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On agency and body-ownership: Phenomenological and neurocognitive reflections

Manos Tsakiris [a,*], Simone Schütz-Bosbach [b], Shaun Gallagher [c]

[a] *Institute of Cognitive Neuroscience and Department of Psychology, University College London,*
Alexandra House, 17 Queen Square, London WC1N 3AR, UK
[b] *Department of Psychology, Cognition and Action, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany*
[c] *Department of Philosophy, University of Central Florida, USA*

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Abstract

The recent distinction between sense of agency and sense of body-ownership has attracted considerable empirical and theoretical interest. The respective contributions of central motor signals and peripheral afferent signals to these two varieties of body experience remain unknown. In the present review, we consider the methodological problems encountered in the empirical study of agency and body-ownership, and we then present a series of experiments that study the interplay between motor and sensory information. In particular, we focus on how multisensory signals interact with body representations to generate the sense of body-ownership, and how the sense of agency modulates the sense of body-ownership. Finally, we consider the respective roles of efferent and afferent signals for the experience of one's own body and actions, in relation to self-recognition and the recognition of other people's actions. We suggest that the coherent experience of the body depends on the integration of efferent information with afferent information in action contexts. Overall, whereas afferent signals provide the distinctive content of one's own body experience, efferent signals seem to structure the experience of one's own body in an integrative and coherent way.

Keywords: Action; Agency; Body-ownership; Phenomenology; Self-awareness; Sensory–motor

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1. Introduction

The recent distinction between sense of agency and sense of body-ownership (see Gallagher, 2000a, 2000b; Marcel, 2003) has attracted considerable empirical and theoretical interest. The sense (experience or awareness) of agency is sometimes regarded as having a "thin" phenomenology (Metzinger, 2003), that is, it does not have to be a complex or reflective cognition; it could be simply a matter of a very brief and minimal awareness of initiating and performing a voluntary movement or causing a certain effect in the world, and in most

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[*] Corresponding author.
E-mail address: e.tsakiris@ucl.ac.uk (M. Tsakiris).

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cases it is just that. One way to get at the concept of a sense of agency is to distinguish it from a sense of body-ownership or ownership for movement (Gallagher, 2000a, 2000b). In the case of involuntary movement, for example, I experience that I am moving, and therefore that it is *my* movement. I thus have a sense of ownership for the movement and the body-part that is moved passively. At the same time, I normally do not have a sense of agency for such movement (since it is not I who caused it).[1]

Distinctions between agency and the sense of ownership may be found both in first-order (immediate) experience and higher-order (reflective or introspective) consciousness. In regard to the latter, for example, Graham and Stephens (1994; Stephens and Graham, 2000) work out their account of introspective alienation in schizophrenic symptoms of delusions of control in terms of two kinds of self-attribution. (1) *Attributions of subjectivity* (or ownership), where the subject reflectively realizes and is able to report that he is moving. (2) *Attributions of agency*, where the subject reflectively realizes and is able to report that he is the cause or author of his movement. It seems reasonable to say that the higher-order attributions of ownership or agency may depend on the first-order experience of ownership or agency, respectively. For example, if I reach to pick up a glass, I have a sense of control over the movement and so have a sense of agency for this movement; if I am then asked, did I reach for the glass, I can correctly attribute agency to myself. In this paper, we are primarily concerned with this distinction at the pre-reflective level, that is, at the level of first-order phenomenal consciousness. We take reports to be reports of pre-reflective, first-order experience of my bodily states and actions. In this regard, the *sense of ownership* is the pre-reflective experience or sense that I am the subject of the movement, that I am the one moving, whether voluntarily or not (e.g., a kinaesthetic experience of movement), or that I am experiencing a certain sensation (e.g., touch). The *sense of agency* is the pre-reflective experience or sense that I am the cause or author of the movement (e.g., an experience that I am in control of my action).

There is some evidence that the sense of agency originates in neural processes responsible for the motor aspects of action (Berti et al., 2005; Haggard, 2005; Lau, Rogers, Haggard, & Passingham, 2004). Consider the (neuro)logic of involuntary movement where there is a sense of ownership but no sense of agency. My awareness of my involuntary movement comes from afferent sensory-feedback (visual and proprioceptive/kinaesthetic information that tells me that I'm moving), but there are no initial motor commands (efference) issued to generate the movement. This suggests that in ordinary voluntary movement the sense of ownership is generated by sensory feedback, while the sense of agency is generated by or at least linked to the motor commands sent to the muscles and the accompanying efference copy that is internally processed within the predictive models of the motor system (Haggard, 2005; Wolpert, 1997). There is a growing consensus on this division of labour (e.g., Blakemore, Wolpert, & Frith, 2002; Frith, Blakemore, & Wolpert, 2000; Gallagher, 2000a, 2000b; Marcel, 2003; Tsakiris & Haggard, 2005a, 2005b; Wolpert & Flanagan, 2001).

To support this kind of account, a number of neuroscientists have attempted to find the neural correlates of the sense of agency. Recent neuroimaging studies (Chaminade & Decety, 2002; Farrer et al., 2003a; Farrer & Frith, 2002; Leube, Knoblich, Erb, & Kircher, 2003) have focused on the sense of *controlling* one's own body movement. A right fronto-parietal network, including superior parietal cortex, the inferior parietal cortex and insular cortex have been consistently activated in such studies of self-attribution of action (Farrer et al., 2003a; Farrer & Frith, 2002). For example, Farrer et al. (2003a) presented subjects with visual feedback of their own actions. The feedback was distorted to varying degrees by an angular bias. The less the subjects felt in control of the viewed action, the more pronounced was the activity in the right inferior parietal lobe. Conversely, the activity in the right posterior insula was correlated with the match between the performed and viewed movement, suggesting, according to the authors, that the insular cortex is related to the sense of agency (see also Farrer & Frith, 2002).

In most of the studies on action- and self-recognition, movements are self-generated. Therefore the subject has an intention-in-action that is translated into a motor command and its accompanying efference copy,

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[1] A terminological note. We do not deny that it is possible that agency for action and the sense of agency for action can be dissociated (as in some experiments and in certain symptoms of schizophrenia [see, e.g., Frith & Done, 1988]), and it seems possible that in some cases the neural correlates of the sense of agency may fail to activate even when there is agency. In the following we will note such cases where relevant, but more generally we'll use the terms 'agency' and 'sense of agency' as synonymous and assume that agency for action and its neural correlates generate a sense of agency.

