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Paula Guedes  
BIAL Foundation  
À Av. da Siderurgia Nacional  
4745-457 S. Mamede do Coronado  
Portugal

## RE: FINAL SCIENTIFIC AND FINANCIAL REPORT FOR RESEARCH GRANT 165/06

Wednesday 16 December 2009

Dear Mrs Guedes

I would like submit the final scientific and financial (see attached, Appendices 1 & 2) reports for Research Grant 165/06 entitled: "The sense of self in the brain: neural correlates of self-recognition".

### **Scientific Report**

#### Project Aims & Objectives:

The research project aimed at understanding the neurophysiological basis of self-recognition by investigating two important dimensions:

1. First, the respective contributions of sensory and motor signals for self-recognition.
2. Second, the similarities and differences between implicit and explicit self-recognition.

The experiments were designed to address these questions using functional magnetic resonance imaging (fMRI) on normal participants.

#### Project Outcomes:

1. Respective contributions of sensory and motor signals for self-recognition. We developed a paradigm to investigate sensory and motor aspects of body representation in the brain using fMRI. Participants (n=20) either made self-generated finger-movements, or remained passive while similar movements were applied to their fingers by an external force, while seeing a video image of their hand either in real-time or with a systematic delay that generated a conflict. With respect to the role of sensory and motor signals for self body-awareness, our study represents a significant advancement of current understanding of the neural correlates of self-recognition because it effectively allows the distinction between a sensory-driven sense of self (i.e. sense of "body-ownership") and a sensori-motor sense of self (i.e. agency). Activations in midline cortical structures were associated with a purely sensory-driven sense of self, while activity in the Supplementary Motor Area (SMA), premotor area BA6 and superior parietal lobe was linked to a motor-driven sense of self. Importantly, no shared activations between the two senses of self were found. The results support an independence model of sensory-driven and motor-driven aspects of self, confirming, thus, our

initial hypothesis. (Please refer to Appendix 6)

2. **Implicit and explicit self-recognition.** We developed an fMRI paradigm in which participants (n=36) saw a series of movies displaying either their own hand or the hand of someone else. They were instructed to make a self-recognition judgment. We analysed the data according to the identity of the stimulus they saw (i.e. self vs. other), according to the judgment they made (i.e. self vs other) and the interaction of the two factors. With respect to the dimensions of implicit and explicit self-recognition of kinematics, the current stage of the analysis of our results show a lack of significant differences in activations for implicit recognition of self versus other-kinematics (i.e. main effect of they identity of the stimulus), while differences in activations for explicit self-recognition (i.e. main effect of the participant's judgement) engage areas in the cingulate cortex and smaller activations in the premotor cortex. Further analyses of the results are currently under way to extract a distinct pattern of activations across the studies. We anticipate that one more research paper will be prepared on these results in due time.

### Overall Progress

In the table below you can see the progress of the research over the award period (September 2007 to September 2009):

Months 1-11 September 2007 – July 2008	Design/Pilot/ Data Collection/ Analysis of Experiment 3 (resulting original research paper is currently under review at the <i>Journal of Neuroscience</i> )
Months 12-14 August 2008 – October 2008	Design and Behavioural Piloting for Experiments 1 & 2
Months 15-24 November 2008 -September 2009	Design/ Data Collection/ Analysis of fMRI Experiments 1 & 2
<i>Parallel Ongoing activities</i>	<i>Scholarship, Dissemination, Writing-up</i>

In our original application, we planned to test 56 participants in 4 fMRI experiment (n=14 per experiment). Because of the need to increase the effect size in our experimental design, the experimental designs of experiment 3 (i.e. active vs. passive movement) and experiment 4 (i.e. synchronous or delayed visual feedback) were combined in one single experiment (now called Experiment 3 that included both factors of active/passive movement and synchronous/delayed feedback) where 20 participants were tested, while experiments 1 and 2 had 18 participants each.

A small delay occurred in the data collection of Experiments 1 and 2 because of a technical problem in the fMRI suite at the Department of Psychology, Royal Holloway, University of London, that had to be dealt with by external contractors. Nevertheless, the data collection was completed within the award period, but further analyses of the results and the writing-up of the research paper are currently under way.

### **Publications**

The following papers have appeared or are currently under review in peer-reviewed edited volumes and journals:

- Tsakiris M (2008) The self-other distinction: insights from self-recognition experiments. In Morganti F, Carassa A, Riva G (Eds) *Enacting Intersubjectivity: A Cognitive and Social Perspective to the Study of Interactions*. IOP Press: Amsterdam.
- Haggard P & Tsakiris M. (2009) The experience of agency: feeling, judgment and responsibility. *Current Directions in Psychological Science*, 18(4), 242-246.

- Tsakiris M, Longo M & Haggard P. Having a body versus moving your body: neural signatures of body-ownership and agency. *Journal of Neuroscience*, currently under review

The contribution of the Bial Foundation Research Grant 165/06 was explicitly acknowledged in all publications. (Please refer to attached reprints of the papers that have been published or are currently under review).

#### **Dissemination activities:**

Our results were presented in the following national and international meetings, where the contribution of the Bial Foundation Research Grant 165/06 was explicitly acknowledged:

- *Symposium on Agency*, International Graduate School of Neuroscience RUB - Ruhr University Bochum, 22.09.2008 (invited oral presentation)
- *Embodiment: from structure and function to experiment*. The Body-Project, funded by the European Platform for Life Sciences, Mind Sciences and the Humanities of the Volkswagen Foundation, Berlin, 01.10-03.10.2008 (oral presentation)
- *Institute of Cognitive Neuroscience*, University College London, 14.10.2008 (poster presentation, see also attached reprint of the poster).
- *38<sup>th</sup> Annual meeting of the Society for Neuroscience*, 15.11-19.11.2008, Washington, DC, USA (poster presentation)
- *Neuroimaging seminar series*, Cognitive Neuroimaging Group, MRC Clinical Sciences Centre, Imperial College London, 26.03.2009 (invited talk)
- *13<sup>th</sup> Annual Meeting of the Association for the Scientific Study of Consciousness (ASSC)*, 05.06-8.06.2009, Berlin, Germany (concurrent talk) \*
- *10<sup>th</sup> International Multisensory Research Forum*, City College of New York, New York City, USA, 29.06-02.07.2009 (conference talk) \*
- *48<sup>th</sup> Annual Conference of the Colombian Psychiatric Association*, 08.10-12.10.2009, Cartagena, Colombia (plenary talk),
- *Philosophy and Psychiatry Group*, Department of Philosophy, National University of Colombia, Bogota, Colombia, 07.10.2009 (invited talk)

\*Travel and conferences expenses were claimed from the Bial Research Grant 165/06.

#### **Comment on Financial Report**

As you can see in the attached Financial Report produced by the Head of Management Accounts, Royal Holloway, University of London, total expenditure and accrued expenditure for estimated publication fees stand to 33,532.27 Euro. The accrued expenditure relates to estimated publication costs that have not been included in our original application. We would like to kindly ask the Bial Foundation to consider our request to reserve some funds (2,000USD) for publication costs of the paper "Tsakiris M, Longo M & Haggard P. Having a body versus moving your body: neural signatures of body-ownership and agency" that is currently under revision at *Journal of Neuroscience*. I have been informed by the Head of the Management Accounts that she will need the bank details of the BIAL Foundation for returning the unused funds (2,467.73 Euro), once the financial report has been approved by the Foundation.

#### **Appendices**

Appendix 1: Financial Report: Statement of Expenditure provided by John Carroll, Head of Management Accounts and copies of past financial reports

Appendix 2: Copies of original documents of costs and expenses

Appendix 3: Poster presented at the 38<sup>th</sup> Annual meeting of the Society for Neuroscience, 15.11-19.11.2008, Washington, DC, USA

Appendix 4: Reprint of Tsakiris M (2008) The self-other distinction: insights from self-recognition experiments. In Morganti F, Carassa A, Riva G (Eds) *Enacting Intersubjectivity: A Cognitive and Social Perspective to the Study of Interactions*. IOP Press: Amsterdam.

Appendix 5: Reprint of Haggard P & Tsakiris M. (2009) The experience of agency: feeling, judgment and responsibility. *Current Directions in Psychological Science*, 18(4), 242-246.

Appendix 6: Reprint of Tsakiris M, Longo M & Haggard P. Having a body versus moving your body: neural signatures of body-ownership and agency. *Journal of Neuroscience*, currently under review

Appendix 7: Abstract of Talk presented at 13<sup>th</sup> Annual Meeting of the Association for the Scientific Study of Consciousness (ASSC), 05.06-8.06.2009, Berlin, Germany

Appendix 8: Abstract of Talk presented at 10<sup>th</sup> International Multisensory Research Forum, City College of New York, New York City, USA, 29.06-02.07.2009

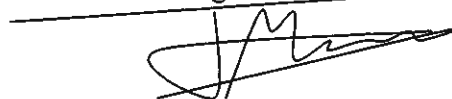
### **Evaluation**

Overall, we believe that the project has progressed successfully. The research outcomes to date have been widely disseminated in international multidisciplinary meetings and conferences, and I anticipate that the publication of the 1<sup>st</sup> paper that will come out of this project will attract further interest (see Tsakiris, Longo & Haggard, under review, Appendix 6). We are also currently completing the final analyses for Experiments 1 and 2 and I anticipate that a second original research paper will be written up and submitted for publication in due course.

I would like to thank the Bial Foundation for its financial and administrative support during the award period. I am grateful for the opportunity you gave us to implement this original research programme on the neural correlates of self-recognition, and I do hope that the outcomes of this project will further enhance the visibility of Bial's contribution to cognitive neuroscience research.

Please do not hesitate to contact me should you require any further information.

Kind Regards

A handwritten signature in black ink, appearing to read 'Manos Tsakiris', written over a horizontal line.

Manos Tsakiris

## **Appendix 3:**

**Poster presented a the 38th Annual  
meeting of the Society for Neuroscience,  
15.11-19.11.2008, Washington, DC, USA**

# Neural Signatures of Agency and Body-ownership

Manos Tsakiris<sup>1,2</sup>, Matt Longo<sup>2</sup>, Henrik Ehrsson<sup>3</sup> & Patrick Haggard<sup>2</sup>

<sup>1</sup>Department of Psychology, Royal Holloway, University of London, UK; <sup>2</sup>Institut of Cognitive Neuroscience, UCL, UK; <sup>3</sup>Department of Neuroscience, Karolinska Institute, Sweden



## Abstract

We developed a new experimental method for investigating sensory and motor contributions to representations of one's own body. In the Rubber Hand Illusion, participants view a prosthetic hand being stimulated in synchrony with their own hand. This gives the experience that the prosthetic hand belongs to them, and is part of their own body. This experience is absent when visual and felt stimulation are asynchronous. We showed participants video images of their own hand, either directly or with an additional feedback delay, to reproduce these conditions. During viewing, their hand was moved either passively, by an experimenter, or by their own voluntary motor command. This design allowed us to isolate the sensory experience of body-ownership, and the motor experience of control over one's own body ('agency'), and to identify their neural bases using fMRI.

## I. Introduction

- Recognising a visual image as oneself is a hallmark of self-consciousness
- In the Rubber Hand Illusion, multisensory correlation between visual and tactile input gives strong evidence that an external object (a rubber hand) belongs to one's own body. This produces a vivid subjective experience, and provides a useful experimental tool to study body ownership.
- Uncorrelated visual and tactile stimulation produces no such effects.
- Previous studies suggested that voluntary movement of the body can also produce a sense of ownership, but the sensory and motor aspects of representing one's own body have not previously been compared directly.
- Here we compared subjective experience and neural correlates of sensory and motor aspects of representing one's own body using a video version of the Rubber Hand Illusion.

## Design

Visual Feedback	Movement Type	
	Active	Passive
Low	Low A & Body ownership	Low P & Body ownership
High	High A & Body ownership	High P & Body ownership

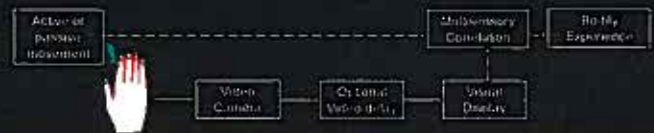
## Set-up



## II. Experimental Design & Methods

- Participants viewed a video image of their right hand.
- This image could be direct (synchronous) or delayed (asynchronous) due to an optional video delay.
- In a passive condition, an experimenter passively lifted and lowered the index finger up and down, at 1 Hz, by pulling a thread attached to the finger.
- In an active condition, the participant themselves actively lifted and lowered their finger at a similar rate.

## Schematic Set-up



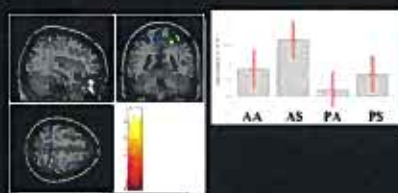
## III. Results

### Introspective Evidence



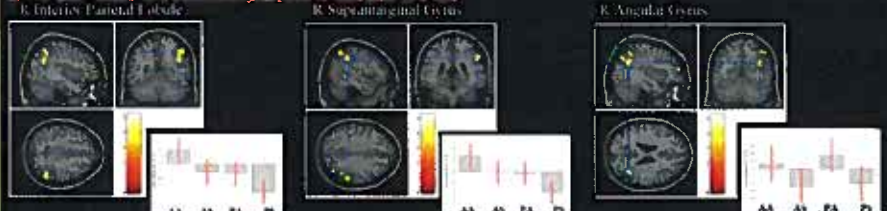
- There was a stronger sense that the viewed image was their own hand for synchronous than for asynchronous views, in both passive and active conditions.
- The passive condition corresponds to a sense of ownership, that the viewed image is linked to one's own body.
- The active condition induces both this sense of ownership, but also a sense of agency, an additional feeling that one can voluntarily control the body at will.
- Comparison of our active and passive conditions allows these two components of body representation to be dissociated for the first time: in previous neuroimaging studies they have generally been confounded.
- Therefore, our fMRI analysis focused on identifying the brain bases of sense of body ownership and sense of agency, and the relations between them.

