, Gentile G, Ehrsson HH. 2013. The invisible hand illusion: multisensory integration leads to the embodiment of a discrete volume of empty space. *Journal of Cognitive Neuroscience* 25: 1078-99

Guterstam A, Larsson DEO, Szczotka J, Ehrsson HH. 2020. Duplication of the bodily self: a perceptual illusion of dual full-body ownership and dual self-location. *Royal Society Open Science* 7: 201911

Guterstam A, Petkova VI, Ehrsson HH. 2011. The illusion of owning a third arm. *PloS One* 6: e17208

Haans A, Kaiser FG, Bouwhuis DG, Ijsselsteijn WA. 2012. Individual differences in the rubber-hand illusion: Predicting self-reports of people's personal experiences. *Acta Psychologica (Amst)* 141: 169-77

Haggard P, Jundi S. 2009. Rubber hand illusions and size-weight illusions: self-representation modulates representation of external objects. *Perception* 38: 1796-803

Hagura N, Takei T, Hirose S, Aramaki Y, Matsumura M, et al. 2007. Activity in the posterior parietal cortex mediates visual dominance over kinesthesia. *Journal of Neuroscience* 27: 7047-53

Hayward V. 2008. A brief taxonomy of tactile illusions and demonstrations that can be done in a hardware store. *Brain Research Bulletin* 75: 742-52

Heed T, Grundler M, Rinkleib J, Rudzik FH, Collins T, et al. 2011. Visual information and rubber hand embodiment differentially affect reach-to-grasp actions. *Acta Psychologica (Amst)* 138: 263-71

Hohwy J, Paton B. 2010. Explaining away the body: experiences of supernaturally caused touch and touch on non-hand objects within the rubber hand illusion. *PLoS One* 5: e9416

Holmes NP, Crozier G, Spence C. 2004. When mirrors lie: "visual capture" of arm position impairs reaching performance. *Cognitive, Affective & Behavioral Neuroscience* 4: 193-200

Holmes NP, Spence C. 2005. Multisensory integration: space, time and superadditivity. *Current Biology* 15: R762-4

Hong SW, Xu L, Kang MS, Tong F. 2012. The hand-reversal illusion revisited. *Frontiers in Integrative Neuroscience* 6: 83

Horváth Á, Ferentzi E, Bogdány T, Szolcsányi T, Witthöft M, Köteles F. 2020. Proprioception but not cardiac interoception is related to the rubber hand illusion. *Cortex* 132: 361-73

Hulliger M, Nordh E, Thelin AE, Vallbo AB. 1979. The responses of afferent fibres from the glabrous skin of the hand during voluntary finger movements in man. *Journal of Physiology* 291: 233-49

Ide M. 2013. The effect of "anatomical plausibility" of hand angle on the rubber-hand illusion. *Perception* 42: 103-11

Iwamura Y. 1998. Hierarchical somatosensory processing. *Current Opinion in Neurobiology* 8: 522-8

Kalckert A, Ehrsson HH. 2012. Moving a Rubber Hand that Feels Like Your Own: A Dissociation of Ownership and Agency. *Frontiers in Human Neuroscience* 6: 40

Kalckert A, Ehrsson HH. 2014a. The moving rubber hand illusion revisited: comparing movements and visuotactile stimulation to induce illusory ownership. *Consciousness & Cognition* 26: 117-32

Kalckert A, Ehrsson HH. 2014b. The spatial distance rule in the moving and classical rubber hand illusions. *Consciousness & Cognition* 30: 118-32

Kalckert A, Ehrsson HH. 2017. The Onset Time of the Ownership Sensation in the Moving Rubber Hand Illusion. *Frontiers in Psychology* 8: 344

Kammers MP, Kootker JA, Hogendoorn H, Dijkerman HC. 2010. How many motoric body representations can we grasp? *Experimental Brain Research* 202: 203-12

Kannape OA, Smith EJT, Moseley P, Roy MP, Lenggenhager B. 2019. Experimentally induced limb-disownership in mixed reality. *Neuropsychologia* 124: 161-70

Kilteni K, Ehrsson HH. 2017. Body ownership determines the attenuation of self-generated tactile sensations. *Proceedings of the National Academy of Sciences U S A* 114: 8426-31

Kilteni K, Maselli A, Kording KP, Slater M. 2015. Over my fake body: body ownership illusions for studying the multisensory basis of own-body perception. *Frontiers in Human Neuroscience* 9: 141

Kilteni K, Normand JM, Sanchez-Vives MV, Slater M. 2012. Extending body space in immersive virtual reality: a very long arm illusion. *PLoS One* 7: e40867

