REVIEW ARTICLE

Subcortical contributions to the sense of body ownership

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Abstract

The sense of body ownership (i.e., the feeling that our body or its parts belong to us) plays a key role in bodily self-consciousness and is believed to stem from multisensory integration. The development of experimental paradigms that allow the controlled manipulation of body ownership in laboratory settings, such as the rubber hand illusion, provide an effective tool to investigate the malleability of the sense of body ownership and the boundaries distinguishing self and other. Neuroimaging studies on body ownership converge on the involvement of several cortical regions, including the premotor cortex and posterior parietal cortex. However, relatively less attention has been paid to subcortical structures that may also contribute to body ownership perception, such as the cerebellum and putamen. Here, on the basis of neuroimaging and neuropsychological observations, we provide an overview of relevant subcortical regions and consider their potential role in generating and maintaining a sense of ownership over the body. We also suggest novel avenues for future research targeting the role of subcortical regions in making sense of the body as our own.

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1. Introduction

We perceive our own body as a coherent blend of various sensory impressions. This multisensory perception of one's own body is believed to arise through multisensory integration, whereby different sources of sensory information (e.g., vision, touch, proprioception) are combined to provide a coherent experience of the own body that is distinct from the surrounding environment (e.g.,[1–9]). This phenomenon is often examined in behavioural studies by using multisensory body illusions. Frequently used is the rubber hand illusion (RHI), in which the synchronous, but not asynchronous, stroking of an individual's hidden hand and a false hand in an anatomically congruent position can induce the feeling that the rubber hand is one's own and part of one's own body[10]. The subjective experience of a limb or body part as being one's own is referred to as the feeling (or sense) of body ownership, and this bodily experience is intimately related to multisensory bodily perception and multisensory integration[4,11]. Thus, the RHI has frequently been used to examine the sense of body ownership, both behaviourally and in neuroimaging experiments. Since it was first reported, many studies have replicated and extended the original finding by Botvinick and Cohen[10], providing important insight into the development and maintenance of the sense of body ownership. These findings also paved the way for the development of further multisensory integration experiments involving different body parts, such as the foot (rubber foot illusion[12]) and the whole body (various full-body illusions[13–16]). Such experiments offer a unique opportunity to investigate the malleability of multisensory body representation and the sensory factors that drive the subjective sense of body ownership.

RHI literature suggests that the illusion takes place under certain sensory stimulation constraints (or 'rules'), including the temporal synchronicity between the felt and seen touch,[8,13] the spatial correspondence of the seen and felt orientations of the rubber hand and real hand,[5,14] the distance between the real and fake hands[7,15,16] (for reviews see[11,17]), and the use of a humanoid shape for the physical embodied object[18]. When the patterns of sensory information in the different modalities obeys these constraints up to a certain degree of tolerable mismatch, the RHI is elicited, but larger discrepancies that violate these constraints cancels the illusion[4,19]. Noteworthy, the spatial, temporal, and other congruence rules are similar to the temporal and spatial principles of multisensory integration,[20] which is in line with the RHI being a multisensory bodily illusion[21]. In recent probabilistic models of body ownership, the rules and constraints are not considered 'fixed', but instead representing continuous probabilistic functions of how likely it is that the different sensory signals have the same cause (e.g., one's own hand), and therefore should be combined as opposed to segregated, based on the degree of spatiotemporal congruence, sensory uncertainty, and prior experiences[13,22–26].

By combining body ownership illusions with neuroimaging, it is possible to evaluate the neural processes underlying the sense of body ownership. Three recent meta-analyses[27–29] of neuroimaging studies on body ownership converge on the involvement of two cortical regions: the ventral premotor cortex (PMv) in the frontal lobe (e.g.,[5,30–32]) and intraparietal sulcus (IPS) in the posterior parietal cortex (e.g.,[5,32,33]); and two meta-analyses[27,29] also observed activation in the anterior or posterior insula (e.g.,[5,34,35]). Activity in the lateral occipital cortex has also been frequently observed (e.g.,[31,36,37]). Notably, damage to some of these areas has also been associated with disordered body ownership in clinical reports[38,39]. Electrocorticography recordings in humans during the RHI suggest that activity in the ventral premotor cortex may reflect the continuous experience of body ownership, whilst activity in the intraparietal sulcus seems to reflect the integration of visual and tactile signals delivered to the real and fake limbs[40]. Electroencephalography studies have associated illusory arm ownership with changes of fronto-parietal cortical dynamics[41] and attenuation of ERPs around 330 ms over frontocentral electrodes[42] in line with engagement of higher order fronto-parietal processes. In sum, the premotor and posterior parietal cortex have been suggested to implement the multisensory integration of visual, tactile, and proprioceptive signals in the RHI, supporting the perceptual illusion[5,25,31,33,43]. In addition to the frontoparietal cortical areas, the insula has been proposed to play an important role in integrating exteroceptive (multisensory) information and interoceptive signals (i.e., informing about the physiological status of the body and its internal organs[44]) to support the subjective experience of the body as being a part of the self[34], along with affective own-body representation[34,45]. The involvement of the insula in manipulations of body ownership during neuroimaging studies[5,34,35] and the association between insular damage and disturbed awareness of one's own limbs[39,46–49] are in line with increasing evidence pointing to the importance of interoceptive signals in creating a coherent representation of one's own body[3,50–52].

Notable in previous neuroimaging and neurophysiological literature is that it has focused its questions and analyses on cortical areas, especially in the frontal and parietal association cortices. Conversely, surprisingly little attention has been paid to subcortical structures, given that it is not uncommon to observe activations in subcortical regions, and it is unlikely that the subcortex fails to contribute to illusory changes in body ownership and multisensory bodily awareness. The subcortex is phylogenetically older than the cortex, playing essential roles in the regulation of visceral and motor processes, both of which arguably should have a relationship to bodily self-perception and body representation[53–56]. Whilst a number of neuroimaging studies do report body ownership-related activity in subcortical areas, the results of different articles are not always consistent in the regions that are reported, which may explain their absence in previous meta-analyses of neuroimaging studies[27–29]. This may be due to the fact that some subcortical areas are small in size and may be more susceptible to noise in an fMRI scanning environment[57]. In the case of the cerebellum, the scanning protocols in some studies were not designed to capture activity in this region (i.e., it falls outside of the field-of-view, e.g.,[36]). Furthermore, in whole-brain analyses, the spatial smoothing and statistical thresholding procedures are typically optimized for detecting large clusters of active voxels in cortical areas, which may lead to false negatives in subcortical areas where activation tends to be smaller, further explaining its absence from meta-analyses. These factors indicate that subcortical contributions to the sense of body ownership are likely to have been understated in meta-analytic coverage of the phenomenon. This is unfortunate, since there is clinical evidence suggesting that damage to subcortical brain regions or white matter tracts deep in the brain (e.g., basal ganglia and periventricular white matter, cortical and subcortical white matter fibre tracts,[58] subcortical white matter,[59] subcortical and cortical-subcortical white matter tracts,[60]) might contribute to disordered awareness of one's own body (e.g.,[61–64]). With this in mind, it is essential to better understand subcortical contributions to the sense of body ownership. In this article we will provide an overview of these regions and their potential role in generating and maintaining a sense of ownership over the body and attempt to integrate these areas into the well-established cortical network[11].

2. Subcortical brain regions associated with the sense of body ownership

2.1. Cerebellum

The cerebellum was one of the first subcortical areas to be observed in a neuroimaging study on the sense of body ownership. Ehrsson *et al.*[5] found that activity in the bilateral cerebellar hemispheres was enhanced when the RHI was induced and maintained. Since then, a large number of fMRI studies on various versions of the RHI and similar full-body illusions have reported cerebellar activations (Figure 1, Supplemental Table 1). For example, follow-up studies using the RHI[33,37,43,65], a somatic version of the RHI,[30] a RHI based on finger movement,[66] a rubber foot illusion,[67] a real limb 'disownership' illusion,[31] an "invisible hand" version of the RHI[68] and a full body illusion[32,45] have all reported cerebellar activation associated with the feeling of ownership over an observed (or sensed) body or body part (Supplemental Table 1). However, these cerebellar activations have received relatively little attention in the broader literature on body ownership and multisensory bodily awareness[4,11,19,69,70].

This is somewhat surprising, given the cerebellum's role in sensory processing and its anatomical connections with the cerebral cortex. The first point to consider is that the lateral portions of the cerebellum receive visual, tactile, and proprioceptive input[71–73], and neuroimaging and clinical studies support a role for the cerebellum in multisensory perception[71–78]. Furthermore, imaging studies have shown that the cerebellum is involved in perceptual and perceptual-cognitive functions in various sensory domains,[75,79–84] including multisensory integration[72,74,78,79] and somatosensory processing[80–82]. With respect to bodily awareness, activation in the cerebellum has also been reported in bodily illusions other than those altering the sense of body ownership, e.g., during illusory arm movement triggered by muscle tendon vibration[83,84] and integration of visual and kinaesthetic signals[73]. Thus, the involvement of the cerebellum in body ownership is consistent with its involvement in higher-order sensory processing.

The precise anatomical location of cerebellar activity in body ownership studies deserves careful consideration since the cerebellum is not a homogenous structure but made up of different lobules with different patterns of cortico-cerebellar connectivity and potentially different functional roles (e.g.,[85,86]). Unfortunately, cerebellar anatomy has not always received the attention it deserves in fMRI studies, and cerebellar activations are sometimes reported without further specification of the exact subregion. We examined published studies that reported active cerebellar peaks and summarise the results by displaying the activation peaks on a probabilistic atlas of the cerebellum[87] (Figure 1). As one can see, fMRI activation related to illusory body ownership is frequently located in lobule VI[5,30,43,68] or lobule VIIa (Crus I and Crus II)[31,66,68] of the bilateral cerebellar hemispheres. These lobules are unlikely to be directly involved with primary sensory or motor processing (that would be lobules IV and V) but fit better with involvement in more high-level perceptual functions and multisensory integration. Lobules VI and VIIa are anatomically connected with frontal and parietal areas involved in body ownership illusions, such as the premotor cortex (lobule VI) and the cortices lining the intraparietal cortex and the supramarginal gyrus (lobules VI and VIIa)[87,88]. Thus, a plausible interpretation is that the co-activation of lobules VI and VIIa and these posterior parietal and premotor areas reflects the engagement of cortico-cerebellar-cortical circuits that links activity in these cortical areas to the specific active sections of the cerebellum which they are connected with during body ownership illusions. This notion is supported by enhanced functional connectivity between lobule VIIa/b and the posterior parietal cortex[31] and between the left lobule VI and premotor and intraparietal cortex[68] observed in previous illusory hand ownership fMRI studies. Whilst lobule VIIa also has connections to regions in the prefrontal cortex, superior temporal, and cingulate cortices[85,87–89], these are not typically activated during body ownership illusions, so engagement of these circuits seems more unlikely.

Lobule VIIa is described as part of the "cognitive cerebellum" in reviews of cerebellar functions,[90–92] which is consistent with the notion that body ownership and bodily illusions requires complex integration and interpretation of sensory information in the association cortex, although these previous reviews have not considered neuroimaging studies investigating higher-order bodily perceptual functions and bodily illusions. However, as can be seen in Figure 1, other regions of the cerebellum are also activated during body ownership illusions, such as lobule IV and V, which are connected to sensorimotor cortical areas, and lobules VIIIa and IX of the vermis, which may be connected with temporal cortex and posterior midline structures[87]. More attention is required when considering the anatomical diversity of different cerebellar regions, the co-activation patterns of anatomically interconnected cerebellar and cortical areas, and how the functional connectivity patterns between specific cerebellar lobules and cortical areas change during the RHI and similar body ownership illusions.

If the cerebellum is involved in body ownership, we must consider its functional role(s). Given the invariant architecture of the cerebellar cortex and the heterogenous pattern of connections to different cortical areas, it has been proposed that the cerebellum performs a universal computation or information "transform",[90,91] although the precise function(s) remains debated. Thus, through a multitude of parallel cortico-cerebellar-cortical loops, the cerebellum could support cortical brain functions by providing a certain type(s) of neural information processing. In contrast to areas in the association cortex, which are densely interconnected with other areas in the association cortex and that receive inputs from different sensory modalities and thus ideal for implementing multisensory integration, different lobules of the cerebellar cortex are not directly interconnected. They are, however, connected to different cortical areas, so a "supporting" role seem plausible. Thus, as Schmahmann[92] proposed that the cerebellum might support higher cognition by "regulating the speed, capacity, consistency, and appropriateness of mental cognitive processes" similar to how "the cerebellum regulates the rate, force rhythm and accuracy of movements",[92] we suggest that the cerebellum may support the timing, spatial patterning, and 'appropriateness' (i.e., the suitability under certain circumstances such as matching information contents or sematic congruence) of multisensory integration in the generation of a coherent perceptual representation of one's own body.

Based on this integrative perspective of cerebellar function, Ehrsson and colleagues suggested that the role of the cerebellum in body ownership may be the detection of multisensory synchrony[11,31,71]. These authors pointed out that cerebellar responses are observed when contrasting synchronous visuotactile stimulation to asynchronous control conditions and that the cerebellum plays an important role in timing functions[93,94]. This would be in keeping with the role of cerebellum in monitoring mental and external events within the context of time, as well as processing temporal information more generally[95,96]; patients with cerebellar damage may show difficulties in perceiving time intervals[93,97,98]. Thus, one possibility is that synchrony detection and temporal sensory processing in the cerebellum supports multisensory integration in higher-level cortical areas such as the intraparietal sulcus and premotor cortex. However, increased cerebellar activity is also observed in RHI studies when synchrony is kept constant in the statistical comparison between conditions and when the spatial congruence was instead manipulated to elicit or supress the RHI[5,30,43,66,68]. Thus, multisensory synchrony detection is unlikely to be the only function of cerebellum in body ownership illusions. An alternative broader view is that the cerebellum supports the frontoparietal areas in implementing effective multisensory integration both in spatial and temporal dimensions. The cerebellum would thus contribute to not only the temporal processing of multisensory signals, but also support spatial and other aspects of the multisensory integration processes (influences of prior knowledge, etc). Future model-based fMRI approaches are needed to investigate how neural computations in the cerebellum and cortical areas may differ or are similar; for example, by comparing neural computational functions associated with changes in body ownership in the cerebellum, premotor cortex[25] and the posterior parietal cortex[33].