### Main Effect of Synchrony: (AS-PS)-(AA-PA)



Right somatosensory cortex → non-primary activation that underpins sense of self in general, both in action and sensation.

### Main Effect of Asynchrony: (AA-PA)-(AS-PS)



Distributed brain areas that detect sensorimotor conflicts from brain areas that detect intersensory conflicts.

### Specific sensory effect of body ownership: PS-(AA+AS+PA)



Medial cortical areas (Frontal Gyrus, Anterior Cingulate, Precentral)

### Specific motoric effect of agency: AS-(AA+PA+PS)



SMA: Superior Parietal Lobule; FBA

## IV. Discussion

- Bodily self-consciousness can be studied scientifically
- Multisensory correlation underlies the sense of one's own body

- Bodily experience has dissociable sensory and motor aspects (ownership and agency)
- These are associated with distinct neural circuits:
  - Sensory: Body ownership → frontopolar cortex
  - Motoric: sense of agency → SMA, right superior parietal

## **Appendix 4:**

**Reprint of Tsakiris M (2008) The self-other distinction: insights from self-recognition experiments. In Morganti F, Carassa A, Riva G (Eds) Enacting Intersubjectivity: A Cognitive and Social Perspective to the Study of Interactions. IOP Press: Amsterdam.**

*New IOS Press Publication*



### **Enacting Intersubjectivity**

A Cognitive and Social Perspective on the Study of Interactions

Volume 10 Emerging Communication: Studies in New Technologies and Practices in Communication

Editors: F. Morganti, A. Carassa and G. Riva

May 2008, approx. 280 pp., hardcover

ISBN: 978-1-58603-850-2

Price: US\$161 / €115 / £81

In recent years a new trend in socio-cognitive research investigates into the mental capacities that allow humans to relate to each other and to engage in social interactions. One of the main streams is the study of intersubjectivity, namely the 'mutual sharing of experiences', conceived of as a basic dimension of consciousness on which socialness is grounded. At the very heart of contemporary studies is an intense debate around some central questions that concern the nature and forms of human intersubjectivity, its development and its role in situated joint activities. Striving to achieve a unified theoretical framework, these studies are characterized by a strong interdisciplinary approach founded on philosophical accounts, conceptual analysis, neuroscientific results and experimental data offered by developmental and comparative psychology.

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# 10 The Self-Other Distinction : Insights from Self-Recognition Experiments

Manos TSAKIRIS

**Abstract.** Recent neuroscientific studies of self-awareness have focused on how the self compares to representations of other people, on the ability to represent and attribute mental states, and on the ability to represent how the external world would appear from other viewpoints. Social cognitive neuroscience tends to emphasize the shared properties of self and others across several dimensions, such as the shared properties of actions, bodies and sensations, rather than the asymmetries between self and other. In the present chapter, we put forward the hypothesis that the experience and representation of one's own body may underpin the distinction between the self and other agents. In every inter-action, there are both private and public states and signals represented in the brain of the agent and the observer. Private signals refer to centrally generated action representations such as intentions, efferent signals (e.g. efference copy, motor commands), and re-afferent signals such as proprioception. Public signals originate from observable sensory events, both re-afferent and ex-afferent, such as visual and auditory signals that may refer to bodies, objects or complex patterns of motor behaviour. How are these signals used to disambiguate the identity of bodies and the origin of actions? By focusing on recent experiments on self-recognition, we propose that the experience of one's actions, which depends largely on the processing of efferent information, may function as a unifying element that structures a coherent representation of the bodily self, as distinct from the other agents.

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## 10.1 Introduction

With the advent of social cognitive neuroscience, recent studies of self-awareness have focused on how the self compares to representations of other people [1], on the ability to represent and attribute own and other people's mental states [2], and on the ability to represent how the external world would appear from other viewpoints [3]. However, the question of how the self can be distinguished from other people, what we would call the "self-other" distinction, has not been fully addressed. Most studies tend to emphasize the shared properties of self and others across several dimensions, such as the shared properties of actions, bodies and sensations (for a review see [4]), rather than the asymmetries between self and other. In the present chapter, we put forward the hypothesis that the experience and representation of one's own body may underpin the distinction between the self and other agents. For our purposes, the self will be treated as the minimal sense of owning a body and the actions originating from that body [5]. This minimal self is a physical entity "which exists in a physical world and has physical effects via its physicality" [6, p. 50]. As such, the minimal self is predominantly an embodied acting self.

## 10.2 On the primacy of the body

There are several unique components in the experience of one's own body, that demonstrate the existence of an intimate link between the body and the self. For example, contrary to the perception of an object, which can be perceived from different perspectives or even cease to be perceived, we experience "the feeling of the same old body always there" [7, p. 242]. When I decide to write something, I do not need to look for my hand, in the same way that I have to look for a pen or a piece of paper. Does this permanent presence make the body special? Merleau-Ponty wrote: "[...] It is particularly true that an object is an object in so far it can be moved away from me, and ultimately disappear from my field of vision. Its presence is such that it entails a possible absence. Now the permanence of my own body is entirely different in kind [...] Its permanence is not a permanence in the world, but a permanence on my part." [8, p.90]. The fact that the body is always present suggests that body-awareness is not like any other form of object-awareness, because the body is an "object" that normally never leaves me.

The body is also a unique perceptual entity by virtue of the versatile ways in which it is perceived. Bodies are perceived from the outside (e.g. vision), but *my* body is also perceived from the inside (e.g. proprioception, interoception). Proprioceptive sense is often conceptualized as the sense of the self par excellence, precisely because no one else can feel my hand moving in the same way I feel it moving from the inside. The fact that the body is perceived from within guarantees an immediate first-personal mode of presentation of bodily experiences.

More importantly, one's own body is the only "object" in the world that can be freely moved according to one's own will. "[...] Body is an organ of the will, the one and only Object which, [...], is moveable immediately and spontaneously and is a means for producing a mediate spontaneous movements in other things [...]" [9, §38, pp.152]. The simple fact that we are capable of action with and sensation

in our bodies is sufficient to distinguish the relation we have with our bodies from our relations with other objects [10].

At the experiential level, the body imposes a point of view of the world [8]. It is the mere fact of embodiment that defines a certain “point de vue” for the embodied self, because it is thanks to the presence of the body, and its position in space that every relation between the self and the world is made possible. In that sense, the bodily self can be thought of as a “perspectival” source from where all actions emanate and to where all experiences are returned [6]. In addition, both the effectors that materialize our intended actions and the sensory organs that provide our perceptual experiences of the world are the constitutive elements of the lived body.

Almost all human activity involves voluntary movements and sensory experiences. Both action and perception are made possible through central motor signals and peripheral sensory signals that are ever present. As agents, we act upon the world with our body, and at the same time we experience ourselves, and the world through the same body. We communicate our intentions to the world through the motor signals that are conveyed into voluntary bodily movements, and we understand the world through the interpretation of sensory signals. In short, the body is an ‘intentional arc’ between the agent and the world [8], a channel of meaningful communication between the self and the world. Having established this intimate relation between the body and the self, it then becomes an empirical question to characterize the functional properties of the bodily self. A preliminary approach to this question can be given by investigating the physiological signals that are used to constitute the bodily self, and possibly distinguish it from other bodies.

### **10.3 On motor and sensory signals**

Two main kinds of physiological signals are used to inform the representation of one’s body: the centrally generated motor (or efferent) signals, and the peripheral sensory (or afferent signals).

Efferent signals are the centrally-generated signals that control every voluntary movement. A key concept in the motor control literature is that of an efference copy. The concept of efference copy was first described as an “effort of will” by Helmholtz [11]. In fact, the idea of an “effort of will” was the answer to Helmholtz’s question regarding our visual experience of the world. When we move our eyes, the retinal image of a perceived object is displaced. Similarly, in the case where we keep our eyes still, but we perceive a moving object, the retinal image of this object is again displaced. The critical question is how the CNS distinguishes between a sensation that is due to the activity of the organism itself from movement that is due to external activity. Helmholtz initially suggested that whenever we make eye movements, the “effort of will”, that is the voluntary effort to produce the eye movement provides critical predictive information about the sensory outcome of the eye movement that will follow. In the 20th century, Helmholtz’s idea was further developed into the concept of an efference copy. Whenever a motor command is issued in the motor cortex, a copy of this command is generated in parallel [12,13]. This information can be used for perceptual compensation, and can help identify the source of the movement (i.e. self vs. non-

self). Von Holst and Mittelstaedt suggested that during voluntary eye movements, an efference copy can be used by visual or motor areas of the brain to predict the sensory outcome of the descending motor command, and therefore anticipate the self-generated stimulation (i.e. the sensory feedback originating from the eye movement itself). More recently, the idea of an efference copy has been generalised to the operation of the motor system, and it is not restricted only to the operation of the oculomotor system. Thus, an efference copy is thought to be generated whenever a motor command that precedes a self-generated movement is issued. This efference copy can then be used by the internal predictive models of the motor system in order to generate accurate predictions about one's own actions [14].

On the other hand, afferent signals are the sensory peripheral signals that can be either the effect of self-generated stimulation (re-afferent) or of externally-generated stimulation (ex-afferent). Taken together, the afferent peripheral signals seem to support an ecological self-awareness [15], in the sense that they provide information about the body and the world within which the body is situated, since information about one's body cannot be perceived in isolation from the environment. According to Gibson each act of perception contains both propriospecific information about the self (i.e. re-afferent), as well as exterospecific information about the distal environment (i.e. ex-afferent): "Egoreception accompanies exteroception, like the other side of the coin...One perceives the environment and coperceives oneself" [15, p.126]. It has been suggested that afference, and especially proprioception, provides us with the phenomenal content of our bodily self-awareness, because proprioceptive information unambiguously pertains to the self [16]. However, the meaning of afferent signals for perception and behaviour is ambiguous, precisely because the afferent signals can be either self- or externally-generated. Recent theories of motor control have shown how an interaction between the efference copy and sensory inflow may reduce this ambiguity. In the case of a self-generated action, intentions and efferent information can predict the consequent multisensory signals produced by one's own movement. This prediction is thought to take place in the internal models of the motor system[14].

We do not normally experience the efferent and afferent components separately. Instead, we have a general awareness of our bodily actions that involves both components. However, the efferent and the afferent signals may support different functions, and may give rise to distinct forms of body-awareness. In fact, recent neuroscientific and phenomenological approaches to selfhood [10, 17, 18] distinguish between two aspects of bodily self consciousness: the sense of agency and sense of ownership.

#### **10.4 From physiological signals to the experience of one's own body**

Sense of agency is the sense of intending and executing an action [5], a sense of oneself as an actor or a sense that one's actions are one's own [6]. In agency, the self is experienced as the source of the experience of the acting, suggesting that the relationship between the self and the action is not simply causal, because that would imply that the agent can be separated from the action. This stance implicitly

suggests that awareness of action cannot be separated from agency, at least not under normal circumstances [6].

The feeling that the body I inhabit is mine and always with me is called body-ownership. This feeling is a fundamental element of the phenomenal experience of my body. Moreover, ownership refers to the sense that "I" am the experiencing subject, my body is the site where the sensory experience takes place, and it is my body the one that experiences a certain sensation, either self- or externally-generated [5,19]. Thus, the sense of body-ownership is present when I move voluntarily, but also when an externally-generated somatic sensation is experienced by me (e.g. passive movement), and also when my body is at rest. The raw basis of body-ownership may be provided by the epistemologically private experience that I have of my body from within (e.g. as provided by the proprioceptive sense), by the body schematic control of movement, and by multisensory integration of body-related sensory signals (e.g. vision of touch and touch).

Following these operational definitions, the sense of agency involves a strong efferent component, because actions are centrally generated. On the other hand, the sense of body-ownership involves a strong afferent component, because the content of body-awareness originates mostly from the plurality of multisensory peripheral signals. An important phenomenological observation is that the sense of body-ownership is present not only during voluntary actions, but also during externally- or passively generated experiences. In contrast, only voluntary actions, or actions that are experienced as voluntary, should produce a sense of agency. To give an example, when I voluntarily move my hand, I have a sense of agency by identifying my intention to move as the source of the movement, and a sense of ownership, by identifying the moving hand as mine. However, if someone else moves my hand, I do not have a sense of agency over the hand movement, yet I retain a sense of ownership of the moving hand as being mine. It is therefore important to ask what is it exactly that the sense of agency adds to the sense of ownership, and more importantly how can agency be used to address the self-other distinction. Recent studies (for a review see [19]) have provided valuable insights on how we experience and represent our bodies in body-ownership and agency, but they have also raised important methodological and epistemological questions.

### **10.5 Who is the agent?**

Several questions regarding the nature of self-specific body- and action-representations were raised with the discovery of the mirror neurons in the macaque brain. The properties of mirror neurons suggest that both self-generated and observed actions, as well as the experience and observation of sensory events, activate overlapping neural networks [4]. These common activations reflect "shared" representations of actions and bodies that are agent-neutral, arguing against a special representation of one's own body.

In every inter-action, there are both private and public states and signals represented in the brain of the agent and/or the observer. Private signals refer to centrally generated action representations such as intentions, efferent signals (e.g. efference copy, motor commands), and re-afferent signals such as proprioception. Public signals originate from observable sensory events, both re-afferent and ex-

afferent, such as visual and auditory signals that may refer to bodies, objects or complex patterns of motor behaviour. How are these signals used to disambiguate the identity of bodies and the origin of actions? The predictive function of the motor system and the resulting anticipation of sensory inflow have been well documented in the literature across different experimental paradigms [14]. However, the link between the operation of the internal models of the motor system and the conscious awareness of action is still debated [20]. A critical issue in this debate relates to the question of the conscious experience of agency.

