

Decomposing the Will

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Print publication date: 2013 Print ISBN-13: 9780199746996

Published to Oxford Scholarship Online: September 2013 DOI: 10.1093/acprof:oso/9780199746996.001.0001

From the Fact to the Sense of Agency

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DOI:10.1093/acprof:oso/9780199746996.003.0006

Abstract and Keywords

This chapter reviews the empirical literature and contrast explicit and implicit tasks investigating the experience of agency with the aim of identifying the functional and neural signatures of the sense of agency. From the design of nonecological situations where there is ambiguity over the authorship of an action to the implementation of control conditions of passive movements that make little sense in our everyday waking life, the reviewed studies have tried to identify the key elements of what constitutes the sense of agency in humans. The exact interplay between conscious intentions and behavior, and the balance between predictive and postdictive processes remain controversial. However, the empirical investigation of the fact of agency, that is, the study of situations where people unambiguously produce voluntary actions, suggests that self-generated behavior changes the perception of one's body and the external world by integrating temporal and spatial representations of movements and their effects on the world.

Keywords: sense of agency, passive movement, authorship of action, predictive processes, postdictive processes, temporal representations, spatial representations

1. The Fact of Agency

Agency refers to a person's ability to control their actions and, through them, events in the external world. In this chapter, we use the term "sense of agency" to refer to the experience of being in control of one's own actions. 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, and we

also feel and know that we control them. As we perform actions in our daily lives, we have a coherent experience of a seemingly simple fluent flow from our prior thoughts, to our body movements, to the effects produced in the outside world. Agency seems to be a single experience because it integrates these three successive stages of sensorimotor control.

We normally experience our own actions as being caused by our intentions that are formed on the basis of our beliefs and desires (Haggard, 2008). However, it is still debated whether intentions are indeed the true causes of our own actions. Libet et al. (1983), who pioneered the experimental study of "free will," suggested that it is neural states preceding our conscious decision to act that cause the action, rather than our conscious intentions. Recently, Wegner (2003) suggested that free will is an illusory reconstructive perception of the relationship between unconscious brain processes and events that occur in the world around us at the right time and the right place. Independently of whether intentions are the true causes of our actions (conscious) intentions and the sense of agency seem to be an integral part of human experience and activity. It is this experiential aspect of the fact of agency that we focus on. Here we will avoid the issue of "free will" and focus on how the different elements of the sensorimotor sequence produce the experience of agency as studied in experimental psychology and cognitive neurosciences.

2. Explicit Tasks of Agency

One influential experimental approach to agency has used tasks that explicitly ask participants to judge whether they caused a particular sensory event. For example, (p.104) participants perform voluntary actions, typically hand movements, in response to a cue or at a time of their own choice within a specific temporal window. They then receive sensory feedback about their movement, which is sometimes distorted (e.g., a different hand configuration is shown, the spatial path of movement is disturbed, or a temporal delay is inserted; see Farrer et al., 2003; Metcalfe & Greene, 2007; Sato & Yasuda, 2005). The sensory feedback given is considered to be the effect of the participant's voluntary movement. Participants explicitly state whether they experience agency over the effect (e.g., by answering the question "Did you produce the movement you saw?" or "Did you cause that tone?"). Converging evidence suggests that greater distortions lead to lower agency scores. However, the interpretations of these results vary. Judgments about agency have been interpreted (Sato & Yasuda, 2005) as outputs from internal predictive models of the motor system (Frith, Blakemore & Wolpert, 2000). Alternatively, the mind may infer and reconstruct a causal connection between conscious intention and effect (Wegner, 2003). Clearly, this reconstructive process only works when the effect was as intended.