A further perspective that has been discussed in the literature is that the cerebellum might play a critical role in multisensory recalibration (or 'adaptation', which is another term used[99]), more precisely the spatial alignment of visual and proprioceptive representations of the upper limb[5]. Ehrsson *et al.*[5] noted greater cerebellar activation in the 10-second period of repeated stroking before the RHI started compared to the period after the illusion had been triggered and was steadily maintained, arguing that the initial activity might reflect visuoproprioceptive recalibration. Chancel *et al.* focused their analysis on the first 12 s of RHI induction and found increased cerebellar activity during this period that was related to the likelihood that the illusion was triggered on a trial-by-trial basis. These findings are consistent with multisensory recalibration in the cerebellum, but, critically, none of these studies included behavioural measures of visuoproprioceptive recalibration, so the link remains speculative. Interestingly, tDCS stimulation over the cerebellum enhances proprioceptive updating of felt real hand position during the RHI elicited by finger movements, according to one recent study[100] which would be consistent with the recalibration hypothesis. However, it has been suggested that the cerebellum may be more important in sensorimotor recalibration when error-based feedback is available during voluntary goal-direct action rather than in "passive" conditions such as when participants experience bodily illusions by visuotactile stimulation, which might speak against the cerebellar recalibration hypothesis[101–103].

A further possible role of the cerebellum is that it may be involved in generating or detecting multisensory prediction errors. This view is inspired by theories that the cerebellum is critical for error detection[104,105] and for encoding internal models for sensorimotor control[82,105,106]. Noteworthy, the cerebellum has been reported to be involved in the generation of sensory predictions and the comparison of expected sensory consequences of movement and afferent sensory feedback from movement[82,107–111]. Thus, the idea with respect to the RHI is that during this initial period of repeated multisensory stimulation before illusion elicitation, the brain tries to minimize prediction errors generated by the conflicting visual and somatosensory signals. These prediction errors arise as a consequence of internal models in the cerebellum (or cortex) that describe the expected relationships between the different sensory signals from the body; and these prediction errors serve as a learning signal that drives the updating of the central body representation, which provides input to the internal model[112]. However, fMRI experiments testing this idea are lacking; the temporal evolution of prediction error signals and signals reflecting the emergence of the RHI should presumably have different temporal profiles and could, thus, theoretically, be disambiguated.

The stronger cerebellar responses reported by Ehrsson *et al.*[5] when contrasting the early period before illusion induction to the later illusion phase would be in line with the prediction error hypothesis but is inconclusive. Interestingly, unpublished data from an fMRI study conducted in our lab[112] investigated prediction error responses in the RHI. Specifically, this study examined brain responses to omissions of expected sensory stimuli during the RHI. In 20% of the synchronous visuotactile stimuli delivered in the RHI condition, there was an unexpected omission of a tactile or a visual stimulus; such omissions generate a prediction error[113] and were associated with cerebellar activation in the right lateral cerebellum (x=28, -58, z=-26; right lobule VI) regardless of omission modality[112]. The control condition was identical sensory omissions in a spatially incongruent condition where synchronous strokes were applied to different parts of the rubber hand and the real hand, suppressing the RHI and its associated prediction errors. Regardless, it should be emphasised that the results from other fMRI studies fit less well with the cerebellar prediction error hypothesis. For example, cerebellar responses correlate positively with the strength of subjective RHI across individuals[5,33,37,43,65] and it is not clear why individuals with a strong illusion should have a strong unresolved conflict and more prediction errors; and crucially, when participants look at their real hand being touched in direct view there are cerebellar responses, which is a situation where there is no prediction error (but multisensory integration[72]).

Ultimately, it is possible that different regions of the cerebellum are involved in each of the aforementioned processes (detection of multisensory synchrony, multisensory recalibration, prediction errors), but at present, the relatively small number of experimental paradigms and statistical contrasts used, most of which focus on temporal and spatial congruence, makes it challenging to verify the precise role(s) of the cerebellum and link function(s) to specific structures. Whilst the involvement of the cerebellum in the RHI and similar body ownership illusions is supported in the imaging literature, it deserves future investigation, especially with respect to its relative functional role and functional connectivity to cortical areas. Experiments designed to directly test and separate the potential roles of the cerebellum would be particularly informative.

2.2. Putamen

Whilst multisensory perception is important for generating a sense of body ownership, it is also essential for representing the space near one's body. Studies of non-human primates have reported cells in the ventral premotor cortex, intraparietal cortex, and putamen that responded to both somatosensory perception of the body and vision of the area surrounding it[114–116]. The receptive fields of these bimodal neurons were anchored to the hand, such that the visual receptive field was updated by changes in the hand position, rather than being retinotopic. This multisensory representation of space surrounding the body, frequently referred to as peripersonal space, is believed to be important for guiding interaction with the external world[117–119]. Activity in the putamen, which has been reported in multiple neuroimaging studies[31,32,43,45,120,121] (Table 1), may reflect the updating of these multisensory receptive fields that encode the space surrounding the body[120]. The putamen contains multisensory neurons[115] and is anatomically interconnected with cortical areas involved in sensory guidance and hand action[72,122]. Indeed, studies in non-human primates showed that the putamen is somatotopically organized and anatomically connected with multisensory frontal and parietal regions[115]. In particular, the putamen receives projection from somatosensory and motor cortex[122], as well as projections from parietal area 7b[122] and ventral premotor area 6[122,123]. These observations, combined with fMRI evidence in humans,[32,72] provide support to the idea that the human putamen is involved in the integration of visual and somatic signals from the body.

During body ownership illusions, the conscious experience of owning a false body part is accompanied by a shift in the perceived location of the body part towards that of the illusory substitute. In the RHI this is typically reflected in 'proprioceptive drift', whereby estimates of the real hand position shift towards the false hand[10,124]. As conscious perception of one's body changes, so too does the internal model of the body's position in space (also sometimes referred to as the 'state estimation')[125,126]. Mirroring work in non-human primates, neuroimaging studies examining multisensory responses to stimulation of the hand suggest that the putamen displays superadditive responses to vision and touch[72]. Brozzoli *et al.* [120] built on these findings by examining brain activity in response to object presentation near the hand. They found evidence to suggest that the putamen, along with frontoparietal cortical areas, was encoding visually-presented objects in hand-centred space. That is, activity was associated with the position of the object relative to the hand,[127] rather than its objective position in the visual field. More importantly, they found that similar responses could be observed when objects were presented near a rubber hand after RHI induction,[120] suggesting a remapping of the hand-centred spatial reference frame onto the false hand. Thus, activity in the putamen might reflect the updating of peripersonal space in line with the perceived limits of the body.

2.3. Other subcortical regions reported in neuroimaging studies of body ownership

In addition to the cerebellum and putamen, there is also evidence that other subcortical regions may contribute to the sense of body ownership (Figure 2). Whilst neuroimaging evidence emphasising a role for these areas is limited, we believe that clinical observations, non-human primate research, and theoretical accounts point towards potentially important roles for these regions. At the very least, the following summary might pave the way for more studies specifically targeting these regions of interest.

2.3.1. Amygdala

The amygdala is a key component of the brain circuits involved in processing of threats and threat-related emotions such as fear, and activity in the amygdala is rarely reported in neuroimaging studies of body ownership. One study found increased amygdala activation in response to physical threat towards the fake body in a full-body illusion[128]. Similarly, presentation of a virtual spider next to a virtual hand during illusory embodiment was related to enhanced amygdala activity[129]. Thus, the amygdala might play a role in emotional defence reactions related to ownership of one's limbs. Amygdala activity was also noted in a PET study when the rubber hand was presented in an anatomically impossible position, rotated 90 degrees clockwise, reducing the illusion[35]. However, such amygdala response was not observed in RHI fMRI studies when the rubber hand was presented in other spatially incongruent orientations that break the illusion, i.e., 180-degree rotation,[5,43,66] so the amygdala's possible involvement in detecting anatomically impossible postures is unclear.

Interestingly, damage to the amygdala may result in faster integration of false limbs into the central body representation[64]. Spengler *et al.*[64] investigated RHI responses in two monozygotic twin sisters with focal bilateral amygdala damage, and 20 healthy women. The twins showed a faster (almost immediate) illusion onset and increased vividness ratings of the illusion as compared to the healthy controls. These findings were followed up by a volumetric brain morphometry study on 57 healthy participants, showing a positive correlation between amygdala volume and RHI onset[64]; smaller amygdala volumes were associated with a faster RHI onset. Spengler *et al.*[64] suggested that the amygdala, given its involvement in threat processing, might constitute the focal area of an evolutionary mechanism that protects us against distortion of body perceptions. However, malleability to bodily illusions might conversely be considered to serve an evolutionary function in that they are examples of efficient perceptual processing in the face of sensory uncertainty and perceptual ambiguity[21,130]. Moreover, bodily illusions are typically not associated with any unpleasant emotions. On the contrary, some participants spontaneously express emotions of surprise, fascination, and joy, so it is not clear to us why a bodily illusion would constitute a threatening perception as suggested by Spengler and colleagues[64]. We also note that the reported illusion onset times in the healthy control group were much longer (mean 134 seconds) than in several other previous RHI studies, where onset times range in the order of 10 to 20 seconds are typically reported[5,13,15,131]; moreover, from the report it was not clear what specific illusory sensations the participants were instructed to base their onset reports on, so the very long onset times are difficult to interpret.

Reader and Crucianelli[132] proposed an alternative interpretation of Spengler and colleagues'[64] findings, by suggesting that the role of the amygdala might rather reflect sensory feedback being prioritised over existing knowledge of how one's body is typically experienced[133]. They proposed that the amygdala may be sensitive to discrepancy between established sensory expectations regarding the real body and incoming sensory information, which could help mediate between bottom-up and top-down processes in the RHI and sense of bodily self. In favour of this, the amygdala is known to be involved in multisensory processing,[134] and seems to respond more vigorously to novel multisensory input,[135,136] suggesting a capacity for distinguishing new from prior (or expected) sensory experience. Furthermore, the functional and anatomical connectivity of the amygdala suggests that it is well situated for supporting cortical areas that are commonly associated with the sense of body ownership,[135–137] such as the posterior parietal cortex and the ventral premotor cortex (e.g.,[40]). As such, the amygdala may be involved in comparing pre-existing knowledge of one's own body (that the hidden real hand is spatially distinct from the rubber hand) with ongoing sensory feedback (the visuotactile correlations) and provide an internal signal for conflict detection that opposes the illusion, i.e., limiting the influence of sensory information until it is strong enough to override experience[133]. However, the lack of amygdala activity in fMRI studies focusing on the period during which the illusion develops[5,33] may speak against this hypothesis. For example, in Chancel *et al.*,[33] analysing the first 12 seconds of illusion induction, no activation in amygdala was observed related to the RHI, visuotactile synchrony, or visuotactile asynchrony (but negative findings in fMRI studies are typically difficult to interpret). Thus, the precise role of amygdala in body ownership is still unclear and require further investigation.

2.3.2. Thalamus

The thalamus is an important 'hub' region of the brain, passing information between the peripheral nervous system and the cortex[138] (see[139] for a recent review) as well as between cortical areas. The thamalus can be divided into 60 or so nuclei, each with different input pathways from the periphery and various projections as outputs, mainly to the cerebral cortex. For example, somatosensory information from the spinal cortex reaches the ventral posterior nucleus (discriminate touch) and the ventral medial posterior nucleus (thermosensation and nociception) and are from here relayed to different sensory cortical areas such as the somatosensory cortex (touch) and the posterior insula (thermosensation and nociception). Other thalamic nuclei receive input from cortical areas and, in turn, relay this information back to other cortical areas through a set of reciprocal "looped" connections to the cortex, forming cortico-thalamo-cortical circuits (see[140] for a review). The thalamus' connectivity with primary sensory areas and the superior colliculus has resulted in its consideration as an important area for multisensory integration, potentially by supporting rapid transfer of information between sensory regions[141]. It may also play a role in guiding selective sensory attention and cross-modal attention,[142–146] which could similarly support multisensory processing.

Interestingly, the first reported activation of the thalamus in response to a body ownership illusion was observed in a situation *not* inducing an illusory sense of body ownership. Tsakiris *et al.*[35] observed increased activity in the thalamus when asynchronous stroking was applied during the RHI, i.e., in the control condition that does not typically induce a sense of ownership over the false hand. However, a number of later studies found increased activity in thalamus in cases when illusory body ownership was induced[32,67,68,128]. Whilst this might be broadly explained by the proposed multisensory processing of the thalamus, not all thalamic nuclei contribute to multisensory processing of body-related stimuli and localising to a specific subregion is likely to be more informative. Whilst the location of thalamic activation across different studies is heterogeneous, thus not permitting the localisation of body-ownership related processing to a particular nucleus, two studies that found activity in the thalamus[36,68] probably overlap in the lateral pulvinar,[147–151] suggesting that this might be a subregion involved in processes related to the sense of body ownership.