It is not clear which signal(s) or state variable(s) of the motor system give rise to the conscious experience of agency. Accumulating evidence suggests that we are not aware of the actual motor commands or motor parameters of our actions [20]. This un-awareness of the actual motor commands was nicely demonstrated by Fourneret and Jeannerod [21] in a replication of the ingenious experiment by Nielsen on volition [22]. Participants were asked to draw lines in a sagittal direction on a digital tablet using a stylus. When tracing a line on the tablet, the subjects could see through the mirror a red line appearing on the computer screen in exact coincidence with the displacements of the tip of the stylus on the tablet. The output of the graphic tablet was processed by the computer using a simple algorithm for adding a linear directional bias. When the bias was set to the right (e.g. at 15°), a line traced in the sagittal direction on the tablet appeared to the subject to deviate to the right at an identical angle. Subjects were able to correct for the introduced bias, and managed to trace lines that appeared to be sagittal. However, when asked after each trial to either report verbally their movement or to reproduce it, it became evident that they were unaware of the corrections they produced during the experimental trials [21].

A theoretical implication of this study is that there seems to be a two-level coding of action-related information [23]. The 1st level codes the sensory and motor signals that are used for the control and monitoring of movements. According to Georgieff and Jeannerod [23], these signals are not made available to consciousness, and therefore they are not the ones used for conscious judgments of actions. The 2nd level coding of action-related information represents the “public” aspects of action, such as the observable effects of the action (see also [24]), whereas the 1st level represents the “private” aspects, such as the efference copy, the motor command, and the sensory feedback. The 2nd level becomes especially important when we adopt a public view of action.

The public view of action-representations is based on the ideomotor theory put forward by James [7]. The basic hypothesis of the ideomotor approach is that actions are coded in terms of the perceptual events resulting from them. Therefore, in action generation, the actual movement is governed by a representation of the goal of the action, which could be agent-neutral. Similarly, in action perception, the generated representations attempt to detect the intended goal. Thus, both own and other's people actions are coded in a common way (see the common coding theory [25,26]). Similarly, perceived events (i.e. perceptions) and to-be-produced events (i.e. actions) are commonly represented by an integrated network of cognitive structures called event-codes (for a review see [25,26]).

With regards to the issue of agency, according to the common coding theory, there are neither quantitative nor qualitative differences in the generation and processing of these common representations that would enable the a priori attribution of the source of the action (i.e. agency), allowing thus a clear-cut

distinction between self and other. Knoblich and Flach [27], in an experiment on action prediction, where participants had to predict the outcome of either self- or other-generated actions (e.g. throwing darts), found an authorship effect in correctly predicting the outcome of self-generated actions. In the light of this evidence, they acknowledge that one problem of the common coding theory is that “[...] first-person and third-person information cannot be distinguished on a common-coding level” [27, p. 468]. The authorship effect reported by Knoblich and Flach could be accounted by the fact that the motor system that perceived the action during the prediction task was the same motor system that generated the action. Thus, the matching process between first-person perspective (i.e. producing the effect) and third-person perspective (i.e. observing the effect) was even more complete, leading to more accurate predictions. Nevertheless, according to the common coding theory, it remains unclear what could be the functional role of the first-person perspective in action generation and perception: “In any case, we see no indication of privileged access to 1st person knowledge, that is, to knowledge referring to the mental preparation of the upcoming action and arising before the fact. Rather, like any other event, both the physical action itself and its mental antecedents appear to be perceived after the fact. The mental representation seems to follow the physical event it represents.” [25, p.149].

According to this public view of action-generation and perception, agency of action is not intrinsically embedded in the generation of the action. Instead, agency of action is the result of an attribution process that takes place at the observational level of public aspects of action that happen after the action itself. The same could be true of the self-other distinction.

Jeannerod and colleagues [23, 28] have argued for the necessity of a specialized neural system that would discriminate between the self and the other, and thus provide the sense of agency. The function of this “who system” is to answer the question “who made the action?”, in other words, who was the agent. The necessity of the “who system” is justified by the fact that several kinds of action representations are independent of the agent who is performing them. It has been shown that both the representations of self-generated and observed actions activate overlapping neural networks [29]. These common activations “share” representations of actions that are agent neutral [30]. According to the “shared representations” model, the “who did it?” question can be answered in computational terms only by disentangling the non-overlapping areas that are active during self- and other-actions. Within this framework, even intentions seem to be agent-neutral: “It could be the case either that intentions [...] are impersonal representations or that, although their form is <agent, action, goal>, the agent parameter can be left unspecified” [31, p.139]. Neither the intention of the acting subject, nor the translation of the intention into an efference copy and a motor command suffice for the experience of agency. Thus, for the “who system”, the default mode of operation seems to be “no agent”. This line of argument implies that the sense of agency arises as a post-action reconstructive meta-representation, and that this meta-representation would be necessary for efficient self-other distinction.

The “who system” seems to be strongly committed to a representational model of agency and self-consciousness, and thus, the problem is no more that of *being* the agent, but it is rather that of *knowing* who the agent is. In this sense, the model ignores all the processes that precede the execution of intentional actions, and

instead focuses on the perception of action as an objective manifestation of “naked intentions” [31]. On a strong view of the attributional perspective on agency, conscious agency could only be “the mind’s best trick” [32]; an “after the fact”, perhaps illusory, ownership of the intention to move. If “shared representations” is the brain’s basic model, then the “who system” is needed in order to reconstruct the representation of an agentic self. In effect, the “shared representations” model and the “who system” raise an epistemological problem, because they leave no room for a phenomenally or epistemologically special self.

However, on the experiential level, the sense of agency seems to presuppose a subjective point of view, a 1<sup>st</sup> person perspective [47], and in addition the sense of agency has to be distinguished from a judgment of agency [33]. By refuting the very possibility of an intrinsic link between intention, efference action, and perception of one’s body, it is impossible to provide an ecological account of agency. The acting body is perceived, not only from the outside (e.g. vision), but also from within (e.g. proprioception), and it is therefore experienced in an epistemologically immediate fashion. Moreover, efferent signals are present only when an action is self-generated, and thus, they could in principle code in an intrinsic way the origin of the action. It may be possible that the sense of agency is a phenomenological correlate of a neural or functional signatures that are unique to voluntary actions, and that such signatures may actually construct rather than reconstruct the conscious sense of agency. On this hypothesis, agency is not embedded in the public aspects of action, but may arise as an intrinsic property of action-execution or even action-generation processes (for a review see [19, 34]). Converging evidence suggests the sense of agency seems to be dependent upon the processing of efferent signals that precede the action itself, and that such signals intrinsically modulate the time-awareness of action, the sensory processing of re-afferent events, and action-attribution [19, 35].

### **10.6 A working example: self-recognition**

A working example that may be used to elucidate this tension between private and public signals, between shared and self-specific representations, and provide some critical insights for the self-other distinction is the self-recognition of bodily movement. Recent research on self-recognition distinguishes between two related computational problems: the problem of action recognition and the problem of self-recognition. In action-recognition, the brain must distinguish between afferent information generated by our own movements, and afferent information that is externally imposed. Action-recognition may involve unconscious operation of internal predictive models of the motor system [34], while self-recognition appears to be a specific cognitive process typically involving conscious experience [36]. Self-recognition, in the current context, involves deciding whether a visual stimulus shows one’s own body or not. Thus, self-recognition is also possible in the absence of any movement or action, for example by purely morphological features. However, we often use voluntary movements as a means of self-recognition. This fact by itself suggests a hierarchical relation between action-recognition and self-recognition: voluntary action can aid self-recognition only if one can be sure that the viewed resulting body movements were caused by one’s own voluntary action. In most studies of self-recognition, participants see a body-

part, which may or may not be related to their own body. The task is to judge whether what they see is their own body or not. The information available to support this judgment is systematically varied across conditions, for example by moving the hand [36, 37], by introducing delays between the movement and the visual feedback [38], or by rotating the hand image [39]. Self-recognition requires the monitoring and integration of various sources of information such as intention, motor command and somatic perception in a short time-window. Only a few studies have explicitly investigated the link between voluntary movement and action-recognition [40, 41], while the specific contribution of efferent signals for self-recognition has been under-investigated (see Table 1).

<b>Summary of Action-Recognition Studies</b>			
	<b>Fournieret &amp; Jeannerod, 1998</b>	<b>Farrer et al., 2003b</b>	<b>MacDonald &amp; Paus, 2003</b>
<b>Participants</b>	Normal Subjects	Normal Subjects & Deafferented Patient GL	Normal Subjects
<b>Experimental Manipulation</b>	Angular Bias	Angular Bias	Temporal Delays
<b>Visual Feedback</b>	Display of the line drawn by the subjects	Computer-reconstructed image of a hand	CyberGlove
<b>Manipulation of Efference</b>	No	Yes	Yes
<b>Results</b>	Subjects automatically compensate for the introduced bias, but they are unaware of these corrections when bias < 15°.	Normal subjects: differences between active and passive movement were significant only for bias > 30°. GL was significantly more impaired.	rTMS over left superior parietal lobule impaired the detection of asynchrony for active but not for passive movement.
<b>Summary of Self-recognition Studies</b>			
	<b>Daprati et al., 1997</b>	<b>Sirigu et al., 1999</b>	<b>Van den Bos &amp; Jeannerod, 2003</b>
<b>Participants</b>	Schizophrenics & Controls	Parietal Patients & Controls	Normal Subjects
<b>Experimental Manipulation</b>	Visual Feedback: 1. Own hand 2. Other's hand/same movement 3. Other's Hand/different movement	Visual Feedback: 1. Own hand 2. Other's hand/same movement 3. Other's hand/different movement	Visual Feedback : 1. Rotation of Hand-Location on screen (0°, 90°, -90°, 180°) 2. Movement (same, different, no movement)
<b>Visual Feedback</b>	Video display of 1 hand	Video display of 1 hand	Video Display of 2 hands (performing same / different / no movement)
<b>Manipulation of Efference</b>	No	No	No
<b>Results</b>	Schizophrenics were significantly impaired in condition 2	Parietal patients were significantly impaired in condition 2	For same movements, self-recognition performance was influenced by the rotation of the hand image.

**Table 1.** A summary of recent experiments on action- and self-recognition

The summary of studies presented in Table 1 shows that only two action-recognition studies have dissociated efferent from afferent information, while none of the self-recognition studies presented above have examined the distinctive roles of efferent and afferent information.

Daprati, Sirigu and colleagues [36,37] investigated the self-recognition of simple and complex gestures in schizophrenic and in parietal patients respectively, using identical experimental designs. Participants were instructed to perform simple or complex self-generated movements (extension of one or two fingers), without direct visual image of their hand. Participants could see on a mirror in front of them (a) their own hand, or (b) the experimenter's hand performing the same movement as the participant's hand, or (c) the experimenter's hand performing a different movement from the participant's hand. Participants were asked to judge whether they saw their hand or not. Consistent results from both experiments revealed that both patients and controls performed almost perfectly when they saw their own hand, and when they saw the experimenter's hand performing a different movement. This suggests that the detection of a mismatch between visual and proprioceptive/efferent information is a relatively easy task, even for patients who display impaired awareness of action [34]. However, both schizophrenics and parietal patients were significantly worse, compared to controls, when they saw the experimenter's hand performing the same movement as them. In this critical condition, they said that they saw their own hand, whereas in fact they saw the experimenter's hand. In other terms, participants tended to misattribute the experimenter's hand to themselves.

In all these studies [36, 37, see also 39], the performed movements were self-generated, that is, participants had both efferent and afferent signals available for comparison against the visual feedback. Efferent information was not dissociated from proprioceptive information, and therefore the relative contributions of these two kinds of information for explicit self-recognition were not clarified. Results showed a significant impairment in the self-recognition performance of schizophrenic and parietal patients when these groups saw someone else's hand performing the same movement as they did. In fact, patients misattributed the viewed hand to themselves. What can account for the enhanced performance of normal participants? In other words, which factor enabled normal participants to distinguish between self and other more efficiently? These studies cannot conclusively answer whether normal subjects integrated in a more efficient way afferent information alone (visual and proprioceptive feedback), that is, an integration of both public and private signals, or whether they used fine-grained efferent information for their self-recognition judgments. According to Jeannerod [30], 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 for self-recognition, over and above multisensory integration.

Moreover, the paradigm of the rubber hand illusion [42, 43] 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 vision and

proprioception were synchronised. In such cases, a dominance of vision which is based on the perception of public "states" would be the main cue for self-recognition. Thus, it may be hypothesized that for highly reliable self-other discrimination, visuo-proprioceptive congruence may not be sufficient. The specific contribution of efference to self-recognition can only be addressed by implementing a situation where visuo-proprioceptive information is kept congruent and maintained constant, while efference is systematically manipulated. This manipulation was implemented in a recent self-recognition experiment. Tsakiris et al. [44] 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. Participants judged whether the right hand they saw was theirs or not. In that experiment, unlike other self-recognition studies [36, 37, 39], 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.

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"). Self-recognition 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 somatic effect of an action 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. This significant difference suggests that efference can also improve the comparison and integration of private (e.g. proprioception) and public (e.g. vision) signals, because these were the same in both the self-generated and externally-generated conditions while participants were looking at their own hand. 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 only 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 [14]. 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 [37, 41].

The results suggest that afferent-driven body-awareness alone may not be sufficient for reliable explicit self-recognition. Similarly, even when there is a perfect match between proprioception and vision, efference does provide a significant advantage for their integration. 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 [45]). This finding also suggests that efferent information is important for self-recognition, and the self-other distinction, and not only for motor control. The distinctive role of efference in self-recognition suggests that central efferent signals have a highly predictive power allowing the correct detection of appropriate afferent signals that pertain to one’s self, and can therefore be used to distinguish between the self and others. It has been suggested [46] that a basic computational mechanism that implements this function may also underpin higher cognitive abilities such as perspective taking and mental states attribution, and that right temporo-parietal areas may underpin this basic computation.