Kondo R, Tani Y, Sugimoto M, Inami M, Kitazaki M. 2020. Scrambled body differentiates body part ownership from the full body illusion. *Scientific Reports* 10: 5274

Lackner JR. 1988. Some proprioceptive influences on the perceptual representation of body shape and orientation. *Brain* 111: 281-97

Lackner JR, DiZio P. 2005. Vestibular, proprioceptive, and haptic contributions to spatial orientation. *Annual Review of Psychology* 56: 115-47

Lackner JR, Taublieb AB. 1984. Influence of vision on vibration-induced illusions of limb movement. *Experimental Neurology* 85: 97-106

Le Franc S, Fleury M, Cogne M, Butet S, Barillot C, et al. 2020. Influence of virtual reality visual feedback on the illusion of movement induced by tendon vibration of wrist in healthy participants. *PLoS One* 15: e0242416

Lenggenhager B, Hilti L, Brugger P. 2015. Disturbed Body Integrity and the "Rubber Foot Illusion". *Neuropsychology* 29: 205-11

Lenggenhager B, Tadi T, Metzinger T, Blanke O. 2007. Video ergo sum: manipulating bodily self-consciousness. *Science* 317: 1096-9

Limanowski J, Blankenburg F. 2013. Minimal self-models and the free energy principle. *Frontiers in Human Neuroscience* 7: 547

Limanowski J, Blankenburg F. 2016. Integration of Visual and Proprioceptive Limb Position Information in Human Posterior Parietal, Premotor, and Extrastriate Cortex. *Journal of Neuroscience* 36: 2582-9

Litwin P. 2019. Extending Bayesian Models of the Rubber Hand Illusion. *Multisensory Research* 33: 127-60

Lloyd DM. 2007. Spatial limits on referred touch to an alien limb may reflect boundaries of visuo-tactile peripersonal space surrounding the hand. *Brain & Cognition* 64: 104-09

Lloyd DM, Shore, D.I., Spence, C., Calvert, G.A. 2003. Multisensory representation of limb position in human premotor cortex. *Nature Neuroscience* 6: 17-18

Longo MR, Schuur F, Kammers MP, Tsakiris M, Haggard P. 2008. What is embodiment? A psychometric approach. *Cognition* 107: 978-98

Louzolo A, Kalckert A, Petrovic P. 2015. When Passive Feels Active--Delusion-Proneness Alters Self-Recognition in the Moving Rubber Hand Illusion. *PLoS One* 10: e0128549

Makin TR, Holmes NP, Ehrsson HH. 2008. On the other hand: dummy hands and peripersonal space. *Behavioral Brain Research* 191: 1-10

Marotta A, Tinazzi M, Cavedini C, Zampini M, Fiorio M. 2016. Individual Differences in the Rubber Hand Illusion Are Related to Sensory Suggestibility. *PLoS One* 11: e0168489

Maselli A, Slater M. 2013. The building blocks of the full body ownership illusion. *Frontiers in Human Neuroscience* 7: 83

Maselli A, Slater M. 2014. Sliding perspectives: dissociating ownership from self-location during full body illusions in virtual reality. *Frontiers in Human Neuroscience* 8: 693

Metral M, Chancel M, Brun C, Luyat M, Kavounoudias A, Guerraz M. 2015. Kinaesthetic mirror illusion and spatial congruence. *Experimental Brain Research* 233: 1463-70

Naito E, Ehrsson HH, Geyer S, Zilles K, Roland PE. 1999. Illusory arm movements activate cortical motor areas: a positron emission tomography study. *Journal of Neuroscience* 19: 6134-44

Naito E, Morita T, Amemiya K. 2016. Body representations in the human brain revealed by kinesthetic illusions and their essential contributions to motor control and corporeal awareness. *Neuroscience Research* 104: 16-30

Naito E, Nakashima T, Kito T, Aramaki Y, Okada T, Sadato N. 2007. Human limb-specific and non-limb-specific brain representations during kinesthetic illusory movements of the upper and lower extremities. *European Journal of Neuroscience* 25: 3476-87

Naito E, Roland PE, Ehrsson HH. 2002. I feel my hand moving: a new role of the primary motor cortex in somatic perception of limb movement. *Neuron* 36: 979-88

Naito E, Roland PE, Grefkes C, Choi HJ, Eickhoff S, et al. 2005. Dominance of the right hemisphere and role of area 2 in human kinesthesia. *Journal of Neurophysiology* 93: 1020-34

Nava E, Steiger T, Röder B. 2014. Both developmental and adult vision shape body representations. *Scientific Reports* 4: 6622