In the primate brain, the lateral pulvinar receives inputs from the superior colliculus and amygdala and displays reciprocal connectivity with areas that include the visual cortex (including extrastriate cortex), premotor cortex, and posterior parietal lobe[152–157]. Strong, direct evidence for pulvinar involvement in multisensory processing remains limited, but neurons in the lateral pulvinar are responsive to visual and tactile stimuli, and it is possibly involved in proprioception ([155] for review). In general, the lateral pulvinar is most typically considered for its role in visual perception and attention[149,153,154,158–161]. This may suggest that activity in this area could reflect changes in cross-modal attention towards a salient multisensory experience, e.g., facilitating attention towards visual processing of the fake hand driven by visuotactile integration in cortical areas. Thus, the pulvinar may mediate top-down modulation of sensory signals that shapes sensory processing as part of sensations of body ownership, rather than implement the core multisensory integration mechanisms related to the generation of body ownership sensations directly. Interestingly, in the relevant studies,[68,128] illusory body-ownership-related activity was also observed in premotor and posterior parietal areas as well as in lateral occipital cortex, so one could speculate the frontoparietal areas may modulate visual processing of the illusory owned limb in the lateral occipital cortex through cortico-thalamic-cortical circuits involving the pulvinar; although this hypothesis needs to be tested in future functional connectivity analyses. Regardless, functional connectivity between IPS and lateral occipital cortex was found, but it was not clarified if this effect was driven by cortico-cortical connections or cortico-thalamic-cortical connections. Ultimately, further work is required to better understand the role of the pulvinar, and other thalamic nuclei. Studies investigating changes in effective connectivity to cortical areas may be particularly informative.

2.3.3. Hippocampus

The hippocampus is involved in associative learning (e.g.,[162]), memory (e.g.,[163]) and spatial navigation[164–166], but lesions and fMRI studies on bodily illusions suggest a potential involvement also in functions related to spatial bodily awareness and sense of bodily self.

Guterstam *et al.*,[128] used a full body ownership illusion to investigate the potential involvement of the hippocampus in the perceptual experience of being physically located at a particular place in the environment. Their results showed an association between left hippocampal activity and the perceived location of the body in the space, suggesting that the human hippocampus might play a crucial role in the interplay between space processing and multisensory body representation[128]. This finding is in line with the idea that the hippocampus is part of a larger network that includes areas of the posterior parietal and posterior cingulate cortices that work in concert to represent perceived embodied self-location[36]. In addition, electrical stimulation of the hippocampus has also been found to elicit illusory changes in perceived self-location[167].

Further support for the potential link between hippocampal activity and the first-person perspective comes from clinical and experimental evidence showing that damage or disruption to hippocampus activity can have dramatic consequences for the ability to recall memories from a first-person perspective[168]. This may also be highlighted in disturbances of bodily awareness observed in anosognosia for hemiplegia, as will be discussed below. In addition, healthy participants that experienced an out-of-body illusion during encoding of naturalistic events show an altered pattern of hippocampal activation during recall[168] and increased third-person perspective at recall[169]. Further, experimental interruption of the sense of body ownership impairs episodic recognition memory[170] and reduced memory accuracy, reliving, and vividness,[171] which is indicative of an influence of body ownership on hippocampal memory processes. Clinically related out-of-body experiences seems to affect the ability to recall events encoded whilst one's own self is displaced outside the real body[172].

An area that, to the best of our knowledge, has not been explored with respect to body ownership and body representation research is the potential involvement of the hippocampus in associative learning[163,173,174] and associative predictions[162] of bodily-related multisensory cues. In the study of bodily illusions and body ownership the focus has been on naturalistic multisensory congruencies, that is relationships between visual and somatosensory information that occur during everyday experiences and are shaped through a lifetime of experiencing statistical regularities of naturally occurring sensory feedback (e.g., what a brushstroke on one's hand look and feel like). However, less is known about the learning of novel associations between arbitrary multisensory cues, and how such learned arbitrarily associations may influence body ownership, and the hypothesis that the hippocampus might be involved in such functions is worth exploring in futures studies. In sum, whilst the hippocampus may not be directly involved in the sense of body ownership, it is likely to contribute to related processes such as sense of bodily self-location, the role of bodily self in memory, and more speculatively, the learning of new associations of multisensory bodily cues.

3. Neuropsychological and psychiatric observations

Disturbances in bodily awareness can offer important insights into the processes underlying the development of a sense of body ownership. Right-hemisphere stroke can result in disorders of self-awareness, such as disturbances of body ownership or disturbances of body agency,[48,62,175] as well as anosognosia for hemiplegia, defined as the unawareness of sensorimotor deficits following stroke[176]. Anosognosia for hemiplegia has been linked to distortions in the sense of body ownership[39]. Traditionally, there has been a relatively strong focus on cortical functions in the neuropsychological literature on disorders of body ownership. For example, subcortical lesions damaging white matter tracts have often been interpreted as interrupting cortical functions of the areas connected by the damaged anatomical pathways (e.g., frontoparietal connections). Still, there is a growing interest in the involvement of subcortical structures themselves and their connections to cortical areas (e.g.,[177]). Lesions caused by subcortical strokes are typically relatively large and involve damage to multiple cortical and subcortical regions as well as cortico-cortical and cortico-subcortical white matter connections. Noteworthy, an examination of 85 patients with anosognosia following right-hemisphere stroke[178] showed the involvement of subcortical damage, with areas including the thalamus, basal ganglia, corpus callosum, internal capsule, corona radiata, insula, lateral ventricles, and amygdala. In particular, basal ganglia and thalamus lesions were the most likely to account for unawareness in 15 cases where there was damage confined to a single subcortical area[178,179]. Additional work on anosognosia showed that this condition is linked to lesions in the rolandic operculum, the insula, subcortical areas including the hippocampus and the thalamus, as well as white matter connections, e.g., basal ganglia and periventricular white matter, cortical and subcortical white matter fibre tracts[58], subcortical white matter[59], subcortical and cortical-subcortical white matter tracts[60,180,181].

Interestingly, people with anosognosia tend to show a dissociation in the experience of their own body from a first and third person perspective, with the latter one dramatically improving body awareness as tested by means of a video reply protocol[182]. By implication, this could suggest that some of the subcortical areas importantly involved in anosognosia, such as basal ganglia, hippocampus, amygdala, and thalamus, might also play a role in the first person experience of the body, that is a fundamental aspect of bodily self-consciousness[19,183,184] as well as an essential condition for body ownership illusions to occur[11,185].

Disorders of body ownership such as asomatognosia (loss of ownership over a limb) or somatoparaphrenia (delusional attribution of one's limb to another individual) have been associated with damage to the putamen, amygdala, thalamus, hippocampus, and basal ganglia[59,60,62,186]. Furthermore, it is essential to also consider the importance of white matter structures when discussing the effects of lesions that involve these subcortical regions (see [187] for a recent review). For example, Moro *et al.*[60] compared lesions in patients with anosognosia for hemiplegia and patients with somatoparaphrenia. They proposed that subcortical grey areas (basal ganglia, thalamus, fornix) and related white matter tracts may be necessary for 'rudimentary feelings of limb ownership', which are then integrated with other aspects of self-awareness (such as higher-order self-representations) within cortical areas[60]. Among white matter tracts, the corona radiata is an arrangement of afferent and efferent fibres passing between subcortical regions and the cerebral cortex[188] that may be of particular importance for interactions between subcortical and cortical areas involved in body ownership. Interestingly, Feinberg *et al.*[61] observed that damage to the corona radiata connecting the supramarginal gyrus with the subcortex was strongly associated with altered limb ownership. Whilst the supramarginal gyrus is not often considered a core component of the cortical network involved in body ownership, there is some evidence that it shows increased fMRI activation during illusory hand ownership[31,120] and multisensory stimulation to one's real hand[72]. Furthermore, its proximity to the intraparietal sulcus and likely connectivity with the premotor cortex for sensorimotor processes might indicate that impaired subcortical inputs to this region could influence the sense of limb ownership. Another patient with damage to the corona radiata was reported in a later article, though none of the other four patients with asomatognosia showed similar damage[189]. However, more recently, Spinazzola *et al.*[190] reported that anterior corona radiata damage was significantly associated with asomatognosia in a sample of ten patients.

The ventral extension of the corona radiata, the internal capsule, has also been found to be damaged in some patients with disrupted body perception[60–63]. Gandola *et al.*[59] proposed a neuroanatomical account of somatoparaphrenia whereby subcortical damage to white matter in the right hemisphere (including the posterior limb of the internal capsule, the corona radiata and the superior longitudinal fasciculus) and of subcortical grey nuclei (thalamus and basal ganglia) plays a crucial role in causing the disorder of body ownership. By comparing 11 patients with and 11 without somatoparaphrenia matched for the presence and severity of other associated symptoms (neglect, motor deficits, and anosognosia), it was possible to identify a lesion pattern involving subcortical grey nuclei as well as damage to the white matter tract linking these structures with cortical sensorimotor and associative areas. These results could explain the occurrence of the feeling of disownership, as a consequence of the deficit in the construction of a coherent body representation including the affected limb. Thus, it has been proposed that the white matter tracts, via their connections to the cortex, can promote the processing and the integration of various bottom-up afferent information arising from the (affected) body part with top-down and pre-existing body representations normally computed in higher-order cortices[59]. Thus, the effects of white matter tract damage suggest that disturbances in the sense of body ownership can arise either from (sub)cortical damage or through damaged connectivity between these cortical areas' regions, in keeping with recent accounts[177,191]. However, more work will be needed to verify exactly what such effects can tell us about the specific body ownership-related processes performed by subcortical regions.

In addition, there are interesting links between subcortical regions and psychiatric and neuropsychiatric disorders. Most notably, some research highlights a potential link between subcortical abnormalities and schizophrenia, a psychiatric condition characterised by disturbances in bodily awareness and sense of self[192] in addition to the classic positive and negative symptoms and cognitive impairments. Individuals with schizophrenia report an increased experience of the RHI in synchronous and asynchronous conditions, which suggests a more malleable body representation and weakened sense of self,[193–195] blurred self-other boundaries,[196] or impaired processing of bottom-up sensory signals, although it is always difficult to rule out effects related to altered higher cognitive functions such as metacognition when these individuals judge and evaluate their subjective experiences, which is also a core feature of schizophrenia. Interestingly, a recent study involving 1117 patients with schizophrenia showed smaller bilateral hippocampus, amygdala, thalamus and accumbens volumes as well as intracranial volume, but larger bilateral caudate, putamen, pallidum and lateral ventricle volumes in patients compared to healthy controls[197]. Functional and neuroanatomical studies also showed an association between the cerebellum and schizophrenia ([198] for a review), with changes in connectivity, blood flow, and structure associated with this mental disorder.

Another interesting condition that is relevant when discussing the link between body ownership and subcortical areas is Body Integrity Identity Dysphoria (BIID). This is a neuropsychiatric disorder characterised by dissatisfaction with one's body and its functionality[199] and a mismatch between the internal representation of bodily self and the physical state and shape of the body[200]. Patients with BIID often report a strong desire for amputation of a particular body part that is considered alien (this variant of BIID is referred to as Xenomelia, [201]), often accompanied with feelings of disownership for that unwanted limb (though these appear to be qualitatively different to those reported in asomatagnosia and somatoparaphrenia). Recent neuroscientific accounts suggest that BIID and xenomelia could result from a disorder in multisensory integration and central body representation,[201–205] and although the focus in the literature has been on anatomical changes in frontal and parietal cortical areas related to body representation (e.g.,[201,205,206]), several studies have described anatomical changes also in subcortical structures. Interestingly, Blom *et al*.[200] analysed the structural data from 8 participants with BIID using voxel-based morphometry and showed a significantly reduced grey matter volume in the left dorsal and ventral premotor cortices as well as a larger grey matter volume in the cerebellum (lobule VIIa, Crus II) of BIID subjects compared to heathy participants. Recall that we discussed how this cerebellar lobule, together with the premotor cortex, has been found activated in several rubber hand illusion fMRI studies, indicating a possible link between BIID and changes in perception of body ownership.

A more recent study focused on the white matter structural connectivity on a larger sample of BIID (n = 16)[207]. In terms of subcortical structures, Saetta *et al.*[207] showed reduced structural connectivity of the right superior parietal lobule with the cuneus and the right orbital frontal cortex with the putamen. They also identified increased structural connectivity between the right paracentral lobule and the right putamen. These results are in line with the changes in the shape of putamen and other parts of the basal ganglia and the left frontolateral thalamus noted by Hängni and colleagues in a group of 13 male BIID patients[208]. Taken together this evidence suggests that BIID might result from alterations in several interconnected cortical-subcortical networks including both cerebellum and putamen. However, one should bear in mind that BIID is a multifaceted and complex mental disorder that may also involves changes in emotion, body image, desire to be disabled, and affective and erotic attraction to non-able bodies and amputees[207,209] meaning that it challenging to separate neuroanatomical changes that specifically relate to alterations in body ownership and multisensory body representation from changes in higher-order bodily representation related to affective and sexual aspects of corporeal awareness.

4. Future directions

There are further subcortical regions that could be involved in the processing of bodily related sensory information and the sense of body ownership that deserve to be examined more closely in future neuroimaging studies. For example, the cuneate nuclei and the gracile nuclei located in the brain-stem process tactile and proprioceptive information and send these signals further to the thalamus. The cuneate process sensory information from the upper body and upper limbs, and the gracile nuclei process information from the lower body and the lower limbs. Although brainstem fMRI is technically challenging[210], future studies could investigate bottom-up sensory processing of somatosensory signals[211,212] in these dorsal column nuclei during altered states of body ownership and explore possible top-down influences. Here, an interesting question for future subcortical studies is how early in the processing steps of somatosensory information from periphery to the cortex does the subjective sense of body ownership modify afferent sensory processing. Only at the level of the cortex, at the level of the thalamus, or even at the brainstem?