Haggard and Tsakiris (2009) suggested that such experiments capture a relatively small part of the experience of agency, for reasons that relate to the experimental design, the dependent variable used, and the theoretical clarity behind the experimental approach. In the agency tasks described earlier, we can assume that a sense of agency is always present and is not manipulated by the experimental design itself. (Daprati et al., 1997; Sato & Yasuda, 2005), because participants are instructed to perform self-generated voluntary movements across all conditions (e.g., lifting their index finger or pressing a key) to produce a specific sensory event either on their body or in the external world (e.g., move a visual cursor or produce an auditory tone). In such cases, the participant is always an agent in the sense of moving her hand voluntarily and controlling it. Because of the self-generated nature of the movement, the neural activity and subjective experience associated with voluntary movements are always present, that is, participants both feel and know that they moved their hand. Therefore, participants' responses to the question "Was that your action?" (or "Was that the effect that you caused?") do not reflect whether they experience agency or not. Instead, the question taps into whether the perceptual consequences of their action correspond to their experience of the action itself. Such judgments can elucidate what information the initial experience of agency contains, but they cannot identify the necessary and sufficient conditions for the experience of agency itself. In fact, many studies that claim to investigate agency focus, instead, on the cross-modal matching process between the internal representation of one's own voluntary actions and the sensory representation of those actions, or their consequences, from an external perspective. For example, angular discrepancies of up to 15 degrees between a voluntary action and its visual feedback are generally not detected (Fourneret & Jeannerod, 1998). Such findings reveal a low sensitivity of cross-modal matching, perhaps reflecting lack of spatial information in efferent motor signals. However, they do not clarify agency in our sense of the experience of being the generator and controller of one's actions.

The use of only voluntary movements within an experiment is problematic for at least two reasons. First, there is not an adequate control condition, where movement parameters would be the same, but the voluntary nature of the movement would be **(p.105)** selectively manipulated; for example, a voluntary key press is compared with a passive key press. This manipulation is important when we want to establish the relative contributions of different sensory and motor cues for agency. Second, to the extent that all these movements are self-generated and voluntary, we can assume the presence of the unique neural events that precede voluntary actions alone, such as the readiness potential and the generation of an efference copy of the motor command. In addition, we can assume that participants experience (at least a minimal) sense of effort as they produce them, and also that they are clearly aware of the fact that they have moved on every trial, despite the fact that they may not be fully aware of all the

low-level movement parameters. These observations beg the question as to what we are actually measuring when we ask participants about their sense of agency. Clearly, we are not asking them whether they felt that they have moved voluntarily, because then the answer would always be affirmative, independently of the discrepancy between their actual movement and the feedback. Thus, most experimental paradigms do not actually investigate a crucial and possibly the most basic experiential component of the sense of agency, namely, the feeling of agency, the feeling that I voluntarily move my body.

3. Feeling and Judgments of Agency

A recent distinction between the feeling of agency and judgment of agency proposed by Synofzik et al. (2008) can clarify the problems encountered when experimenting with agency. Feelings of agency refer to the subjective experience of fluently controlling the action one is currently making, and is considered as being nonconceptual. Judgments of agency refer to explicit conceptual attributions of whether one did or did not make an action or cause an effect. As recent reviews of the experimental literature on agency suggest (Haggard & Tsakiris, 2009; Synofzik et al., 2008), most studies have focused on explicit judgments of agency rather than feelings of agency. They therefore reflect metacognitive beliefs (Metcalfe & Greene, 2007) about agency rather than the more basic experiential component, namely, the *feeling* that I voluntarily move my body.

What, then, is the link between the feeling of agency and the judgment of agency? Under normal circumstances, the feeling seems to be a *necessary* condition for judgment, and indeed forms the evidence base for the judgment: my belief that I turned on my laptop depends on my phenomenal experience that I pressed the switch. However, this principle fails in a few special circumstances, suggesting that the feeling of agency alone might not be necessary. For example, when several people's actions simultaneously aim to produce a single effect, people accept agency over events when they did not in fact make the relevant action (Wegner, 2003). Note, however, that even in these special circumstances, such as the ones implemented in Wegner's experiments, the presence of an intention to perform an action seems a necessary element for the sense of agency that people report.

In addition, as neuropsychiatric (e.g., schizophrenic delusions of control) and neuropsychological (e.g., anarchic hand syndrome) cases aptly suggest, the experience of action by itself is not normally sufficient for veridical judgments of agency. As suggested by accounts of the internal models of the motor system, a separate (p.106) cognitive function monitors the effects of actions (Frith, Blakemore & Wolpert, 2000). Explicit judgments of agency require successful completion of the monitoring process: only when I see the laptop booting up, would I judge that I actually turned it on. For mundane actions, 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 neuropsychological condition reveals this interplay between an advance intention-based prediction of the sensory feedback of action that may underpin the feeling of agency, and a delayed postdictive attribution of sensory feedback to the self that may underpin judgments of agency. Some patients with hemiplegia deny that their affected limb is paralyzed (ansognosia for hemiplegia, AHP). For example, the patient may assert that they performed an action using their paralyzed limb, which in fact remains immobile. Judgments of agency in these patients seem to be based only on the feeling that they prepare appropriate motor commands for the action, and bypass the normal stage of monitoring whether appropriate effects of limb movement actually occur (Berti et al., 2005). In AHP, the feeling of intending an action becomes sufficient for a judgment of agency. This suggests that the monitoring is a specific cognitive function that normally provides the appropriate link between feelings of agency and explicit judgments of agency.