Newport R, Gilpin HR. 2011. Multisensory disintegration and the disappearing hand trick. *Current Biology* 21: R804-5

Newport R, Pearce R, Preston C. 2010. Fake hands in action: embodiment and control of supernumerary limbs. *Experimental Brain Research* 204: 385-95

Newport R, Preston C. 2010. Pulling the finger off disrupts agency, embodiment and peripersonal space. *Perception* 39: 1296-98

Newport R, Wong DY, Howard EM, Silver E. 2016. The Anne Boleyn Illusion is a Six-Fingered Salute to Sensory Remapping. *i-Perception* 7: 2041669516669732

Nishio S, Watanabe T, Ogawa K, Ishiguro H. 2012. Body Ownership Transfer to Teleoperated Android Robot. In: Ge SS, Khatib O, Cabibihan JJ, Simmons R, Williams MA (eds) *Social Robotics*. Presented at Social Robotics. ICSR 2012. Lecture Notes in Computer Science, vol 7621. Berlin, Heidelberg: Springer

O'Kane SH, Ehrsson HH. 2021. The contribution of stimulating multiple body parts simultaneously to the illusion of owning an entire artificial body. *PLoS One* 16: e0233243

Parise CV, Ernst MO. 2016. Correlation detection as a general mechanism for multisensory integration. *Nature Communications* 7: 11543

Parise CV, Spence C, Ernst MO. 2012. When Correlation Implies Causation in Multisensory Integration. *Current Biology* 22: 46-49

Pavani F, Spence C, Driver J. 2000. Visual capture of touch: out-of-the-body experiences with rubber gloves. *Psychological Science* 11: 353-9

Peck TC, Seinfeld S, Aglioti SM, Slater M. 2013. Putting yourself in the skin of a black avatar reduces implicit racial bias. *Consciousness & Cognition* 22: 779-87

Perera AT, Tan JT, Mu PS, Newport R. 2021. Differential effects of minified and magnified mirror visual feedback on the underlying misperception of hand size. *Attention, Perception & Psychophysics* 83:2281-2290

Perez-Marcos D, Sanchez-Vives MV, Slater M. 2012. Is my hand connected to my body? The impact of body continuity and arm alignment on the virtual hand illusion. *Cognitive Neurodynamics* 6: 295-305

Petkova VI, Bjornsdotter M, Gentile G, Jonsson T, Li TQ, Ehrsson HH. 2011a. From part- to whole-body ownership in the multisensory brain. *Current Biology* 21: 1118-22

Petkova VI, Ehrsson HH. 2008. If I were you: perceptual illusion of body swapping. *PLoS One* 3: e3832

Petkova VI, Ehrsson HH. 2009. When right feels left: referral of touch and ownership between the hands. *PLoS One* 4: e6933

Petkova VI, Ehrsson HH. 2010. Body self-perception. In *McGraw-Hill Yearbook of Science & Technology*, pp. 51-53. New York: McGraw-Hill

Petkova VI, Khoshnevis M, Ehrsson HH. 2011b. The perspective matters! Multisensory integration in ego-centric reference frames determines full-body ownership. *Frontiers in Psychology* 2: 35

Preston C, Ehrsson HH. 2014. Illusory changes in body size modulate body satisfaction in a way that is related to non-clinical eating disorder psychopathology. *PLoS One* 9: e85773

Preston C, Ehrsson HH. 2016. Illusory Obesity Triggers Body Dissatisfaction Responses in the Insula and Anterior Cingulate Cortex. *Cerebral Cortex* 26: 4450-60

Preston C, Ehrsson HH. 2018. Implicit and explicit changes in body satisfaction evoked by body size illusions: Implications for eating disorder vulnerability in women. *PLoS One* 13: e0199426

Preuss N, Ehrsson HH. 2019. Full-body ownership illusion elicited by visuo-vestibular integration. *Journal of Experimental Psychology: Human Perception and Performance* 45: 209-23

Proske U, Gandevia SC. 2018. Kinesthetic Senses. *Comprehensive Physiology* 8: 1157-83

Radziun D, Ehrsson HH. 2018. Auditory cues influence the rubber-hand illusion. *Journal of Experimental Psychology: Human Perception and Performance* 44: 1012-21

Ramachandran VS, Hirstein W. 1997. Three Laws of Qualia: Clues From Neurology About the Biological Functions of Consciousness and Qualia. *Journal of Consciousness Studies* 4: 28

Ramachandran VS, Rogers-Ramachandran D. 1996. Synaesthesia in phantom limbs induced with mirrors. *Proceedings of the Royal Society B*: 377-86

Rao RP, Ballard DH. 1999. Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience* 2: 79-87