### **10.7 Towards an implicit self-recognition measure?**

A methodological confound present in almost all the self-recognition studies is the use of explicit measures of self-processing. Participants in self-recognition studies are asked to explicitly recognize the identity of a moving hand they see on a screen in front of them which could be theirs or not. The experience that participants have during these tasks does not do justice to the actual experience (or even representation) that one has about one’s own body, because we rarely represent explicitly and reflectively our sense of embodied selfhood [47]. A recent study [49] showed that the primary motor cortex forms an agent-specific, not neutral, representation of observed actions. Observing another agent acting facilitates the observer’s motor system [48], whereas observing one’s own actions tends to suppress the excitation of the motor system [49]. This novel finding implies that the motor system may be sensitive to representations of other agents as qualitatively different from the self, and as such, it may underpin a distinction between self and other, providing thus an important addition to the “self-other equality” of the mirror system. Further studies should investigate whether this low-level sensorimotor representation might underpin 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, as distinct from other agents.

## 10.8 Conclusions

We constantly feel, see and move our body, and have no doubt that it is our own. Correct demarcation of the physical body's boundaries seems to be essential for goal-directed action, for our sense of who we are and for our successful interaction with other agents. It has been proposed that the experience of one's body and related sensory events are characterized by a sense of body-ownership, and actions generated by one's own body are characterized by a sense of agency. Converging evidence suggests that the sense of agency is efferent-driven, whereas the contents of body-ownership are predominantly afferent in their origins [19, 43]. This effect of efference is not surprising since our main way of being-in-the-world is to voluntarily act on it, rather than passively perceiving it. In this sense, bodily self-awareness is not simply another form of object consciousness. Models of self-awareness that over-emphasize the shared self-other representations ignore the mere fact that my body is not so much an object of perception, but rather it is given to me as a subject, and that agency actually structures the experience of one's body. The sense of body-ownership and the sense of agency may underpin a minimal model of the self as distinct from other agents. This model would process efferent and afferent signals to inform and update representations of the body and structure its experience. Perhaps, this self-model would be a prerequisite for higher cognitive abilities, such as perspective taking and action understanding.

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## 10.10 References

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## **Appendix 5:**

**Reprint of Haggard P & Tsakiris M. (2009)  
The experience of agency: feeling,  
judgment and responsibility. Current  
Directions in Psychological Science,  
18(4), 242-246.**

# The Experience of Agency

## Feelings, Judgments, and Responsibility

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**ABSTRACT**—*The experience of agency refers to the experience of being in control both of one's own actions and, through them, of events in the external world. Recent experimental studies have investigated how people recognise a particular event as being caused by their own action or by that of another person. These studies suggest that people match sensory inputs to a prediction based on the action they are performing. Other studies have contrasted voluntary actions to physically similar but passive body movements. These studies suggest that voluntary action triggers wide-ranging changes in the spatial and temporal experience not only of one's own body but also of external events. Prediction and monitoring of the consequences of one's own motor commands produces characteristic experiences that form our normal, everyday feeling of being in control of our life. We conclude by discussing the implications of recent psychological work for our notions of responsibility for action.*

**KEYWORDS**—agency; action; prediction; volition; monitoring

Agency refers to a person's ability to control their actions and, through them, events in the external world. We experience agency throughout our waking lives to the extent that we control the movements of our body in walking, talking, and other voluntary actions. In addition, we also feel and know that we control these events: We have a "sense of agency" to accompany the fact of our agency. Although everybody knows what agency is, psychological debates about agency have generally been controversial. Many psychologists think of agency more as an illusion or a confabulation than as a bona fide mental state. In this article, we first discuss how the human mind generates the sense of agency and how the sense of agency can be assessed empirically. We then consider how the sense of agency may malfunction and what role agency plays in the social concept of responsibility for one's own actions.

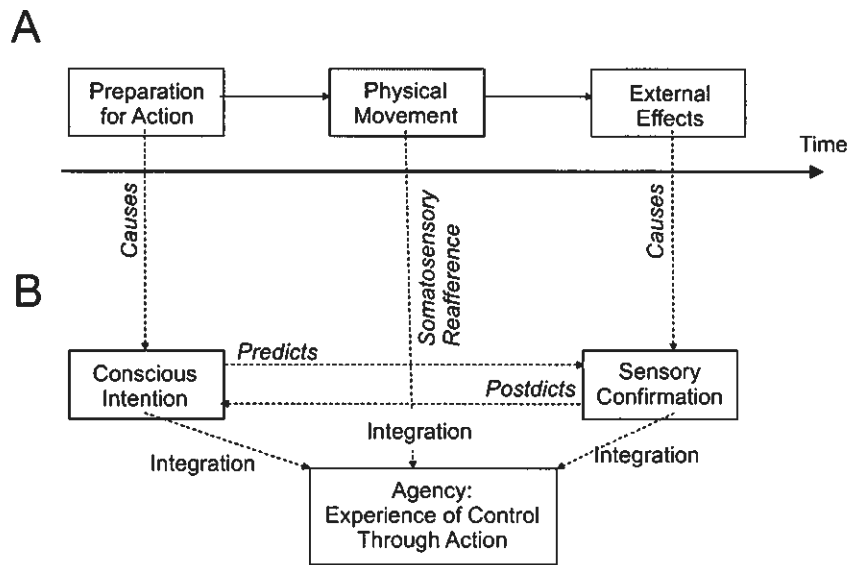
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As we perform actions in our daily lives, we have a coherent experience of a seemingly simple fluent flow from our thoughts, to our body movements, to the effects produced in the world. I want to have something to eat, I go to the kitchen, I eat a piece of bread. We have a single experience of agency—of control over these events—because our cognitive representations of the successive stages of sensorimotor control are tightly linked together (Fig. 1). Action prediction is the key mechanism underlying this coherent linkage. For example, my intention to eat something already anticipates the taste of the bread and the feeling of satiety. More generally, the "I did that" aspect of the sense of agency depends on our ability to predict what will follow from each specific motor act we perform.

### "WHODUNNIT?": EXPLICIT JUDGMENTS OF AGENCY

Several experimental studies have investigated agency by asking participants to judge whether they caused a particular sensory event. Typically, participants perform voluntary actions, in response to a cue and then receive sensory feedback about their movement, which is sometimes veridical and sometimes distorted (e.g., the spatial path of movement is disturbed, a temporal delay is inserted; see Farrer et al., 2003; Metcalfe & Greene, 2007; Sato & Yasuda, 2005; Wegner, 2003). Participants explicitly state whether they experience agency over the effect (e.g., by answering the question "did you produce the movement you saw?"). An important distinction should be made between situations in which another possible agent is present, for example a second person performing a similar movement at the same time (Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005), and situations without an alternative agent. In the former case, participants generally view a visual feedback of a hand action and must judge if they made the action or not. Judging agency is then essentially the same as recognising oneself. These studies generally find a bias to judge oneself to be the author of action. They also emphasise that agency plays a major role in distinguishing oneself from non-self, including other people.

In other studies, no alternative agent is present, and participants judge whether they caused a sensory event (e.g., a tone occurring sometime after their action). In general, greater delays or distortions



**Fig. 1.** Objective physical events (A) and subjective experiences (B) during action that contribute to the sense of agency. As shown in (A), actions are preceded by neural preparation, which includes motivation for action, selection of appropriate movement parameters, and activation of cortical motor networks. Physical movement of the body is signalled by the somatosensory systems (somatosensory reafference), and forms the core of our experience of action. Finally, actions are generally performed to achieve specific desired effects (goals) in the external world, which are signalled by exteroceptive perception (sensory confirmation). Preparation, body movement, and sensory effect are objective physical events that necessarily occur in strict temporal sequence. In contrast to the objective physical events that it reflects, the subjective experience of action has a strong coherence and unity. The experience of preparing an action already predicts the effect of the action; and sensory information that an intended effect has occurred is retrospectively matched with the prediction (i.e., “postdiction”).

make people less likely to experience agency over the effect. Therefore, the perception of one’s own agency depends on detecting spatio-temporal correlations between one’s actions and its effects. These same principles of spatio-temporal correlation underlie perception of causality in general, suggesting that agency is a special case of causation in which one is oneself the cause of an external event.

However, two quite different explanations have been offered for such judgments about agency. On one view (Sato & Yasuda, 2005), agency judgments are outputs from internal predictions by the motor system of what the consequences of an action are likely to be (Frith, Blakemore, & Wolpert, 2000). If there is no discrepancy between prediction and sensory feedback, then “I” am the agent responsible for this particular event. An alternative view treats agency as an inference, rather than a prediction. Thus, the mind may infer and reconstruct a path between conscious intention and effect. According to Wegner (2003), the sense of voluntary control is effectively a reconstructive illusion that one’s intention has caused an external event, analogous to Hume’s view of causation as an illusory inference from the constant conjunction of cause and effect.

#### FEELINGS OF AGENCY AND JUDGMENTS OF AGENCY

Synofzik, Vosgerau, and Newen (2008) drew an important distinction between the judgment of agency (JoA) and the feeling of

agency (FoA). JoA refers to explicit conceptual attributions of whether one did or did not make an action or cause an effect. A jury’s verdict, for example, is a JoA. FoA refers to the subjective experience of fluently controlling the action one is currently making, and is nonconceptual. What, then, is the link between FoA and JoA? Under normal circumstances, the FoA is a *necessary* condition for JoA, and indeed forms the evidence base for the judgment: My belief that I switched on the lights depends on my experience of reaching for the light switch. This principle fails in a few special circumstances. For example, when several people’s actions simultaneously aim to produce a single effect, a person may judge that he or she has agency over an event because he or she *thought* of making an action, even though the event was in fact caused by someone else (Wegner, 2003).

However, FoA is not normally *sufficient* for JoA. Explicit JoAs require an additional cognitive function of monitoring the effects of action. Only when I see that the lights have come on would I judge that I switched them on. This monitoring process is often unconscious: Indeed, the motor system includes specific mechanisms for predicting the sensory consequences of our own actions (Frith, Blakemore, & Wolpert, 2000).

An interesting neurological condition reveals that the experience of making an action can be dissociated from monitoring the effects of action. Patients with anosognosia for hemiplegia (AHP; hemiplegia is weakness following a stroke affecting motor

areas of the brain) deny that their affected limb is paralysed. For example, patients may assert that they performed an action using their paralysed limb, which in fact remains immobile. The patients' JoA seems to be based *only* on the feeling that they prepare appropriate motor commands for the action. Anosognosic patients seem to skip the normal stage of monitoring whether appropriate effects of limb movement actually occur (Fotopoulou et al., 2008). In AHP, the feeling of intending an action becomes sufficient for a JoA, and the effects of the intention are no longer monitored in the normal way. This suggests that effect monitoring is a specific cognitive function that normally provides the appropriate link between FoA and explicit JoA but that has been selectively compromised in these patients.

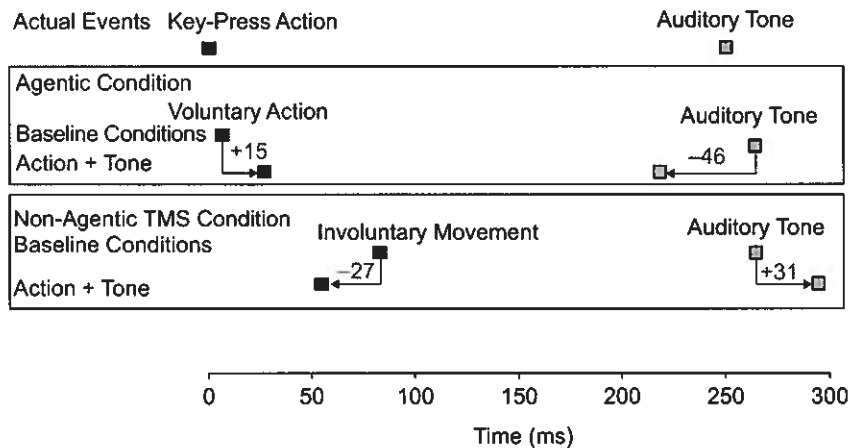
**AN ALTERNATIVE APPROACH: FACT AND SENSE OF AGENCY**

An important source of confusion in the literature on sense of agency comes from the nonagency control conditions to which agency is compared. Most previous studies of JoA involve comparing sensory events caused by one's own action to sensory events caused by another person's action. Therefore, these studies are really comparing first- and third-person perspectives on action feedback, rather than comparing representations of action itself.

An alternative approach involves comparing voluntary action and passive movement within a single individual. Voluntary action and a passive limb displacement may involve physically

identical movements but are different both physiologically and psychologically. Voluntary movement depends on a cascade of cognitive-motor processes within the brain's frontal lobes (Haggard, 2008): These processes give us a sense of agency over our own voluntary movement, and over the effects of our movement on the external world, while passive movement does not. Comparing active with passive movements recalls Wittgenstein's (1953/1998) question "What is left over if I subtract the fact that my arm goes up from the fact that I raise my arm?" This approach views agency as an addition to or modification of somatic experience. Experimental studies show that agency changes the experience of the body and the outside world in three ways: effects on perceived time, effects on sensory intensity, and effects on the spatial representation of the body itself.

**Temporal Attraction: Agency Influences Time Perception**  
 Action fundamentally changes the experience of time. In fact, time perception has been one of the most important indirect methods for studying agency. In one approach, participants are asked to judge the onset of voluntary actions (a key press) and of a sensory event (a tone) occurring shortly afterward. The perceived time of the action is shifted later in time, toward the ensuing tone, relative to the perceived time of an action in a baseline condition in which no tone occurs. In other blocks, participants are asked to judge the onset of tones. The perceived time of a tone that follows the participant's voluntary action is shifted earlier in time, back toward the action that caused it, relative to a baseline condition in which tone occurs without any



**Fig. 2.** Changes in time perception associated with agency. A simple key-press causes an auditory tone. In baseline conditions, participants note on a rotating clock the time at which they press the key in the absence of a tone or the time at which the tone occurs in the absence of a keypress. In agency conditions, the keypress is associated with a tone, and the perceived time of action and tone are perceived as shifted from their baseline values toward each other. The magnitude of each shift (in milliseconds, ms) is shown in red. In a nonagency control condition, the voluntary key-press was replaced by an involuntary contraction of the same muscles used to press the key (triggered by stimulating the motor areas of the brain using transcranial magnetic stimulation). This produces a perceptual repulsion (i.e., the key-press and tone are perceived as farther apart) in contrast to the shifts found in the agency condition. Data taken from Haggard, Clark, and Kalogeras (2002).

action being made. This “intentional binding” effect, shown in Figure 2, suggests that the sense of agency may involve a specific cognitive function that links actions and effects across time, producing a temporal attraction between them (Haggard, Clark, & Kalogeras, 2002). Crucially, no such effects were found for passive involuntary movements, suggesting that intentional binding is a specific marker of agency.

