FISEVIER

Contents lists available at ScienceDirect

### Consciousness and Cognition

journal homepage: www.elsevier.com/locate/concog



## Beyond differences between the body schema and the body image: insights from body hallucinations



Victor Pitron<sup>a,b,\*</sup>, Frédérique de Vignemont<sup>a</sup>

- a Institut Jean Nicod, UMR 8129, ENS/EHESS/CNRS, IEC, PSL Research University, 29 rue d'Ulm, 75005 Paris, France
- b AP-HP, Hôpitaux Universitaires Paris Ouest, Service de Psychiatrie de l'adulte et du sujet âgé, 20 rue Leblanc, 75015 Paris, France

#### ARTICLE INFO

# Keywords: Alice in Wonderland syndrome Body schema Body image Bayesian model Hallucination Schizophrenia

#### ABSTRACT

The distinction between the body schema and the body image has become the stock in trade of much recent work in cognitive neuroscience and philosophy. Yet little is known about the interactions between these two types of body representations. We need to account not only for their dissociations in rare cases, but also for their convergence most of the time. Indeed in our everyday life the body we perceive does not conflict with the body we act with. Are the body image and the body schema then somehow reshaping each other or are they relatively independent and do they only happen to be congruent? On the basis of the study of bodily hallucinations, we consider which model can best account for the body schema/body image interactions.

#### 1. A dialogue between the body schema and the body image?

The distinction between the body schema and the body image has become the stock in trade of much recent work in neuropsychology, cognitive neuroscience and philosophy (e.g., de Vignemont, 2010; Dijkerman & de Haan, 2007; Di Vita, Boccia, Palermo, & Guariglia, 2016; Gallagher, 1986; Paillard, 1999). In brief, the body schema is involved in action, whereas the body image corresponds to how we perceive our body. This distinction is in line with the general functional hypothesis according to which perception and action require different transformations of the sensory signals, obey different rules, and are thus subserved by different cortical and subcortical pathways. This has been shown for visual and auditory signals (Milner & Goodale, 1995; Milner & Goodale, 2008; Romanski et al., 1999; Zatorre et al., 2002; Hall, 2003; Warren, Wise, & Warren, 2005; Dyson, Dunn, & Alain, 2010), but also for somatosensory ones (Dijkerman & de Haan, 2007). The so-called Perception-Action model, however, is controversial (Rossetti, 2003). In particular, the nature and the extent of the interactions between the two types of sensory processing are often left underspecified. Little has been said about the links between the body schema and the body image. To what extent do they communicate with each other? Are the body image and the body schema somehow reshaping each other or on the contrary, are they relatively independent? In most situations in our day-to-day life, the body we perceive does not conflict with the body we act with. In this case, are body representations converging precisely because they are co-constructed or are they built separately and do they only happen to be congruent? And if they are congruent, how can we know that actions are guided by the body schema only, and that the body image does not contribute to their guidance?

One of the difficulties that one has to face is that there is still little agreement on the definition of the notions themselves (de Vignemont, 2010). How should one draw the boundary between the body schema and the body image? In purely functional terms (action versus perception) (Paillard, 1999; Djikerman & de Haan, 2007)? Or could it depend also on their availability to the subject (unconscious versus conscious) (Head & Holmes, 1911)? A further dimension that might be relevant is their malleability: one can

<sup>\*</sup> Corresponding author at: Institut Jean Nicod, UMR 8129, ENS/EHESS/CNRS, IEC, PSL, 29 rue d'Ulm, 75005 Paris, France. E-mail address: victor.pitron@ens.fr (V. Pitron).

distinguish between short-term and long-term body representations (O'Shaughnessy, 1980).

A second difficulty is that there are very rare 'pure' cases in which only one type of representation is disturbed. Why are the body schema and the body image usually impaired together? Does the deficit of one affect the other? Or do their respective impairments have a common cause? Interestingly, when dissociations are found, they mainly concern short-term bodily information, either tactile or proprioceptive one. For instance, the patient KE failed to accurately localize tactile stimulations when asked to point to his own hand, but not to a pictorial representation of his hand, whereas the patient JO displayed the reverse pattern and failed to accurately localize tactile stimulations when asked to point to a pictorial representation of her hand, but not to her own hand (Anema et al., 2009; see also Paillard, 1999). In healthy participants similar dissociation has been found with the sensation of bodily position using the Rubber Hand Illusion (RHI). Participants saw a rubber hand in front of them while their own hand is hidden from sight. Both hands – the rubber one and the real one – are stroked on the same finger. After synchronous stroking only, participants mislocalize their hand in the direction of the location of the rubber hand (Botvinick & Cohen, 1998). Interestingly they still correctly localize their hand in motor responses, as shown by normal kinematics in reaching their hand and in using it (Kammers, Vignemont, Verhagen, & Dijkerman, 2009).