More recent accounts, capitalizing on recent computational models of motor control (Frith et al., 2000), proposed that AHP results from specific impairments in motor planning. Under normal circumstances, the formation of an intention to move will be used by "forward models" to generate accurate predictions about the impending sensory feedback. If an intended movement is not performed as planned, a comparator will detect a mismatch between the predicted sensory feedback and the absence of any actual sensory feedback. The error signal at the level of the comparator can be then used to inform motor awareness. Berti et al. (2007), following Frith et al. (2000), hypothesized that patients with AHP form appropriate representations of the desired and predicted positions of the limb, but they are not aware of the discrepancy between their prediction and the actual position. On this view, patients' awareness is dominated by intention and does not take into account the failure of sensory evidence to confirm the execution of the intended action. AHP arises because action awareness is based on motor commands sent to the plegic limb, and sensory evidence about lack of movement is not processed. Accordingly, AHP may involve damage to the brain areas that underpin the monitoring of the correspondence between motor outflow and sensory inflow (e.g., Brodmann premotor areas 6 and 44 [BA6 and BA44]; Berti et al., 2005), or else contrary sensory information is neglected (Frith et al., 2000). Consequently, the mismatch between the predicted state (i.e., movement of the limb) and the actual state (i.e., no movement) is not registered.

The account of Berti and Frith can explain why patients with AHP fail to perceive the failure to move. However, an equally important question relates to the nonveridical awareness of action that they exhibit, that is, their subjective experience that they have moved. An experimental demonstration that motor

intention dominates over sensory information about the actual effects of movement in AHP patients was provided by Fotopoulou et al. (2008). Four hemiplegic patients with anosognosia (p.107) (AHP) and four without anosognosia (nonAHP) were provided with false visual feedback of movement in their left paralyzed arm using a prosthetic rubber hand. This allowed for realistic, three-dimensional visual feedback of movement, and deceived patients into believing the rubber hand was their own. Crucially, in some conditions, visual feedback that was incompatible with the patient's intentions was given. For instance, in a critical condition, patients were instructed to move their left hand, but the prosthetic hand remained still. This condition essentially mirrored the classic anosognosic scenario within an experimentally controlled procedure. In this way the study was able to examine whether the ability to detect the presence or absence of movement, based on visual evidence, varied according to whether the patient had planned to move their limb or not. The key measure of interest was the patient's response to a movement detection question (i.e., "Did your left hand move?"), which required a simple yes/no response. The results revealed a selective effect of motor intention in patients with AHP; they were more likely than nonAHP controls to ignore the visual feedback of a motionless hand and claim that they moved it when they had the intention to do so (selfgenerated movement) than when they expected an experimenter to move their own hand (externally generated movement), or there was no expectation of movement. In other words, patients with AHP only believed that they had moved their hand when they had intended to move it themselves, while they were not impaired in admitting that the hand did not move when they had expected someone else to move it. By contrast, the performance of nonAHP patients was not influenced by these manipulations of intention, and they did not claim they moved their hand when the hand remained still.

These results confirm that AHP is influenced by motor planning, and in particular that motor "awareness" in AHP derives from the processing of motor intentions. This finding is consistent with the proposals made by Frith et al. (2000; see also Berti et al., 2007) that the illusory "awareness" of movement in anosognosic patients is created on the basis of a comparison between the intended and predicted positions of the limbs, and not on the basis of a mismatch between the predicted and actual sensory feedback. According to this hypothesis, patients with AHP are able to form appropriate representations of the desired and predicted positions of the limb. However, conflicting information derived from sensory feedback that would indicate a failure of movement is not normally available, because of brain damage to regions that would register the actual state of the limbs, or else because this contrary information is neglected. A recent lesion mapping study suggested that premotor areas BA6 and BA44, which are implicated in action monitoring, are the most frequently damaged areas in patients with AHP (Berti et al., 2005). This finding may explain why these patients fail to register their inability to move, but it does not address the

