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EXPERIMENTING WITH THE ACTING SELF

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Recent neuroscientific research has developed the concept of the embodied agent as a scientifically viable approach to the psychological concept of the self. Both the awareness of one's own actions and awareness of one's own body are necessary conditions for the experience of selfhood. The relative contributions of efferent and afferent information in self-awareness are yet to be fully understood. We review experimental evidence that highlights the phenomenological and functional differences between the "acting self" and the "sensory self." These differences may underlie the ubiquitous modulation of perception in voluntary action. We focus on three main research fields: somatosensory perception, time-awareness, and self-recognition. A series of experiments, designed so as to dissociate afferent from efferent information, are reviewed. As a whole the results suggest that intentional action functions as a general context for awareness, modulating the perception of one's own body. The "acting self," owner of the efferent information, modulates the phenomenal experience of the "sensory self" because of the intrinsically agentic nature of voluntary movement. Finally, it is suggested that this sense of agency is efferent-driven, originating from pre-action processes.

INTRODUCTION

The quest to understand what is "the body in the brain" (Berlucchi & Aglioti, 1997) is intrinsically linked to the emergence of a new topic in neuroscientific research: the embodied agent. The aim of the present review is to investigate the way in which perception of one's own body is modulated by the intentional and agentic nature of voluntary action.

In this context, agency is defined according to the phenomenological distinction between "sense of agency" and "sense of ownership" proposed by Gallagher (2000a, 2000b). Sense of agency is the sense of intending and executing an action, whereas ownership refers to the sense that one's own body experiences a certain sensation, either externally or self-generated. A crucial phenomenological observation is that sense of ownership is present not only during voluntary actions, but also during externally or passively generated bodily experiences. In contrast, only voluntary actions can produce a sense of agency. Following these operational definitions, the sense of agency involves a strong *efferent* component, because actions are centrally generated. The sense of ownership involves a strong *afferent* component, because the content of body-awareness originates mostly by the plurality of multisensory peripheral signals. We do not normally experience the efferent and afferent components separately. Instead, we have a general awareness of our body that involves both components. This body-awareness can be defined as a nonconceptual and prelinguistic form of self-awareness, which is ontogenetically more primitive than the higher

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form of reflectional self-consciousness (Bermúdez, 1998; Rochat, 2003; Zahavi, 2002).

There is a clear link between body-awareness and self-consciousness. My experience of my body reflects the fact that this particular body responds to my intentional actions, and is the site of my bodily feelings (Merleau-Ponty, 1962). Therefore, the sense of agency arising from controlling one's own body movements is quite different from the feeling of controlling an independent object, such as a machine. We deal here with the first, "embodied" variety of agency. The main issue under investigation is the exact contribution of this sense of embodied agency to body-awareness in general.

This emphasis on the agentic self is justified and supported by a renewed interest of cognitive neurosciences in the functional and phenomenological properties of sensory and motor processes. The concept of agency underlies many recent research trends, including the primacy of goal-directed movement in cognitive development (for a review, see Rochat & Striano, 2000), the constitution of a "sense of agency" and its relation to bodily self-awareness (for a review, see Blakemore, Frith, & Wolpert, 2002), the status of "free will" (Libet, Gleason, Wright, & Pearl, 1983), and the neural processes underpinning the understanding of actions (Decety & Grèzes, 1999). The sensorimotor functions of the brain are no longer considered as low-level processes that cannot account for the existence of self-consciousness, agency, and symbolic thought. For example, the discovery of mirror neurons demonstrated that the firing of these special classes of pre-motor neurons is not related to a command for action, but to an internal representation of the motor behaviour they code (for a review, see Rizzolatti, Fogassi, & Gallese, 2001). The presence of a motor vocabulary within area F5, which operates by means of neuronal sensitivity to specific actions performed with different effectors (Buccino et al., 2001) and across different modalities (Kohler, Keysers, Umiltà, Fogassi, Gallese, & Rizzolatti, 2002), implies that these actions are represented at the level of goals rather than at the level of movements (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Such evidence suggests that motor systems might be representational systems, as well as executive (for a review, see Gallese, 2000).