Dissociations of these types have been used to show that there must be at least two distinct types of body representations, which seems relatively accepted nowadays. However, what may be true at the short-term level may not be true at the long-term level of the enduring properties of the body (i.e. bodily configuration and metrics). Instead, it has been suggested that there is a unique type of long-term representation used for both action and bodily experiences (O'Shaughnessy, 1980; Brewer, 1995; Bermúdez, 2005; Alsmith, 2009). This hypothesis has the advantage to be relatively parsimonious:

"This first category of body-relative information performs two tasks. First, it is responsible for the felt location of sensations. Sensations are referred to specific body-parts in virtue of a body of information about the structure of the body. Second, *the same body of information* informs the motor system about the body-parts that are available to be employed in action." (Bermúdez, 2005, p. 305, our underline).

Here we shall focus exclusively on long-term body representations. We will ask the following two questions: (i) is there a unique multifunctional representation of bodily metrics and configuration or does the distinction body schema/body image also apply for enduring bodily properties? (ii) if there are two functionally defined long-term body representations, how do they interact? We shall discuss three theoretical options (see Fig. 1):

- a. The Fusion model: There is a unique representation of the enduring properties of the body that both spatially frames bodily experiences and guide bodily movements (O'Shaughnessy, 1980; Brewer, 1995; de Bermúdez, 2005; Alsmith, 2009);
- b. The Independence model: There are two distinct functionally defined representations of the enduring properties of the body, a long-term body schema for action and a long-term body image for perception, and they work independently of each other;
- c. The Co-construction model: There are two distinct functionally defined representations of the enduring properties of the body, a long-term body schema for action and a long-term body image for perception, and they can interact and reshape each other.

We shall consider each model in light of the existing literature but as mentioned earlier almost no studies have directly addressed the question of the body schema/body image in the specific context of long-term body representations (Carruthers, 2008). Here we

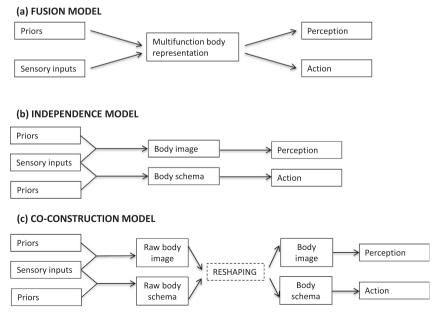


Fig. 1. Models of interactions between body representations.

want to open a new path to investigate this question by analysing a series of disorders that are rarely, if ever, considered in this context, that is, cases of clinical bodily hallucinations, and in particular in the Alice in Wonderland syndrome. We will rely exclusively on introspective reports. We believe that they afford unique direct insights into what it is like to experience bodily hallucinations and that they can shed new light on the three models. Although one may question their reliability, it is worth noting that subjective reports have presented us a consistent pattern of symptoms over the 70 years in which the Alice in Wonderland syndrome has been studied. Hopefully this work will be the first step for further investigations in patients with bodily hallucinations, including kinematics studies.

#### 2. Building up hallucinations

Why study hallucinations? The phenomenology of hallucination resembles the phenomenology of perception so that one may be unaware that one is hallucinating. This is particularly true in schizophrenia. Even when schizophrenic patients have experienced hallucinations for years they rarely agree that the voices that they hear come out of their head. Even when told so, patients do not believe that their perceptions are false (Ey, 1973). The feeling of reality associated with hallucinations can be explained by the cortical overlap with the sensory areas involved in perception. For instance, auditory verbal hallucinations are concomitant with cortical activations involved in speech perception (Jardri, Pouchet, Pins, & Thomas, 2011). Moreover, there is some evidence showing that inhibition of symptom-oriented sensory areas with repetitive trans-cranial magnetic stimulation (rTMS) diminishes hallucinations. In a case report of coenesthesic hallucinations, fMRI-guided rTMS treatment on the somatosensory cortex seemed to reduce the symptoms (Jardri, Pins, & Thomas, 2008, but see Koops, Schutte, & Neggers, 2016).

It has recently been suggested that one can account for hallucinations in Bayesian terms (Adams, Stephan, Brown, Frith, & Friston, 2013). More specifically, in schizophrenia there is an increase of reverse inferences between top down and bottom up signals (Jardri & Denève, 2013). One single signal gets over-confidence weighted, accounting for the hallucination all by itself. This explains how hallucinations can pop up despite the fact that presumably sensory inputs are absent. For instance, auditory hallucinations have been reported in deaf schizophrenic patients: although they receive no auditory inputs from the outside, it seems to these patients that they hear sounds and even voices that are speaking (Pedersen & Ernst Nielsen, 2013). Confidence weighting is so high that schizophrenic patients might take the hallucination for granted and imagine a delusory reality fitting with it. One deaf patient had such blind faith in her auditory hallucinations that instead of realizing that she could not be hearing real voices, she thought she was not deaf anymore (Schonauer, 1998).