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resulting in the generation of proprioceptive, tactile and visual events. The usual manipulation in these experiments is to provide incongruent visual feedback. For example, in the study by Farrer et al. (2003a), the experimenters introduced angular deviations in the visual feedback, from 0° to 50°. In such conditions, and given the self-generated nature of movement, across all trials the motor command is congruent with the resulting proprioceptive signals. When visual feedback is congruent (i.e., 0° angular deviation), there is a sensory–motor match between efferent signals and visual feedback, but also a sensory–motor match between efferent signals and proprioceptive feedback and an inter-sensory match between proprioceptive and visual feedback. Conversely, when the visual feedback is incongruent, there is a sensory–motor conflict between efferent signals and visual feedback, but also an inter-sensory conflict between proprioceptive and visual feedback, and a sensory–motor match between efferent signals and proprioceptive feedback. Given this analysis of the experimental design, it is essential to ask whether the observed neural activities reflect sensory–motor or inter-sensory matching/conflict? If, for example, activity in the right posterior insula was coding the inter-sensory match between proprioception and vision, it would be wrong to conclude that this area underpins the sense of agency *per se*.

The foregoing studies used *action* recognition tasks to investigate the sense of controlling one's body (agency) rather than the sense of ownership for movement of one's body. Sense of agency normally implies ownership (one knows one is controlling one's own body), but ownership does not imply a sense of agency since the presence of self-generated movements is necessary for the sense of agency, but not for body-ownership, as the example of involuntary movement shows. Voluntary action always involves an inseparable combination of efferent and afferent information. This makes it difficult to isolate experimentally the specific contributions of efferent and afferent signals to representations of one's own body and one's own actions (Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005). To that extent, it is unclear whether the activated brain areas in experiments that only used voluntary movements reflect the experience of agency or the experience of body-ownership. In fact, a recent neuroimaging study (Tsakiris, Hesse, Boy, Haggard, & Fink, in press) on the neural signatures of body-ownership during the Rubber Hand Illusion (see Section 2) shows that the same area in the right posterior insula as the one reported in Farrer et al. (2003a) is positively correlated with body-ownership. In the study by Tsakiris et al. (in press), activity in the right posterior insula was correlated with ownership of a body-part in the absence of any motor command or actual movement. This finding suggests that the functional role of the right posterior insula may be related to the sense of body-ownership *per se*, and not to the sense of agency.

Similar methodological confounds relate to the respective roles of efferent and afferent information for action- and body-awareness. Even though efferent and afferent information jointly constitute the core of our bodily self-awareness (Bermúdez, Marcel, & Eilan, 1995), their respective contributions to different aspects of action- and body-awareness, as well as action recognition in self and others, are still the subject of ongoing research. In fact, a long-standing debate regarding the influence of efferent and afferent information on action-awareness started more than 100 years ago. In the "Williams debate" (see Petit, 1999), William James argued that knowledge of our movements originates from peripheral information, whereas Wilhelm Wundt emphasised the role of central motor signals. Both these sources may produce distinctive phenomenologies of bodily experience. Although the "Williams debate" originally concerned the representation of actions, it has wider implications: how do efferent and afferent signals interact, how do they underpin the experience of one's own body, and how do they contribute to the perception of other people? Questions about the sense of agency and the sense of ownership, about efference and afference, about action recognition in self, action recognition in others, and self–other discrimination, thus cut across the whole field of the cognitive neuroscience of motor cognition.

In the present review, we focus on different varieties of bodily experiences. We begin by considering how afferent signals underpin the sense of body-ownership, and we then discuss the way the sense of agency modulates body-ownership. We then focus on the interplay between afferent and efferent signals in relation to recognition of self-actions and other people's actions, and finally in relation to self–other distinction.

2. Body-ownership and agency during the Rubber Hand Illusion

As aforementioned, one fundamental difference between agency and ownership lies in the contexts within which these two varieties of body experience can occur. Under normal circumstances, agency is experienced only for voluntary actions, while body-ownership is present during voluntary actions, but also during passive or externally generated sensory experiences. This implies that the sense of ownership may give rise to different forms of body-awareness, depending on the presence or absence of the sense of agency. It seems that the sense of agency contributes something additional to ownership at the functional and the experiential level,[2] but what? To answer this question agency must be methodologically subtracted from ownership. In order to approach this issue empirically, a methodological framework is needed to compare (i) the sense of body-ownership in the absence of a sense of agency with (ii) the sense of body-ownership in the presence of a sense of agency. To that end, the methodological framework put forward here allows for the comparison between the perception of purely afferent body-related events and the perception of similar afferent events that are voluntarily generated (i.e., efferent-driven). Thus, one way to approach the differences between sense of agency and sense of body-ownership is to investigate the specific ways in which comparable afferent body-related events are differentially experienced depending on the presence or absence of efference. The experimental implementation of this manipulation facilitates the investigation of how the sense of body-ownership is generated during purely sensory events, but more importantly, how the presence of agency modulates body-ownership. This methodological manipulation has been implemented in studies related to time-awareness (Haggard, Clark, & Kalogeras, 2002; Tsakiris & Haggard, 2003), somatosensory perception (Blakemore, Frith, & Wolpert, 1999; Shergill, Bays, Frith, & Wolpert, 2003; Tsakiris & Haggard, 2003), self-recognition (MacDonald & Paus, 2003; Tsakiris et al., 2005) and body-ownership (Tsakiris, Prabhu, & Haggard, 2006). In all these studies, the experience of afferent events that were self-generated was compared to the experience of similar afferent events that were either passively or externally generated. Such manipulations allow a two-step investigation of the role played by afferent signals alone and of the afferent-efferent interaction for the experience of one's own body.

2.1. *Afference and body-ownership*

One experimental paradigm that enables us to investigate the pure sense of body-ownership in the absence of movement and efferent information is the Rubber Hand Illusion. The Rubber Hand Illusion (RHI) allows for an external object to be treated as part of the body, or not, under experimental control. Watching a rubber hand being stroked synchronously with one's own unseen hand causes the rubber hand to be attributed to one's own body, to "feel like it's my hand" (Botvinick & Cohen, 1998). How does the rubber hand come to be experienced as part of one's own body?

In a series of psychophysical studies, Tsakiris and Haggard (2005b), following Botvinick and Cohen (1998), used an induced change in the perceived location of the participant's hand as a behavioural/phenomenal correlate of the RHI. Participants judged the felt position of their own unseen hand before and after visuo-tactile stimulation of the rubber hand and their own hand. Participants perceived their hand to be closer to the rubber hand after stimulation than before, suggesting an integration of the visually perceived rubber hand and the tactile experience on the subject's own hand. Importantly, this misperception of the proprioceptively felt position of one's own hand towards the rubber hand occurred only when the stimulation between the participant's hand and the rubber hand was synchronized, and was absent or even reversed when visual and tactile stimulation was temporally asynchronous. Thus, one factor that modulates body-ownership in the RHI is multisensory correlation.