Reader AT, Ehrsson HH. 2019. Weakening the subjective sensation of own hand ownership does not interfere with rapid finger movements. *PLoS One* 14: e0223580

Reader AT, Trifonova VS, Ehrsson HH. 2021. The Relationship Between Referral of Touch and the Feeling of Ownership in the Rubber Hand Illusion. *Frontiers in Psychology* 12: 629590

Reuschel J, Drewing K, Henriques DY, Rosler F, Fiehler K. 2010. Optimal integration of visual and proprioceptive movement information for the perception of trajectory geometry. *Experimental Brain Research* 201: 853-62

Rijntjes M, Dettmers C, Buchel C, Kiebel S, Frackowiak RS, Weiller C. 1999. A blueprint for movement: functional and anatomical representations in the human motor system. *Journal of Neuroscience* 19: 8043-8

Roel Lesur M, Weijs ML, Simon C, Kannape OA, Lenggenhager B. 2020. Psychometrics of Disembodiment and Its Differential Modulation by Visuomotor and Visuotactile Mismatches. *iScience* 23: 100901

Roll JP, Albert F, Thyrion C, Ribot-Ciscar E, Bergenheim M, Mattei B. 2009. Inducing any virtual two-dimensional movement in humans by applying muscle tendon vibration. *Journal of Neurophysiology* 101: 816-23

Roll JP, Vedel JP. 1982. Kinaesthetic role of muscle afferents in man, studied by tendon vibration and microneurography. *Experimental Brain Research* 47: 177-90

Roll JP, Vedel JP, Ribot E. 1989. Alteration of proprioceptive messages induced by tendon vibration in man: a microneurographic study. *Experimental Brain Research* 76: 213-22

Romaiguere P, Anton JL, Roth M, Casini L, Roll JP. 2003. Motor and parietal cortical areas both underlie kinaesthesia. *Brain Research Cognitive Brain Research* 16: 74-82

Romano D, Maravita A, Perugini M. 2021. Psychometric properties of the embodiment scale for the rubber hand illusion and its relation with individual differences. *Scientific Reports* 11: 5029

Rosa N, Veltkamp RC, Hurst W, Nijboer T, Gilbers C, Werkhoven P. 2019. The Supernumerary Hand Illusion in Augmented Reality. *ACM Transactions on Applied Perception* 16: 1-20

Samad M, Chung AJ, Shams L. 2015. Perception of body ownership is driven by Bayesian sensory inference. *PLoS One* 10: e0117178

Sanchez-Vives MV, Spanlang B, Frisoli A, Bergamasco M, Slater M. 2010. Virtual hand illusion induced by visuomotor correlations. *PLoS One* 5: e10381

Schilder P. 1950. *The Image and Appearance of the Human Body*. New York, USA: International Universities Press.

Schmalzl L, Ragno C, Ehrsson HH. 2013. An alternative to traditional mirror therapy: illusory touch can reduce phantom pain when illusory movement does not. *The Clinical Journal of Pain* 29: e10-8

Seizova-Cajic T, Azzi R. 2011. Conflict with vision diminishes proprioceptive adaptation to muscle vibration. *Experimental Brain Research* 211: 169-75

Senna I, Maravita A, Bolognini N, Parise CV. 2014. The Marble-Hand Illusion. *PLoS One* 9: e91688

Shapiro AG, Todorovic D. 2017. *The Oxford Compendium of Visual Illusions*. Oxford, UK: Oxford University Press.

Shimada S, Fukuda K, Hiraki K. 2009. Rubber hand illusion under delayed visual feedback. *PLoS One* 4: e6185

Shimada S, Suzuki T, Yoda N, Hayashi T. 2014. Relationship between sensitivity to visuotactile temporal discrepancy and the rubber hand illusion. *Neuroscience Research* 85: 33-8

Slater M, Perez-Marcos D, Ehrsson HH, Sanchez-Vives MV. 2008. Towards a digital body: the virtual arm illusion. *Frontiers in Human Neuroscience* 2: 6

Slater M, Perez-Marcos D, Ehrsson HH, Sanchez-Vives MV. 2009. Inducing illusory ownership of a virtual body. *Frontiers in Human Neuroscience* 3: 214-20

Smit M, Kooistra DI, van der Ham IJM, Dijkerman HC. 2017. Laterality and body ownership: Effect of handedness on experience of the rubber hand illusion. *Laterality* 22: 703-24

Stein BE, Stanford TR. 2008. Multisensory integration: current issues from the perspective of the single neuron. *Nature Reviews Neuroscience* 9: 255-66