As in auditory hallucinations, bodily hallucinations can emerge though there are no sensory inputs. After amputation for instance, people may perceive a phantom limb, a reminiscence of their ancient limb that they feel and even claim to be able to control. Likewise, in some rare cases, people who were born without arms or legs can nevertheless feel their presence and they feel that they can control them (Brugger et al., 2000). Among all hallucinations, the case of bodily ones is especially interesting because they involve multiple sensory modalities. For instance, one patient transiently experienced the presence of a supernumerary phantom hand in addition to her two biological hands after a subcortical capsulolenticular haemorrhage (Khateb et al., 2009). She reported controlling her supernumerary hand reaching her shoulder, experiencing sensations both in her supernumerary hand and in her shoulder. When she scratched herself with her supernumerary hand, she felt relief from the itching sensation. In addition, she reported seeing her supernumerary hand, which looked "pale," "milk-white," and "transparent." Her brain activity in somatosensory, motor and visual areas during movements of the supernumerary hand confirmed her introspective reports. The hypothesis is that bodily hallucinations involve multisensory body representations, which are based on the integration of all available body-related sensory signals, including proprioceptive, tactile, visual and vestibular information (de Vignemont, 2014; Kaliuzhna, Ferrè, Herbelin, Blanke, & Haggard, 2016).

#### 3. Alice in Wonderland syndrome: Alice did not fall

The Alice in Wonderland syndrome has known an increase of interest these last few years (Blom, 2016; Lanska & Lanska, 2013; Mastria, Mancini, Viganò, & Di Piero, 2016; O'Toole and Modestino, 2017; Perdices, 2016). Its name finds its origin in Lewis Carroll's novel, in which Alice perceives her body growing bigger or shrinking after she ate and drank magic food: "now I'm opening out like the largest telescope that ever was! Good-bye, feet!" (for when she looked down at her feet, they seemed to be almost out of sight, they were getting so far off)" (Carroll, 1865, Chapter 2, p. 12). Similarly, during Alice in Wonderland hallucinations, the perception of the size of one body part is altered: patients experience their limbs as smaller or larger than they really are. Like other hallucinations, the Alice in Wonderland syndrome occurs in a large range of neurological and psychiatric diseases such as epilepsy, migraine with aura, and schizophrenia. They pop up spontaneously and erratically. The Alice in Wonderland syndrome has been described as a disruption of the body image (Lippman, 1952; Todd, 1955). The crucial question is: is the body schema also disturbed (see Table 1)? In other words, was Alice clumsy when she suddenly became very tall? To our knowledge no motor deficits have ever been reported in the clinical descriptions of the Alice in Wonderland syndrome. Unfortunately motor performance has never been explicitly investigated. Here we decided to include five case studies, which well illustrate how the patients experience the size of their body as well as their movements (see Table 1). We shall see that although for most of them the distortion of their body image has no impact on the way they act, it can affect their kinaesthetic experiences and their sensorimotor expectations.

The Alice in Wonderland syndrome is classically described as a purely perceptual disorder. It can actually be conceived of as a prototypical example of dissociation between perception and action. Consider the case report n°1: the person experienced being very short while she was walking. Her case is interesting for two reasons. On the one hand, it shows that her hallucination had no effect on

**Table 1**Actions during Alice in Wonderland hallucinations.

Case report n°1: "Often preceding and during the migraine attack I have a very peculiar feeling of being very close to the ground as I walk along. It is as though I were short and wide, as the reflection in one of those broadening mirrors one sees in carnivals, etc. Of course I know it isn't true." (Lippman, 1952, p. 349)

Case report n°2: "A patient, for instance, reported: "A feeling that I was very tall. When walking down the street I would think I would be able to look down on the tops of others' heads, and it was very frightening and annoying not to see as I was feeling. The sensation was so real that when I would see myself in a window or full-length mirror, it was quite a shock to realize that I was still my normal height of under five feet." "(Lippman, 1952, p. 349)

Case report n°3: " "... sometimes I feel myself to be six inches tall and sometimes twelve feet." She was occasionally conscious of an illusory feeling that her feet were a yard long, or that she was going up or down hill, when actually walking over flat ground." (Todd, 1955)

Case report n°4: "While seated, the patient felt her four limbs growing longer in a bilateral and symmetrical way and her trunk enlarging to make her more straight and like "draped with a long train". While standing, she perceived the floor as distant and soft and felt she had a very light walk, full of ease, or "like on stilts". She was happy to feel like dominating the others, not only with her height but also with her intense well-being. This sensation lasted for approximately 30 min." (Bayen, Cleret de Langavant, and Fénelon, 2012, our translation)