Another brainstem region that has been largely ignored in the body ownership literature is the superior colliculus. The superior colliculus contains maps of auditory and visual space and tactile maps of body surface and is critically involved in reflexive orientation movements of head and eyes to auditory and visual cues[213]; output pathways from multisensory neurons in superior colliculus target motor pathways within the same structure that control orienting movements of eyes and head. Importantly, the visual, auditory, and tactile map are not rigid and fixed, but display dynamic plasticity to maintain behaviourally meaningful alignments of the different sensory maps, thus reflecting multisensory representation of the extrapersonal space[214]. Moreover, since the representations of egocentric external space and bodily space including the head are functionally related in bodily self-consciousness,[166] body ownership[183,185] and bodily self-location,[34,128]and the superior colliculus is anatomically connected to cortical areas related to body ownership and bodily self-consciousness such as the premotor cortex[215], one may ask if processing in superior colliculus is related to body ownership. Interestingly, one fMRI study[208] reported changes in ipsilateral superior colliculus activity during the RHI and increases in functional connectivity between the superior colliculus, the right temporoparietal junction, bilateral ventral premotor cortex, and bilateral postcentral gyrus during the RHI. Thus, it is possible that sensory processing and dynamic multisensory map alignments in the superior colliculus may contribute to the spatial representations of extrapersonal and egocentric peripersonal space that is relevant for body ownership and bodily self-consciousness more generally; this is a hypothesis that is worth exploring further, but the findings of Olivé *et al.*[216] also need to be replicated.

A further subcortical structure that has been discussed in the recent behavioural neuroscience literature on body ownership is the hypothalamus. The hypothalamus is an important hub for controlling the autonomic functions of the body, including energy levels, metabolism, and thermoregulation[217]. An indirect way in which the hypothalamus may influence the sense of body ownership is via the release of neuropeptides such as oxytocin. Oxytocin is synthesised in the hypothalamus, and it has a dual function; it acts as a hormone peripherally on the body and as a neuromodulator centrally in the brain. Recent studies showed that peripheral levels of oxytocin can modulate the extent to which participants experience the RHI,[218] and vice versa, intranasal intake of oxytocin can enhance the subjective experience of ownership during the illusion, potentially by promoting processes of multisensory integration[64,219,220]. A recent study provides further support to the idea that intranasal oxytocin might promote an adaptive balance between the bottom-up and top-down attention system[221], a process that is of importance for the RHI as attention can modify sensory processing in different modalities and thus influence multisensory perception. Thus, future combined neuropharmacological and neuroimaging studies could possibly help us to better understand the potential role of the hypothalamus in body ownership and test the hypothesis of a neuromodulatory role related to oxytocin in the perception of the body, as well as the affective dimension of the somatosensory experience related to bodily illusions[220].

According to some views, changes in thermoregulation could potentially be considered as a physiological signature of the occurrence of the RHI. In other words, it has been suggested that the body might react to the acquisition of a new body part (rubber hand) by downregulating autonomic control of one's own hand, which is out of view[222] or both hands[223]. However, these findings have been difficult to replicate and current literature suggest that hand temperature changes little during the RHI (e.g.,[3,52,224,225]). Nevertheless, it would be interesting to explore possible neural links between hypothalamus-related thermoregulatory processes and the sense of body ownership. Thermosensory-affective experiences such as thermal comfort or discomfort and deviations from thermoneutrality are critical for survival and for the physiological integrity of the body[226], so functional links to the sense of body ownership seems plausible. Thus, future ultra-high-field strength fMRI studies could investigate the hypothalamus during RHI experiments involving thermosensory stimuli, deviations from thermoneutrality and thermal discomfort and associated thermoregulatory physiological reactions to test the hypothesis of potential links between thermoregulatory processes and the sense of body ownership. So far, 1.5T and 3T fMRI studies with standard imaging sequences for whole brain coverage have not noted activations in the hypothalamus during the RHI or similar full-body ownership illusions so more targeted imaging studies with MRI sequences and analysis protocols optimal for imaging the hypothalamus will be needed to further explore this hypothesis (e.g.,[227]).

Indeed, from the methodological point of view, a pressing concern for clarifying the role of subcortical areas, especially small structures in the brain stem and thalamus, in the sense of body ownership is optimising fMRI approaches to detect their activity. For example, imaging of brainstem structures poses a significant challenge, and requires special sequences, coils, and spatial preprocessing steps,[210] and if one is interested in studying specific thalamic nuclei or other small subcortical structures whole brain 3T fMRI imaging and group averaging of functional images is not ideal, but 7T and single subject analysis based on anatomical masks drawn from each individual participant's structural scans is a better approach. Moreover, the cerebellum is occasionally excluded from the field of view during "whole brain" fMRI experiments, and deep brain structures are particularly susceptible to noise. Thus, ROI-based approaches, ultra-high field fMRI (7 Tesla), or imaging sequences designed to improve signal-to-noise ratio in midbrain areas may be of use (e.g.,[228]). Furthermore, recent advances in machine learning can help to tackle difficult segmentation problems observed in small areas with an accuracy higher than both multi-atlas and manual segmentation methods (e.g., see [229] for an automated segmentation of the whole hypothalamus and its subnuclei). Such methods may improve the detection of activity in midbrain regions, which is often lost during neuroimaging pre-processing (e.g., spatial smoothing). Finally, electrophysiological and neurophysiological methods, such as single neuron recording, local field-potential and intracortical EEG recordings in neurosurgical or neurological patients, can provide unique opportunities to investigate activity in subcortical structures of the human brain[167,230].

6. Conclusions

We have outlined the subcortical areas of the brain most commonly associated with the sense of body ownership, namely the cerebellum and the putamen, but also the thalamus and the hippocampus. However, it is clear that more research is needed to further clarify their role as well as to expand on other areas of interest that deserve more attention, such as the hypothalamus and the amygdala. Furthermore, we discussed clinical evidence from the neurological and psychiatric fields, providing important direct and indirect insight into subcortical contributions to body ownership. Overall, we show that it is possible to integrate subcortical areas into the more established cortical network underlying the emergence, maintenance, and update of the feeling that the body belongs to oneself. By highlighting outstanding issues in the field of body ownership we hopefully pave the way for further research on subcortical regions.

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Competing interests

None declared.

References

1. Bekrater-Bodmann R, Foell J, Diers M, Flor H. The perceptual and neuronal stability of the rubber hand illusion across contexts and over time. *Brain Res*. 2012;1452:130-139. doi:10.1016/j.brainres.2012.03.001

2. Costantini M, Robinson J, Migliorati D, Donno B, Ferri F, Northoff G. Temporal limits on rubber hand illusion reflect individuals' temporal resolution in multisensory perception. *Cognition*. 2016;157:39-48. doi:10.1016/j.cognition.2016.08.010

3. Crucianelli L, Krahé C, Jenkinson PM, Fotopoulou A (Katerina). Interoceptive ingredients of body ownership: Affective touch and cardiac awareness in the rubber hand illusion. *Cortex*. 2018;104:180-192. doi:10.1016/j.cortex.2017.04.018

4. Ehrsson HH. The concept of body ownership and its relation to multisensory integration. *New Handb Multisensory Process*. Published online January 1, 2012:775-792.

5. Ehrsson HH, Spence C, Passingham RE. That's My Hand! Activity in Premotor Cortex Reflects Feeling of Ownership of a Limb. *Science*. 2004;305(5685):875-877. doi:10.1126/science.1097011

6. Fahey S, Charette L, Francis C, Zheng Z. Multisensory integration of signals for bodily self-awareness requires minimal cognitive effort. *Can J Exp Psychol Rev Can Psychol Expérimentale*. 2018;72:244-252. doi:10.1037/cep0000152

7. Preston C. The role of distance from the body and distance from the real hand in ownership and disownership during the rubber hand illusion. *Acta Psychol (Amst)*. 2013;142(2):177-183. doi:10.1016/j.actpsy.2012.12.005

8. Shimada S, Fukuda K, Hiraki K. Rubber Hand Illusion under Delayed Visual Feedback. *PLOS ONE*. 2009;4(7):e6185. doi:10.1371/journal.pone.0006185

9. Shimada S, Suzuki T, Yoda N, Hayashi T. Relationship between sensitivity to visuotactile temporal discrepancy and the rubber hand illusion. *Neurosci Res*. 2014;85:33-38. doi:10.1016/j.neures.2014.04.009

10. Botvinick M, Cohen J. Rubber hands ‘feel’ touch that eyes see. *Nature*. 1998;391(6669):756-756. doi:10.1038/35784

11. Ehrsson HH. Chapter 8 - Multisensory processes in body ownership. In: Sathian K, Ramachandran VS, eds. *Multisensory Perception*. Academic Press; 2020:179-200. doi:10.1016/B978-0-12-812492-5.00008-5

12. Crea S, D’Alonzo M, Vitiello N, Cipriani C. The rubber foot illusion. *J NeuroEngineering Rehabil*. 2015;12(1):77. doi:10.1186/s12984-015-0069-6

13. Chancel M, Ehrsson HH, Ma WJ. Uncertainty-based inference of a common cause for body ownership. van Wassenhove V, Makin TR, Dienes Z, Wang L, Aller M, eds. *eLife*. 2022;11:e77221. doi:10.7554/eLife.77221

14. Ide M. The Effect of “Anatomical Plausibility” of Hand Angle on the Rubber-Hand Illusion. *Perception*. 2013;42(1):103-111. doi:10.1068/p7322

15. Lloyd DM. Spatial limits on referred touch to an alien limb may reflect boundaries of visuo-tactile peripersonal space surrounding the hand. *Brain Cogn*. 2007;64(1):104-109. doi:10.1016/j.bandc.2006.09.013

16. Kalckert A, Ehrsson HH. The spatial distance rule in the moving and classical rubber hand illusions. *Conscious Cogn*. 2014;30:118-132. doi:10.1016/j.concog.2014.08.022

17. Riemer M, Trojan J, Beauchamp M, Fuchs X. The rubber hand universe: On the impact of methodological differences in the rubber hand illusion. *Neurosci Biobehav Rev*. 2019;104:268-280. doi:10.1016/j.neubiorev.2019.07.008

18. Tsakiris M, Carpenter L, James D, Fotopoulou A. Hands only illusion: multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. *Exp Brain Res*. 2010;204(3):343-352. doi:10.1007/s00221-009-2039-3

19. Blanke O, Slater M, Serino A. Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness. *Neuron*. 2015;88(1):145-166. doi:10.1016/j.neuron.2015.09.029

20. Stein BE, Stanford TR. Multisensory integration: current issues from the perspective of the single neuron. *Nat Rev Neurosci*. 2008;9(4):255-266. doi:10.1038/nrn2331

21. Ehrsson HH. Bodily illusions. In: *The Routledge Handbook of Bodily Awareness*. Routledge; 2022.

22. Sato Y, Toyoizumi T, Aihara K. Bayesian Inference Explains Perception of Unity and Ventriloquism Aftereffect: Identification of Common Sources of Audiovisual Stimuli. *Neural Comput*. 2007;19(12):3335-3355. doi:10.1162/neco.2007.19.12.3335

23. Samad M, Chung AJ, Shams L. Perception of Body Ownership Is Driven by Bayesian Sensory Inference. *PLOS ONE*. 2015;10(2):e0117178. doi:10.1371/journal.pone.0117178

24. Kilteni K, Maselli A, Kording KP, Slater M. Over my fake body: body ownership illusions for studying the multisensory basis of own-body perception. *Front Hum Neurosci*. 2015;9. Accessed June 20, 2023. https://www.frontiersin.org/articles/10.3389/fnhum.2015.00141

25. Fang W, Li J, Qi G, Li S, Sigman M, Wang L. Statistical inference of body representation in the macaque brain. *Proc Natl Acad Sci*. 2019;116(40):20151-20157. doi:10.1073/pnas.1902334116

26. Körding KP, Beierholm U, Ma WJ, Quartz S, Tenenbaum JB, Shams L. Causal Inference in Multisensory Perception. *PLOS ONE*. 2007;2(9):e943. doi:10.1371/journal.pone.0000943

27. Grivaz P, Blanke O, Serino A. Common and distinct brain regions processing multisensory bodily signals for peripersonal space and body ownership. *NeuroImage*. 2017;147:602-618. doi:10.1016/j.neuroimage.2016.12.052

28. Nilsson M, Kalckert A. Region-of-interest analysis approaches in neuroimaging studies of body ownership: An activation likelihood estimation meta-analysis. *Eur J Neurosci*. 2021;54(11):7974-7988. doi:10.1111/ejn.15534

29. Salvato G, Richter F, Sedeño L, Bottini G, Paulesu E. Building the bodily self-awareness: Evidence for the convergence between interoceptive and exteroceptive information in a multilevel kernel density analysis study. *Hum Brain Mapp*. 2020;41(2):401-418. doi:10.1002/hbm.24810

30. Ehrsson HH, Kito T, Sadato N, Passingham RE, Naito E. Neural Substrate of Body Size: Illusory Feeling of Shrinking of the Waist. *PLOS Biol*. 2005;3(12):e412. doi:10.1371/journal.pbio.0030412

31. Gentile G, Guterstam A, Brozzoli C, Ehrsson HH. Disintegration of Multisensory Signals from the Real Hand Reduces Default Limb Self-Attribution: An fMRI Study. *J Neurosci*. 2013;33(33):13350-13366. doi:10.1523/JNEUROSCI.1363-13.2013

32. Petkova VI, Björnsdotter M, Gentile G, Jonsson T, Li TQ, Ehrsson HH. From Part- to Whole-Body Ownership in the Multisensory Brain. *Curr Biol*. 2011;21(13):1118-1122. doi:10.1016/j.cub.2011.05.022

33. Chancel M, Iriye H, Ehrsson HH. Causal Inference of Body Ownership in the Posterior Parietal Cortex. *J Neurosci*. 2022;42(37):7131-7143. doi:10.1523/JNEUROSCI.0656-22.2022

34. Ehrsson HH, Wiech K, Weiskopf N, Dolan RJ, Passingham RE. Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. *Proc Natl Acad Sci*. 2007;104(23):9828-9833. doi:10.1073/pnas.0610011104