As a result of this re-conceptualisation of sensory and motor processes, "motor" theories of cognition are currently widespread and popular (Blakemore et al., 2002; Cruse, 2003; Frith, 1992; Paillard, 1999). A common presumption among diverse "motor theories" is that our perception of the world is guided by sensorimotor dependences, in other words "[…] perception consists of perceptually guided action" (Varela, 1999, p. 12; for a similar argument, see also O'Regan & Noë, 2001). It is postulated that these recurrent sensorimotor patterns that guide our actions give birth to higher cognitive structures. The same basic initial mechanisms, which are used by our sensorimotor system in the execution and understanding of simple goal-directed actions, can be generalised to higher cognitive tasks (Rizzolatti & Gallese, 1997). Within this theoretical framework, recent neuroscientific research has developed the concept of the embodied agent as a scientifically viable approach to the psychological concept of the self.

Almost every human activity involves voluntary movements. Central motor signals (i.e., efferent) and peripheral sensory signals (i.e., afferent) are ever present. As agents, we act upon the world with our bodies, and at the same time we experience ourselves, and the world, through the same bodies. The fact that the body is this "intentional arc" (Merleau-Ponty, 1962) between the agent and the world implies that the sense of self is crucially dependent on sensory-motor signals. In effect, a long-standing debate regarding the influence of efferent and afferent information on action-awareness started more than 100 years ago. In the "Williams debate" (see Petit, 1999), W. James argued that knowledge of our movements originates from peripheral information, whereas W. Wundt emphasised the role of a central corollary efference of the motor command. Traditionally, proprioception is conceptualised as the modality of the self *par excellence*, especially in relation to body awareness (Bermúdez, 1998; Gibson, 1979), because proprioceptive information unambiguously pertains to the sensing subject. On the other hand, efferent information (Helmholtz, 1995) and the function of the internal models of the motor system have been linked to the sense of agency (Blakemore, Frith, & Wolpert, 1999a; Wolpert, 1997). These two sources may produce the distinctive phenomenologies of the "sensory self" and the "acting self" respectively. Although the "Williams debate" originally concerned the representation of actions, it has wider implications: Is the "self" primarily a *proprioceptive* experience of our bodies, or primarily a *motor* experience of our actions?

In an attempt to answer this question, we will review experimental evidence that highlights the phenomenological and functional differences between the "acting self" and the "sensory self." The "acting" self is the author of an action and also the owner of the consequent bodily sensations. The "sensory" self is solely the owner of bodily sensations that were not intentionally generated, but on the contrary were passively experienced. This distinction is principally a methodological one, because the experience of one's self in the world does not entail these two separate entities. Nevertheless, this distinction can be of great use for a neuroscientific approach on agency, because it allows for the comparison between purely afferent events and similar afferent events that are voluntarily generated (i.e., efferent-driven).

We focus on recent experiments from three main research paradigms: sensory suppression, time-awareness, and self-recognition. By sensory suppression we refer to the well-known phenomenon of attenuating the sensory consequences of self-generated movements. Recent studies link sensory suppression to prediction of the consequences of action, perhaps within a forward model of the motor system (Blakemore et al., 2002). The question we address is whether such attenuation occurs even when the motor system *cannot* accurately predict the sensory consequences of self-generated movements. By time-awareness we refer to the perceived time of actions and their sensory effects (Haggard, 2003). The question we address is whether the time perception of voluntary actions and their effects is different from the time-perception of involuntary movements and comparable effects. By self-recognition, we refer to the process of integrating different sources of information (i.e., intentions, efference and afference) in order to ascribe a visual representation of a body-part to its proper agent (Jeannerod, 2003). The question we address refers to the specific role of efferent information in such experimental tasks.

In all three research areas, we use a single simple experimental design to compare the "acting" and the "sensory" self. This design involves manipulating efference, and maintaining afference constant (Tsakiris & Haggard, 2003; Tsakiris, Haggard, Franck, Mainy, & Sirigu, in press). Such studies suggest a distinctive contribution of efference to body- awareness, based on laboratory experiments in which both subjective experience and objective performance has been compared across conditions in which efference was either present or absent. We propose a theoretical model of agency based on a synthesis of these three research areas.