Case report n°5: "In 1940, during the period of headaches, he felt his fingers lengthening, and even looking at them he found them very long; when he wanted to touch his head with his fingers he couldn't calculate his movement and his fingers always went higher than his head [...]. He wouldn't dare to tell anyone for fear of passing as a madman." (Hécaen and Ajuriaguerra, 1952, p. 262, our translation)

her movements because she walked normally. On the other hand, it shows that her movements had no effect on her hallucination: her normal steps did not cancel the illusion of being short. One can draw a parallel here with patients suffering from numbsense who are completely anaesthetized on their right side. It has been shown that although they are not able to detect, localize and describe tactile stimuli on their right arm, even in a forced choice condition, they are able to guide their opposite hand toward the approximate site at which they are touched when so instructed, and to their own surprise (Paillard, 1999). Interestingly, they are not better in judging the location of their sensation when they are performing the motor task at the same time (Rossetti, Rode, & Boisson, 1995). The case of numbsense has been taken as evidence for a dissociation between the body schema and the body image, but we can now generalize that for the representation of enduring properties of the body. Case report n°1 indeed clearly argues in favour of a dissociation between two distinct long-term body representations, one that is affected leading to the hallucination and the other that is preserved guiding her movements. It also seems to indicate that these two body representations can work independently of each other and do not communicate.

Case report n°2 also illustrates the same disconnection between an affected body image and an intact body schema, although this time the patient felt she was very tall. Again, she had her hallucination while walking and again it did not prevent the hallucination to happen. What is interesting in her case, however, is that her hallucination was associated with a strong feeling of confidence. It has been repeatedly shown that action can be immune to illusions (Milner & Goodale, 1995, 2008). However, in illusions perceptual distortions can be faint, only on the "as-if" mode. One might then easily conceive that participants would not trust the illusion, and thus would not guide their actions accordingly. Part of the interest of hallucination is the high feeling of confidence that these patients usually have in their experience. They are more prone to believe their experience to be true than healthy subjects in illusory experimental paradigms. They do not merely feel as if their lower limbs were enlarged but believe them to be longer. Yet despite their feeling of confidence they move correctly. Still their hallucination is not completely isolated with no impact on the rest of their mental life. In case report n°2 the patient indeed generated visuomotor expectations: if she looked at people, she expected to see the top of their heads as if she was far taller than them. This is a first indication that bodily hallucinations can have an impact beyond the patient's own body image.

Further confirmation for the larger scope of the syndrome can be found in the case report n°3. As in the previous two cases, the patient perceived her feet three times longer than their real size but she did not make extra large steps. Hence, the body schema seemed to be intact. Nonetheless, she also experienced vestibular and kinaesthetic hallucinations: she felt that she was walking up and down a hill. Again she did not stumble. Likewise, patient n°4 described how she felt her legs as growing in size and although she was walking normally, she experienced her walk as if she were "standing on stilts". These two cases show that bodily hallucinations can have a motor component: the hallucination encompasses movement perception. This is consistent with patients with phantom limbs who can feel them moving. For example, Ramachandran and Blakeslee (1998) describe the case of a patient who felt that he was grasping a mug and who began to scream when the examiner moved the mug away from him. One may then wonder whether in some cases the body schema cannot be affected too. Consider now the last report, case n°5. The patient perceived his fingers longer and seemed to act on the basis of this false percept. He failed to scratch his head, possibly because he raised his elbow too much and his arm landed too high above his scalp. In this case at least, it seems that the content of both body representations was distorted. Although case report n°5 might appear as an oddball and one may question its reliability, it is consistent with some findings with patients with phantom limbs. A study using EEG has shown that "phantom" actions have the same neural signature in the motor cortex as physical actions (Walsh, Long, & Haggard, 2015).

What this series of cases highlights is the complexity of the relationship between the body schema and the body image. In short, either the body schema is spared and the two representations are dissociated, or the body schema is affected and they converge. We shall now revisit the three models briefly described in Introduction in light of those results.

#### 4. A claim for independence?

When the body schema and the body image are fully convergent, it is difficult to individuate distinct types of body representations for action and perception. One may thus be tempted to posit a unique multifunctional body representation. However, although what

we call the *fusion model* (Fig. 1a) seems more parsimonious than the other models, it needs to account for dissociations as described in the previous section. We have seen indeed that it is possible to perceive the body in one way and act in another. Contrary to what Bermudez (2005) claims, it is not the same body of information about the enduring properties of the body that govern both our bodily experiences and our actions. Bodily experiences can be detached from practical knowledge of how to move. The only way out for advocates of the fusion model is to assume that there is a unique long-term body representation under normal conditions, and that it can be split into two distinct representations during illusions and hallucinations. However, claiming that the body image and the body schema exist only when their contents diverge seems to be an odd move. The fusion model no longer appears as parsimonious. On the contrary, it now needs to posit two sets of rules, one when things are normal and one when things are abnormal. Furthermore, the hypothesis that we have two types of body representations in abnormal situations only is purely post hoc. There is no explanation of the reason for which we have them only in some rare circumstances. Finally, the fusion model conflicts with previous results about the dual anatomical pathways in visual processing: the ventral pathway for perception and the dorsal pathway for action. For what reason would we have two distinct dedicated systems if most of the time only one representation is constructed? Although this is not a fully conclusive argument against the fusion model, it seems preferable to favour a common understanding for all situations.