However, not all multisensory stimuli are experienced as part of one's body. Correlation of visual and tactile percepts is a necessary, but perhaps not sufficient condition for the sense of body-ownership (see Fig. 1). In one experiment, participants were stimulated on their hand, while viewing either a rubber hand in a congruent posture, in an incongruent posture or a neutral object being touched either synchronously or asynchronously with respect to the subject's own hand (see Experiment 1 in Tsakiris & Haggard, 2005b). When subjects viewed a rubber hand in a congruent posture, they perceived their hand to be significantly closer to the rubber hand after synchronous stimulation than after asynchronous stimulation. Conversely, when subjects viewed a

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[2] By functional we refer to the information processing of efferent and afferent signals within the CNS; and by experiential we refer to the way by which the body and/or movement is experienced by the subject.

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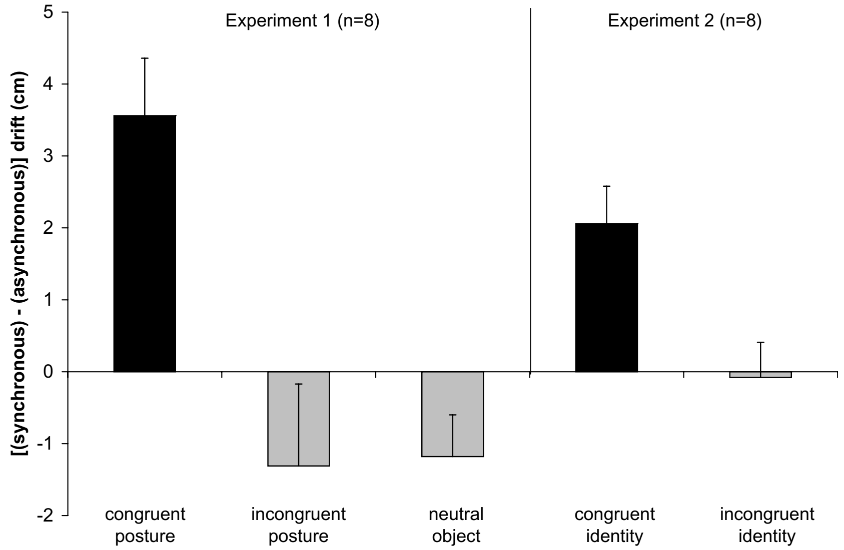

Fig. 1. Mean perceptual shifts across conditions for Experiments 1 and 2. The interest in these experiments is on the part of the proprioceptive drift due to visual–tactile integration. This integration component can be defined as the increase in proprioceptive drift when visual and tactile stimulation are correlated (i.e., synchronous conditions), over and above the drift caused by the same stimuli when they are not correlated (i.e., asynchronous conditions). Therefore, the proprioceptive drifts obtained in the asynchronous conditions were subtracted from the proprioceptive drifts obtained in the synchronous conditions. The term 'perceptual shifts' refers to this quantity. In Experiment 1, the comparison between the perceptual shifts after viewing a rubber hand at congruent posture versus viewing a rubber hand at incongruent posture showed a significant difference, $t(7) = 2.9$, $p < .05$, two-tailed. Similarly, the comparison between the perceptual shifts after viewing a rubber hand at congruent posture versus the condition of viewing a neutral object showed a significant difference, $t(7) = 4.31$, $p < .05$, two-tailed, suggesting that simple association of synchronous visuo-tactile events between the participant's hand and the neutral viewed object did not suffice to induce large proprioceptive drifts. In Experiment 2, the mean perceptual shifts for the middle finger when participants watched a left or a right rubber hand were compared. The difference was significant, $t(7) = 2.9$, $p < .03$, two-tailed, suggesting that the RHI occurred only when felt and seen hand identities match were congruent. Error bars indicate standard errors (data from Tsakiris and Haggard, 2005b).

rubber hand positioned in an incongruent posture (i.e., rotated by −90° with respect to the subjects own hand), differences in the proprioceptive judgments between synchronous and asynchronous conditions were not significant. That is, synchronous stimulation between the participant's hand and the rubber hand no longer induced the illusion. Similarly, looking at a neutral object being touched at the same time as one's own hand did not elicit the RHI (compare with Armel & Ramachandran, 2003). In another experiment, participants were stimulated on their left hand, while viewing either a left or a right rubber hand being touched either synchronously or asynchronously with respect to their own hand (see Experiment 2 in Tsakiris & Haggard, 2005b). The RHI as measured by proprioceptive drift was present only when subjects saw a left rubber hand, that is, a rubber hand of the same handedness as their own hand, being stimulated synchronously (see Fig. 1). The first conclusion to be drawn from these experiments is that multisensory correlation is not a sufficient condition for inducing the RHI. Body-ownership during the RHI seems to require the viewed object to fit in a general pre-existing representation of one's body. Thus, Tsakiris and Haggard (2005b) suggested that body-ownership is also modulated by top–down influences based on prior visual and functional (e.g., proprioceptive, postural) representations of the body (see also Blanke & Arzy, 2005).

These experiments on the RHI imply that three factors originating from body representations constrain the effects of intermodal afferent matching: body-specificity, anatomical constraints, and body-part identity. The viewed object has to be a body-part, and not a neutral object that has no functional connection with the body. The body-part has to be in a posture that is anatomically plausible and congruent with the posture of the subject's own body-part, and of the same handedness as the subject's stimulated body part. These top–down constraints on body-related afferent percepts suggest that body-ownership is not a purely bottom–up process driven only by afferent signals. Yet body-ownership cannot be a purely top–down process driven by abstract

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cognitive body-representations, because that would not explain how an incorporation process of an external object is possible at all. Instead, body-ownership seems to arise as an *interaction* between bottom–up processes originating from multisensory integration and top–down body-image influences originating from cognitive body representations.

Of course, the body is not merely a sensing entity. As agents we usually move our bodies voluntarily. In that sense, even though the RHI paradigm may help us in understanding the necessary and sufficient conditions for inducing a purely sensory form of body-ownership, it does lack ecological validity. In order to develop a naturalistic account of bodily experiences it is essential to understand how body-ownership is experienced during action, that is, to study how agency interacts with body-ownership.