SENSING WHEN I AM ACTING: THE PERCEPTION OF SENSORY STIMULATION IS MODULATED BY AUTHORSHIP OF ACTION

In this section we focus on the processes underlying the perception of self-generated bodily effects. Touching and being touched at the same time characterise our tactile relations with the world. An active and a receptive element coexist, which generate a computational problem for the brain of separating these two elements. Especially during action, one should pay attention not to the self-generated bodily effects, but to the externally generated bodily effects and also to the effects in the external world. The process of separating and distinguishing self-generated from externally generated events has been linked to the sense of selfhood and agency (Blakemore et al., 1999a).

This process seems to begin early in life. Developmental studies showed that newborn infants (24 hours old) are able to discriminate between double touch stimulation combined with proprioception, and single touch of exogenous origin (Rochat & Hespos, 1997). It seems that even at birth, infants can discriminate between external and self-stimulation, suggesting, that an early sense of the body as a differentiated entity exists, and even more importantly, that self-generated sensory stimulation is processed and perceived differently from externally generated stimulation.

Sensory suppression is a key concept in recent accounts of the link between perception and action, because it highlights the way that perception of sensory events is modulated by the voluntary nature of the movement. Numerous studies have shown that the perceptual consequences of self-generated actions are attenuated (Blakemore et al., 1999a; Blakemore, Wolpert, & Frith, 1998, 1999b, 2000; Claxton, 1975; Collins, Cameron, Gillard, & Prochazka, 1998; Weiskrantz, Elliot, & Darlington, 1971). The reasons for sensory suppression are probably twofold. First, any body movement potentially increases the amount of afferent information to the brain. Sensory suppression would reduce the possibility of computational overload. Second, the sensory consequences of my own actions can be predicted internally, so there is no need to sense them. The phenomenon of sensory suppression suggests that the acting self is hierarchically positioned above the passive, sensory self, since the acting self can temporarily block afferent sensation.

Blakemore and colleagues (1998, 1999a, 1999b, 2000) investigated the way that somatosensory consequences of our own actions are perceived differently from identical somatosensory inputs that are externally generated in a series of psychophysical and neuroimaging experiments. The perceptual consequences of self-generated actions are attenuated because internal models of the motor system use the efference copy to predict the consequences of our own actions, and subsequently an internal "forward model" (Wolpert, 1997) compares the predicted sensory outcome of our own actions with the actual somatosensory feedback. It has been suggested that the intact function of this comparative mechanism is a prerequisite for correct attribution of actions and recognition of agents (Blakemore et al., 2002).

At the core of this model lies the concept of an "efference copy" or copy of the motor command (Sperry, 1950; Von Holst & Mittelstaedt, 1950, cited in Nelson, 1996). The concept of efference copy was initially proposed in answer to Helmholtz's (1995) question: "how is it that, when we move our eyes, the world remains stable, despite the fact that the retinal image has moved?" In other words, how do we know whether the movement can be attributed to the eye or to the object; whether the perceived movement originates from us or from the world (Pachoud, 1999)? By generating an efference copy of the motor command, the motor system can simulate the motor execution, and therefore it can predict and anticipate the sensory consequences of self-generated movements. Any sensory input that is not predicted from the motor command would reflect an external event.

In the study by Blakemore and colleagues (1999a), tactile stimulation by means of a piece of foam was applied to the participant's right hand. The stimulation was either produced by a voluntary movement of the participant's left hand, or it was externally generated. Crucially, for the self-generated condition, between the movement of the right hand and the stimulated left hand a robotic interface was mediated, so that the experimenters could manipulate and parametrically vary (a) the delay between movement and stimulation, and (b) the degrees of trajectory perturbations. Participants' task was to judge the "ticklishness" of the sensory stimulation. Participants perceived the tactile stimulation as significantly less ticklish when it was self-generated compared to the externally generated condition, suggesting that relevant perceptual attributes of stimulation were attenuated. When a time delay of 200 ms was artificially introduced between the motion and the resulting sensation, the attenuation effect was absorbed. The authors attributed this absence of attenuation to sensory discrepancy, or the error between the predicted sensory feedback during voluntary action and the *actual* sensory feedback from the right hand. The results showed that even in the case of self-generated stimulation, the tactile sensation and its causative movement should correspond in time and space for the attenuation to take place.