#### Sensory Attenuation: Agency and Perceived Sensory Intensity

A self-generated sensory stimulus is perceived as less intense than an identical externally generated stimulus. For example, one cannot tickle oneself (Frith, Blakemore, & Wolpert, 2000). Internal models within the motor system use internal copies of voluntary motor commands (efference copies) to predict and thus cancel or attenuate the sensory consequences of the action (Frith, Blakemore, & Wolpert, 2000). These models compare the predicted and actual sensory input during action. When there is little or no discrepancy between predicted and actual state, then one is oneself the agent. This approach can correctly discriminate between internally generated and externally produced sensory events, and can therefore ascribe agency. However, models based on attenuation treat agency as absence of externally generated perceptual experience, and not as an experience in itself. They cannot therefore explain why there is a positive experience of agency in the first place.

#### Agency and the Unity of Bodily Awareness

Comparisons of active and passive movement define agency as an additional component, over and above the normal experience of one’s own body. Recent evidence suggests that agency transforms the experience of the body itself. In keeping with this definition, a number of studies have compared the effects of voluntary action and passive movement on the awareness of one’s body. Agency generally enhances both spatial and temporal (Tsakiris et al., 2005) processing of proprioceptive information from sensory receptors in the body. We recently used the rubber hand illusion (Botvinick & Cohen, 1998) to show that voluntary actions produce a more coherent and unified proprioceptive representation of the body than do passive movements (Tsakiris, Prabhu & Haggard, 2006). In the rubber hand illusion, synchronous stimulation of both a rubber hand (or a video image of it) and the participant’s unseen hand produces a strong illusion that the rubber hand is part of the participant’s own body. A reliable behavioral proxy of the illusion is a shift in the perceived location of the participant’s hand toward the rubber hand. In our experiment, when the stimulation involved passively displacing the participant’s hand and monitoring the movement via a video image of the hand, the effect was confined to the individual finger that was passively displaced. In contrast, when the participant actively moved the same finger, the illusion transferred to other fingers also. Voluntary action appeared to integrate distinct body

parts into a unified awareness of the body, whereas equivalent passive stimulation produced local and fragmented proprioceptive awareness. The experience of one’s body as a unified and continuous entity across space and time may be an important component of the sense of agency (Tsakiris et al., 2005).

#### CHALLENGES AND FUTURE DIRECTIONS: RESPONSIBILITY FOR ACTION

Society requires that individuals are responsible for their actions and the consequences of those actions. The subjective experience of agency generally tells us when we are responsible and when we are not. Therefore, an accused’s first-person *sense* of agency often simplifies the process of establishing the facts of agency: If I clearly know that I did it, then I should plead guilty and accept responsibility rather than evade it. Equally, I may know that I did not perform the relevant action. Therefore, the social practices surrounding responsibility are closely associated with the psychology of agency.

The sense of agency is relevant to social and legal responsibility in several ways. First, abnormal sense of agency may provide grounds for diminished responsibility. In particular, our concept of responsibility assumes conscious prediction of the effect of one’s own action and full voluntary control over the action at the time it is made. Thus, diminished responsibility is sometimes recognized in cases of sleep-walking assault. This implies that real-time conscious experience of performing an action is necessary for responsibility. Further, specific conscious prediction of consequences of one’s action is often held to increase responsibility (cf. premeditated actions vs. actions made “in the heat of the moment”). People are often held more responsible for direct and immediate effects of an actions than for effects that are only distantly, unspecifically, and unpredictably related to it (Lagnado & Channon, 2008).

Judgments of whether or not individuals should be held responsible for their actions involve one of several very different questions about the person’s mental processes—questions that touch on quite different areas of psychological theory. First, one might ask whether an individual was aware of making the action. This question addresses the individual’s sense of agency, and answering it depends on knowing about internal sensorimotor signals in the brain. Second, one might ask whether the individual could have, should have, or did predict the consequences of his or her action. This question addresses the predictive match between action and effect that underlies JoA, and the answer bears on general aspects of cognitive ability, such as associative learning and intelligence. Third, one might ask whether the individual understood that the consequence of the action was wrong. This addresses the individual’s moral judgment and relates to the theory of value rather than theory of agency. In the next decades, expanding knowledge about the psychological and neural bases of agency will become increasingly relevant to neuroethics and law.

**Recommended Reading**

Fotopoulou A., Tsakiris M., Haggard P., Vagopoulou A., Rudd A., & Kopelman M. (2008). (See References). An experimental demonstration that motor intention dominates over sensory information about the actual effects of movement in patients with anosognosia for hemiplegia, suggesting that effect monitoring is a specific cognitive function that normally provides the appropriate link between feelings of agency and explicit judgments of agency but that has been selectively compromised in these patients.

Haggard, P., Clark, S., & Kalogeras, J. (2002). (See References). Reports a novel effect of agency on the experience of time: Voluntary action causes a temporal attraction between the perception of an action and the perception of a subsequent sensory event, an effect that is absent when a physically similar passive movement is followed by the same sensory event.

Wegner, D.M. (2002). *The illusion of conscious will*. Cambridge, MA: MIT Press. An extensive psychological exposition of the view that our behavior is generated unconsciously but that the processes that generate it may produce an illusory experience of conscious control.

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Synofzik, M., Vosgerau, G., & Newen, A. (2008). Beyond the comparator model: A multifactorial two-step account of agency. *Consciousness and Cognition*, 17, 219–239.

Tsakiris, M., Haggard, P., Franck, N., Mainy, N., & Sirigu, A. (2005). A specific role for efferent information in self-recognition. *Cognition*, 96, 215–231.

Tsakiris, M., Prabhu, G., & Haggard, P. (2006). Having a body versus moving your body: How agency structures body-ownership. *Consciousness and Cognition*, 15, 423–432.

Wegner, D.M. (2003). The mind’s best trick: How we experience conscious will. *Trends in Cognitive Sciences*, 7, 65–69.

Wittgenstein, L. (1998). *Philosophical investigations*. Oxford: Basil Blackwell. (Original work published 1953)

## **Appendix 6:**

**Reprint of Tsakiris M, Longo M & Haggard P. Having a body versus moving your body: neural signatures of body-ownership and agency. *Journal of Neuroscience, currently under review***

Journal Section : Behavioral/Systems/Cognitive

**Title: Having a body versus moving your body: neural signatures of agency and body-ownership**

**Abbreviated title: Neural signatures of agency and body-ownership**

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†MT & ML declare equal contribution for this paper

Number of figures: 4

Number of tables: 3

Contents of supplemental material (if applicable)

Number of pages: 23 (including text and references), 33 (including text, references, tables & figures)

Number of words for Abstract (238), Introduction (497), and Discussion (1,489)

Keywords: agency, body-ownership, supplementary motor area, angular gyrus, parietal cortex, cortical midline structures

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**Abstract**

Two important aspects of self-consciousness are the sense of one's own body (so-called 'body-ownership') and the sense that one controls one's own bodily actions (agency). remains unknown. The exact relation between these has been the focus of much speculation, but remains unclear. We distinguish two models of the ownership-agency relation. On an 'additive' model, agency and body-ownership are strongly related, because the ability to control actions is a powerful cue to body-ownership. This view implies a component common to the senses of body-ownership and agency, plus possible additional components unique to agency. An alternative 'independence' model holds that agency and body-ownership are qualitatively different experiences, triggered by different inputs, and recruiting distinct brain networks. We tested these two specific models, by investigating the sensory and motor aspects of body representation in the brain using fMRI. Activations in midline cortical structures were associated with a purely sensory-driven sense of body-ownership, and were absent in agency conditions. In contrast, activity in the pre-SMA was linked to the sense of agency, but distinct from the sense of body-ownership. Importantly, no shared activations that would support the additive model were found. The results support an independence model of agency and body-ownership, and do not support the additive model. Body-ownership involves a psychophysiological baseline, linked to activation of the brain's default mode network. Agency over one's body is linked to premotor and parietal areas involved in generating motor intentions and subsequent action monitoring.

## **Introduction**

The feeling that the body I inhabit is 'my own' (sense of body-ownership, SoB), is normally experienced not only during voluntary actions, but also during passive movement and at rest. In contrast, only voluntary actions generally produce the feeling that I can move and control my body (sense of agency, SoA). On one view, the relation between SoB and SoA is additive, meaning that agency entails body-ownership, because one can control movements of one's own body, but not other objects, at will. Thus, agency offers a strong cue to body ownership. Accordingly, the SoA should involve the SoB, plus a possible additional experience of voluntary control. An alternative view holds that SoA and SoB are qualitatively different experiences, without any common component.

The exact neural bases of SoB and SoA remain unclear. Right posterior insula activation have been associated with SoB (Tsakiris et al., 2007), and SoA (Farrer et al., 2003), while right inferior parietal activations have been associated with breakdowns of SoA (Farrer et al., 2003, 2008) and SoB (Shimada, Hiraki & Oda, 2005). These studies of agency manipulated visual feedback to either match or mismatch proprioceptive and motor signals. However, such manipulations confound agency and body-ownership (Tsakiris, Schütz-Bosbach & Gallagher, 2007), because the brain activations reported could reflect sensori-motor comparisons, which would be relevant to agency, or proprioceptive-visual comparisons, which would be relevant to body-ownership. Instead, SoA and SoB can be disentangled experimentally by comparing voluntary action to passive movement. Both involve physically comparable movement and proprioceptive feedback, but are physiologically and psychologically very different (Haggard, 2008). Comparing active with passive movements can test whether agency represents the addition of action programming to the somatic experience of body movement or whether agency and body-ownership are qualitatively different. It also allows a clear operationalisation of body-

ownership, without confounding by agency. We therefore manipulated the SoB by presenting real-time or delayed visual feedback of movements, and the SoA, by comparing voluntary and passive movements.

We tested two specific models of the relation between body-ownership and agency. The first, ‘additive’ model, holds that SoA entails body-ownership. Thus, active movements of the body producing SoA should also produce SoB, plus an additional component specific to agency. This produces three concrete predictions about brain activations in agency and body-ownership conditions: first there should be some activations common to agency and body-ownership conditions. Second, there should be an additional activation in agency, which is absent from body-ownership. Third, there should be no activation in the body-ownership condition that is not also present in the agency. A second ‘independence’ model holds that the senses of agency and body-ownership are qualitatively different experiences, without any common component. Accordingly, the brain could contain distinct networks for body-ownership and agency. This produces three concrete predictions: first, there should be *no* common activations between agency and ownership. Second, there should be a specific activation in agency conditions that is absent from ownership. Third, there should be a specific activation in body-ownership that is absent from agency.

## **Materials and Methods**

### Experimental Design

A 2x2 factorial design was used (see Figure 1a). The first factor was the type of movement (active or passive), and the second factor was the visual feedback (real-time or delayed). Participants viewed a video image of their right hand that was covered with a woollen glove. This image could be direct (synchronous) or delayed (asynchronous, 500 ms video delay).

In the passive condition, an experimenter passively lifted and lowered the index finger up and down, at approximately 0.5 Hz, by pulling a thread attached to a ring around the participant's finger. In the active condition, the participant actively lifted and lowered their finger at a similar rate. Thus, there were four conditions: active synchronous (AS), active asynchronous (AA), passive synchronous (PS), and passive asynchronous (PA).

INSERT FIGURE 1 AROUND HERE

### Experimental Set-up and Methods

The methods were based on a previous behavioural study (Tsakiris, Prabhu & Haggard, 2007) with modifications appropriate for the fMRI scanning environment (see Figure 1B). Whilst the brain scans were being performed, the participant rested comfortably in a supine position on the bed in the MRI scanner. All participants wore headphones to reduce noise and to communicate with the experimenters between runs. The right arm was extended and placed on a support so that the right hand was positioned in a relaxed position. Within the cylindrical head coil the head was tilted approximately 20-30 degrees by placing foam wedges underneath. Thus the natural direction of gaze was oblique so that the participants saw a projection screen attached to the bore of the scanner through direct vision without discomfort. The participant's arm was placed on a tilted (30-45°) plastic table that was positioned over the stomach of the participant. The table was covered with a soft black material. Finally, to reduce potential head movements, we fixed the position of the head using foam pads. Participants did not have direct vision of their hand.

A mirror was placed above the participant's hand at approximately a 45° angle and a colour MRI-compatible video camera recorded the mirror image of the hand. This video image was fed to a PC in the control room which projected the image of the hand onto a projection screen either with minimal delay (synchronous condition) or with a systematic delay

(asynchronous condition). The video presentation was controlled by a custom LabView (National Instruments, Austin, TX) script. In the synchronous condition, there was a irreducible delay of approximately 100 ms due to digitisation and projection of the image. In the asynchronous condition the delay was approximately 500 ms. Healthy adults perceive viewed actions as self-generated at delays up to 150 ms (Franck et al., 2001), suggesting that the 100 ms delay should not adversely affect illusion of body-ownership and agency (Blakemore et al., 1999). The script also flipped the image to undo the reversal created by filming the mirror image of the hand. The resulting image mimicked the perspective the participant would have had they directly viewed their hand. The distance of the camera from the hand was adjusted before the experiment so that the image of the hand on the projection screen was approximately life size.

