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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Keywords: body ownership; multisensory integration; cerebellum; putamen; amygdala; thalamus; hippocampus

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.

Acknowledgements

Preparation of this article was supported by a Marie Skłodowska-Curie Intra-European Individual Fellowship to LC (Grant agreement no 891175); the Swedish Research Council (#2017-03135), European Research Council under the European Union's Horizon 2020 research and innovation program (SELF-UNITY #787386), and Göran Gustafssons Stiftelse to HHE.

Competing interests

None declared.

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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.

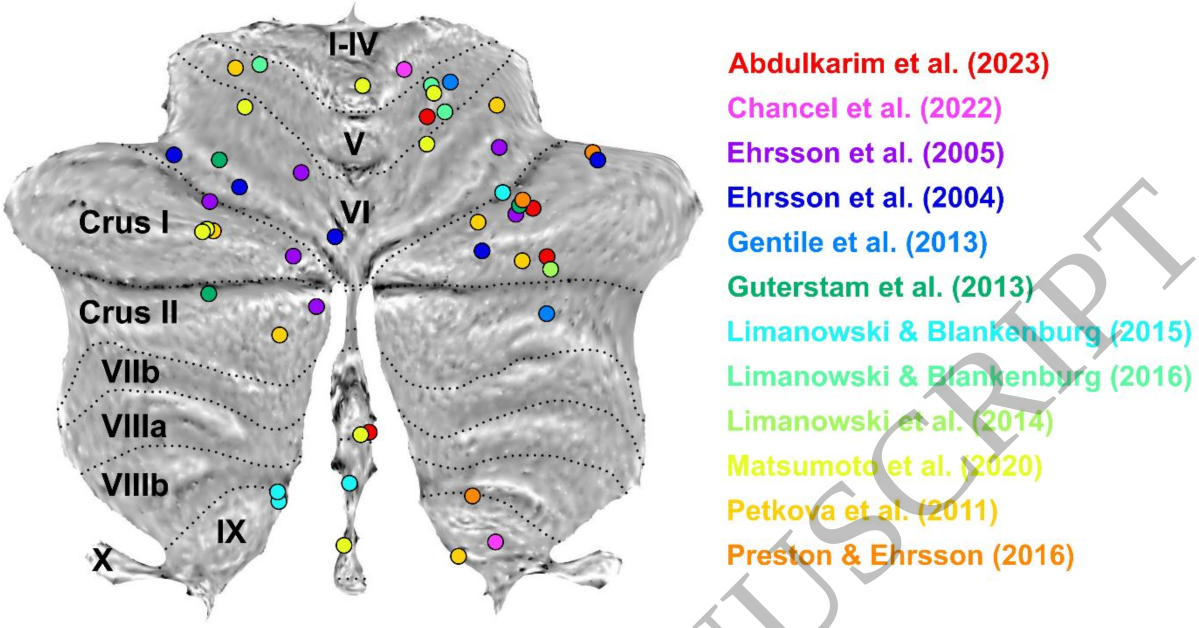

Figure 1
159x85 mm (x DPI)

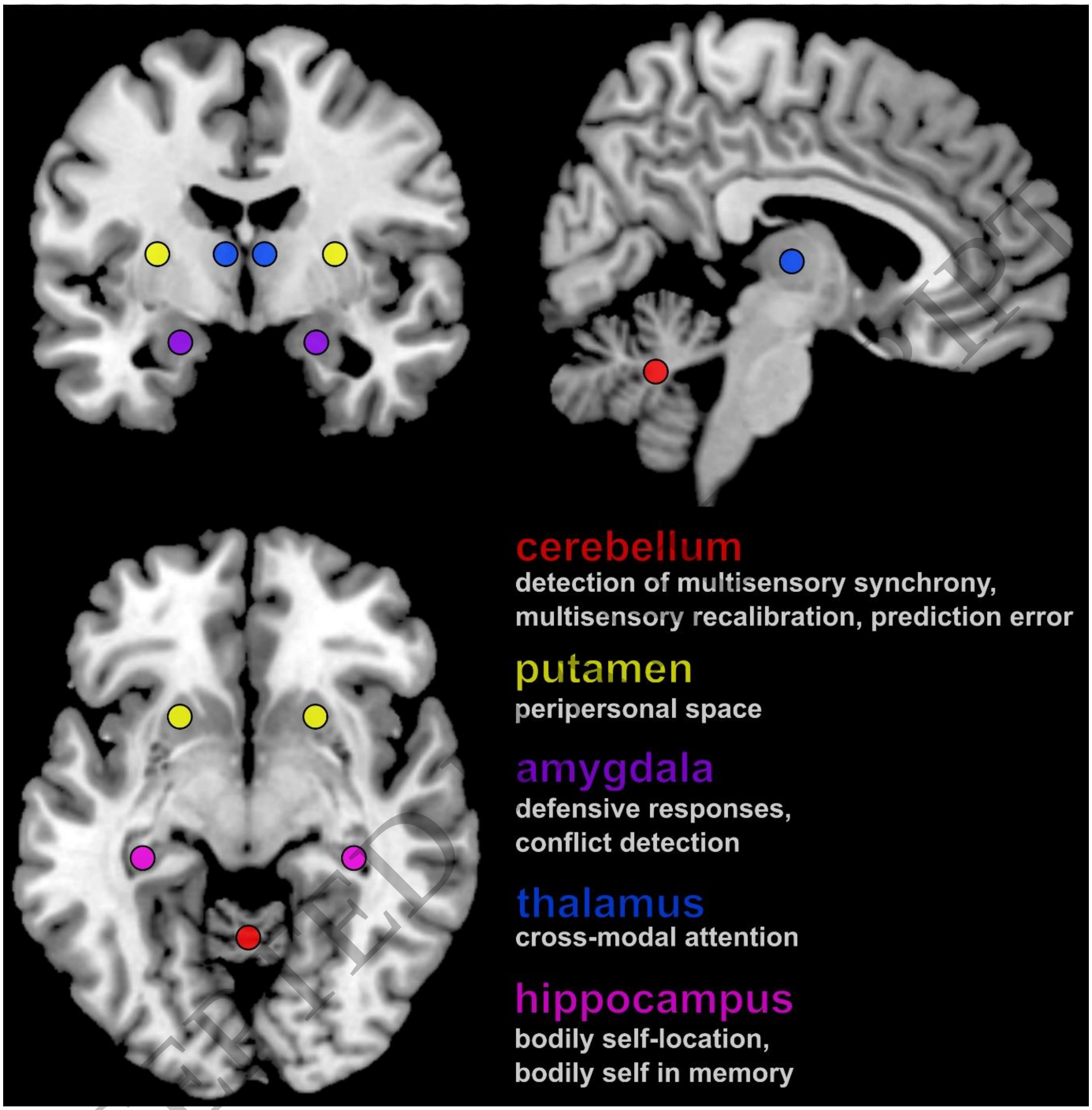

Figure 2
159x162 mm (x DPI)

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.