Follow-up imaging experiments suggested that the cerebellum is crucially involved in the comparison between predicted and actual sensory feedback (Blakemore, Frith, & Wolpert, 2001), and that it provides the signal used for sensory attenuation in the somatosensory cortex (Blakemore et al., 1998, 1999b). According to this model (Blakemore et al., 2002), awareness of our own actions is largely dependent on the outcome of the comparison between the predicted and the actual state of our bodies. In the case of little or no discrepancy between predicted and actual state, one can be reassured that she was the agent. Therefore, it may seem as if ascription of agency is a post-action verificational judgment.

Of course, under normal circumstances, the mere presence of efferent information should constitute an infallible, or at least a necessary, index of the ownership of action, and it is debatable whether agency attribution is a post hoc judgment. One way to investigate this hypothesis is to create a situation where the efferent copy cannot directly predict the sensory outcome. It is an empirical question whether similar sensory attenuation would occur in such conditions.

In a recent experiment (Tsakiris & Haggard, 2003) we showed that identical somatic effects, induced with transcranial magnetic stimulation (TMS) over the motor cortex, are perceived as less intense when caused by a voluntary action than when caused by an involuntary movement. Figure 1 shows the experimental set-up.

A key press triggered the TMS, which was applied over the motor cortex of the participant, producing a twitch of the right index finger 270 ms later. The key was pressed either voluntarily by the participant's left index finger (voluntary condition) or by a mechanical motor pressing the participant's finger on to the key (involuntary condition), or by the experimenter (control condition). Participants were asked to judge the *intensity* of the TMS