functional mechanism that underpins their illusory awareness of action per se. This study provides direct evidence for the hypothesis that awareness of action is based on the stream of motor commands and not on sensory inflow. While previous studies have suggested that conflicting sensory information may not be capable of altering anosognosic beliefs (Berti et al., 2005), they did not demonstrate that sensory feedback about the affected limb was ignored even when it was demonstrably available. Accordingly, this study demonstrated for the first time why anosognosic beliefs are formed in the first place: the altered awareness (p.108) of action in AHP depends predominantly on motor intention rather than sensory inflow. Actual sensory feedback has a remarkably limited role in the experience of action in neurologically healthy individuals (Sarrazin et al., 2008). To this extent, AHP may be a pathological exaggeration of the role of proactive and predictive information in motor awareness, arguing against the view that the sense of agency is solely postdictive.

4. An Alternative Experimental Approach to the Study of Agency: The Search for the Functional Signatures of Agency The careful analysis of the experimental designs used in agency studies and the distinction between feeling and judgment of agency beg a key theoretical question: What should be the nonagency control condition to which agency is compared? Most previous studies compare conditions where participants' actions cause a sensory effect relatively directly with conditions involving some appropriate transformation between action and effect. We consider that a feeling of agency cannot be experimentally manipulated in a consistent way, unless the action component itself is systematically manipulated. Accordingly, an alternative approach put forward by Tsakiris and Haggard (2005) involves the systematic manipulation of the action component itself, by comparing voluntary action and passive movement conditions. A voluntary movement and a passive displacement applied externally may be physically identical but are psychologically different: the voluntary movement supports a sense of agency while the passive movement does not. Implicit in this alternative experimental approach to agency is the assumption that a sense of body-ownership (i.e., the sense that this is my body, independently of whether it is moving or not) is present during both active and passive movement. What therefore distinguished the two conditions is the critical addition of agency: only during an active voluntary movement do I have a sense of agency over my moving hand, whereas during a passive movement or a purely sensory situation (e.g., see Rubber Hand Illusion [RHI]), I have only a sense of body-ownership (e.g., that's my hand moving or I experience touch on my hand). This approach recalls Wittgenstein's (1953) question, "What is left over if I subtract the fact that my arm goes up from the fact that I raise my arm?" Recent experimental studies have inverted the philosophical question, to ask, "What is added when I raise my arm over and above the fact that my arm goes up?" This view treats agency as an addition to or modification of somatic experience.

Studies of this kind have manipulated the intention/preparation stage of the motor sequence. However, since the experience of intention itself is thin and elusive, most studies have measured the experience of later stages, such as bodily movement and its external effects. The aim here is to understand how voluntary actions structure the perception of events that relates to one's own moving body and/or the effects of such movements in the external world, and use this indirect or implicit evidence to inform psychological theories about agency. Such an approach has been adopted in recent studies that focus on time awareness, somatosensory perception, and proprioceptive awareness during voluntary action. Importantly, a significant (p.109) methodological advantage of studying these domains is that one can directly compare how the agentive nature of movement affects these three domains over and above the mere presence of movement cues, that is, one can directly compare voluntary with passive movements. Consistent results have shown how the fact of agency changes the experience of the body and the outside world, measured using dependent variables such as temporal awareness and spatial representation of the body. They thus provide indirect or implicit evidence about agency. Three fundamental and robust features of agency emerge: a temporal attraction effect, a sensory attenuation effect, and a change in the spatial representation of the body itself.

4.1. Agency and Temporal Attraction Effects

Action fundamentally changes the experience of time. Both actions and their effects occur at specific measurable points in time, making correlation between subjective (i.e., the perceived time onset of events) and objective (i.e., the actual time onset of events) time possible. Therefore, time perception has been one of the most important indirect methods for studying agency. In one approach, participants are asked to judge the perceived onset of voluntary actions, and of a sensory event (a tone) occurring shortly afterward. The perceived time of the action was shifted later in time, toward the ensuing tone, compared with a baseline condition where no tone occurred. The perceived time of tones, in contrast, was shifted earlier, back toward the action that caused the tone, relative to a baseline condition in which no action was made. This intentional binding effect (Haggard et al., 2002; Tsakiris & Haggard, 2003) suggests that the experience of agency reflects a specific cognitive function that links actions and effects across time, producing a temporal attraction between them (cf. Ebert & Wegner, 2010; Moore & Haggard, 2010). Crucially, no such effects were found when passive, involuntary movements were applied, suggesting intentional binding is a specific marker of the sense of agency.