There were three functional runs. Each run began with 15 seconds of rest followed by four blocks of stimulation. Each block was comprised of four trials, one of each of the four conditions in random order. Trials began with four seconds of written instructions ('Passive' or 'Active') indicating to the participant whether the upcoming trial would involve active or passive movements. Following the instructions, the video image was displayed and finger movements began. The video image was displayed for 36 seconds. Following each block, there was a rest period of 25 seconds in which participants saw a black screen. Thus, there were a total of 16 trials (4 of each condition) in each run.

Following the experiment, participants were asked to rate their agreement or disagreement with ten statements concerning their experience during the various conditions (see Table 1). Responses were made using a 7-point Likert scale, where a score of +3 indicated strong agreement with the statement, -3 strong disagreement with the statement, and 0 neither agreement nor disagreement. Judgments for each statement were made separately for each of

the four conditions. The order of statements was randomised for each participant. This questionnaire has been used previously to measure subjective experiences of body-ownership and agency in a similar experimental situation (Longo & Haggard, 2009). An overall measure of body-ownership was computed by averaging across items (1) – (3), with items (2) and (3) being scored in reverse. An overall measure of agency was computed by averaging across items (4) – (6), with item 6 being scored negatively.

### Participants

Twenty naïve healthy right-handed volunteers (eight female), between 18 and 36 years of age ( $M = 24.8$ ,  $SD = 5$ ), with no history of neurological or psychiatric illness participated with informed consent. All but one were right handed ( $M = 77.2$ ,  $SD = 43.6$ , range:  $-81.8 - 100$ ) as assessed by the Edinburgh Inventory (Oldfield, 1971). The study was approved by the local ethics committee. One participant was excluded because of large head-movement artefacts. The analyses reported refer to the 19 remaining participants.

### fMRI Methods: Image Acquisition and data analysis

The functional imaging was conducted in a Siemens Sonata 1.5T Scanner to acquire gradient echo T2\*-weighted echo-planar images with blood oxygenation level dependent contrast (BOLD) as an index of local increases in synaptic activity. A functional image volume comprised 48 continuous slices of 3mm thickness which ensured that the whole brain was within the field of view. Volumes were acquired continuously with a TR of 4.32 s. A total of 175 scans were collected during each functional run (12.6 min), with the first four volumes subsequently discarded to allow for T1 equilibration effects. Thus during the three experimental runs performed for each participant a total 525 image volumes were collected.

Data analyses were conducted using Statistical Parametric Mapping (SPM5; Wellcome Trust Centre for Neuroimaging, London, UK, <http://www.fil.ion.ucl.ac.uk/spm>) using MATLAB 7.3 (Mathworks, Natick, MA). All volumes were realigned and unwarped to correct for head movements. The voxel size of normalized images was 2 x 2 x 2 mm. Resulting volumes were normalized to a standard EPI template based on the Montreal Neurological Institute (MNI) reference brain, and smoothed with an isotropic 8 mm full-width half-maximum Gaussian kernel. For each run, time series in each voxel were high-pass filtered at 1/128 Hz to remove low-frequency confounds.

For each individual participant, we fitted a linear regression model (general linear model) to the data (first level analysis). First-level analyses were conducted for each participant by modelling the four experimental conditions and instructions with box-car functions and convolving them with a canonical hemodynamic response function. To eliminate confounds associated with the total amount of movement in each condition, the number of finger movements in each block was included as a separate block-level regressor. We defined linear contrasts in the general linear model. The results of this analysis were contrast estimates for each condition from each of the 19 participants (contrast images). To accommodate inter-subject variability, the contrast images from all participants were entered into a random effect group analysis (second level analysis) using a 2x2 factorial (movement [active, passive], synchrony [synchronous, asynchronous]) analysis of variance (ANOVA).

To analyse the main effects of our experimental manipulations, we computed differential activation patterns associated with synchronous in contrast to asynchronous visual feedback [(AS+PS)-(AA+PA)] and vice versa [(AA+PA)-(AS+PS)]. We similarly computed differential patterns of activations associated with active movement in contrast to passive movement [(AS+AA)-(PS+PA)] and vice versa [(PS+PA)-(AS+AA)]. Activations were identified using a

corrected (with False Discovery Rate; Genovese, Lazar, & Nichols, 2002) two-tailed height threshold of  $p < 0.05$  and an extent threshold of  $k > 10$  contiguous voxels throughout the brain. We also report areas predicted that survive  $p < 0.05$  small volume correction using a 10 mm sphere over coordinates from previous studies. We additionally report regions surviving a two-tailed uncorrected threshold of  $p < 0.001$ .

In addition, to evaluate the different models of agency discussed in the introduction, we performed a structured series of contrasts using the masking procedure of SPM5. Both the additive and independence models predict that there should be agency-related activations specific to the AS condition, that do not appear in the PS condition. The interaction term of the classic ANOVA, expressed as  $[(AS - PS) - (AA - PA)]$ , does not specifically isolate such activations, since it identifies voxels active in *both* the AS and PA conditions, relative to the PS and AA conditions. Because our a priori hypothesis was that activations related to the sense of agency should be specific to the AS condition, and absent from the PA condition, we instead used a more specific contrast based on, an *exclusive* masking procedure:  $[(AS-PS) \text{ at } p < 0.0005 \text{ masked exclusively by } (AA-PA) \text{ at } p < 0.0005, \text{ and } k > 10]$ . This contrast identifies voxels selective for active movements with synchronous visual feedback that were not due to making active movements alone.

Second, the additive model predicts that the ownership-related activations in the PS condition should also appear in the AS condition. Thus, activations in the PS condition should be a subset of those in the AS condition and there should be no activations specific to PS. The independence hypothesis, in contrast, predicts that agency-related activations in the AS condition and ownership-related activations in the PS conditions should differ qualitatively. Thus, the independence model predicts that there should be activations found uniquely in the PS condition, while the additive model predicts that there should not. To identify any such

activations, we used an exclusive masking procedure [(PS-AS) at  $p < 0.0005$  masked exclusively by (PA-AA) at  $p < 0.0005$ , and  $k > 10$ ], to identify voxels that were selective for synchronous visual feedback following passive, but not active, movements.

Third, the additive model predicts that ownership-related activations should be common to the PS and the AS conditions. The independence model, in contrast, predicts that there should not be activations common to the PS and AS conditions, that are not also shared by the asynchronous conditions. To identify such regions, we used an inclusive masking procedure [(AS-AA) at  $p < 0.0005$  masked *inclusively* with (PS-PA) at  $p < 0.0005$ , and  $k > 10$ ] to identify voxels that were *commonly* activated during synchronous video feedback, independent of movement type.

Thus, the two models make one common prediction, that the AS condition should involve an activation unique to agency. More importantly, the models also make two divergent predictions. The independence model predicts some activations unique to the PS condition, whereas the additive model predicts no such activations. Second, the additive model predicts activations common to the PS and AS conditions, while the independence model predicts no such activations. The set of masked contrasts described above, therefore, allow the two models to be directly tested.

## **Results**

### Subjective Reports

The mean ratings for the body-ownership questions per condition were submitted to a 2x2 ANOVA (see Table 1). There were significant main effects of type of movement and feedback ( $F(1,18)=17.48$ ,  $p<0.05$ ) and  $F(1,18)=28.25$ ,  $p<0.05$ , respectively). The interaction between the two factors, however, was not significant ( $F(1,18)=.1$ ,  $p>0.05$ ). Participants reported a stronger sense that the viewed image was their own hand for synchronous than for asynchronous views, in both passive and active conditions. The passive condition corresponds to a pure sense of body-ownership (i.e., that the viewed image is linked to one's own body), uncontaminated by sense of agency. Active movement with synchronous feedback also elicited a significantly stronger sense of body-ownership than the equivalent passive movement condition ( $t(18)=4.4$ ,  $p<0.05$ ).

The mean ratings for the agency questions were analysed with a 2x2 ANOVA. There were significant main effects of type of movement and feedback ( $F(1,18)=40.85$ ,  $p<0.05$ ) and  $F(1,18)=64.61$ ,  $p<0.05$ , respectively). The interaction between the two factors was also significant ( $F(1,18)=4.35$ ,  $p =.05$ ). This interaction shows that the feeling that one can voluntarily control the body at will is selectively present in the AS condition. As predicted, active movement with synchronous feedback elicited a significantly stronger sense of agency than the equivalent passive movement condition ( $t(18)=7.1$ ,  $p<0.0001$ ).

INSERT FIGURE 2 AROUND HERE

### Number of Movements

The mean number of movements performed in each condition were analysed using a 2x2 ANOVA. The main effect of type of movement (i.e. active vs passive) was not significant ( $F(1,18)=2.62$ ,  $p>0.05$ ). Significantly more finger movements occurred in synchronous than asynchronous blocks (15.5 vs. 14.5) ( $F(1,18)=124.62$ ,  $p<0.0001$ ). This effect was modulated by movement type, ( $F(1,18)=11.34$ ,  $p<0.05$ ); the difference between synchronous and asynchronous conditions was larger for active (15.9 vs. 14.4) than for passive (15.1 vs. 14.5) movement blocks. To eliminate confounds associated with total amount of movement, the number finger movements in each block was included as a separate block-level regressor in analyses of fMRI data.

### fMRI Data

#### Main effects

First, we investigate the main effects of movement type and visual feedback. Table 2 shows the local maxima of brain areas with increased neural activity assessed for the main effects of the experimental design.

The main effect of active movement [(AA+AS)-(PA+PS)] was associated with bilateral activity in the cerebellum, primary motor cortex, the postcentral gyrus, and the inferior parietal lobule. The main effect of passive movement [(PA+PS) - (AA+AS)] was associated with bilateral activations in the postcentral gyrus, the medial frontal gyrus, the right precuneus, and the anterior cingulate.

The main effect of synchronous visual feedback [(AS+PS)-(AA+PA)] elicited activations in the right (ipsilateral) postcentral gyrus, the left posterior insula, and the cerebellum bilaterally. The main effect of asynchronous delayed visual feedback [(AA+PA)-(AS+PS)] elicited activations in the right inferior parietal lobule, and more precisely in the supramarginal gyrus and the angular gyrus. As shown in Figure 3, the patterns of activations in the

supramarginal (BA40) and the angular gyri (BA39) are different. Mean beta values calculated in the supramarginal gyrus show that activity in this cluster was mainly driven by the AA condition (Figure 3a), while the mean beta values in the angular gyrus show that activity in this area was elicited both in the AA and PA conditions (Figure 3b). Therefore, the supramarginal gyrus may code for sensorimotor conflicts, while the angular gyrus may code for intersensory conflicts.

#### Specific activations related to agency

As described above, both models predict activations related to the sense of agency to be observed specifically in the AS condition. Thus, we performed an exclusive masking procedure [(AS-PS) at  $p < 0.0005$  masked exclusively by (AA-PA) at  $p < 0.0005$ , and  $k > 10$ ] to determine activations that were unique to the difference between active and passive movements with synchronous visual feedback, but that cannot be accounted by a general confound of the presence of intentional movement. Table 3 shows the local maxima of brain areas that were active for this contrast, including the right superior parietal cortex, the supplementary motor area (see Figure 4a), the dorsal premotor cortex (BA6) bilaterally, and the cerebellum bilaterally. A distributed neural network of sensorimotor brain areas in frontal and parietal areas was more active in the AS than the PS condition. These differences cannot be explained simply by the presence of movement alone or by synchronous visual feedback alone. The observed pattern suggests that the sense of agency is underpinned by different brain areas from those related to the sense of body-ownership. Importantly no activations in the primary motor cortex were observed.

#### Activations common to AS and PS conditions

The additive model predicts that body-ownership is common to conditions with synchronous video feedback, regardless of whether active or passive movements are made. We implemented an inclusive masking procedure [(AS-AA) at  $p < 0.0005$  masked inclusively with

(PS-PA) at  $p < 0.0005$ , and  $k > 10$ ] to determine voxels that were commonly activated in the two contrasts. No suprathreshold activations were observed. This absence of activation is predicted by the independence model, but is inconsistent with the additive model.

#### Activations specific to the PS condition

To examine whether the sense of body-ownership in the absence of movement is underpinned by a distinct set of brain areas independent from those underlying the sense of agency we performed an additional analysis. We implemented an exclusive masking procedure [(PS-AS) at  $p < 0.0005$  masked exclusively by (PA-AA) at  $p < 0.0005$ , and  $k > 10$ ] to determine activations that were unique to a purely sensory sense of body-ownership (PS), that cannot be accounted for by the experiences present in AS condition (see Table 3). Brain areas that were uniquely activated in the PS condition included medial anterior and posterior brain areas such as the superior medial gyrus (see Figure 4b), the precuneus, and the posterior cingulate gyrus. In sharp contrast to the activations observed uniquely in the AS condition, the present contrast revealed activations in midline cortical structures. These activations suggest that the sense of body-ownership generated during sensory stimulation is underpinned by a different neural network from the one engaged during active movement and experienced agency. This finding provides direct support for the independence model, and is inconsistent with the additive model.

## Discussion

We investigated the neural signatures of the SoA and SoB. We manipulated whether finger movements were actively generated by participants or passively generated by an experimenter, while presenting either real-time or systematically delayed visual feedback. Manipulating the timing of visual feedback caused the observed hand to be either attributed to the participant or not. Previous studies showed that temporal congruency can cause a sense of body-ownership in purely sensory situations such as the RHI (Botvinick & Cohen, 1998; Longo et al., 2008; Tsakiris & Haggard, 2005) and a sense of agency during voluntary movement (Longo & Haggard, 2009; Tsakiris et al., 2006). Analysis of subjective reports collected after the fMRI session supported this view. The main effect of feedback was significant suggesting that synchronous video feedback produced the feeling that participants were seeing their own body, while asynchronous video feedback did not. In contrast, a sense of agency over the perceived hand appeared only following actively generated movements combined with synchronous video feedback.