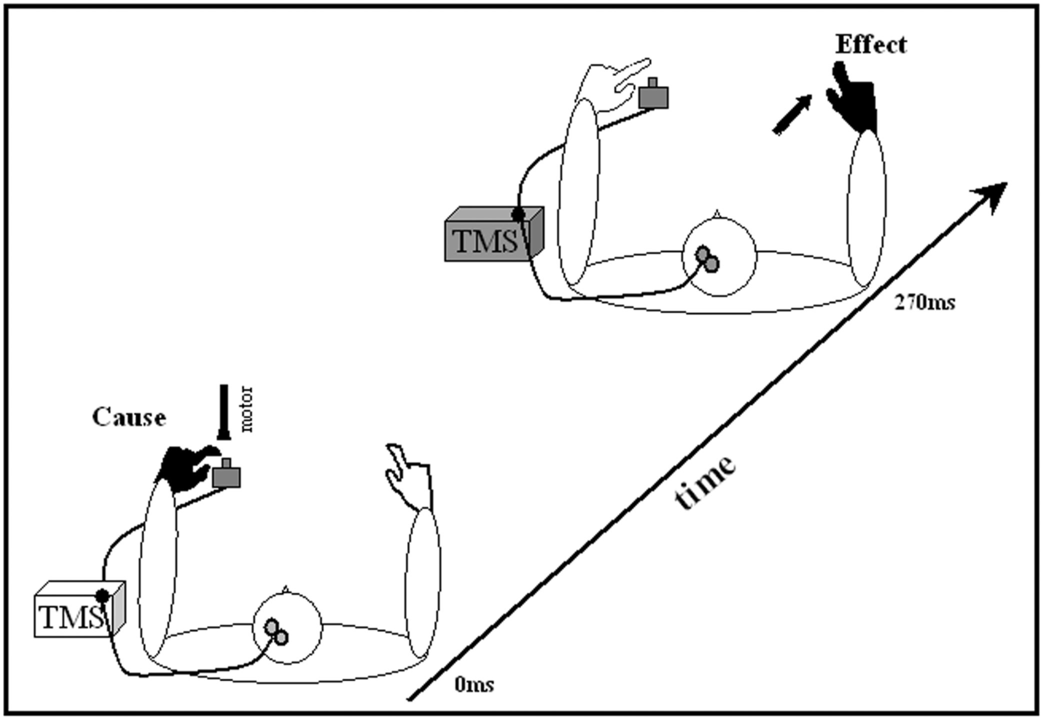

Figure 1. *Experimental set-up from Tsakiris and Haggard (2003). A key press triggered the TMS, which was applied over the motor cortex of the participant, producing a twitch of the right index finger 270 ms later. The key was pressed either voluntarily by the participant's left index finger or by an involuntary movement (e.g., the motor was pressing the participant's finger onto the key). Participants had to judge the intensity of the TMS-induced twitch.*

induced twitch of their right index finger by using a subjective scale from 1 to 10, 1 being not intense at all, and 10 extremely intense. To achieve a wide range of actual twitch intensities, the TMS output was varied randomly across trials between 110%, 130%, and 150% of relaxed motor threshold in the first dorsal interosseus. The participants were unaware of the TMS intensity that would be used in each trial. In both voluntary and involuntary conditions, a physically comparable movement of the left hand preceded the somatic effect. However, only in the voluntary condition did the subject intentionally cause the somatic effect. No prior movement of the left hand occurred in the control condition.

Mean subjective intensity ratings and mean objective MEP sizes across conditions are shown in Figure 2.

Participants perceived the TMS twitches in the control condition as more intense than a physically comparable twitch occurring as a somatic effect of a previous movement. More interestingly, somatic effects that were induced involuntarily were judged to be significantly more intense than when caused voluntarily. This finding confirms the sensory suppression observation of Blakemore and other authors. However, by separating the action and its sensory consequences in both space and time, our study provides a more controlled experiment. For example, previous measures of sensory suppression have confounded agency with predictability, by comparing the perceived intensity of highly predictable somatic effects of action with less predictable external events. Our result shows that sensory suppression is not an artefact of predictability because across conditions, the intensity of the somatic effect was unpredictable, whereas its time-occurrence was the same. Moreover, intentional action, and not mere body movement, is a necessary condition of sensory suppression.

We also investigated *how* sensory suppression occurs. Does it act as a proportional attenuator, or does it shift perceived intensity of all somatic effects by a fixed amount? Because we varied the actual size of the somatic effect in a measurable way, we could address this problem by regressing perceived intensity on objective MEP size, and investigating whether the slopes or intercepts of this regression changed across conditions, using dummy regression analysis (Kleinbaum, Kupper, & Muller, 1988).