4.2. Agency and Sensory Attenuation Effects

Sensory stimulation of equal magnitude is perceived as being less intense when it is self-generated than when it is externally or passively generated. This phenomenon of sensory attenuation is a robust feature of voluntary motor control. Computational models suggest that it reduces the possibility of

computational overload by reafferent signals reflecting self-generated actions. Since the sensory consequences of such actions can be predicted internally, there is no need to sense them, and they are accordingly attenuated. This prediction is thought to involve efference copies of the motor command, and internal neural models of the motor system (Frith, Blakemore & Wolpert, 2000). This concept has been extended from computational motor control to the experience of agency. On this view, the experience of one's own actions depends on the outcome of the comparison between the predicted and the actual state of our bodies. Sensory stimulation generated by one's voluntary actions is predicted and attenuated. Therefore, when there is little or no discrepancy between the predicted and actual state of the body, a subject can be reassured that she was the agent. This approach can correctly discriminate between internally (p.110) generated and external sensory events and can therefore ascribe agency. However, since it suppresses perception of self-generated information, it cannot explain why there is a positive experience of agency at all. Models based on attenuation treat agency as absence of exteroceptive perceptual experience, not as a positive experience in itself. However, the phenomenon of sensory attenuation may be a reliable functional signature of agency, which can be used as an implicit measure in experimental studies.

4.3. Agency and Spatial Body-Representation Effects

We previously defined agency as an addition to normal experience of the body. Recent evidence suggests that agency transforms the experience of the body, as well as adding to it. A number of studies have compared the effects of voluntary action and passive movement on proprioceptive awareness of one's body. Agency generally enhances both spatial and temporal (Tsakiris et al., 2005) processing of proprioceptive information. Tsakiris, Prabhu, and Haggard (2006) used the RHI (Botvinick & Cohen, 1998) to show that voluntary actions produce a more coherent and global proprioceptive representation of the body than do passive movements. In the RHI, synchronous stimulation of both a rubber hand, or a video image of the hand, and the participant's unseen hand produces a strong illusion that the rubber hand is part of one'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. When the stimulation involves 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 coherent, unified awareness of the body, while equivalent passive stimulation produced local and fragmented effects on proprioceptive awareness. This result suggests that the unity of bodily self-consciousness may be an important result of agency.

5. The Search for the Neural Correlates of Agency

The framework of comparing active to passive movements to study agency implies that agency is added to the normally continuous and omnipresent sense of body-ownership. Thus, we experience body-ownership not only during voluntary actions but also during passive movement and at rest. In contrast, only voluntary actions should produce a sense of agency. Several studies confirm that agency is closely linked to the generation of efferent motor signals and the monitoring of their effects (e.g., Blakemore, Wolpert & Frith, 2002). In contrast, the sense of body-ownership can be induced by afferent sensory signals alone (Botvinick & Cohen, 1998). However, the exact relation between agency and body-ownership remains unknown. On one view, as argued earlier, the relation between agency and body-ownership is additive, meaning that agency entails body-ownership. This view follows from the observation that one can control movements of one's own body, but not other objects, at will, as Descartes suggested. Thus, agency offers a strong (p.111) cue to body-ownership. On this view, the sense of agency should involve the sense of body-ownership, plus a possible additional experience of voluntary control. An alternative view holds that sense of agency and sense of body-ownership are qualitatively different experiences, without any common component.

Previous accounts based on introspective evidence favor the additive model, since they identified a common sense of body-ownership, plus an additional component unique to action control (Longo & Haggard, 2009). Recent behavioral and neuroimaging studies have also focused on the neurocognitive processes that underpin body-ownership and agency (Fink et al., 1999; Farrer & Frith, 2002; Farrer et al., 2003; Ehrsson, Spence & Passingham, 2004; Tsakiris et al., 2007), but the exact neural bases of these two aspects of self-consciousness remain unclear. For example, neuroimaging studies that investigated the sense of body-ownership using the RHI (see Botvinick & Cohen, 1998) report activations in the bilateral premotor cortex and the right posterior insula associated with the illusion of ownership of the rubber hand, and present only when visual and tactile stimulations are synchronized (Ehrsson et al., 2004; Tsakiris et al., 2007). Studies investigating the neural signatures of the sense of agency have used similar methods, such as the systematic manipulation of visual feedback to alter the experience of one's body in action. Activity in the right posterior insula was correlated with the degree of match between the performed and viewed movement, and thus with self-attribution (Farrer et al., 2003). Conversely, activity in the right dorsolateral prefrontal cortex (Fink et al. 1999; Leube et al., 2003), right inferior parietal lobe, and temporoparietal junction (Farrer et al., 2003, 2008) was associated with degree of disparity between performed and viewed movement, and thus with actions not attributed to the self.