35. Tsakiris M, Hesse MD, Boy C, Haggard P, Fink GR. Neural Signatures of Body Ownership: A Sensory Network for Bodily Self-Consciousness. *Cereb Cortex*. 2007;17(10):2235-2244. doi:10.1093/cercor/bhl131

36. Guterstam A, Björnsdotter M, Gentile G, Ehrsson HH. Posterior Cingulate Cortex Integrates the Senses of Self-Location and Body Ownership. *Curr Biol*. 2015;25(11):1416-1425. doi:10.1016/j.cub.2015.03.059

37. Limanowski J, Lutti A, Blankenburg F. The extrastriate body area is involved in illusory limb ownership. *NeuroImage*. 2014;86:514-524. doi:10.1016/j.neuroimage.2013.10.035

38. Arzy S, Overney LS, Landis T, Blanke O. Neural Mechanisms of Embodiment: Asomatognosia Due to Premotor Cortex Damage. *Arch Neurol*. 2006;63(7):1022-1025. doi:10.1001/archneur.63.7.1022

39. Baier B, Karnath HO. Tight Link Between Our Sense of Limb Ownership and Self-Awareness of Actions. *Stroke*. 2008;39(2):486-488. doi:10.1161/STROKEAHA.107.495606

40. Guterstam A, Collins KL, Cronin JA, et al. Direct Electrophysiological Correlates of Body Ownership in Human Cerebral Cortex. *Cereb Cortex*. 2019;29(3):1328-1341. doi:10.1093/cercor/bhy285

41. Casula EP, Tieri G, Rocchi L, et al. Feeling of Ownership over an Embodied Avatar's Hand Brings About Fast Changes of Fronto-Parietal Cortical Dynamics. *J Neurosci*. 2022;42(4):692-701. doi:10.1523/JNEUROSCI.0636-21.2021

42. Rao IS, Kayser C. Neurophysiological Correlates of the Rubber Hand Illusion in Late Evoked and Alpha/Beta Band Activity. *Front Hum Neurosci*. 2017;11. Accessed June 20, 2023. https://www.frontiersin.org/articles/10.3389/fnhum.2017.00377

43. Limanowski J, Blankenburg F. That's not quite me: limb ownership encoding in the brain. *Soc Cogn Affect Neurosci*. 2016;11(7):1130-1140. doi:10.1093/scan/nsv079

44. (Bud) Craig A. Interoception: the sense of the physiological condition of the body. *Curr Opin Neurobiol*. 2003;13(4):500-505. doi:10.1016/S0959-4388(03)00090-4

45. Preston C, Ehrsson HH. Illusory Obesity Triggers Body Dissatisfaction Responses in the Insula and Anterior Cingulate Cortex. *Cereb Cortex*. 2016;26(12):4450-4460. doi:10.1093/cercor/bhw313

46. Ronchi R, Bello-Ruiz J, Lukowska M, et al. Right insular damage decreases heartbeat awareness and alters cardio-visual effects on bodily self-consciousness. *Neuropsychologia*. 2015;70:11-20. doi:10.1016/j.neuropsychologia.2015.02.010

47. Heydrich L, Blanke O. Distinct illusory own-body perceptions caused by damage to posterior insula and extrastriate cortex. *Brain*. 2013;136(3):790-803. doi:10.1093/brain/aws364

48. Jenkinson PM, Papadaki C, Besharati S, et al. Welcoming back my arm: affective touch increases body ownership following right-hemisphere stroke. *Brain Commun*. 2020;2(1):fcaa034. doi:10.1093/braincomms/fcaa034

49. Kirsch LP, Besharati S, Papadaki C, et al. Damage to the right insula disrupts the perception of affective touch. Liberles S, Büchel C, eds. *eLife*. 2020;9:e47895. doi:10.7554/eLife.47895

50. Suzuki K, Garfinkel SN, Critchley HD, Seth AK. Multisensory integration across exteroceptive and interoceptive domains modulates self-experience in the rubber-hand illusion. *Neuropsychologia*. 2013;51(13):2909-2917. doi:10.1016/j.neuropsychologia.2013.08.014

51. Monti A, Porciello G, Tieri G, Aglioti SM. The "embreathment" illusion highlights the role of breathing in corporeal awareness. *J Neurophysiol*. 2020;123(1):420-427. doi:10.1152/jn.00617.2019

52. Crucianelli L, Ehrsson HH. Visuo-thermal congruency modulates the sense of body ownership. *Commun Biol*. 2022;5(1):1-12. doi:10.1038/s42003-022-03673-6

53. McHaffie JG, Stanford TR, Stein BE, Coizet V, Redgrave P. Subcortical loops through the basal ganglia. *Trends Neurosci*. 2005;28(8):401-407. doi:10.1016/j.tins.2005.06.006

54. Critchley HD, Harrison NA. Visceral Influences on Brain and Behavior. *Neuron*. 2013;77(4):624-638. doi:10.1016/j.neuron.2013.02.008

55. Azzalini D, Rebollo I, Tallon-Baudry C. Visceral Signals Shape Brain Dynamics and Cognition. *Trends Cogn Sci*. 2019;23(6):488-509. doi:10.1016/j.tics.2019.03.007

56. Park HD, Tallon-Baudry C. The neural subjective frame: from bodily signals to perceptual consciousness. *Philos Trans R Soc B Biol Sci*. 2014;369(1641):20130208. doi:10.1098/rstb.2013.0208

57. Marquis R, Muller S, Lorio S, et al. Spatial Resolution and Imaging Encoding fMRI Settings for Optimal Cortical and Subcortical Motor Somatotopy in the Human Brain. *Front Neurosci*. 2019;13. Accessed June 20, 2023. https://www.frontiersin.org/articles/10.3389/fnins.2019.00571

58. Zeller D, Gross C, Bartsch A, Johansen-Berg H, Classen J. Ventral Premotor Cortex May Be Required for Dynamic Changes in the Feeling of Limb Ownership: A Lesion Study. *J Neurosci*. 2011;31(13):4852-4857. doi:10.1523/JNEUROSCI.5154-10.2011

59. Gandola M, Invernizzi P, Sedda A, et al. An anatomical account of somatoparaphrenia. *Cortex*. 2012;48(9):1165-1178. doi:10.1016/j.cortex.2011.06.012

60. Moro V, Pernigo S, Tsakiris M, et al. Motor versus body awareness: Voxel-based lesion analysis in anosognosia for hemiplegia and somatoparaphrenia following right hemisphere stroke. *Cortex*. 2016;83:62-77. doi:10.1016/j.cortex.2016.07.001

61. Feinberg TE, Haber LD, Leeds NE. Verbal asomatognosia. *Neurology*. 1990;40(9):1391-1391. doi:10.1212/WNL.40.9.1391

62. Martinaud O, Besharati S, Jenkinson PM, Fotopoulou A. Ownership illusions in patients with body delusions: Different neural profiles of visual capture and disownership. *Cortex*. 2017;87:174-185. doi:10.1016/j.cortex.2016.09.025

63. Romano D, Maravita A. The dynamic nature of the sense of ownership after brain injury. Clues from asomatognosia and somatoparaphrenia. *Neuropsychologia*. 2019;132:107119. doi:10.1016/j.neuropsychologia.2019.107119

64. Spengler FB, Scheele D, Kaiser S, Heinrichs M, Hurlemann R. A Protective Mechanism against Illusory Perceptions Is Amygdala-Dependent. *J Neurosci*. 2019;39(17):3301-3308. doi:10.1523/JNEUROSCI.2577-18.2019

65. Limanowski J, Blankenburg F. Network activity underlying the illusory self-attribution of a dummy arm. *Hum Brain Mapp*. 2015;36(6):2284-2304. doi:10.1002/hbm.22770

66. Abdulkarim Z, Guterstam A, Hayatou Z, Ehrsson HH. Neural Substrates of Body Ownership and Agency during Voluntary Movement. *J Neurosci*. 2023;43(13):2362-2380. doi:10.1523/JNEUROSCI.1492-22.2023

67. Matsumoto N, Nakai R, Ino T, Mitani A. Brain activity associated with the rubber foot illusion. *Neurosci Lett*. 2020;721:134820. doi:10.1016/j.neulet.2020.134820

68. Guterstam A, Gentile G, Ehrsson HH. The Invisible Hand Illusion: Multisensory Integration Leads to the Embodiment of a Discrete Volume of Empty Space. *J Cogn Neurosci*. 2013;25(7):1078-1099. doi:10.1162/jocn_a_00393

69. Makin TR, Holmes NP, Ehrsson HH. On the other hand: Dummy hands and peripersonal space. *Behav Brain Res*. 2008;191(1):1-10. doi:10.1016/j.bbr.2008.02.041

70. Tsakiris M. My body in the brain: A neurocognitive model of body-ownership. *Neuropsychologia*. 2010;48(3):703-712. doi:10.1016/j.neuropsychologia.2009.09.034

71. Bushara KO, Grafman J, Hallett M. Neural Correlates of Auditory–Visual Stimulus Onset Asynchrony Detection. *J Neurosci*. 2001;21(1):300-304. doi:10.1523/JNEUROSCI.21-01-00300.2001

72. Gentile G, Petkova VI, Ehrsson HH. Integration of Visual and Tactile Signals From the Hand in the Human Brain: An fMRI Study. *J Neurophysiol*. 2011;105(2):910-922. doi:10.1152/jn.00840.2010

73. Hagura N, Oouchida Y, Aramaki Y, et al. Visuokinesthetic Perception of Hand Movement is Mediated by Cerebro–Cerebellar Interaction between the Left Cerebellum and Right Parietal Cortex. *Cereb Cortex*. 2009;19(1):176-186. doi:10.1093/cercor/bhn068

74. Kavounoudias A, Roll JP, Anton JL, Nazarian B, Roth M, Roll R. Proprio-tactile integration for kinesthetic perception: An fMRI study. *Neuropsychologia*. 2008;46(2):567-575. doi:10.1016/j.neuropsychologia.2007.10.002

75. Naumer MJ, Ratz L, Yalachkov Y, et al. Visuohaptic convergence in a corticocerebellar network. *Eur J Neurosci*. 2010;31(10):1730-1736. doi:10.1111/j.1460-9568.2010.07208.x

76. Ronconi L, Casartelli L, Carna S, Molteni M, Arrigoni F, Borgatti R. When one is Enough: Impaired Multisensory Integration in Cerebellar Agenesis. *Cereb Cortex*. 2017;27(3):2041-2051. doi:10.1093/cercor/bhw049

77. Stevenson RA, Kim S, James TW. An additive-factors design to disambiguate neuronal and areal convergence: measuring multisensory interactions between audio, visual, and haptic

sensory streams using fMRI. *Exp Brain Res*. 2009;198(2):183-194. doi:10.1007/s00221-009-1783-8

78. Ishikawa T, Shimuta M, Häusser M. Multimodal sensory integration in single cerebellar granule cells in vivo. Marder E, ed. *eLife*. 2015;4:e12916. doi:10.7554/eLife.12916

79. Baumann O, Greenlee MW. Neural Correlates of Coherent Audiovisual Motion Perception. *Cereb Cortex*. 2007;17(6):1433-1443. doi:10.1093/cercor/bhl055

80. Blakemore SJ, Wolpert DM, Frith CD. The Cerebellum Contributes to Somatosensory Cortical Activity during Self-Produced Tactile Stimulation. *NeuroImage*. 1999;10(4):448-459. doi:10.1006/nimg.1999.0478

81. Borsook D, Moulton EA, Tully S, Schmahmann JD, Becerra L. Human cerebellar responses to brush and heat stimuli in healthy and neuropathic pain subjects. *The Cerebellum*. 2008;7(3):252-272. doi:10.1007/s12311-008-0011-6

82. Kilteni K, Ehrsson HH. Functional Connectivity between the Cerebellum and Somatosensory Areas Implements the Attenuation of Self-Generated Touch. *J Neurosci*. 2020;40(4):894-906. doi:10.1523/JNEUROSCI.1732-19.2019

83. Naito E, Roland PE, Grefkes C, et al. Dominance of the Right Hemisphere and Role of Area 2 in Human Kinesthesia. *J Neurophysiol*. 2005;93(2):1020-1034. doi:10.1152/jn.00637.2004

84. Naito E, Nakashima T, Kito T, Aramaki Y, Okada T, Sadato N. Human limb-specific and non-limb-specific brain representations during kinesthetic illusory movements of the upper and lower extremities. *Eur J Neurosci*. 2007;25(11):3476-3487. doi:10.1111/j.1460-9568.2007.05587.x

85. Schmahmann JD, Guell X, Stoodley CJ, Halko MA. The Theory and Neuroscience of Cerebellar Cognition. *Annu Rev Neurosci*. 2019;42(1):337-364. doi:10.1146/annurev-neuro-070918-050258

86. Strick PL, Dum RP, Fiez JA. Cerebellum and Nonmotor Function. *Annu Rev Neurosci*. 2009;32(1):413-434. doi:10.1146/annurev.neuro.31.060407.125606

87. Bernard J, Seidler R, Hassevoort K, et al. Resting state cortico-cerebellar functional connectivity networks: a comparison of anatomical and self-organizing map approaches. *Front Neuroanat*. 2012;6. Accessed June 20, 2023. https://www.frontiersin.org/articles/10.3389/fnana.2012.00031

88. Bostan AC, Strick PL. The basal ganglia and the cerebellum: nodes in an integrated network. *Nat Rev Neurosci*. 2018;19(6):338-350. doi:10.1038/s41583-018-0002-7

89. O'Reilly JX, Beckmann CF, Tomassini V, Ramnani N, Johansen-Berg H. Distinct and Overlapping Functional Zones in the Cerebellum Defined by Resting State Functional Connectivity. *Cereb Cortex*. 2010;20(4):953-965. doi:10.1093/cercor/bhp157