2.2. How agency modulates body-ownership during the Rubber Hand Illusion

Whereas the RHI paradigm allows us to study the link between afferent signals and body-ownership, it lacks ecological validity, mainly because it does not involve bodily movement. Perhaps this absence of movement can account for a somewhat puzzling finding regarding proprioceptive awareness observed in RHI experiments. Two experiments in Tsakiris and Haggard (2005b) showed that proprioceptive awareness during the RHI is partly fragmented, in the sense that only the stimulated finger was perceived to be closer to the rubber hand than it really was. In one experiment, participants viewed a rubber hand being stroked by a paintbrush on either the index or the little finger. The participant was always stroked by a similar paintbrush on the same finger as the rubber hand was stroked, synchronously for the experimental conditions and asynchronously for the control conditions. After synchronous stimulation, the stimulated finger was perceived to be significantly closer to the rubber hand than it really was, whereas the unstimulated finger was not (see Experiment 3 in Tsakiris & Haggard, 2005b). This pattern was replicated in a second experiment, in which both index and little fingers were stimulated across all conditions, one synchronously and one asynchronously with respect to the rubber hand (see Experiment 4 in Tsakiris & Haggard, 2005b). Again, only the finger that was synchronously stimulated was perceived to be significantly closer to the rubber hand. This fragmented pattern of localized proprioceptive drifts suggests that visual–tactile associations operate to produce integration only at a very local level. The more general sense of owning my own body as a coherent unit seems to involve a second mechanism, which may or may not be an extension or generalisation of this visuo-tactile associative mechanism. At the phenomenal level, the question of whether participants experience a sense of ownership of the whole rubber hand or of the stimulated finger alone has not been formally addressed. However, introspective evidence collected from Botvinick and Cohen (1998) and during debriefing in Tsakiris and Haggard (2005b) suggests that probably at the phenomenal level, subjects experience ownership of the whole hand, rather than of the stimulated finger(s) alone. The feeling of ownership needs to be distinguished from its cause, namely the pattern of sensory stimulation. In other words, the participants who experience the RHI report that they feel as if the touch they experience on their own hand is caused by the brush touching the rubber hand, and this correlation between touch and vision of touch creates a feeling of ownership of the rubber hand. Thus, the feeling of body-ownership may go beyond the mere perception of the pattern of stimulation, in the sense that phenomenology of the experience is not a description of the stimulation or of the visual capture of touch.

What can account for the observed pattern of localized proprioceptive drifts? The literature on sensory and motor representation in the brain seems relevant here, because the representations in primary somatosensory cortex (SI) and primary motor cortex (MI) have quite different organizing principles. Although both have comparable gross somatotopy, fine somatotopy differs sharply between these two areas. Recent neuroimaging studies support this observation by showing an overlap of activations evoked by different movements. On the contrary, the receptive field of neurons in SI corresponds to a small well-defined skin area, confirming the presence of an orderly, segregated representation in human SI (Blankenburg, Ruben, Meyer, Schwiemann, & Villringer, 2003). These studies confirm the difference between motor and sensory somatotopy, in the sense that "the somatotopy in SI is more discrete and segregated, in contrast to the more integrated and overlapping somatotopy in MI" (Hlustik, Solodkin, Gullapalli, Noll, & Small, 2001, p. 319; see also Lemon, 1988; Sanes, Donoghue, Thangaraj, Edelman, & Warach, 1995). This view is also in line with the phenomenology of the body image—which is experienced in a piecemeal way, in contrast to the body schematic processes for motor

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control which operate more holistically (Gallagher, 2005). It may be possible that the localised RHI effects arise from activation of local, segregated representations in S1. That would suggest that during active movement of a single digit, quantitative measures of the RHI should be global and generalized to the other digits. Thus, it was hypothesized that active movements, compared to passive sensory stimulation, would induce a more global and coherent form of proprioceptive awareness.

This hypothesis was tested in a recent experiment (Tsakiris et al., 2006) that compared the spread of the RHI from a stimulated finger to other fingers, after inducing RHI by three different kinds of stimulation. Participants viewed a video-projected image of their hand, while they were actively or passively moving either their index or little finger. The active movement was self-generated, whereas the passive movement was externally generated by the experimenter without any voluntary control by the participants. It was assumed that participants acquire a sense of owning the projected hand in both active and passive conditions, but they acquire a sense of agency over the projected hand in the active condition only. A third tactile stimulation condition was included for comparison with previous studies. The video-projected hand was viewed either online (synchronous) or after a computer-controlled delay (asynchronous). In the same way as in the previous

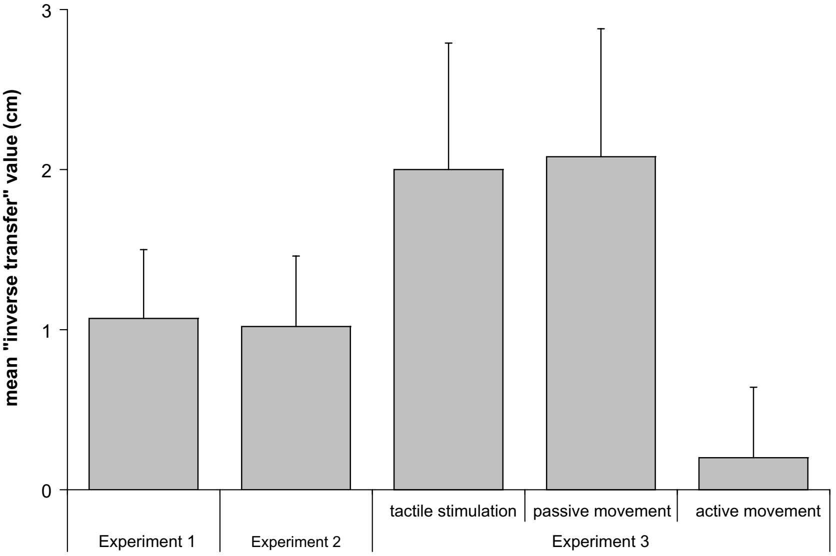

Fig. 2. In Experiment 1 (Tsakiris & Haggard, 2005b), tactile stimulation was delivered either on the little or the index finger, synchronously or asynchronously with respect to the rubber hand, and subjects judged the felt location of either the index or the little finger in different blocks. In Experiment 2 (Tsakiris & Haggard, 2005b), both the index and the little fingers were stroked across blocks, but only one of the two was stroked synchronously with respect to the rubber hand. Subjects judged the felt location of either their little or index finger in difference blocks. In Experiment 3, subjects judged the felt location of either their index or little finger, after (a) active movement of index or little, (b) passive movement of index or little, (c) tactile stimulation of index or little, while they were looking at synchronized or delayed video feedback of the hand projected on a different location.The figure shows the mean "inverse transfer" values across experiments and conditions. This quantity represents the degree to which proprioceptive judgments for stimulated fingers differ from judgments for unstimulated fingers (see Tsakiris et al., 2006). High positive values of this measure occur when they are large shifts for the stimulated finger, and small shifts for the unstimulated one. This would imply a localised RHI which does not transfer across fingers. Perfect transfer across fingers would give a value of 0. Note that the "inverse transfer" measure is equivalent to quantifying the interaction between finger stimulated and finger judged for each type of stimulation shown.In Experiment 1, the inverse transfer value was significantly different from zero ($t(9) = 2.46$, $p < .05$). In Experiment 2, the inverse transfer value was again significantly different from zero $t(13) = 2.3$, ($p < .05$). In Experiment 3, the inverse transfer measure was significantly greater than zero in the tactile ($t(11) = 2.52$, $p < .05$) and passive ($t(11) = 2.37$, $p < .05$) conditions, but not in the active condition ($t(11) = 0.46$, $p > .05$). In Experiment 3 (see Tsakiris et al., 2006), a directional planned comparison was performed to compare the inverse transfer measure following active movement with that following passive movement. The difference between active and passive conditions was significant ($t(11) = 1.84$, $p < .05$, one-tailed). This arose because perceptual shifts in the active, but not the passive condition, spread from the stimulated to the unstimulated finger. The difference between active movement and tactile stimulation were also significant ($t(11) = 1.98$, $p < .05$, one-tailed), for the same reason. Overall, these comparisons support the hypothesis that active movements would reduce the localised pattern of proprioceptive shifts reported in Tsakiris and Haggard (2005b).