By contrast, the *independence model* (Fig. 1b) can easily account for dissociations in borderline cases. On this new model, there are two distinct kinds of body representations that work independently once built up. We have seen that in most cases of the Alice in Wonderland syndrome the body schema and the body image indeed do not influence each other. The false body image and the preserved body schema do not reshape each other one way or the other. Neither does the false body image alter the body schema, nor does the preserved body schema restore the distorted body image. In a nutshell, the body schema appears to be informationally encapsulated, at least to some extent. It is less prone to errors than the body image. This makes sense from a pragmatic perspective. Roughly speaking, it does not matter if the perception of the body is false as long as actions remain unaffected. However, the independence model seems to suffer from the problem opposite to the one that the fusion model encounters. It can account for dissociations, but can it succeed as well to account for the convergence between the two representations? Under normal conditions, when perception is not distorted, contents of the body schema and of the body image are congruent and the action we perform does not conflict with the perception that we have of our body. How does the independence model explain this congruency? Do the body schema and the body image just happen to be similar? An advocate of the independence model may reply that this is not a mere coincidence. After all, we have only one body from which we receive information. When the body schema and the body image do their job well, they both represent this body and are thus consistent.

So far we have focused on cases in which the body schema is immune to the distortion of the body image but there are other cases in which it is not. Disruption of the body schema can indeed be found in phantom movements as well as the case of the patient n°5. Even when one considers the short-term properties of the body, both types of representations can be biased in some cases. For instance, several studies have found that motor responses can be sensitive to the RHI in specific contexts (Heed et al., 2011; Holmes, Snijders, & Spence, 2006; Kalckert & Ehrsson, 2012; Riemer, Kleinböhl, Hölzl, & Trojan, 2013; Tieri, Tidoni, Pavone, & Aglioti, 2015). Let us just focus on the following study by Kammers, Kootker, Hogendoorn, and Dijkerman (2010). Unlike the classic version of the RHI, the participant's hand and the rubber hand were shaped as if they were ready to grasp an object and both the index fingers and the thumbs of the real hand and of the rubber hand were stroked. Participants were then asked to grasp an object in front of them. It was found that after synchronous stroking, their actual grip aperture was significantly influenced by the size of the seen grip aperture of the rubber hand: there is a lack of dissociation between the body schema and the body image. Do these results entail that the distorted body image influences the body schema? Not necessarily. According to the independence model, both types of representation are fed by the same inputs and if the inputs are distorted or manipulated the same way, then they can end up being both erroneous. Their common bias does not show that one has reshaped the other. Rather it suggests that, to some extent, the construction process of the two body representations may obey the same rules.

To recapitulate, according to the independence model, the reason for which we generally perceive the same body as the one we act with is because they have a common pathway that exploits the same sensory signals. The independence model can thus account for both congruencies and incongruences between the body schema and the body image. But at what cost? One might legitimately wonder to what extent the two body representations are still independent. Not only are the inputs common, but it also seems that part of the processing involved in the construction of the two types of representations is shared too. Hence, they do not happen to converge; they converge because they have a lot in common. We now want to consider an alternative model, which we call the *co-construction model* (Fig. 1c). On this new view, the content of the body schema and the body image converge thanks to a dialogue between the two, which can happen at several stages. Here we shall sketch the main outlines of a computational model of body representations.

#### 5. Modelling interactions

Our starting point is Marr's three-step model of visual perception: the primal sketch, the 2.5D sketch and the 3D sketch (Marr, 1982). At each step, more information is extracted from the original visual input until it switches from a viewer-centred perspective to an object-centred perspective. Recent work on body representations suggests similar serial processing and that at each stage, the representation of the body gains in complexity and spatial richness (Haggard, Cheng, Beck, & Fardo, 2017; Longo, 2017). One may further account for the generation of each body sketch in Bayesian terms. A Bayesian model starts with some a priori knowledge about the body and its constraints. It is represented by a prior probability distribution for a model's structure and parameters—what the variables are and how they influence each other. It aims at computing the posterior probability, that is, the degree of belief in the prior hypothesis conditioned on the observation of sensory evidence. A body sketch is thus normally the result of the interplay

between the inputs, prior knowledge that models the body, and expectation for uncertainty due to internal and external noise. Presumably, as for Marr's model of vision, there are several sketches in the construction process of body representations. The system works in loops where posteriors from preceding computations become priors for next ones. To construct body representations, information comes from various sensory modalities. The visual system generates a visual representation of the body, compelling sensory inputs and related priors. So does each of the other sensory systems. These representations become inputs for a new Bayesian computation whose posterior is a multisensory body sketch. Bayesian rules may favour one input on the other depending on the context. For instance, at sunset if outside light is dark and the visual sensory signal is noisy, then vision may be downgraded in favour of proprioception.