Stone KD, Bullock F, Keizer A, Dijkerman HC. 2018. The disappearing limb trick and the role of sensory suggestibility in illusion experience. *Neuropsychologia* 117: 418-27

Tacikowski P, Fust J, Ehrsson HH. 2020a. Fluidity of gender identity induced by illusory body-sex change. *Scientific Reports* 10: 14385

Tacikowski P, Weijs ML, Ehrsson HH. 2020b. Perception of Our Own Body Influences Self-Concept and Self-Incoherence Impairs Episodic Memory. *iScience* 23: 101429

Tajadura-Jimenez A, Vakali M, Fairhurst MT, Mandrigin A, Bianchi-Berthouze N, Deroy O. 2017. Contingent sounds change the mental representation of one's finger length. *Scientific Reports* 7: 5748

Tastevin J. 1937. En partant de l'expérience d'Aristotle [Starting from Aristotle'sexperience]. *L'Encephale* 1: 140-58

Thiéry A. 1895. *Ueber geometrisch-optische Täuschungen*. Universität Leipzig, Leipzig, Germany. 307-70 pp.

Thyrion C, Roll JP. 2010. Predicting any arm movement feedback to induce three-dimensional illusory movements in humans. *Journal of Neurophysiology* 104: 949-59

Tieri G, Tidoni E, Pavone EF, Aglioti SM. 2015. Mere observation of body discontinuity affects perceived ownership and vicarious agency over a virtual hand. *Experimental Brain Research* 233: 1247-59

Tinazzi M, Marotta A, Fasano A, Bove F, Bentivoglio AR, et al. 2013. Aristotle's illusion reveals interdigit functional somatosensory alterations in focal hand dystonia. *Brain* 136: 782-9

Trojan J, Fuchs X, Speth SL, Diers M. 2018. The rubber hand illusion induced by visual-thermal stimulation. *Scientific Reports* 8: 12417

Tsakiris M. 2010. My body in the brain: a neurocognitive model of body-ownership. *Neuropsychologia* 48: 703-12

Tsakiris M, Carpenter L, James D, Fotopoulou A. 2010. Hands only illusion: multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. *Experimental Brain Research* 204: 343-52

Tsakiris M, Haggard P. 2005. The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance* 31: 80-91

Tsakiris M, Prabhu G, Haggard P. 2006. Having a body versus moving your body: How agency structures body-ownership. *Consciousness & Cognition* 15: 423-32

Tsuge M, Izumizaki M, Kigawa K, Atsumi T, Homma I. 2012. Interaction between vibration-evoked proprioceptive illusions and mirror-evoked visual illusions in an arm-matching task. *Experimental Brain Research* 223: 541-51

van Beers RJ, Sittig AC, Gon JJ. 1999. Integration of proprioceptive and visual position-information: An experimentally supported model. *Journal of Neurophysiology* 81: 1355-64

van Beers RJ, Wolpert DM, Haggard P. 2002. When feeling is more important than seeing in sensorimotor adaptation. *Current Biology* 12: 834-7

van der Hoort B, Guterstam A, Ehrsson HH. 2011. Being Barbie: the size of one's own body determines the perceived size of the world. *PloS One* 6: e20195

van Riper C. 1935. An Experimental Study of the Japanese Illusion. *American Journal of Psychology* 47: 252-63

van Stralen HE, van Zandvoort MJ, Hoppenbrouwers SS, Vissers LM, Kappelle LJ, Dijkerman HC. 2014. Affective touch modulates the rubber hand illusion. *Cognition* 131: 147-58

Verschueren SM, Cordo PJ, Swinnen SP. 1998. Representation of wrist joint kinematics by the ensemble of muscle spindles from synergistic muscles. *Journal of Neurophysiology* 79: 2265-76

Walsh LD, Moseley GL, Taylor JL, Gandevia SC. 2011. Proprioceptive signals contribute to the sense of body ownership. *Journal of Physiology* 589: 3009-21

Weiller C, Juptner M, Fellows S, Rijntjes M, Leonhardt G, et al. 1996. Brain representation of active and passive movements. *Neuroimage* 4: 105-10

White RC, Weinberg JL, Davies AMA. 2015. The nonvisual illusion of self-touch: Misaligned hands and anatomical implausibility. *Perception* 44: 436-45

Zeller D, Litvak V, Friston KJ, Classen J. 2015. Sensory processing and the rubber hand illusion--an evoked potentials study. *Journal of Cognitive Neuroscience* 27: 573-82

Zopf R, Savage G, Williams MA. 2013. The crossmodal congruency task as a means to obtain an objective behavioral measure in the rubber hand illusion paradigm. *Journal of Visualized Experiments* 77: 50530