These studies were largely based on manipulating visual feedback to either match or mismatch the participant's manual action, similar to the behavioral experiments on agency described earlier. However, such manipulations cannot separate the contributions of efferent and afferent signals that are both inevitably present in manual action. The imaging data from these studies may therefore confound the neural correlates of agency and body-ownership. For example, with undistorted visual feedback of an action, there is a three-way match between efferent motor commands, afferent proprioceptive signals, and vision. Thus, any effects seen in such conditions could be due to congruence between (1) efferent and proprioceptive signals, (2) efferent signals and visual feedback, (3) proprioceptive signals and visual feedback, or (4) some complex interaction of all three signals. Conversely, when visual feedback is distorted (spatially or temporally), there is sensorimotor conflict between efferent signals and vision, but also intersensory conflict between proprioception and vision. As a result, any differences between match and mismatch conditions could reflect sensorimotor comparisons (relating to sense of agency) or proprioceptive-visual comparisons (relating to sense of body-ownership). As a result, such experimental designs cannot distinguish between the additive and the independence model of agency and body-ownership.

However, as suggested previously, the senses of agency and body-ownership can be disentangled experimentally by comparing voluntary action with passive movement, as shown earlier. Tsakiris, Longo, and Haggard (2010) implemented (p.112) this experimental design in a neuroimaging study to disentangle the neural basis of the relation between the sense of body-ownership and agency using fMRI. Body-ownership was manipulated by presenting real-time or delayed visual feedback of movements, and agency, by comparing voluntary and passive movements. Synchronous visual feedback causes body parts and bodily events to be attributed to one's own self (Longo & Haggard, 2009). The experiment aimed at testing two specific models of the agency and body-ownership relations. The first, additive model, holds that agency entails body-ownership. On this view, active movements of the body should produce both a sense of body-ownership and a sense of agency. The feeling of being in control of one's body should involve the sense of body-ownership, plus an additional sense of agency. This produces three concrete predictions about brain activations in agency and 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 condition. A second model, the independence model, holds that sense of agency and sense of body-ownership are qualitatively different experiences, without any common component. On this view, the brain could contain distinct networks for sense of body-ownership and sense of agency. The independence model 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 ownership that is absent from agency. In addition to the collection and analysis of fMRI data, participants were asked to answer a series of questions referring to their experience of agency and/or body-ownership during the various experimental conditions.

Overall, the introspective evidence broadly supported the additive model of agency. According to the additive model, a similar sense of body-ownership would be present for both active and passive movement conditions with synchronous visual feedback, but the sense of agency would additionally be present following voluntary movements. Indeed, participants reported significantly more agreement with questionnaire items reflecting agency in the active/synchronous condition compared with the other three conditions. In particular, body-ownership questions were also more highly rated in the active/ synchronous condition as compared with the passive/synchronous condition, suggesting that agency strengthens the experience of body-ownership. In terms of expected brain activations, 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 the neural predictions of the additive and independence models, the first analysis focused on brain areas that are commonly activated by agency (induced via active movement) and a sensory-driven body-ownership (induced via passive movement). This analysis revealed no suprathreshold activations common to the two conditions, inconsistent with the additive model that predicted at least some common activations. A second hypothesis derived from the (p.113) additive models is that there should be no activations for body-ownership that are not also present for agency. However, the analysis did not support this prediction as the activated networks for agency and bodyownership were sharply distinct. Both body-ownership and agency were associated with distinct and exclusive patterns of activation, providing direct evidence that their neural substrates differ. In particular, agency was specifically associated with activations in the presupplementary motor area, the superior parietal lobe, the extrastriate body area, and the dorsal premotor cortex bilaterally (BA6). In relation to a purely sensory-driven body-ownership, suprathreshold activations were observed in a network of midline cortical structures, including the precuneus, the superior frontal gyrus, and the posterior cingulate. Notably, these midline cortical activations recall recent suggestions of a dedicated self-referential processing network (Northoff & Bermpohl, 2004;

Northoff et al., 2006) in the default mode network (Gusnard et al., 2001; Schneider et al., 2008).