Importantly, the construction of body representations never stops and it is continuously fed by new inputs. Not only do Bayesian equations shape at each moment how all the available body-related information is compiled, but they also rule how body representations are integrated overtime. The system is able to learn from its errors. If the posterior is somewhat different from predictions, then for next computations priors are reshaped. Priors are always updated accordingly to new body information, they rearrange and adapt in order to get as accurate as possible at predicting future bodily states. This is therefore one major property of the Bayesian system: it tends to improve predictions. This model is compatible with some recent accounts of bodily awareness in terms of predictive coding (Apps & Tsakiris, 2014; Tsakiris, 2017). On this view, the brain always aims at decreasing prediction errors. In the case of body representations, one way to refine predictions is to integrate information from various sensory modalities. Arguably, the combination of proprioception and vision increases reliability and is more accurate than proprioception only. However, in case of multisensory discrepancies, false body representations might pop up, leading to the RHI for instance: the visual system is tricked, and it biases the construction of body representations even if proprioception is not modified.

This computational model gives the general framework for the construction of body representations. However, it stays silent about the functional perception/action distinction. Here we propose that two distinct kinds of intermediate body sketches are generated, which can be conceived of as raw body schema and raw body image. Each is built up on its own complex set of rules accordingly to its function. Raw body schema might favour metrical information that is relevant for action. Priors come from past experiences of acting, each time refined by new actions. Raw body image focuses on information about the outlines of the body part. Although they are both fed by the same sensory inputs, differences between them can be explained by different priors, different weights ascribed to inputs and different decision criteria (Kammers, Mulder, de Vignemont, & Dijkerman, 2009). Hence because raw body representations are built for different purposes, their constructions obey different rules and their contents can differ. According to the Bayesian view, however, the system tends to decrease prediction errors whenever it is possible. To do so, the two body representations can take advantage of each other. The body image refines its content thanks to information hold in the body schema and vice versa. There is thus a second step at which the two raw contents are compared and averaged. This does not imply that they match perfectly but only that their respective content is tempered in light of the other in order to maximize efficiency and get to as accurate predictions as possible. Hence, each body representation keeps its own functional identity and there is no merging between them. The averaging process obeys its own Bayesian rules and given the context it can give more or less weight to the body image, which therefore has more or less impact on the body schema, or vice versa. This explains why in some situations actions are immune to bodily illusions and hallucinations while they are not in other conditions.

The co-construction model can thus explain not only cases of congruence between the body schema and the body image, but also cases of divergence. Constructions of the body image and the body schema are intertwined. Most of the time, the two body representations use each other to maximize their chance of being correct and their contents get coherent. But under some rare circumstances, namely in some cases of body illusions and hallucinations, the averaging system fails and the two body representations diverge. Why is it so? Possibly, the discrepancy is tolerated because confidence-weighting ascribed to each body representation is stronger than the proneness to average. Alternatively, there is a failure at the level of the comparison between the two raw contents: if the system fails to detect inconsistency, then there is no attempt to eliminate it. A definite answer is there to be found by mathematical computational modelling, for which further research will be needed.

#### 6. Conclusions

We reviewed several cases of bodily hallucinations and showed that, depending on the context, they do or do not disturb actions. Therefore, sometimes only the body image is affected, while other times the body image and the body schema are biased. We discussed three possible models of the relationship between these two representations: fusion, independence, and mutual co-construction. On this last model, the two representations are compared and averaged within iterative loops of Bayesians computations. The two body representations remain inherently distinct with respect to their function; the body schema and the body image hold the information for action and perception respectively. Nevertheless, body representations tend to get as precise and refined as possible. They reshape each other in order to minimize prediction error and increase their reliability. We argued this co-construction model has the most explanatory power to account for the wide variety of possible interplays between the body image and the body schema.

#### Acknowledgements

This work was supported by la Fondation pour la Recherche Médicale (DEA20140630450), the French association of patients Schizo?...Oui!, and grants ANR-10-LABX-0087 IEC and ANR-10-IDEX-0001-02 PSL. We are also deeply thankful to Géraldine Carranante, Therese Collins, Terry Eskenazi, Pierre Jacob and Renaud Jardri, for helpful comments.

Alsmith, A. J. (2009). Acting on (bodily) experience. Psyche, 15(1), 82-99.

processing for perception and action. Neuropsychologia, 47(6), 1615–1620.