experiments reviewed on the RHI, participants again judged the proprioceptively perceived location of their index or little finger.

The results confirmed the prediction that active, but not passive, movement would induce a global change in proprioceptive awareness (see Fig. 2). A significant overall RHI, defined as greater drifts following synchronous than asynchronous stimulation, was found in all cases. However, the distribution of the RHI across stimulated and non-stimulated fingers depended on the kind of stimulation. Localized proprioceptive drifts, specific to the stimulated finger, were found for tactile and passive stimulation. Conversely, during active movement of a single digit, the proprioceptive drifts were not localized to that digit, but were spread across the whole hand. It was suggested that active movements integrate distinct body-parts into a coherent, unified awareness of the body in contrast to a fragmented proprioceptive awareness observed after sensory stimulation alone.

3. Afference, efference and self/other recognition

3.1. Afferent information in action recognition of self and others

As we have seen, afferent inputs from one's body provide important information for internally based body and motor representations. This has significance for more than just generating a sense of ownership. Here we want to consider action recognition in self; action recognition in others; and self–other discrimination. To do this we turn to an alternative way of investigating the respective contributions of efferent and afferent signals in action awareness and body awareness, namely, the examination of patients who are deprived of afferent signals. GL and IW are two well-known deafferented patients who have been tested in a variety of experimental designs. Due to a rare viral infection, nerve fibers that normally transmit peripheral kinaesthetic, cutaneous and muscular information to the brain are completely and selectively degenerated in these subjects. GL and IW have recovered a remarkable degree of control of their movements relying solely on visual feedback and cognitive control. However, when prevented from seeing their bodies they are unable to locate or to make controlled movements of their body parts (see Gallagher & Cole, 1995). Testing GL and IW may provide a unique opportunity for investigating whether action recognition is supported by these peripheral inputs.

GL, for instance, was tested in the "action conflict task" that was originally developed by Nielsen (1963) and recently adapted by Fourneret and Jeannerod (1998). In this experimental paradigm, participants are asked to trace a continuous line, as straight as possible, with a stylus on a surface hidden from direct view. The visual feedback, manipulated by the experimenters who introduce angular biases, is presented on a monitor screen. There are two issues under investigation. The first one refers to the motor performance: Will the participants be able to compensate for the angular biases after a certain number of trials? The second issue refers to the content of motor awareness: Will the participants become aware of the discrepancy? Normal participants are able to compensate after some trials and therefore to produce the desired straight line (Fourneret & Jeannerod, 1998), and they do become aware of their actual behaviour only when the biases are large. When GL was tested in the same paradigm (Fourneret et al., 2002), she was able to compensate for the angular biases in a similar way as the control participants, suggesting that her motor performance was intact. However, "GL never became aware of the bias and, consequently, of any strategy of correction she had to apply to correct" (Fourneret et al., 2002, p. 545), suggesting that the content of awareness of one's own movements is derived not from the efferent signals alone, but from the comparison of the predicted to the real sensory consequences of the executed movement. In a deafferented patient like GL, this process never takes place, since she is deprived of proprioceptive signals.

GL was also tested in a self-recognition task developed by Farrer and colleagues (Farrer et al., 2003a, Farrer, Franck, Paillard, & Jeannerod, 2003b). The results were consistent with her performance in the action conflict task. Her motor performance was not significantly different compared to controls, but her motor awareness was significantly impaired. GL was also tested in a "sense of effort" task (Lafargue, Paillard, Lamarre, & Sirigu, 2003). In this task, controls and GL were asked to produce and judge isometric forces: The force was produced with one hand and, three seconds later, participants were asked to match the force with the other hand. Again, GL's motor performance was not significantly different compared to con-

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trols, suggesting that she did have a sense of muscular effort derived from efferent signals, even though she reported being unaware of any fatigue or of how hard she tried to match the produced forces. These consistent results seem to suggest that the content of body awareness is largely dependent on afferent signals. However, the fact that GL's performance was accurate, and that she did have a sense of effort, suggest that the sense of agency may be crucially dependent on efferent, rather than afferent, signals (for a similar argument, see Marcel, 2003).

There is reason to assume that afferent information from one's own body contributes to recognition and interpretation of others' actions (Bosbach, Cole, Prinz, & Knoblich, 2005). A recent study tested the two deafferented individuals, GL and IW, during an action recognition task originally devised by Runeson and Frykholm (1983), and further developed by Grezes and colleagues (Grezes, Frith, & Passingham, 2004a, 2004b). Bosbach et al. (2005) confronted GL and IW with videos showing a person lifting a box of varying weights. The actor was always given correct information about the box' weight prior to lifting. The subjects were asked to estimate the weight of the box by the mere observation of that action. GL and IW performed this task as well as a group of neurologically healthy controls. Thus, they could deduce the box's weight purely from observing and interpreting the actor's lifting movement. GL and IW probably solved this task by making use of a visual- and knowledge-based strategy. That is, they correctly interpreted the available visual cues; for instance, the faster and higher the movement is the lighter the object must be (cf. Fleury et al., 1995). Note that the first task focused on questions about the box rather than on questions about the actor.

In a second task GL and IW again observed videos of a person lifting a box. However, the actor had sometimes been given correct information about the weight of the box and had sometimes been deceived about its weight. The subjects were now asked to guess whether the actor had a correct or false expectation regarding the weight of the box. Again, the only source of information for making this judgment was the movement of the lifter. This time, GL and IW's accuracies were significantly below that of controls indicating a deficit in deducing another's expectation of weight from observing his/her actions. If the actor's expectation of weight is false there is a mismatch between his/her prepared and resulting movement. GL and IW may have difficulties in detecting match or mismatch between another's prepared and resulting movement as an indicator of his/her expectation of weight.