90. Dow RS. Some novel concepts of cerebellar physiology. *Mt Sinai J Med N Y*. 1974;41(1):103-119.

91. Schmahmann JD. An Emerging Concept: The Cerebellar Contribution to Higher Function. *Arch Neurol*. 1991;48(11):1178-1187. doi:10.1001/archneur.1991.00530230086029

92. Schmahmann JD. The cerebellum and cognition. *Neurosci Lett*. 2019;688:62-75. doi:10.1016/j.neulet.2018.07.005

93. Ivry RB, Keele SW. Timing Functions of The Cerebellum. *J Cogn Neurosci*. 1989;1(2):136-152. doi:10.1162/jocn.1989.1.2.136

94. Ullén F, Forssberg H, Ehrsson HH. Neural Networks for the Coordination of the Hands in Time. *J Neurophysiol*. 2003;89(2):1126-1135. doi:10.1152/jn.00775.2002

95. Aso Y, Siwanowicz I, Bräcker L, Ito K, Kitamoto T, Tanimoto H. Specific Dopaminergic Neurons for the Formation of Labile Aversive Memory. *Curr Biol*. 2010;20(16):1445-1451. doi:10.1016/j.cub.2010.06.048

96. Kalmbach BE, Voicu H, Ohyama T, Mauk MD. A Subtraction Mechanism of Temporal Coding in Cerebellar Cortex. *J Neurosci*. 2011;31(6):2025-2034. doi:10.1523/JNEUROSCI.4212-10.2011

97. Gooch CM, Wiener M, Wencil EB, Coslett HB. Interval timing disruptions in subjects with cerebellar lesions. *Neuropsychologia*. 2010;48(4):1022-1031. doi:10.1016/j.neuropsychologia.2009.11.028

98. Lee KH, Bhaker RS, Mysore A, Parks RW, Birkett PBL, Woodruff PWR. Time perception and its neuropsychological correlates in patients with schizophrenia and in healthy volunteers. *Psychiatry Res*. 2009;166(2):174-183. doi:10.1016/j.psychres.2008.03.004

99. Templeton WB, Howard IP, Wilkinson DA. Additivity of components of prismatic adaptation. *Percept Psychophys*. 1974;15(2):249-257. doi:10.3758/BF03213941

100. Marotta A, Re A, Zampini M, Fiorio M. Bodily self-perception during voluntary actions: The causal contribution of premotor cortex and cerebellum. *Cortex*. 2021;142:1-14. doi:10.1016/j.cortex.2021.05.012

101. Block HJ, Bastian AJ. Cerebellar involvement in motor but not sensory adaptation. *Neuropsychologia*. 2012;50(8):1766-1775. doi:10.1016/j.neuropsychologia.2012.03.034

102. Henriques DYP, Filippopulos F, Straube A, Eggert T. The cerebellum is not necessary for visually driven recalibration of hand proprioception. *Neuropsychologia*. 2014;64:195-204. doi:10.1016/j.neuropsychologia.2014.09.029

103. Therrien AS, Bastian AJ. Cerebellar damage impairs internal predictions for sensory and motor function. *Curr Opin Neurobiol*. 2015;33:127-133. doi:10.1016/j.conb.2015.03.013

104. FIEZ JA, PETERSEN SE, CHENEY MK, RAICHLE ME. IMPAIRED NON-MOTOR LEARNING AND ERROR DETECTION ASSOCIATED WITH CEREBELLAR DAMAGE: A SINGLE CASE STUDY. *Brain*. 1992;115(1):155-178. doi:10.1093/brain/115.1.155

105. Ito M. Control of mental activities by internal models in the cerebellum. *Nat Rev Neurosci*. 2008;9(4):304-313. doi:10.1038/nrn2332

106. Kawato M, Gomi H. A computational model of four regions of the cerebellum based on feedback-error learning. *Biol Cybern*. 1992;68(2):95-103. doi:10.1007/BF00201431

107. Blakemore SJ, Frith CD, Wolpert DM. The cerebellum is involved in predicting the sensory consequences of action. *NeuroReport*. 2001;12(9):1879.

108. Molinari M, Restuccia D, Leggio MG. State Estimation, Response Prediction, and Cerebellar Sensory Processing for Behavioral Control. *The Cerebellum*. 2009;8(3):399-402. doi:10.1007/s12311-009-0112-x

109. Popa LS, Ebner TJ. Cerebellum, Predictions and Errors. *Front Cell Neurosci*. 2019;12. Accessed June 20, 2023. https://www.frontiersin.org/articles/10.3389/fncel.2018.00524

110. Schlerf J, Ivry RB, Diedrichsen J. Encoding of Sensory Prediction Errors in the Human Cerebellum. *J Neurosci*. 2012;32(14):4913-4922. doi:10.1523/JNEUROSCI.4504-11.2012

111. Therrien AS, Bastian AJ. The cerebellum as a movement sensor. *Neurosci Lett*. 2019;688:37-40. doi:10.1016/j.neulet.2018.06.055

112. Gentile G. *Investigating the Multisensory Representation of the Hand and the Space around It Using FMRI*. Inst för neurovetenskap / Dept of Neuroscience; 2013. Accessed June 20, 2023. http://openarchive.ki.se/xmlui/handle/10616/41790

113. Lee H, Noppeney U. Temporal prediction errors in visual and auditory cortices. *Curr Biol*. 2014;24(8):R309-R310. doi:10.1016/j.cub.2014.02.007

114. Duhamel JR, Colby CL, Goldberg ME. Ventral Intraparietal Area of the Macaque: Congruent Visual and Somatic Response Properties. *J Neurophysiol*. 1998;79(1):126-136. doi:10.1152/jn.1998.79.1.126

115. Graziano MSA, Gross CG. A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields. *Exp Brain Res*. 1993;97(1):96-109. doi:10.1007/BF00228820

116. Graziano MSA. Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proc Natl Acad Sci*. 1999;96(18):10418-10421. doi:10.1073/pnas.96.18.10418

117. di Pellegrino G, Làdavas E. Peripersonal space in the brain. *Neuropsychologia*. 2015;66:126-133. doi:10.1016/j.neuropsychologia.2014.11.011

118. Graziano MS, Gross CG. Spatial maps for the control of movement. *Curr Opin Neurobiol*. 1998;8(2):195-201. doi:10.1016/S0959-4388(98)80140-2

119. Maravita A, Spence C, Driver J. Multisensory integration and the body schema: close to hand and within reach. *Curr Biol*. 2003;13(13):R531-R539. doi:10.1016/S0960-9822(03)00449-4

120. Brozzoli C, Gentile G, Ehrsson HH. That's Near My Hand! Parietal and Premotor Coding of Hand-Centered Space Contributes to Localization and Self-Attribution of the Hand. *J Neurosci*. 2012;32(42):14573-14582. doi:10.1523/JNEUROSCI.2660-12.2012

121. Gentile G, Björnsdotter M, Petkova VI, Abdulkarim Z, Ehrsson HH. Patterns of neural activity in the human ventral premotor cortex reflect a whole-body multisensory percept. *NeuroImage*. 2015;109:328-340. doi:10.1016/j.neuroimage.2015.01.008

122. Künzle H. Bilateral projections from precentral motor cortex to the putamen and other parts of the basal ganglia. An autoradiographic study inMacaca fascicularis. *Brain Res*. 1975;88(2):195-209. doi:10.1016/0006-8993(75)90384-4

123. Parthasarathy HB, Schall JD, Graybiel AM. Distributed but convergent ordering of corticostriatal projections: analysis of the frontal eye field and the supplementary eye field in the

macaque monkey. *J Neurosci*. 1992;12(11):4468-4488. doi:10.1523/JNEUROSCI.12-11-04468.1992

124. Tsakiris M, Haggard P. The Rubber Hand Illusion Revisited: Visuotactile Integration and Self-Attribution. *J Exp Psychol Hum Percept Perform*. 2005;31:80-91. doi:10.1037/0096-1523.31.1.80

125. Kilteni K, Ehrsson HH. Body ownership determines the attenuation of self-generated tactile sensations. *Proc Natl Acad Sci*. 2017;114(31):8426-8431. doi:10.1073/pnas.1703347114

126. Medendorp WP, Heed T. State estimation in posterior parietal cortex: Distinct poles of environmental and bodily states. *Prog Neurobiol*. 2019;183:101691. doi:10.1016/j.pneurobio.2019.101691

127. Brozzoli C, Gentile G, Petkova VI, Ehrsson HH. fMRI Adaptation Reveals a Cortical Mechanism for the Coding of Space Near the Hand. *J Neurosci*. 2011;31(24):9023-9031. doi:10.1523/JNEUROSCI.1172-11.2011

128. Guterstam A, Björnsdotter M, Bergouignan L, Gentile G, Li TQ, Ehrsson HH. Decoding illusory self-location from activity in the human hippocampus. *Front Hum Neurosci*. 2015;9. Accessed June 20, 2023. https://www.frontiersin.org/articles/10.3389/fnhum.2015.00412

129. Fourcade A, Schmidt TT, Nierhaus T, Blankenburg F. Enhanced processing of aversive stimuli on embodied artificial limbs by the human amygdala. *Sci Rep*. 2022;12(1):5778. doi:10.1038/s41598-022-09603-0

130. Lanfranco RC, Chancel M, Ehrsson HH. Quantifying body ownership information processing and perceptual bias in the rubber hand illusion. *Cognition*. 2023;238:105491. doi:10.1016/j.cognition.2023.105491

131. Kalckert A, Ehrsson HH. The Onset Time of the Ownership Sensation in the Moving Rubber Hand Illusion. *Front Psychol*. 2017;8. Accessed June 20, 2023. https://www.frontiersin.org/articles/10.3389/fpsyg.2017.00344

132. Reader AT, Crucianelli L. A Multisensory Perspective on the Role of the Amygdala in Body Ownership. *J Neurosci*. 2019;39(39):7645-7647. doi:10.1523/JNEUROSCI.0971-19.2019

133. Reader AT, Crucianelli L. A Multisensory Perspective on the Role of the Amygdala in Body Ownership. *J Neurosci*. 2019;39(39):7645-7647. doi:10.1523/JNEUROSCI.0971-19.2019

134. Morrow J, Mosher C, Gothard K. Multisensory Neurons in the Primate Amygdala. *J Neurosci*. 2019;39(19):3663-3675. doi:10.1523/JNEUROSCI.2903-18.2019

135. Ishida H, Inoue K ichi, Takada M. Multisynaptic Projections from the Amygdala to the Ventral Premotor Cortex in Macaque Monkeys: Anatomical Substrate for Feeding Behavior. *Front Neuroanat*. 2018;12. Accessed June 20, 2023. https://www.frontiersin.org/articles/10.3389/fnana.2018.00003

136. Roy AK, Shehzad Z, Margulies DS, et al. Functional connectivity of the human amygdala using resting state fMRI. *NeuroImage*. 2009;45(2):614-626. doi:10.1016/j.neuroimage.2008.11.030

137. Rizzo G, Milardi D, Bertino S, et al. The Limbic and Sensorimotor Pathways of the Human Amygdala: A Structural Connectivity Study. *Neuroscience*. 2018;385:166-180. doi:10.1016/j.neuroscience.2018.05.051

138. Hwang K, Bertolero MA, Liu WB, D'Esposito M. The Human Thalamus Is an Integrative Hub for Functional Brain Networks. *J Neurosci*. 2017;37(23):5594-5607. doi:10.1523/JNEUROSCI.0067-17.2017

139. Shine JM, Lewis LD, Garrett DD, Hwang K. The impact of the human thalamus on brain-wide information processing. *Nat Rev Neurosci*. 2023;24(7):416-430. doi:10.1038/s41583-023-00701-0

140. Shepherd GMG, Yamawaki N. Untangling the cortico-thalamo-cortical loop: cellular pieces of a knotty circuit puzzle. *Nat Rev Neurosci*. 2021;22(7):389-406. doi:10.1038/s41583-021-00459-3

141. Cappe C, Rouiller EM, Barone P. Multisensory anatomical pathways. *Hear Res*. 2009;258(1):28-36. doi:10.1016/j.heares.2009.04.017

142. Baluch F, Itti L. Mechanisms of top-down attention. *Trends Neurosci*. 2011;34(4):210-224. doi:10.1016/j.tins.2011.02.003

143. McAlonan K, Cavanaugh J, Wurtz RH. Guarding the gateway to cortex with attention in visual thalamus. *Nature*. 2008;456(7220):391-394. doi:10.1038/nature07382

144. Noudoost B, Chang MH, Steinmetz NA, Moore T. Top-down control of visual attention. *Curr Opin Neurobiol*. 2010;20(2):183-190. doi:10.1016/j.conb.2010.02.003

145. Saalmann YB, Kastner S. Gain control in the visual thalamus during perception and cognition. *Curr Opin Neurobiol*. 2009;19(4):408-414. doi:10.1016/j.conb.2009.05.007

146. Wimmer RD, Schmitt LI, Davidson TJ, Nakajima M, Deisseroth K, Halassa MM. Thalamic control of sensory selection in divided attention. *Nature*. 2015;526(7575):705-709. doi:10.1038/nature15398

147. Barron DS, Eickhoff SB, Clos M, Fox PT. Human pulvinar functional organization and connectivity. *Hum Brain Mapp*. 2015;36(7):2417-2431. doi:10.1002/hbm.22781

148. Battistella G, Najdenovska E, Maeder P, et al. Robust thalamic nuclei segmentation method based on local diffusion magnetic resonance properties. *Brain Struct Funct*. 2017;222(5):2203-2216. doi:10.1007/s00429-016-1336-4

149. Guedj C, Vuilleumier P. Functional connectivity fingerprints of the human pulvinar: Decoding its role in cognition. *NeuroImage*. 2020;221:117162. doi:10.1016/j.neuroimage.2020.117162

150. Iglesias JE, Insausti R, Lerma-Usabiaga G, et al. A probabilistic atlas of the human thalamic nuclei combining ex vivo MRI and histology. *NeuroImage*. 2018;183:314-326. doi:10.1016/j.neuroimage.2018.08.012

151. Najdenovska E, Alemán-Gómez Y, Battistella G, et al. In-vivo probabilistic atlas of human thalamic nuclei based on diffusion- weighted magnetic resonance imaging. *Sci Data*. 2018;5(1):180270. doi:10.1038/sdata.2018.270

152. Arcaro MJ, Pinsk MA, Kastner S. The Anatomical and Functional Organization of the Human Visual Pulvinar. *J Neurosci*. 2015;35(27):9848-9871. doi:10.1523/JNEUROSCI.1575-14.2015

153. Bridge H, Leopold DA, Bourne JA. Adaptive Pulvinar Circuitry Supports Visual Cognition. *Trends Cogn Sci*. 2016;20(2):146-157. doi:10.1016/j.tics.2015.10.003

154. Grieve KL, Acuña C, Cudeiro J. The primate pulvinar nuclei: vision and action. *Trends Neurosci*. 2000;23(1):35-39. doi:10.1016/S0166-2236(99)01482-4

155. Froesel M, Cappe C, Ben Hamed S. A multisensory perspective onto primate pulvinar functions. *Neurosci Biobehav Rev*. 2021;125:231-243. doi:10.1016/j.neubiorev.2021.02.043

156. Kaas JH, Lyon DC. Pulvinar contributions to the dorsal and ventral streams of visual processing in primates. *Brain Res Rev*. 2007;55(2):285-296. doi:10.1016/j.brainresrev.2007.02.008

157. Stepniewska I. The pulvinar complex. (2003). In J. H. Kaas, & C.E. Collins (Eds.), The Primate Visual System (pp/ 53-80). CRC Press.