The fMRI data shows that the main effect of synchronous visual feedback resulted in activations in the ipsilateral (right) somatosensory cortex. The ipsilateral, rather than contralateral, location suggests that this activation did not primarily reflect afferent input. Other studies suggested a role for the right somatosensory cortex in self-other distinction (Agnew & Wise, 2008; Ruby & Decety, 2001, 2003) and in body-awareness (Hari et al., 1998; Schwartz et al., 2005). In contrast, the main effects of asynchronous visual feedback resulted in activations in the right inferior parietal lobule, and the angular and supramarginal gyri. Interestingly, the profile of mean beta values in these clusters was not homogeneous (see Figure 3). Activation of the supramarginal gyrus was most prominent in the AA condition, while the angular gyrus was activated in both the AA and PA conditions. This pattern extends previous findings (Balslev,

Nielsen, Paulson, & Law, 2005; Farrer et al., 2008), suggesting that the angular gyrus codes for an intersensory conflict between vision and sensory information, that affects body-ownership and agency. In contrast, the supramarginal gyrus may code for sensorimotor conflicts that are critical only for the SoA.

A recent study (Farrer et al. 2008) showed a key role of angular gyrus in action awareness. Activity in the right angular gyrus (conjunction analysis inferior parietal lobule BA39 angular gyrus: 46, -50, 48) was associated with both the awareness of discrepancy between intended and movement consequences (study 1) and the awareness of action authorship (study 2). Another study (Shimada et al., 2005) that used only passive movements reported activity in the right inferior parietal cortex during detection of a conflict between proprioception and visual feedback. This activation would contribute to body-ownership but not agency. In our study, one cluster (centred at 52, -38, 38) showed highest mean beta values for the AA condition, corresponding to the activation reported by Farrer et al (2008), while another, more inferior, cluster (40, -58, 26) in angular gyrus showed comparable activity for both the AA and PA conditions, suggesting that it reflects neural responses to intersensory conflict between proprioception and vision. Overall, these results suggest that the right supramarginal gyrus is activated during sensori-motor conflicts (relevant to agency and action awareness), while the right inferior parietal cortex is activated during intersensory conflicts (relevant to body-ownership).

Timing information alone cannot distinguish the SoB from the SoA, or identify the relation between them. According to the additive model, a similar SoB would be present both for active and passive movement conditions with synchronous visual feedback, but the SoA would additionally be present following voluntary movements. The introspective evidence broadly supported this view: participants reported significantly more agreement with questionnaire items

reflecting agency in the AS condition compared to the other three conditions. Interestingly, body-ownership questions were also more highly rated in the AS condition as compared to the PS condition, suggesting that agency strengthens the experience of body-ownership. If the addition of agency to body-ownership enhances the same kind of experience, then we would expect to find at least some shared activations between agency and body-ownership. Another hypothesis suggests that agency is not simply an addition to body-ownership, but a qualitatively different process. This independence model would predict different patterns of brain activity in the two cases.

To distinguish between these possibilities, we first used an inclusive masking analysis to look for brain areas that are commonly activated by agency (induced via active movement) and a sensory-driven body-ownership (induced via passive movement) [(AS-AA) masked inclusively with (PS-PA)]. This analysis revealed no suprathreshold activations common to the two conditions, inconsistent with the additive model. A second analysis based on exclusive masking was used to evaluate the model of independence between agency and body-ownership. Both body-ownership and agency were associated with distinct and exclusive patterns of activation, providing direct evidence that their neural substrates differ. This may seem surprising given the similar responses in our questionnaire. The finding of activity present in the PS, but not the AS, condition, and vice versa, directly contradicts the additive model, in which activations related to body-ownership should be a subset of those related to agency.

The specific brain areas associated with agency and with ownership shed further light on these two components of self-consciousness. Suprathreshold activations unique to the experience of agency [(AS-PS) masked exclusively by (AA-PA)] were observed in the pre-supplementary motor area, the superior parietal lobe, the extrastriate body area and the dorsal premotor cortex bilaterally (BA6). The pre-SMA is strongly involved in the voluntary control of

action (Goldberg, 1985). Neurosurgical stimulation studies further suggest that it contributes to the experience of volition itself: stimulation here can produce an 'urge' to move, at stimulation levels below threshold for evoking physical movement (Fried et al., 1991). In our study, voluntary action was present in both the AS and AA conditions: these differed only in timing of visual feedback, and the resulting sense of agency. However, the pre-SMA activation was greater in the AS condition, where visual feedback confirms that the observed movement is temporally related to the voluntary motor command. Our findings therefore suggest that the pre-SMA plays an important role not only in conscious intention (Lau et al., 2004), but also in the SoA. Interestingly, lesions to the supplementary motor area and/or the anterior corpus callosum may result in Anarchic Hand Syndrome (Della Sala, Marchetti & Spinnler, 1994; Goldberg, Mayer, & Toglia, 1981), in which the contralateral hand performs goal-directed actions which are not intended by the patient. Despite the autonomous behaviour of the affected hand, these patients retain a SoB of the moving hand, but they report an inability to control it (see also Marcel, 2003). These results are consistent with our findings of a pre-SMA activation related specifically to agency.

The observed premotor activation (BA6) is also of relevance to a different type of action-awareness deficit. Anosognosia for hemiplegia involves denial of motor deficits after right hemisphere stroke. It arises, in part, by a failure to monitor signals related to one's own movement, and is associated with lesions in right BA44 and BA6 (Berti et al. 2005). Interestingly, anosognosic patients seem to 'ignore' the conflict between their own intention to move, and the manifest lack of movement of the left hand. They appear to perceive their intention, but not the failure of their intention to trigger appropriate proprioceptive and visual feedback (Fotopoulou et al., 2008). Our findings are consistent, therefore, with an involvement of this area in SoA, based on conflicts between sensory and motor signals.

In relation to a purely sensory-driven body-ownership [(PS-AS) masked exclusively by (PA-AA)], we observed suprathreshold activations in a network of midline cortical structures including the precuneus, the superior frontal gyrus and the posterior cingulate. These midline cortical activations recall recent suggestions of a dedicated self-referential processing network (Northoff & Bermpohl, 2004). Meta-analyses of imaging studies revealed activations in medial regions of the brain during processing of self-related stimuli (Northoff et al., 2006; Wicker et al., 2003). In particular, ventral and posterior cortical midline structures seem to underpin distinct self-related processes, with more anterior structures related to the processing of extero- and interoceptive stimuli for their relation to the self (Northoff & Bermpohl, 2004), and the more posterior areas with higher-order self-representations such as self-identity and perspective taking (Vogeley et al, 2001). These midline activations are also similar to regions of the so-called ‘default mode network’, activated in the absence of any goal-directed task (Raichle et al., 2001). Intriguingly, several lines of evidence suggest that this default network is involved in self-referential processes (Gusnard et al., 2001; Schneider et al., 2008). Northoff and Bermpohl (2004) ask ‘is there a ‘psychological baseline’?’ corresponding to this apparent physiological baseline. We suggest that the feeling of ownership over one’s body, ‘the feeling of the same old body always there’ in James’ (1890) terms, comprises an important (and perhaps dominant) part of this psychological baseline. Importantly, this baseline for the bodily self appears to have a neural basis quite distinct from that for volition.

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**Table Captions**

**Table 1. Mean responses (plus SD) to subjective report questionnaire.**

**Table 2. Transformed Z scores from an SPM{F} for the main effects.** We show areas predicted that survive  $p < 0.05$  small volume correction using a 10 mm sphere over coordinates from previous studies ( $x=44, y=-54, z=38$ , see Farrer et al., 2008), areas that were not predicted, but that survive correction for multiple comparisons across whole brain (FDR) at  $p < 0.05$ , areas for which no prediction was made, which are significant at  $p < 0.001$  uncorrected for clusters of more than 10 voxels. L/R: left and right hemispheres. [†  $p < 0.001$  uncorrected, ‡ FDR, \* SVC]

**Table 3. Transformed Z scores from an SPM{F} for the planned comparisons for the independence models of agency and body-ownership.** Each contrast and its mask were thresholded at  $p < 0.0005$  and  $k > 10$  voxels. L/R: left and right hemispheres.

**Figure Captions**

**Figure 1:** The experimental design (1A), and the experimental set-up (1B).

**Figure 2:** Psychometric Data. Error bars indicate standard errors.

**Figure 3:** Mean bold responses across conditions for the main effect of asynchronous visual feedback in the supramarginal (see 3a) and angular gyri (see 3b). Error bars indicate standard errors.

**Figure 4:** Mean bold responses across conditions for the independence model of agency (see 4a) and body-ownership (see 4b). Error bars indicate standard errors.

**Table 1**

Questionnaire item:	Synchronous		Asynchronous	
	Active	Passive	Active	Passive
“During the block there were times when...”				
1) “...it felt like the hand I was looking at was my own hand.” (Ownership)	2.42 (1.17)	1.58 (1.22)	1.11 (1.66)	-.03 (2.03)
2) “...it felt like the hand I was looking at wasn't mine.” (Ownership)	-1.79 (1.51)	-.47 (1.58)	.16 (1.71)	1.05 (1.75)
3) “...it felt like the hand I was looking at was somebody else's hand.” (Ownership)	-1.74 (1.63)	-.63 (1.67)	-.42 (1.77)	.61 (1.89)
4) “...it felt like I was in control of the hand I was looking at.” (Agency)	2.74 (.56)	.42 (1.92)	.63 (1.57)	-1.42 (1.77)
5) “...it felt like I could move the hand I was looking at if I wanted.” (Agency)	2.58 (.61)	1.16 (1.83)	.84 (1.54)	-.29 (1.98)
6) “...it felt like the hand I was looking at was out of my control.” (Agency)	-2.11 (1.05)	.21 (1.69)	-.05 (1.75)	1.58 (1.54)
7) “...it felt like my hand was somewhere between the table and the location where the video image was projected.”	-.42 (1.98)	-.26 (1.91)	-.63 (1.77)	-.58 (1.68)
8) “...it felt like I could not really tell where my hand was.”	-1.47 (1.81)	-.37 (2.09)	-.74 (2.00)	.26 (2.13)
9) “...it felt like my hand was in the location where the video image was projected.”	.47 (2.20)	.26 (1.91)	-.42 (1.80)	-.63 (1.83)
10) “...it felt like I was looking directly at my hand, rather than at a video image.”	.37 (2.17)	-.37 (1.86)	-1.42 (1.54)	-1.82 (1.45)

Table 2

Brain Regions	MNI Coordinates			Z-score	
	x	y	z		
<b><i>Main Effect of Synchronous Stimulation (AS+PS)-(AA+PA)</i></b>					
L Cerebellum VI	-22	-54	-24	4.44	†
R Postcentral Gyrus (BA 5)	24	-40	54	4.15	†
R Postcentral Gyrus (BA7)	38	-42	58	3.72	†
R Cerebellum, Culmen	12	-48	-20	3.69	†
L Posterior Insula / Rolandic Operculum (BA13)	-44	-18	18	3.56	†
R Precuneus (BA31)	24	-72	36	3.46	†
<b><i>Main Effect of Asynchronous Stimulation (AA+PA)-(AS+PS)</i></b>					
R Inferior Parietal Lobule (BA 39)	42	-52	46	4.82	*
R Supramarginal Gyrus (BA 40)	52	-38	38	4.53	*
R Inferior Parietal Lobule (BA39) (Ag)	40	-58	26	4.44	*
L Insula (BA 13)	-38	20	2	4.01	†
L Cerebellum,Uvula	-16	-84	-26	3.88	†
L Cerebellum, Cerebellar Tonsil	-12	-62	-38	3.85	†
R Middle Frontal Gyrus (BA 10)	40	52	14	3.8	†
R Middle Orbital Gyrus	24	48	-14	3.56	†
R Middle Temporal Gyrus	50	-46	-2	3.51	†
R Inferior Frontal Gyrus (BA44)	60	20	6	3.5	†
<b><i>Main Effect of Active Movement (AS+AA)-(PS+PA)</i></b>					
R Cerebellum III	20	-58	-26	6.03	‡
L Cerebellum Crus I	-40	-64	-28	5.43	‡
R Superior Parietal Lobule	32	-54	56	5.8	‡
R Inferior Parietal Lobule (BA 40)	40	-38	46	4.97	‡
R Precentral Gyrus (BA 6)	54	4	42	5.43	‡

R Middle Occipital Gyrus	52	-72	0	5.31	‡
L Inferior Parietal Lobule (BA 40)	-34	-38	46	5	‡
L Postcentral Gyrus (BA 3)	-38	-26	52	4.96	‡
L Middle Occipital Gyrus	-42	-86	4	4.3	‡
L Insula (BA 13)	-46	0	-2	4.2	‡
L Cingulate Gyrus (BA 24)	-22	-16	46	3.7	‡
L Putamen	-14	2	8	3.69	‡
L Precentral Gyrus (BA 6)	-54	-2	40	3.66	‡
R Cerebellum VIII	16	-62	-48	3.57	‡
R Middle Frontal Gyrus	44	36	36	3.54	‡
R Superior Frontal Gyrus (BA 8)	42	26	46	3.51	‡
R Inferior Frontal Gyrus	36	6	32	3.5	‡
<b><i>Main Effect of Passive Movement (PS+PA) -(AS+AA)</i></b>					
R Precuneus	0	-58	22	4.72	‡
R Medial Frontal Gyrus (BA 10)	4	64	8	4.67	‡
L Anterior Cingulate (BA 32)	-4	50	-2	4.09	‡
R Superior Temporal Gyrus (BA 39)	60	-58	22	4.36	‡
L Medial Frontal Gyrus (BA 10)	-6	66	14	3.73	†
R Middle Temporal Gyrus (BA 39)	54	-72	24	3.46	†
L Precuneus	-4	-50	52	4.15	†
R Medial Frontal Gyrus	2	52	34	3.96	†
R Superior Frontal Gyrus (BA 9)	8	62	24	3.8	†
L Superior Frontal Gyrus (BA 8)	-12	62	34	3.5	†
L Postcentral Gyrus	-26	-40	72	3.71	†
R Postcentral Gyrus	22	-48	76	3.39	†
L Middle Temporal Gyrus	-52	-64	24	3.37	†