It is known that due to the deafferentation GL and IW's movement kinematics generally differ from the kinematics of controls. Thus, it is possible that their deficit in action recognition is a result of being less familiar with those kinematic cues that signal a false expectation of weight in normal controls. To test this assumption in a third part of the study the task was reversed. Now IW was asked to lift a box by himself. Prior to lifting he had been given correct or false information regarding the box' weight. The authors recorded IW's movements and then showed these videos to him and to a group of healthy controls. The subject's task was to decide whether IW had a correct or false expectation about the weight of the box. The accuracies of controls were close to chance. They could not deduce IW's expectation of weight from observing his lifting movements; but also IW was not more accurate at judging his own expectations than those of others. Normally there are characteristic movement adaptations when one has a false weight expectation. It is therefore notable that the movement kinematics of IW did not differ depending on whether he expected a correct or false weight. Obviously he was not able to attune his movements to his expectations and it is likely for this reason that he was not able to deduce the expectations of others from their movements. In other words, these results suggest that information about one's body and actions grounds the recognition of others' actions.

A well-established and widely supported hypothesis states that action recognition involves a direct mapping of a certain observed action onto a motoric representation for the same action in the observer. In other words, action recognition requires at some point action mirroring (for review see Rizzolatti & Craighero, 2004). The results of Bosbach et al. (2005) are in line with this hypothesis and furthermore suggest that action mirroring (indirectly) accesses the somatic experience of action as provided by afferent information from one's body. Somatic experience seems to feed internal models or motor representations which are not only used for action control but also for action recognition. The somatic experience associated with a certain action might be stored in a particular motor representation which is automatically activated when observing this action. It might also be that these motor representations need constant reinforcement by sensory feedback for their

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maintenance. A lack of this feedback might then explain GL and IW's deficit in extracting certain types of information from other's actions by observation.

3.2. The specific role of efferent information in self-recognition

In experiments on self-recognition of movements and body-parts, subjects are presented with a visual image of a still or moving hand of ambiguous identity. For example, the subject could see either her own hand, or someone else's hand on a screen. Both hands are covered with identical gloves, and therefore, discrimination of hand identity on the basis of morphological differences is far from easy. In these cases, afferent signals such as vision and proprioception need to be integrated with efferent signals in order to generate a coherent self-representation, i.e., "that's my hand" (for a review see Jeannerod, 2003). This self-representation is accompanied by an explicit form of self-awareness (e.g., "this is *me*"). In most recent studies on the self-recognition ability of adults (Daprati et al., 1997; Sirigu, Daprati, Pradat-Diehl, Franck, & Jeannerod, 1999; van den Bos & Jeannerod, 2002), participants perform a self-generated movement, while they are looking at (a) their own hand, (b) someone else's hand performing the *same* movement, or (c) someone else's hand performing a *different* movement. Subjects are then asked to make an explicit judgment about the identity of the seen hand. According to Jeannerod (2003), one main conclusion of these studies is that 'action cues' are used when distinctive movements are made (e.g., in the different movement condition), and that afferent signals (i.e., vision and proprioception) are used when action cues are ambiguous (e.g., in the same movement condition). In these studies, the movements performed by the subjects were always self-generated, and therefore across conditions, both efferent and afferent information were present. To that extent, these studies did not quantify the specific contribution of efferent information. Moreover, the paradigm of the RHI suggests that if only afferent information were present or used for self-recognition, then the viewed hand would always be attributed to the self, provided that there were no conflicts between vision and proprioception. Thus, it may be hypothesized that for highly reliable self–other discrimination, visuo-proprioceptive congruence may not be sufficient.[3] Efference may play a critical role in structuring the perception of bodily related multisensory signals, and it may therefore also play a critical role in self-recognition.

Tsakiris et al. (2005) investigated the specific role of efferent information for self-recognition. Subjects experienced a passive extension of the right index finger via a lever, either as an effect of moving their left hand ('self-generated action'), or imposed externally by the experimenter ('externally generated action'). The visual feedback was manipulated so that subjects saw either their own right hand ('view own hand' condition) or someone else's right hand ('view other's hand condition) undergoing the same passive displacement of the right index finger. Thus, across all trials, subjects experienced a passive displacement of their right index finger. In one block, this passive displacement was self-generated, and in another block, the same passive displacement was externally generated. In half of the trials, subjects saw their own right hand, and in the other half, subjects saw someone else's hand. Both hands were covered with identical gloves, so that discrimination on the basis of morphological differences was not possible. Participants judged whether the right hand they saw was theirs or not. In that experiment, unlike other self-recognition studies, efferent information was selectively manipulated because the right hand's displacement could be effected either by the participant or by the experimenter. In the former case, participants had two kinds of information about the passive displacement of the right hand: efferent information from the left hand that caused the displacement of the right hand, and also afferent information from the right hand itself. When the displacement of the right hand was externally generated, afferent information was similar, but efferent information was absent. Participants viewed only the effect of the action in visual display of the right hand, and never saw the left hand or left side of the lever (Fig. 3).

Overall, performance was significantly better when the passive displacement of the right index finger was self-generated across both viewing conditions (i.e., viewing "self" and "other", see Fig. 3). Self-recognition

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[3] The following discussion of reliable self-recognition should not be confused with the issue of immunity to error through misidentification which pertains only to "as subject" attributions. The question addressed here pertains to "as object" judgments. For more on the distinction (first made by Wittgenstein (1958)) between "as subject" and "as object" attributions, and proprioception, see Cassam (1994, 1995) and Gallagher (2003).

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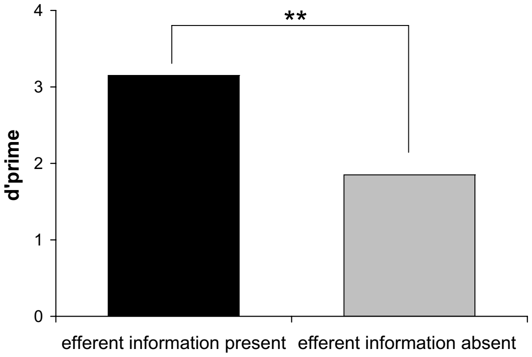

Fig. 3. A signal detection analysis for the self-generated condition *vs.* the externally generation condition was performed, as an informational measure of self-recognition, which would be independent of the response bias. The hits and false alarms were used to calculate the *d'prime* measures for self-detection, for each subject and in each condition (i.e., self-generated and externally generated). The *d'primes* were submitted to the non-parametric Wilcoxon matched-pairs tests. Differences between self-generated and externally generated conditions were significant ($Z = 2.635$, $p < .05$), suggesting that participants had access to more discriminative information for self-recognition in the self-generated condition. Asterisks indicate significant differences.