#### References

```
Blom, J. D. (2016). Alice in Wonderland syndrome: A systematic review. Neurology: Clinical Practice, 6(3), 259-270.
Botvinick, M., & Cohen, J. (1998). Rubber Hands 'feel' touch that eyes see. Nature, 391(6669), 756.
Brewer, B. (1995). Bodily Awareness and the self. In: J.L. Bermudez, A. Marcel, N. Eilan (Eds.), The body and the self. Cambridge (Mass.): MIT Press. p. 302.
Brugger, P., Kollias, S. S., Müri, R. M., Crelier, G., Hepp-Reymond, M. C., & Regard, M. (2000). Beyond re-membering: Phantom sensations of congenitally absent limbs.
    Proceedings of the National academy of Sciences of the United States of America, 97(11), 6167-6172.
Carroll, L. (1865) Alice in Wonderland. Macmillan & Co.
 Carruthers, P. (2008). Types of body representation and the sense of embodiment. Consciousness and Cognition, 17(4), 1302-1316.
de Vignemont, F. (2010). Body Schema and Body image -pros and cons. Neuropsychologia 48(3), 669-680.
de Vignemont, F. (2014). A multimodal conception of bodily awareness. Mind, 123(492), 989-1020.
Dijkerman, H. C., & de Haan, E. (2007). Somatosensory processes subserving perception and action. Behavioral and Brain Sciences, 30(02), 189.
Di Vita, A., Boccia, M., Palermo, L., Guariglia, C. (2016). To move or not to move, that is the question! Body schema and non-action oriented body representations: An fMRI meta-
    analytic study. Neuroscience & Biobehavioral Reviews 68, 37-46.
Dyson, B.J., Dunn, A.K., Alain, C. (2010). Ventral and dorsal streams as modality-independent phenomena. Cognitive Neuroscience 1(1), 641.
Ey, H. (1973). Traité des hallucinations. Masson. pp. 774-777.
Gallagher, S. (1986). Body image and body schema: A conceptual clarification. Journal of Mind and Behaviour, 7(4), 541-554
Haggard, P., Cheng, P., Beck, B., & Fardo, F. (2017). Spatial perception and the sense of touch. In F. de Vignemont, & A. Alsmith (Eds.), The subject's matter: Self-consciousness and
    the body. Cambridge (Mass.): The MIT Press.
Hall, D. A. (2003). Auditory pathways: Are 'what' and 'where' appropriate? Current Biology, 13(10), R406-R408.
Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. Brain, 34(2-3), 102.
Hecaen, H., Ajuriaguerra, J. (1952). Méconnaissances et hallucinations corporelles: Intégration et désintégration de la somatognosie. p. 262. Masson.
Heed, T., Gründler, M., Rinkleib, J., Rudzik, F.H., Collins, T., Cooke, E., O'Regan, J.K. (2011). Visual information and rubber hand embodiment differentially affect reach-to-grasp
    actions. Acta Psychologica 138(1): 263: 26.
Holmes, N.P., Snijders, H.J., Spence, C. (2006). Reaching with alien limbs: visual exposure to prosthetic hands in a mirror biases proprioception without accompanying illusions
    of ownership. Perception & Psychophysics 68(4), 685-701.
Jardri, R., Denève, S. (2013). Circular inferences in schizophrenia. Brain 136(Pt 11), 3227-3241.
Jardri, R., Pins, D., Thomas, P. (2008). A case of fMRI-guided rTMS treatment of coenesthetic hallucinations. American Journal of Psychiatry 165(11).
Jardri, R., Pouchet, A., Pins, D., & Thomas, P. (2011). Cortical activations during auditory verbal hallucinations in schizophrenia: A coordinate-based meta-analysis. American
    Journal of Psychiatry, 168(1), 73.
Kalckert, A., Ehrsson, H.H. (2012). Moving a rubber hand that feels like your own: A dissociation of ownership and agency. Frontiers in Human Neuroscience 6, 40.
Kaliuzhna, M., Ferrè, E.R., Herbelin, B., Blanke, O., Haggard, P. (2016). Multisensory effects on somatosensation: A trimodal visuo-vestibular-tactile interaction. Scientific Reports
Kammers, M., Mulder, J., de Vignemont, F., & Dijkerman, H. C. (2009). The weight of representing the body: A dynamic approach to investigating multiple body representations
    in healthy individuals. Experimental Brain Research, 204(3), 333-342.
```

Adams, R. A., Stephan, K. E., Brown, H. R., Frith, C. D., & Friston, K. J. (2013). The computational anatomy of psychosis. Frontiers in Psychiatry, 4, 47.

Apps, M. A., & Tsakiris, M. (2014). The free-energy self: A predictive coding account of self-recognition. Neuroscience and Biobehavioral Reviews, 41, 85–97. Bayen, E., Cleret de Langavant, L., & Fenelon, G. (2012). The Alice in Wonderland syndrome: an unusual aura in migraine. Revue Neurologique, 168(5), 457-459. Bermudez, J. L. (2005). The phenomenology of bodily awareness. In: D. Woodruff Smith, A. Thomasson (Eds.), Phenomenology and philosophy of mind. Oxford: Clarendon Press, pp.

Anema, H. A., van Zandvoort, M. J., de Haan, E. H., Kappelle, L. J., de Kort, P. L., Jansen, B. P., & Dijkerman, H. C. (2009). A double dissociation between somatosensory

findings from a double-blind-randomized trial. Schizophrenia Bulletin 42(1),250-257. Lanska, J.R., Lanska, D.J. (2013). Alice in Wonderland Syndrome: somesthetic vs visual perceptual disturbance. Neurology 80(13), 1262-1264.

Kammers, M. P. M., Vignemont, F., Verhagen, L., & Dijkerman, H. C. (2009). The rubber hand illusion in action. Neuropsychologia, 47(1) 204n Act.