Table 3

Brain Regions	MNI Coordinates			Z-score
	x	y	z	
<i>(AS-PS) exclusively masked by (AA-PA)</i>				
R Cerebellum (VI)	24	60	24	5.97
L Cerebellum (Crus 1)	-34	-68	30	5.70
R Precentral Gyrus (BA6)	54	4	38	5.14
R Anterior Insula	40	10	-2	4.95
R Precentral Gyrus (BA6)	38	-10	58	4.84
R Superior Parietal Lobule (BA2)	32	-58	58	4.68
L Postcentral Gyrus (BA3)	-36	-26	54	4.76
L Precentral Gyrus (BA6)	-38	-14	54	4.75
R Inferior Occipital Gyrus (BA19)	42	-82	0	4.69
L SMA (BA6)	-12	6	48	4.55
R SMA (BA6)	6	10	48	4.46
R SMA (BA6)	10	0	68	4.20
R Middle Frontal Gyrus (BA45)	52	44	14	4.44
L Superior Temporal Gyrus	-48	0	-2	4.31
L Inferior Parietal Lobule (BA40)	-36	-42	52	4.26
L Middle Occipital Gyrus (BA19)	-52	-78	6	3.70
L Middle Frontal Gyrus (BA44)	-34	14	38	4.06
R Superior Frontal Gyrus (BA8)	42	26	46	3.95
L precentral Gyrus (BA6)	-28	-10	62	3.90
L Thalamus	-22	-18	-4	3.87
L Precentral Gyrus (BA6)	-58	2	32	3.86
L Cerebellum	-16	-52	-50	3.74
R Middle Frontal Gyrus	36	50	30	3.62
<i>(PS-AS) exclusively masked by (PA-AA)</i>				
L Inferior Temporal Gyrus (BA20)	-58	-20	-34	4.69
L Fusiform gyrus (BA20)	-52	-12	-30	4.15
L Fusiform gyrus (BA20)	-64	-8	-28	3.74
L Superior Medial Gyrus (BA9)	-8	66	16	4.40

R Superior Medial Gyrus (BA9)	8	62	24	4.40
L Superior Medial Gyrus (BA9)	-4	62	24	4.32
L Posterior Cingulate (BA23)	-2	-56	18	4.40
L Precunues (BA19)	-46	-68	48	4.05
R Middle Temporal Gyrus (BA41)	48	-38	0	3.96
R Fusiform Gyrus (BA20)	56	-14	-30	3.90
L Postcentral Gyrus (BA5)	-28	-38	74	3.78
L Cuneus (BA18)	-2	-86	28	3.77
L Precuneus (BA7)	-4	-50	52	3.66
L Cuneus (BA7)	2	-72	30	3.64

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Figure 1: The experimental design (1A), and the experimental set-up (1B).

1a

		<u>Movement</u>	
		Active	Passive
<u>Feedback</u>	Synchronous		
	Asynchronous		

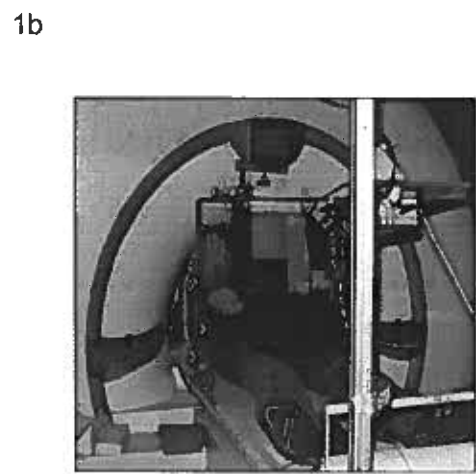


Figure 2: Psychometric Data. Error bars indicate standard errors.

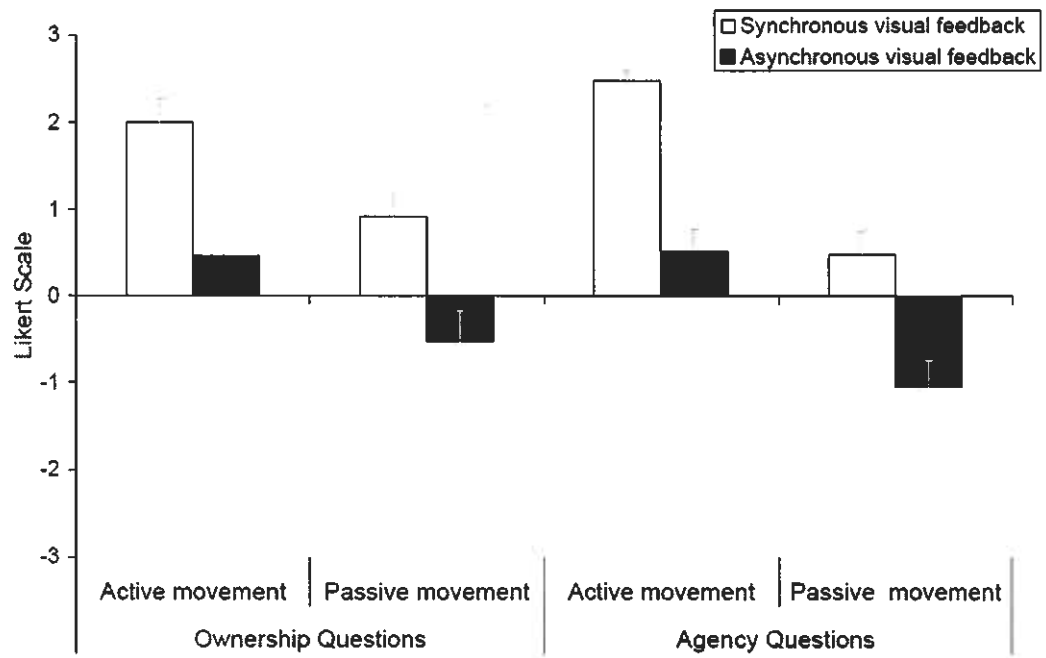
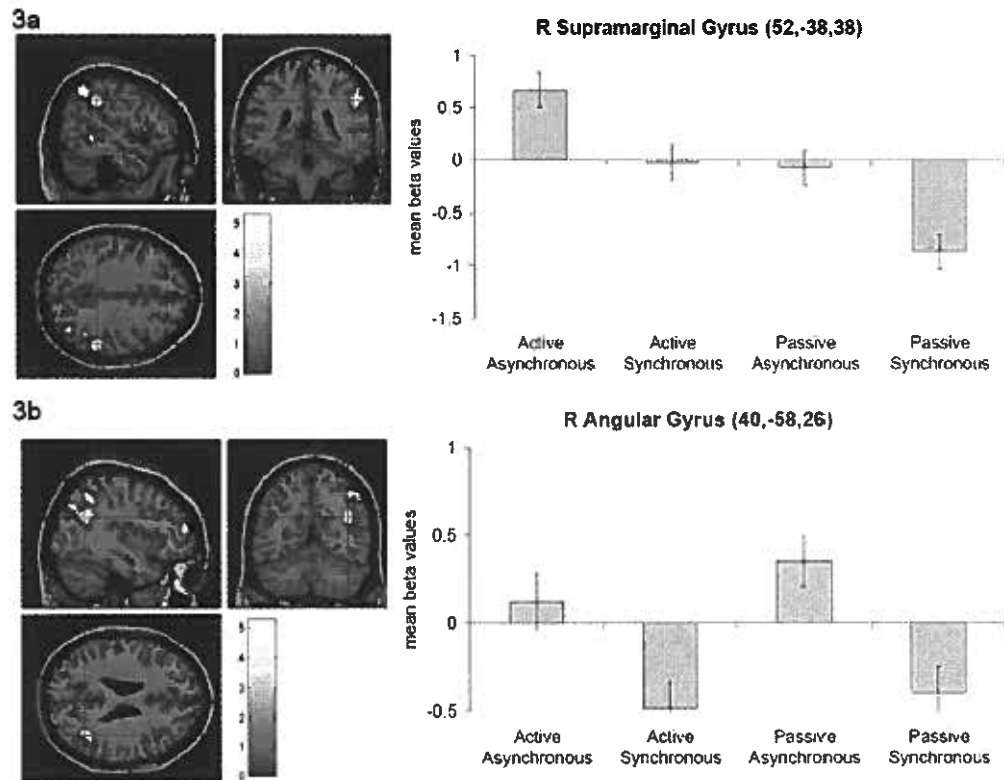
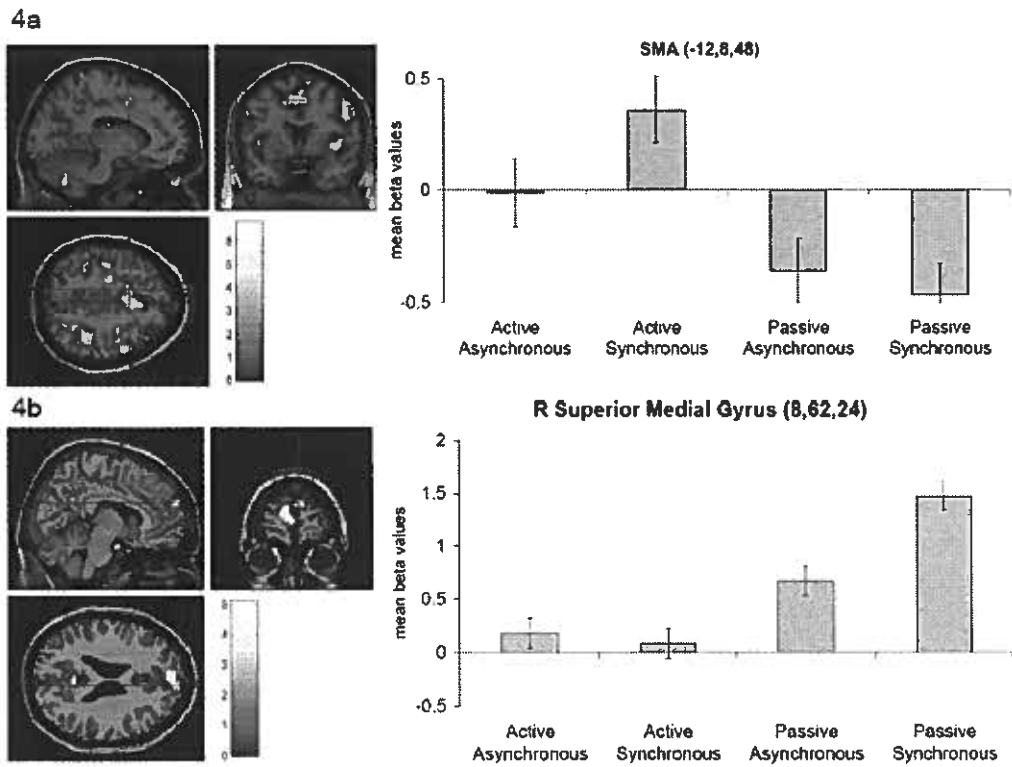


Figure 3 : Mean bold responses across conditions for the main effect of asynchronous visual feedback



**Figure 4:** Mean bold responses across conditions for the independence model of agency (see 4a) and body-ownership (see 4b). Error bars indicate standard errors.



## **Appendix 7:**

**Abstract of Talk presented at *13th Annual Meeting of the Association for the Scientific Study of Consciousness (ASSC)*, 05.06-8.062009, Berlin, Germany**

# Neural Signatures of Body-ownership and Agency

Manos Tsakiris, Royal Holloway University of London

Matthew Longo, University College London

Patrick Haggard, University College London

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Sunday, June 7th, 16:00–16:30: Room 2097, Humboldt-Universität zu Berlin

Body ownership can be easily confounded with the sense of controlling one's body because agency is a powerful cue to ownership: my body feels like mine because I can control it at will. As a result, interactions between body-ownership and agency are difficult to investigate. We developed an fMRI paradigm to investigate multisensory and sensorimotor aspects of body representation in the brain. Movements of the participant's hand were either self-generated or externally-generated, and video-feedback was relayed in real-time or with a systematic delay. Analyses showed different activations in the right parietal lobe for intersensory and sensorimotor conflicts. Activity in the SMA was linked to a sense of agency over and above the sense of body-ownership, while activations in midline cortical structures were associated with a purely sensory-driven sense of body-ownership. The results are discussed in the light of recent neurocognitive models of self.

## **Appendix 8:**

**Abstract of Talk presented at *10th International Multisensory Research Forum*, City College of New York, New York City, USA, 29.06-02.07.2009**



# 10<sup>th</sup> INTERNATIONAL MULTISENSORY RESEARCH FORUM

The City College of New York - New York City - June 29 - July 4, 2009

IMRF Home > IMRF 2009 > Presentations > Tsakiris

## Having a body versus moving your body: neural signatures of body-ownership and agency

*Manos Tsakiris, Matthew Longo, Patrick Haggard*

Talk

Time: 2009-06-30 05:10 PM – 05:30 PM

Last modified: 2009-06-04

### Abstract

Body ownership can be easily confused with the sense of controlling one's body because agency is a powerful cue to ownership: my body feels like 'mine' in part because I can control it at will. As a result, interactions between body-ownership and agency are difficult to investigate. A first imaging study using PET reveals that the right posterior insula that has been previously linked to agency, may in fact encode body-ownership. Because agency typically involves both efferent and afferent signals, previous studies have been unable to distinguish between these alternatives. We therefore developed an fMRI paradigm to investigate multisensory and sensorimotor aspects of body representation in the brain in an attempt to disambiguate the neural signatures of agency and body-ownership. Movements of the participant's hand were either self-generated or externally-generated, and video-feedback was relayed either in real-time or with a systematic delay. Analyses showed different activations in the right parietal lobe for intersensory and sensorimotor conflicts. Activity in the SMA was linked to a sense of agency distinct from the sense of body-ownership, while activations in midline cortical structures were associated with a purely sensory-driven sense of body-ownership. The results are discussed in the light of recent neurocognitive models of self.

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