was significantly more accurate when subjects themselves were the authors of the action, even though visual and proprioceptive information always specified the same posture, and despite the fact that subjects judged the effect and not the action *per se*. In fact, even when subjects saw their own hand, they were significantly better at correctly recognizing it as their own when they produced the passive displacement themselves, than when the passive displacement was externally generated. In the critical condition where participants saw someone else's right hand and the displacement of their right hand was externally generated, they incorrectly attributed the viewed hand to themselves in 55% of the trials. When the passive displacement was self-generated and they saw someone else's hand, incorrect attribution to self occurred in 38% of the trials. The difference between these two conditions shows the specific role of efferent information in the accuracy of self-recognition. Therefore, efferent information clearly contributes to the ability to match proprioceptive and visual representations of a remote bodily effect. The observed efferent advantage could occur for two reasons. First, efferent information might provide an advantage in monitoring the timing of sensory events. In the case of a self-generated action, forward models of the motor system use the efferent information so as to generate a prediction about the anticipated sensory feedback (Wolpert, 1997). Second, efference might modulate the on-line comparison between vision and proprioception by providing detailed temporal and kinematic information, and integrating these signals in posterior parietal areas (MacDonald & Paus, 2003; Sirigu et al., 1999; Tsakiris & Haggard, 2005a).

The results suggest that proprioceptive self-consciousness alone may not be sufficient for reliable explicit self-recognition. Self-recognition, in the sense of correctly recognizing a visual object or event as "me" or "mine" seems to depend largely on efference and agency. This is consistent with recent experiments on action recognition and prediction, where an agentive effect was observed in recognizing and predicting actions that were performed by the participants themselves, when compared to actions performed by other agents (for a review, see Knoblich & Flach, 2003). This finding also suggests that efferent information is important for self-recognition and self-awareness (see also Blakemore et al., 2002; Tsakiris & Haggard, 2003), and not only for motor control. This distinctive role of efference in self-recognition experiments suggests that central efferent signals have a highly predictive power allowing the correct detection of appropriate afferent signals that pertain to one's self.

3.3. *Pre-reflective self-consciousness in the motor system?*

Social understanding of action seems to involve the mapping of another's action onto the observer's own motor representations. This implies that the brain represents others' actions in partly the same way as it represents one's own (see Rizzolatti & Craighero, 2004). In line with this hypothesis, so far, studies on action

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observation have tended to emphasize commonality and not distinction between self and other. The proposed overlapping neural system that appears to be involved in the execution and observation of actions raises important questions for the neurocognitive processes responsible for constructing a sense of self as distinct from others. It may be argued that the "mirror system" can not account for a unique representation of one's own body. How do we solve the problem of action attribution given the idea that the brain represents others' actions in the same way as it represents one's own (cf. Jeannerod & Pacherie, 2004)? Georgieff and Jeannerod's (1998) concept of a "who system" which discriminates between self and non-self on the basis of non-overlapping areas of neuronal activation simultaneous with mirror system activation is one proposal. Consistent with this idea,it has recently been shown that although actions of others are represented in the observer's motor system, the extent of involvement of the motor system does depend on the agent to whom an observed action is attributed (Schütz-Bosbach, Mancini, Aglioti, & Haggard, 2006).

Schütz-Bosbach et al. (2006) used the RHI as an established method for manipulating the sense of body ownership. They compared motor facilitation to transcranial magnetic stimulation (TMS) when observing another's actions with the facilitation when the same actions appeared to be one's own (cf. Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). During the experiment subjects observed the index finger of a "rubber hand" (actually an experimenter's hand) being stroked, while feeling identical tactile stroking of their own unseen index finger. The tactile stimulation was synchronous or asynchronous with the visual stimulation. This caused the subject to feel that the experimenter's hand was part of their own body only in the synchronous condition, but not the asynchronous condition (see above Section 2). The subject observed the experimenter's hand occasionally and unpredictably making abduction movements with her index finger. The authors recorded motor evoked potentials (MEPs) to TMS at the time of these observed actions, during interleaved control trials when the experimenter's hand was at rest, and also in baseline fixation blocks.

Motor facilitation was then analysed relative to baseline as a function of the experimenter's action (rest, action), and as a function of the subject's attribution of the experimenter's hand (self, other). The results show that observed movements of an experimenter's hand tended to suppress the motor system when the subject viewed the experimenter's hand as their own (i.e., synchronous condition), but significantly facilitated the motor system when the same hand actions were clearly attributable to another (i.e., asynchronous condition, see Fig. 4). This finding seems to confirm that a distinction between self and other is even present on a low-level sensorimotor representation.

Taken together, these results confirm the hypothesis that the mere observation of others' actions facilitates the motor system (Fadiga et al., 1995; Strafella & Paus, 2000). More importantly, though, they suggest that facilitation strongly depends on the agent to whom the observed action is attributed: observing another agent acting facilitates the observer's motor system, whereas observing one's own actions tends to suppress the observer's motor system. A suppression of a tendency to "imitate" oneself might reflect a natural reaction

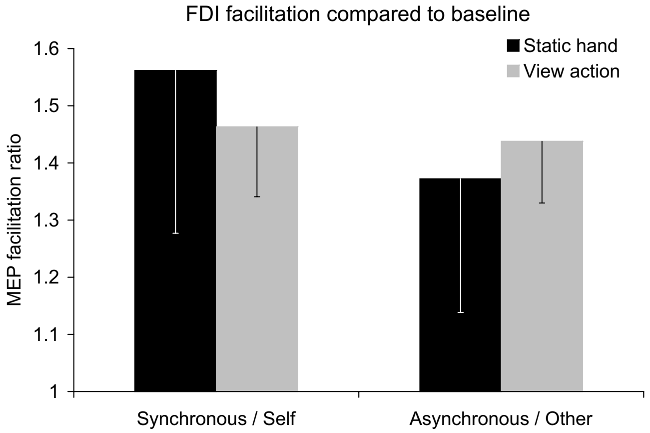

Fig. 4. Mean (+SE) cortical motor excitability of First Dorsal Interosseus (FDI) following action observation, or while viewing a static hand, in each ownership condition.

to avoid inappropriate perseverations or responses when viewing one's own actions. This novel result implies that the motor system includes a representation of other agents as qualitatively different from the self, and as such, it may underpin a distinction between the self and the other that normally trumps the self–other identity of the mirror system. Further studies should investigate whether this low-level sensorimotor representation might reflect a form of pre-reflective self-consciousness and whether and how it may be used to build up a conscious sense of agency and a sense of self.