Lippman, C. W. (1952). Certain hallucinations peculiar to migraine. Journal of Nervous and Mental Disease, 116, 110-116.

Longo, M. (2017). Body representations and sense of self. In F. de Vignemont, & A. Alsmith (Eds.), The subject's matter: Self-consciousness and the body. Cambridge (Mass.): The MIT

Kammers, M. P. M., Kootker, J. A., Hogendoorn, H., & Dijkerman, H. C. (2010). How many motoric body representations can we grasp? Experimental Brain Research, 202(1), 203.

Koops S., van Dellen E., Schutte M.J., Nieuwdorp W., Neggers S.F., Sommer I.E. (2016). Theta burst transcranial magnetic stimulation for auditory verbal hallucinations: negative

Khateb, A., Simon, S.R., Dieguez, S., Lazeyras, F., Momjian-Mayor, I., Blanke, O., Landis, T., Pegna, A.J., Annoni, J.M. (2009). Seeing the phantom: A functional magnetic

Marr, D. (1982). Vision: A computational investigation into the human representation and processing of Visual Information, New York, W.H. Freeman and Company. pp. 302-309. Mastria, G., Mancini, V., Viganò, A., & Di Piero, V. (2016). Alice in wonderland syndrome: A clinical and pathophysiological review. BioMed Research International, 2016,

Milner, A.D., Goodale, M.A. (1995). The visual brain in action. Oxford University Press. 2d ed. (2006), pp. 157-181.

Milner, A.D., Goodale, M.A. (2008). Two visual systems re-viewed. Neuropsychologia 46(3), 774: 77.

O'Shaughnessy, B. (1980). The will: A dual aspect theory. Cambridge University Press. pp. 273-282.

resonance imaging study of a supernumerary phantom limb. Annals of Neurology 65(6), 698nal M.

O'Toole, P., Modestino, E.J. (2017). Alice in Wonderland Syndrome: A real life version of Lewis Carroll's novel. Brain Dev. Feb 8.

Paillard, J. (1999). Body Schema and Body Image-a Double Dissociation in deafferented patients. In G. Gantchev, S. Mori, & J. Massion (Eds.), Motor control today and tomorrow. Sofia, Bulgaria: Academic Publishing House,

Pedersen, N., Ernst Nielsen, R. (2013). Auditory hallucinations in a deaf patient: A case report. Case Reports in Psychiatry. Volume 2013, Article ID 659698.

Perdices, M. (2016). The Alice in Worderland Syndrome. Neuropsychological Rehabilitation, 1-10.

Ramachandran, V. S., & Blakeslee, S. (1998). Phantoms in the brain: Probing the mysteries of the human mind. HarperCollins: William Morrow and Company.

Riemer, M., Kleinböhl, D., Hölzl, R., & Trojan, J. (2013). Action and perception in the rubber hand illusion. Experimental Brain Research, 229(3).

Romanski, L. M., Tian, B., Fritz, J., Mishkin, M., Goldman-Rakic, P. S., Rauschecker, J. P. (1999). Dual streams of auditory afferents target multiple domains in theprimate prefrontal cortex. Nature Neuroscience 2(12), 1131-1136.

Rossetti, Y. (2003). Abstraction from a sensori-motor perspective: can we get a quick hold on simple perception? Philosophical Transactions of the Royal Society of London B: Biological Sciences 358(1435), 1269-75.

Rossetti, Y., Rode, G., & Boisson, D. (1995). Implicit processing of somaesthetic information: A dissociation between where and how? NeuroReport, 6, 506-510.

Schonauer, K., Achtergarde, D., Gotthardt, U., & Folkerts, H. W. (1998). Hallucinatory modalities in prelingually deaf schizophrenic patients: A retrospective analysis of 67 cases. Acta Psychiatrica Scandinavica, 98(5), 377.

Tieri, G., Tidoni, E., Pavone, E. F., & Aglioti, S. M. (2015). Mere observation of body discontinuity affects perceived ownership and vicarious agency over a virtual hand. Experimental Brain Research, 233(4), 1247-1259.

Todd, J. (1955). The syndrome of Alice in Wonderland. Canadian Medical Association Journal, 73(9), 701.

Tsakiris, M. (2017). The material me: Unifying the exteroceptive and interoceptive sides of the bodily self. In de Vignemont, & A. Alsmith (Eds.), The subject's matter: Selfconsciousness and the body. Cambridge (Mass.): The MIT Press.
Walsh, E., Long, C., & Haggard, P. (2015). Voluntary control of a phantom limb. Neuropsychologia, 75, 341–348.

Warren, J. E., Wise, R. J., & Warren, J. D. (2005). Sounds Do-Able: Auditory-motor transformations and the posterior temporal plane. Trends in Neurosciences, 28(12), 636-643. Zattore, R. J., Bouffard, M., Ahab, P., & Belin, P. (2002). Where is "where" in the human auditory cortex? Nature Neuroscience.