158. Arend I, Rafal R, Ward R. Spatial and temporal deficits are regionally dissociable in patients with pulvinar lesions. *Brain*. 2008;131(8):2140-2152. doi:10.1093/brain/awn135

159. Bourgeois A, Guedj C, Carrera E, Vuilleumier P. Pulvino-cortical interaction: An integrative role in the control of attention. *Neurosci Biobehav Rev*. 2020;111:104-113. doi:10.1016/j.neubiorev.2020.01.005

160. Fiebelkorn IC, Kastner S. Functional Specialization in the Attention Network. *Annu Rev Psychol*. 2020;71(1):221-249. doi:10.1146/annurev-psych-010418-103429

161. Zhou H, Schafer RJ, Desimone R. Pulvinar-Cortex Interactions in Vision and Attention. *Neuron*. 2016;89(1):209-220. doi:10.1016/j.neuron.2015.11.034

162. Kok P, Turk-Browne NB. Associative Prediction of Visual Shape in the Hippocampus. *J Neurosci*. 2018;38(31):6888-6899. doi:10.1523/JNEUROSCI.0163-18.2018

163. Cohen NJ, Eichenbaum H. *Memory, Amnesia, and the Hippocampal System*. MIT Press; 1993.

164. Burgess N, Maguire EA, O'Keefe J. The Human Hippocampus and Spatial and Episodic Memory. *Neuron*. 2002;35(4):625-641. doi:10.1016/S0896-6273(02)00830-9

165. Howard LR, Javadi AH, Yu Y, et al. The Hippocampus and Entorhinal Cortex Encode the Path and Euclidean Distances to Goals during Navigation. *Curr Biol*. 2014;24(12):1331-1340. doi:10.1016/j.cub.2014.05.001

166. Moon HJ, Gauthier B, Park HD, Faivre N, Blanke O. Sense of self impacts spatial navigation and hexadirectional coding in human entorhinal cortex. *Commun Biol*. 2022;5(1):1-12. doi:10.1038/s42003-022-03361-5

167. Dary Z, Lenggenhager B, Lagarde S, Medina Villalon S, Bartolomei F, Lopez C. Neural bases of the bodily self as revealed by electrical brain stimulation: A systematic review. *Hum Brain Mapp*. 2023;44(7):2936-2959. doi:10.1002/hbm.26253

168. Bergouignan L, Nyberg L, Ehrsson HH. Out-of-body–induced hippocampal amnesia. *Proc Natl Acad Sci*. 2014;111(12):4421-4426. doi:10.1073/pnas.1318801111

169. Bergouignan L, Nyberg L, Ehrsson HH. Out-of-body memory encoding causes third-person perspective at recall. *J Cogn Psychol*. 2022;34(1):160-178. doi:10.1080/20445911.2021.1958823

170. Tacikowski P, Weijs ML, Ehrsson HH. Perception of Our Own Body Influences Self-Concept and Self-Incoherence Impairs Episodic Memory. *iScience*. 2020;23(9):101429. doi:10.1016/j.isci.2020.101429

171. Iriye H, Ehrsson HH. Perceptual illusion of body-ownership within an immersive realistic environment enhances memory accuracy and re-experiencing. *iScience*. 2022;25(1):103584. doi:10.1016/j.isci.2021.103584

172. Vargha-Khadem F, Gadian DG, Watkins KE, Connelly A, Van Paesschen W, Mishkin M. Differential Effects of Early Hippocampal Pathology on Episodic and Semantic Memory. *Science*. 1997;277(5324):376-380. doi:10.1126/science.277.5324.376

173. Davachi L. Item, context and relational episodic encoding in humans. *Curr Opin Neurobiol*. 2006;16(6):693-700. doi:10.1016/j.conb.2006.10.012

174. Garvert MM, Dolan RJ, Behrens TE. A map of abstract relational knowledge in the human hippocampal–entorhinal cortex. Davachi L, ed. *eLife*. 2017;6:e17086. doi:10.7554/eLife.17086

175. Fotopoulou PMJ Valentina Moro, Aikaterini (Katerina). Disorders of body ownership. In: *The Routledge Handbook of Bodily Awareness*. Routledge; 2022.

176. Cocchini G, Beschin N, Cameron A, Fotopoulou A, Della Sala S. Anosognosia for motor impairment following left brain damage. *Neuropsychology*. 2009;23:223-230. doi:10.1037/a0014266

177. Moro V, Pacella V, Scandola M, et al. A fronto-insular-parietal network for the sense of body ownership. *Cereb Cortex*. 2023;33(3):512-522. doi:10.1093/cercor/bhac081

178. Pia L, Neppi-Modona M, Ricci R, Berti A. The Anatomy of Anosognosia for Hemiplegia: A Meta-Analysis. *Cortex*. 2004;40(2):367-377. doi:10.1016/S0010-9452(08)70131-X

179. Besharati S, Crucianelli L, Fotopoulou A. Restoring awareness: a review of rehabilitation in anosognosia for hemiplegia. Published online 2014.

180. Fotopoulou A, Pernigo S, Maeda R, Rudd A, Kopelman MA. Implicit awareness in anosognosia for hemiplegia: unconscious interference without conscious re-representation. *Brain*. 2010;133(12):3564-3577. doi:10.1093/brain/awq233

181. Moro V, Pernigo S, Zapparoli P, Cordioli Z, Aglioti SM. Phenomenology and neural correlates of implicit and emergent motor awareness in patients with anosognosia for hemiplegia. *Behav Brain Res*. 2011;225(1):259-269. doi:10.1016/j.bbr.2011.07.010

182. Besharati S, Kopelman M, Avesani R, Moro V, Fotopoulou A (Katerina). Another perspective on anosognosia: Self-observation in video replay improves motor awareness. *Neuropsychol Rehabil*. 2015;25(3):319-352. doi:10.1080/09602011.2014.923319

183. Ehrsson HH. The Experimental Induction of Out-of-Body Experiences. *Science*. 2007;317(5841):1048-1048. doi:10.1126/science.1142175

184. Dijkerman HC. How do different aspects of self-consciousness interact? *Trends Cogn Sci*. 2015;19(8):427-428. doi:10.1016/j.tics.2015.06.003

185. Petkova V, Khoshnevis M, Ehrsson HH. The Perspective Matters! Multisensory Integration in Ego-Centric Reference Frames Determines Full-Body Ownership. *Front Psychol*. 2011;2. Accessed June 20, 2023. https://www.frontiersin.org/articles/10.3389/fpsyg.2011.00035

186. Feinberg TE, Venneri A, Simone AM, Fan Y, Northoff G. The neuroanatomy of asomatognosia and somatoparaphrenia. *J Neurol Neurosurg Psychiatry*. 2010;81(3):276-281. doi:10.1136/jnnp.2009.188946

187. Forkel SJ, Friedrich P, Thiebaut de Schotten M, Howells H. White matter variability, cognition, and disorders: a systematic review. *Brain Struct Funct*. 2022;227(2):529-544. doi:10.1007/s00429-021-02382-w

188. Kim JS, Pope A. Somatotopically located motor fibers in corona radiata: Evidence from subcortical small infarcts. *Neurology*. 2005;64(8):1438-1440. doi:10.1212/01.WNL.0000158656.09335.E7

189. Feinberg TE, Roane DM, Ali J. Illusory limb movements in anosognosia for hemiplegia. *J Neurol Neurosurg Psychiatry*. 2000;68(4):511-513. doi:10.1136/jnnp.68.4.511

190. Spinazzola L, Pagliari C, Facchin A, Maravita A. A new clinical evaluation of asomatognosia in right brain damaged patients using visual and reaching tasks. *J Clin Exp Neuropsychol*. 2020;42(5):436-449. doi:10.1080/13803395.2020.1757040

191. Ronchi R, Bassolino M, Viceic D, et al. Disownership of body parts as revealed by a visual scale evaluation. An observational study. *Neuropsychologia*. 2020;138:107337. doi:10.1016/j.neuropsychologia.2020.107337

192. Park S, Baxter T. Schizophrenia in the flesh: Revisiting schizophrenia as a disorder of the bodily self. *Schizophr Res*. 2022;242:113-117. doi:10.1016/j.schres.2021.12.031

193. Thakkar KN, Nichols HS, McIntosh LG, Park S. Disturbances in Body Ownership in Schizophrenia: Evidence from the Rubber Hand Illusion and Case Study of a Spontaneous Out-of-Body Experience. *PLOS ONE*. 2011;6(10):e27089. doi:10.1371/journal.pone.0027089

194. Ferri F, Costantini M, Salone A, et al. Upcoming tactile events and body ownership in schizophrenia. *Schizophr Res*. 2014;152(1):51-57. doi:10.1016/j.schres.2013.06.026

195. Costantini M, Salone A, Martinotti G, et al. Body representations and basic symptoms in schizophrenia. *Schizophr Res*. 2020;222:267-273. doi:10.1016/j.schres.2020.05.038

196. van der Weiden A, Prikken M, van Haren NEM. Self–other integration and distinction in schizophrenia: A theoretical analysis and a review of the evidence. *Neurosci Biobehav Rev*. 2015;57:220-237. doi:10.1016/j.neubiorev.2015.09.004

197. Okada N, Fukunaga M, Yamashita F, et al. Abnormal asymmetries in subcortical brain volume in schizophrenia. *Mol Psychiatry*. 2016;21(10):1460-1466. doi:10.1038/mp.2015.209

198. Andreasen NC, Pierson R. The Role of the Cerebellum in Schizophrenia. *Biol Psychiatry*. 2008;64(2):81-88. doi:10.1016/j.biopsych.2008.01.003

199. First MB. Desire for amputation of a limb: paraphilia, psychosis, or a new type of identity disorder. *Psychol Med*. 2005;35(6):919-928. doi:10.1017/S0033291704003320

200. Blom RM, Van Wingen GA, Van Der Wal SJ, et al. The Desire for Amputation or Paralyzation: Evidence for Structural Brain Anomalies in Body Integrity Identity Disorder (BIID). Jaencke L, ed. *PLOS ONE*. 2016;11(11):e0165789. doi:10.1371/journal.pone.0165789

201. McGeoch PD, Brang D, Song T, Lee RR, Huang M, Ramachandran VS. Xenomelia: a new right parietal lobe syndrome. *J Neurol Neurosurg Psychiatry*. 2011;82(12):1314-1319. doi:10.1136/jnnp-2011-300224

202. Van Dijk MT, Van Wingen GA, Van Lammeren A, et al. Neural Basis of Limb Ownership in Individuals with Body Integrity Identity Disorder. Tsakiris M, ed. *PLoS ONE*. 2013;8(8):e72212. doi:10.1371/journal.pone.0072212

203. Weijs ML, Ho JT, Roel Lesur M, Lenggenhager B. Is this my foot? Experimentally induced disownership in individuals with body integrity dysphoria. *Conscious Cogn*. 2022;106:103432. doi:10.1016/j.concog.2022.103432

204. Lenggenhager B, Hilti L, Brugger P. Disturbed body integrity and the “rubber foot illusion.” *Neuropsychology*. 2015;29(2):205-211. doi:10.1037/neu0000143

205. Saetta G, Hänggi J, Gandola M, et al. Neural Correlates of Body Integrity Dysphoria. *Curr Biol*. 2021;31(16):3702. doi:10.1016/j.cub.2021.07.037

206. Hilti LM, Hänggi J, Vitacco DA, et al. The desire for healthy limb amputation: structural brain correlates and clinical features of xenomelia. *Brain*. 2013;136(1):318-329. doi:10.1093/brain/aws316

207. Saetta G, Ruddy K, Zapparoli L, et al. White matter abnormalities in the amputation variant of body integrity dysphoria. *Cortex*. 2022;151:272-280. doi:10.1016/j.cortex.2022.03.011

208. Hänggi J, Bellwald D, Brugger P. Shape alterations of basal ganglia and thalamus in xenomelia. *NeuroImage Clin*. 2016;11:760-769. doi:10.1016/j.nicl.2016.05.015

209. Brugger P, Christen M, Jellestad L, Hänggi J. Limb amputation and other disability desires as a medical condition. *Lancet Psychiatry*. 2016;3(12):1176-1186. doi:10.1016/S2215-0366(16)30265-6