4. Discussion

We reviewed recent findings on the neurocognitive processes that underpin the sense of agency and the sense of body-ownership. In the absence of action, the body can be perceived only through afferent signals, some of which are thought to be ego-receptive (e.g., proprioception) and some of which are not (e.g., vision). These afferent signals need to be integrated in order to provide a unified percept of one's own body as distinct from the world. The interactions between these signals have been at the centre of the research on self- and body-perception. The experiments presented on body-ownership and self-recognition (see Sections 2.1 and 3.2) suggest that proprioceptive information can be overridden or altered to produce an "erroneous" sense of self. For example, when subjects experience a passive movement of their own hand, while they are looking at someone else's hand moving in a similar way, they frequently misattribute the moving hand as being theirs. Likewise, when subjects see a rubber hand being stroked synchronously with respect to their own unseen hand, they feel as if their own tactile sensation is caused by the paintbrush touching the rubber hand and not their own hand. The effect of this visuo-tactile integration is an alteration in the proprioceptively sensed location of their hand. These results seem to suggest that intermodal matching is not only a necessary but also a sufficient condition for self-attribution, and hence body-ownership.

On one view, any object can become part of me, simply because of strong statistical correlations between different sensory modalities which are both necessary and sufficient conditions for self-attribution. On this view, psychological concepts such as embodiment and selfhood may seem unnecessary, because multisensory statistical correlations are sufficient to extend the body representation, to include as body parts elements as implausible as tables (Armel & Ramachandran, 2003). However, not all objects are experienced as being part of my body, simply because in some cases there is no functional reason for an external object to be part of me. For example, the RHI experiments show that neutral objects are not experienced as part of one's own body, not even after synchronous visuo-tactile stimulation (see Section 2.1). It is possible though that once this neutral object has to be used by the body (e.g., a tool), then it will become a "bodily auxiliary, an extension of the bodily synthesis" (Merleau-Ponty, 1962, p. 152), and it will cease to be simply an external object (see Iriki, Tanaka, & Iwamura, 1996).

Interestingly, when subjects saw a neutral object being stimulated synchronously with their own hand (see Section 2.1), the induced perceptual shifts were in an opposite direction, namely away from the neutral object. This "perceptual repulsion" might reflect a behavioural correlate of the dissociation between events that either do or do not produce self-attribution. When, however, the rubber hand is experienced as one's own hand, we observe a perceptual attraction of the prorioceptively felt position of the subject's own hand towards the rubber hand. Interestingly, this effect is compatible with the results of studies on time-awareness and intentional binding (Haggard et al., 2002; Tsakiris & Haggard, 2003). In these studies, the results showed a perceptual attraction between the time-awareness of one's own action and its sensory consequence, and a perceptual repulsion for a physically comparable involuntary movement followed by the identical external consequence. It may be argued that perceptual attraction is the experiential hallmark of the bodily self, both in the sense of body-ownership and the sense of agency, while perceptual repulsion may be characteristic of events not linked to the bodily self.

Voluntary action significantly improves self-recognition performance, as shown in Section 3.2, and suggests that efferent information contributes to the sense of body-ownership. In the absence of efferent information, congruent visual and proprioceptive feedback, as is the case in the RHI, leads to a self-attribution of an alien moving hand. Overall, the results showed that efferent information clearly contributes to the ability to match proprioceptive and visual representations of a remote bodily effect. One interpretation of these results focused on the precise temporal information that efference carries with it. This temporal signal can be used to predict the onset of the movement and also the arrival of the impending somatic effect in line with the internal predictive models of the motor system (Wolpert, 1997). The effect of agency on body-ownership was further assessed in a modified version of the RHI (see Tsakiris et al., 2006). The results showed that whereas a purely proprioceptive sense of body-ownership is local and fragmented, the motor sense of agency integrates distinct body-parts into a coherent, unified awareness of the body. In a sense, it may be argued that the constitutive units involved in body-ownership in the absence of agency are anatomical (e.g., fingers), whereas the constitutive units of body-ownership during agentic movements are functional (i.e., effectors). In the self-recognition experiment presented in Section 3.2, the movements were confined to one finger, and had minimal spatial detail. Self-generated actions provided a precise temporal signal which could be used to predict proprioceptive and/or visual feedback. In the video version of the RHI presented in Section 2.2, the difference between action and passive movement was studied using a *spatial* rather than a *temporal* measure. Taken together, the observed differences between active and passive conditions reflect a distinctive contribution of efferent information to both *temporal* and *spatial* aspects of body awareness.

The importance of afferent signals in action-recognition is demonstrated by the study of two individuals who are selectively deprived of any afferent signals (see Section 3.1). The results demonstrate that the sense of one's own body as provided by proprioceptive information plays a role in perceiving others' bodies. One's own body mirrors the actions of others and may mediate action understanding. As a possible mechanism information about somatic experiences associated with one's own actions, carried by afferent inputs, feed forward models and allow accurate kinematic predictions for both one's own and others' actions. Thus, the chronic lack of afference in deafferented subjects may lead to deficits not only in action execution but also in action-recognition.

On the other hand, although it seems as if we generalise from our own body to others' bodies, our brain discriminates between our own actions and the actions of other people even as our own motor system is selectively entrained when observing others' actions. In the experiment on motor excitability presented in Section 3.2, the observation of hand movements that were clearly attributable to another led to strong activation in the observer's motor system (i.e., M1), whereas the opposite pattern was found when subjects interpreted the same hand actions as belonging to the self. In this sense the motor system seems to prioritise the actions of others over the self, which means that a distinction between self and other is present even on a low-level sensorimotor representation. Further studies should assess whether this sensorimotor self/other distinction may be the source of an explicit self-recognition, that is, an explicit judgement of whether a seen action belongs to oneself or to another, or vice versa.

5. Conclusions

The experiments reviewed here focused on understanding the relations between the sense of ownership and the sense of agency, and on showing how afference and efference can modulate these forms of self-awareness, action recognition and attribution to self and other. If there is no sense of agency without the sense of ownership, it is also true that the efferent signals that contribute to the sense of agency also contribute to a more fluid and integrated sense of body ownership. Distinctions between sensory aspects and motor aspects of experience are indeed abstractions from the full experience of embodied existence. This review of the relevant literature suggests that the sense of ownership depends on the interaction of afferent feedback and a top–down contribution from body representations. Afferent feedback alone, even with contributions with top–down representations, however, likely generates a fragmented experience of the body. A more coherent experience of the body depends on the integration of efferent information with afferent information in action contexts. On this view, the sense of agency contributes to a more unified experience of one's body.

The sense of ownership and sense of agency are part of a pre-reflective experience of embodied experience. They are generated in low-level, albeit complex, sensory–motor processes. They tend to remain phenomenologically recessive or attenuated. That is, they involve a thin or minimal although not necessarily simple phenomenology. Furthermore, the same processes that support a minimal self-awareness of embodied action, contribute to the resonance systems that support our perception and understanding of another person's action. Within the pre-reflective experience of my own body in action there is both resemblance to and differ-

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ence from others. Self-awareness and the meaningful awareness of others are not entirely separate forms of cognition.

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