Thus, neuroimaging data supported an independence model, while questionnaire data supported an additive model. This somewhat surprising inconsistency may be explained in at least two distinct ways. First, the questionnaire data may reflect a limitation of the folk-psychological concepts used to describe our embodied experience during sensation and movement. Folk psychology suggests that agency is a very strong cue for ownership, so that I experience ownership over more or less any events or object that I control. However, the experience of ownership of action during agency may represent a distinctive type of ownership that should not be necessarily conflated with ownership of sensations or body parts. Second, the apparent dissociation between neural activity and introspective reports may suggest that there is not a one-to-one mapping between brain activity and conscious experience. Qualitatively similar subjective experiences of ownership appear to be generated by quite different brain processes in the passive/synchronous and active/synchronous condition. Models involving a single neural correlate of each specific consciousness experience have been highly successful in the study of individual sensory percepts, particularly in vision (Haynes & Rees, 2006). However, the aspects of selfconsciousness that we call sense of body-ownership and sense of agency are not unique elemental percepts or qualia in the same way. Rather, they may be a cluster of subjective experiences, feelings, and attitudes (Synofzik, Vosgerau & Newen, 2008; Gallagher, this volume).

Suprathreshold activations unique to the experience of agency were observed in the presupplementary motor area (pre-SMA), 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 of pre-SMA can produce an "urge" to move, at stimulation levels below threshold for evoking physical movement (Fried et al., 1991). Voluntary action was present in both the active/synchronous and the active/asynchronous conditions: these differed only in timing of visual feedback, and the resulting sense of agency. However, the pre-SMA activation was greater in the active/synchronous condition, where visual feedback confirms that the observed movement is temporally related to the voluntary motor command, suggesting that the pre-SMA plays an important role not only in conscious intention (Lau et al., 2004) but also in the sense of agency.

(p.114) 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). The roles of pre-SMA and BA6 in this experiment could reflect either an advance intention-based prediction of the sensory feedback of action or a delayed postdictive attribution of sensory feedback to the self.

6. Concluding Remarks

This chapter has presented some of the ways with which experimental psychology and cognitive neurosciences have experimented with the sense of agency. Several experimental approaches to the study of agency have emerged with recent advance in research method. From the design of nonecological situations where there is ambiguity over the authorship of an action to the implementation of control conditions of passive movements that make little sense in our everyday waking life, the reviewed studies have tried to identity some key elements of what constitutes the sense of agency in humans. The exact interplay between conscious intentions and behavior and the balance between predictive and postdictive processes remain controversial. However, the empirical investigation of the fact of agency, that is, the study of situations where people unambiguously produce voluntary actions, suggests that selfgenerated behavior changes the perception of one's body and the external world by integrating temporal and spatial representations of movements and their effects on the world. One important implication of the experiments described in this chapter is that the sense of agency seems to be closely linked to the appropriate processing of efferent information within the motor system. For example, the experiments on intentional binding and sensory attenuation suggest that efferent signals are sufficient for eliciting these effects, and support the conceptualization of the sense of agency as an efferent-driven predictive process. From a conceptual point of view, the efference copy can be considered as a pragmatic index of the origin of movement that operates at the interface between the psychological and the physiological sides of our actions. The psychological content can be described as an intention-in-action, and the physiological side relates to the descending motor command and the sensory feedback. The reviewed agentic effects that are specific to the cascade of the cognitive-motor processes that underpin voluntary movements allude to the important functional role of agency for interacting biological organisms.

Acknowledgments

Dr. Tsakiris and Dr. Fotopoulou were supported by the "European Platform for Life Sciences, Mind Sciences, and the Humanities" grant by the Volkswagen Stiftung for "Body-Project: Interdisciplinary Investigations on Bodily Experiences." Dr. Tsakiris **(p.115)** was supported by the European Science

Foundation EUROCORES Programme CNCC, supported by funds from the EC Sixth Framework Programme under contract no. ERAS-CT-2003-980409.

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Notes:

(1.) For example, Marcel distinguished between attributing an action to one's self, and attributing the intentional source of the action to one's self. Patients with anarchic hand have a clear sense that their involuntary movements are their own, but they strongly deny intending them (Marcel, 2003). Since the patients often themselves report this dissociation as surprising, folk psychology may not adequately capture the difference between ownership of intentional action and ownership of bodily sensation.

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