210. Beissner F. Functional MRI of the Brainstem: Common Problems and their Solutions. *Clin Neuroradiol*. 2015;25(2):251-257. doi:10.1007/s00062-015-0404-0

211. Henderson L, Macefield V. Functional Imaging of the Human Brainstem during Somatosensory Input and Autonomic Output. *Front Hum Neurosci*. 2013;7. Accessed June 20, 2023. https://www.frontiersin.org/articles/10.3389/fnhum.2013.00569

212. Versteeg C, Chowdhury RH, Miller LE. Cuneate nucleus: the somatosensory gateway to the brain. *Curr Opin Physiol*. 2021;20:206-215. doi:10.1016/j.cophys.2021.02.004

213. Stein BE, Meredith MA. *The Merging of the Senses*. MIT Press; 1993.

214. King A. The superior colliculus.

215. Liu X, Huang H, Snutch TP, Cao P, Wang L, Wang F. The Superior Colliculus: Cell Types, Connectivity, and Behavior. *Neurosci Bull*. 2022;38(12):1519-1540. doi:10.1007/s12264-022-00858-1

216. Olivé I, Tempelmann C, Berthoz A, Heinze HJ. Increased functional connectivity between superior colliculus and brain regions implicated in bodily self-consciousness during the rubber hand illusion. *Hum Brain Mapp*. 2015;36(2):717-730. doi:10.1002/hbm.22659

217. Fealey RD. Chapter 7 - Interoception and autonomic nervous system reflexes thermoregulation. In: Buijs RM, Swaab DF, eds. *Handbook of Clinical Neurology*. Vol 117. Autonomic Nervous System. Elsevier; 2013:79-88. doi:10.1016/B978-0-444-53491-0.00007-9

218. Ide M, Wada M. Salivary Oxytocin Concentration Associates with the Subjective Feeling of Body Ownership during the Rubber Hand Illusion. *Front Hum Neurosci*. 2017;11. Accessed June 20, 2023. https://www.frontiersin.org/articles/10.3389/fnhum.2017.00166

219. Crucianelli L, Paloyelis Y, Ricciardi L, Jenkinson PM, Fotopoulou A. Embodied Precision: Intranasal Oxytocin Modulates Multisensory Integration. *J Cogn Neurosci*. 2019;31(4):592-606. doi:10.1162/jocn_a_01366

220. Crucianelli L, Serpell L, Paloyelis Y, et al. The effect of intranasal oxytocin on the perception of affective touch and multisensory integration in anorexia nervosa: protocol for a double-blind placebo-controlled crossover study. *BMJ Open*. 2019;9(3):e024913. doi:10.1136/bmjopen-2018-024913

221. Xin F, Zhou X, Dong D, et al. Oxytocin Differentially Modulates Amygdala Responses during Top-Down and Bottom-Up Aversive Anticipation. *Adv Sci*. 2020;7(16):2001077. doi:10.1002/advs.202001077

222. Moseley GL, Olthof N, Venema A, et al. Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *Proc Natl Acad Sci*. 2008;105(35):13169-13173. doi:10.1073/pnas.0803768105

223. Crivelli D, Polimeni E, Crotti D, Bottini G, Salvato G. Bilateral skin temperature drop and warm sensibility decrease following modulation of body part ownership through mirror-box illusion. *Cortex*. 2021;135:49-60. doi:10.1016/j.cortex.2020.11.015

224. de Haan AM, Van Stralen HE, Smit M, Keizer A, Van der Stigchel S, Dijkerman HC. No consistent cooling of the real hand in the rubber hand illusion. *Acta Psychol (Amst)*. 2017;179:68-77. doi:10.1016/j.actpsy.2017.07.003

225. Lang VA, Zbinden J, Wessberg J, Ortiz-Catalan M. Hand Temperature Is Not Consistent With Illusory Strength During the Rubber Hand Illusion. In: *2021 43rd Annual International Conference of the IEEE Engineering in Medicine & Biology Society (EMBC)*. ; 2021:1416-1418. doi:10.1109/EMBC46164.2021.9630200

226. Crucianelli L, Ehrsson HH. The Role of the Skin in Interoception: A Neglected Organ? *Perspect Psychol Sci*. Published online August 15, 2022:17456916221094508. doi:10.1177/17456916221094509

227. Roger C, Lasbleiz A, Guye M, Dutour A, Gaborit B, Ranjeva JP. The Role of the Human Hypothalamus in Food Intake Networks: An MRI Perspective. *Front Nutr*. 2022;8. Accessed June 20, 2023. https://www.frontiersin.org/articles/10.3389/fnut.2021.760914

228. Miletić S, Bazin PL, Weiskopf N, van der Zwaag W, Forstmann BU, Trampel R. fMRI protocol optimization for simultaneously studying small subcortical and cortical areas at 7 T. *NeuroImage*. 2020;219:116992. doi:10.1016/j.neuroimage.2020.116992

229. Billot B, Bocchetta M, Todd E, Dalca AV, Rohrer JD, Iglesias JE. Automated segmentation of the hypothalamus and associated subunits in brain MRI. *NeuroImage*. 2020;223:117287. doi:10.1016/j.neuroimage.2020.117287

230. Pereira M, Faivre N, Bernasconi F, et al. Subcortical correlates of consciousness with human single neuron recordings. Published online January 30, 2023:2023.01.27.525684. doi:10.1101/2023.01.27.525684

Figure legends

Figure 1 Flatmap representation of the cerebellum and locations of activity reported in published studies on body ownership. Reference citations in the figure refer to: Abdulkarim *et al.*,[66] Chancel *et al.*,[33] Ehrsson *et al.*,[5,30] Gentile *et al.*,[31] Guterstam *et al.*,[68] Limanowski *et al.*,[37,43,65] Matsumoto *et al.*,[67] Petkova *et al.*[32] and Preston *et al.*[45]. Locations are approximate and some have been shifted to avoid overlap. Details of the studies in terms of MNI coordinates and contrasts reported in the literature are provided in Supplementary Table 1.

Figure 2 Subcortical brain areas associated with the sense of body ownership, along with possible functions.

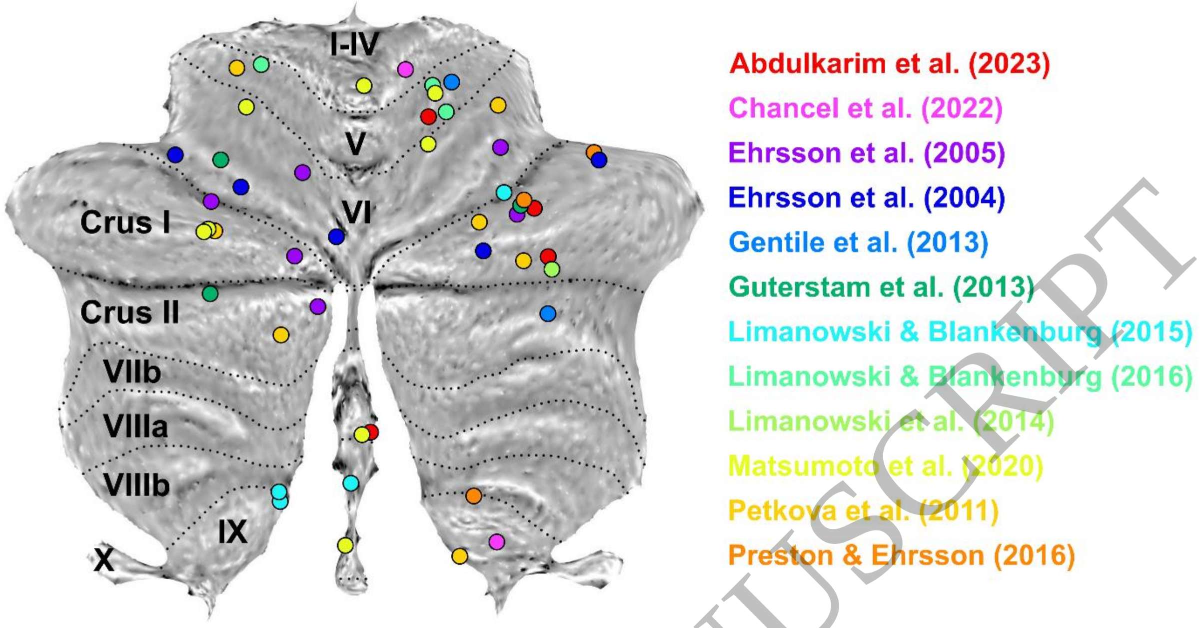

Figure 1
159x85 mm (x DPI)

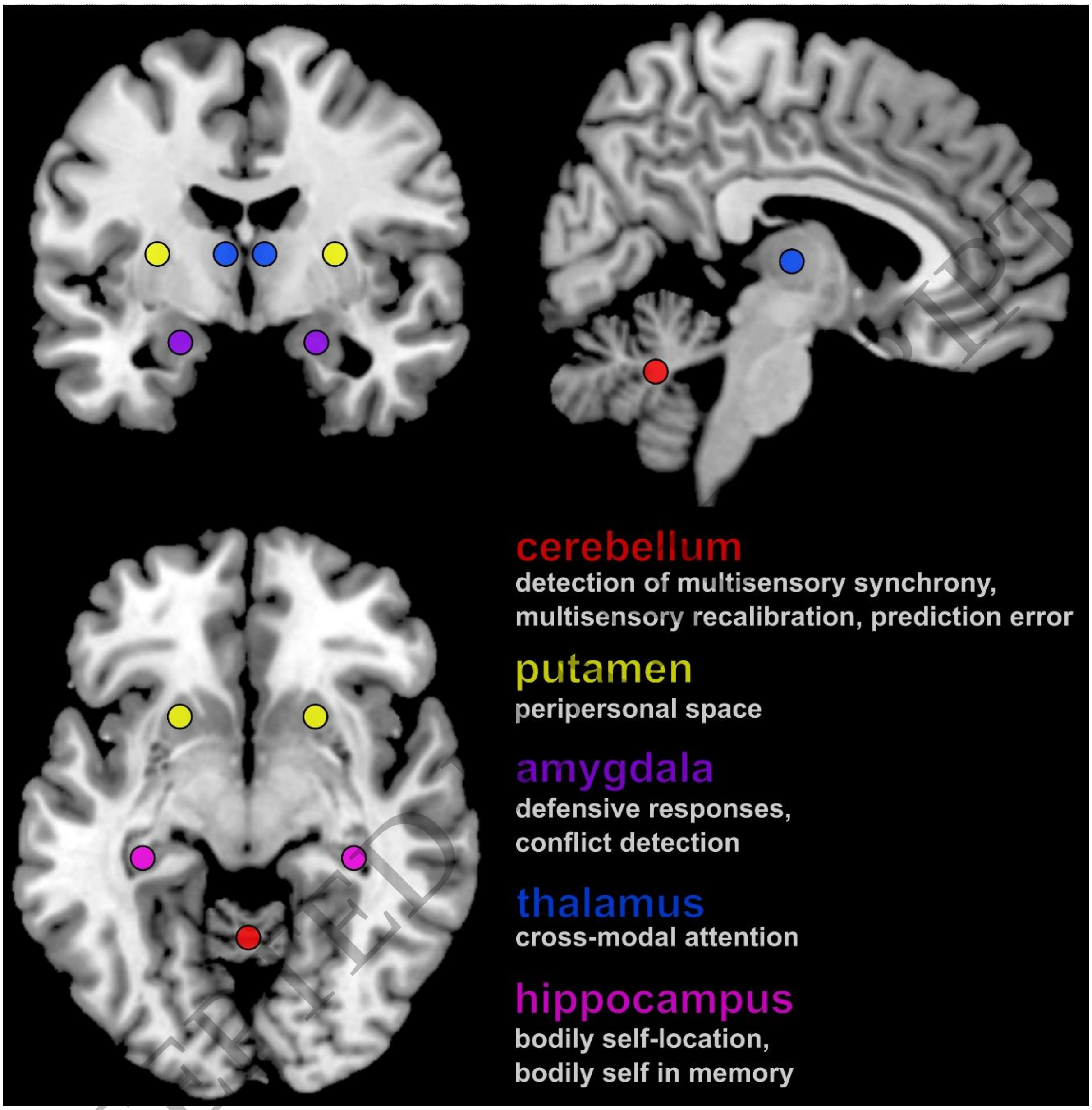

Figure 2
159x162 mm (x DPI)

Table 1 Summary of putamen activation reported in neuroimaging studies of body ownership.

Article	Paradigm	Reported effect	Peak coordinate (MNI)		
			x	*y*	*z*
Brozzoli *et al.*[120]	Rubber hand illusion	Remapping of hand-centred space onto owned rubber hand	−20	6	0
			20	12	−8
Chancel *et al.*[33]	Rubber hand illusion	Illusion detection (yes) vs no detection (no) response	−28	−14	−2
			−24	−8	10
Gentile *et al.*[31]	Real hand disownership	Integration of visual and tactile signals from the hand under conditions of full temporal and spatial congruence	−28	6	4
Gentile *et al.*[121]	Full body illusion	Multivoxel pattern analysis decoding accuracy (synchronous vs. asynchronous condition)	−28	−16	−6
Limanowski *et al.*[43]	Real hand, rubber hand illusion	Increased activity during synchronous fake arm stimulation compared with asynchronous fake stimulation and compared with real arm stimulation	24	4	−10
Petkova *et al.*[32]	Full body illusion	Effect of visuotactile synchrony applied to a fake body vs. block of wood	−22	−8	8
		Effect of visuotactile synchrony in first-person perspective vs. third-person perspective	−26	−8	6
			24	−8	8
		Effect of visuotactile synchrony for visually attached limb vs. visually detached limb	−26	4	−8
		Activity related to subjective illusion strength	30	10	4
Preston *et al.*[45]	Full body illusion	Regression analysis (illusion score with main effect of synchrony)	30	−18	4

All relevant coordinates reported in each article are provided. See individual articles for details of correction methods.