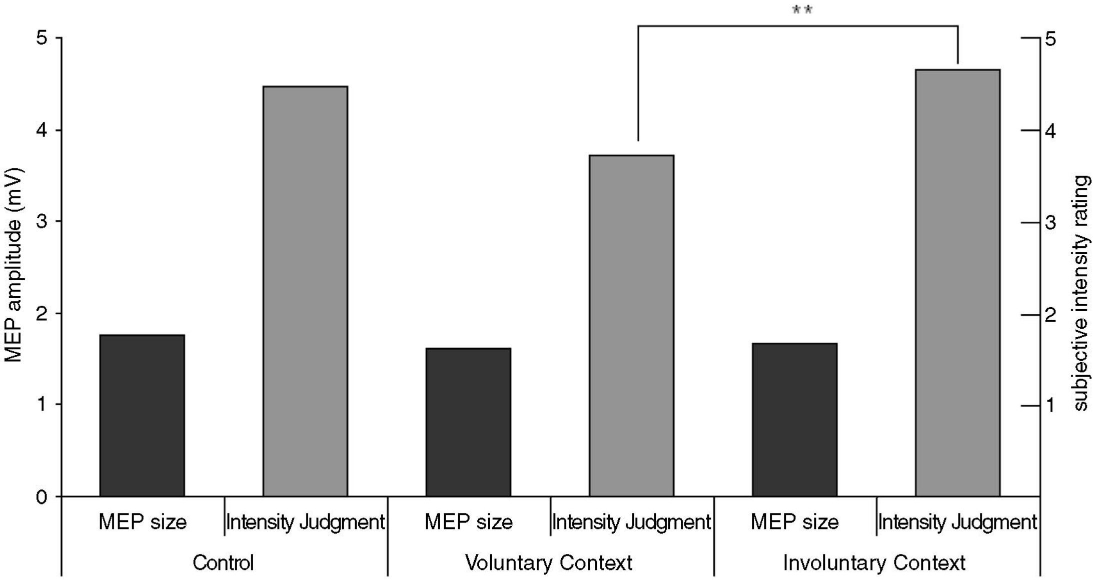

Figure 2. *Mean MEP size (mV) and subjective intensity rating across conditions. Asterisks indicate significant differences.*

This revealed that there was a significant effect on the intercept of the psychophysical relation between perceived intensity and objective MEP size, with significantly lower perceived intensity after voluntary action than after passive involuntary movement. However, the slope coefficients did not differ significantly between voluntary and involuntary conditions. Therefore, we concluded that agency shifts the perceived intensity of all subsequent somatic effects by a fixed amount, but does not attenuate percepts in a proportional manner. It is due to the operation of the forward model 392 that sensory events are attenuated in a proportional manner, because of the detailed comparison between motor parameters, predicted, and actual sensory feedback.

In the light of this evidence, intention and efference act as a general context for awareness, shifting the perceived intensity by fixed amounts. This context effect could be applied predictively in the form of a "sensory bias." We have shown that this bias occurs quite generally, even when the details of the action do not predict the details of its sensory consequences. The mere intention to act would therefore be sufficient to apply this bias. Sensory suppression may be an important index of agency (Blakemore et al., 2002). Our sensory suppression results suggest that the sense of agency could arise at an early stage in the planning of action, and before the precise details of the impending movement are determined.

TIMING WHEN I AM ACTING: THE TIME-AWARENESS OF SENSORY EFFECTS IS MODULATED BY AUTHORSHIP OF ACTION

Apart from perceiving the somatic effects of self-generated actions, we also perceive the time occurrence of these events. Voluntary actions have a distinctive temporal structure: generation of intention, "translation" of the intention to the motor command and the accompanying efference copy, execution, and perception of the effects. Early neuroscientific research on time-awareness focused on the perceived time of intending to act (Libet et al., 1983). However, both the methodology of the "psychophysics of intention" and the interpretation of Libet's experiments have been criticised on various neuroscientific and philosophical grounds (see Libet, 1985, commentaries).

Investigation of the time-awareness of action, rather than intention, might be a more viable research topic for two main reasons (Haggard, Aschersleben, Gehrke, & Prinz, 2002a). First, actions and effects can be self-generated or externally generated. Therefore, by comparing the perceived times of self-generated vs. externally generated events we can investigate the role of agency on time-awareness, using the basic experimental design proposed in the introduction. Moreover, studying the perceived time of *actions* offers an indirect way of studying *intentions*, by comparing awareness of intentional movements with awareness of physically identical movements, which are nonintentional.

A series of experiments on the time-awareness of actions has demonstrated the anticipatory nature of the acting self (Haggard & Eimer, 1999; Haggard & Magno, 1999; Haggard et al., 2002a; Libet et al., 1983). Overall, these studies show that the perceived time of action is influenced by intentional processes preceding the action itself. The perceived time of sensory effects of operant actions is also modulated by the intentional nature of the action that caused them (Haggard et al., 2002a; Haggard, Clark, & Kalogeras, 2002b; Tsakiris & Haggard, 2003).

By using a modified version of the Libet method (Libet et al., 1983), subjects were asked to make time judgments for actions (such as a key press) or for sensory stimuli caused by the action after a short delay. Haggard and colleagues (2002b) compared the perceived times of voluntary actions with the perceived times of involuntary movements induced by TMS over the motor cortex (single-event conditions), as well as the perceived times of these events (voluntary action vs. TMS-induced movement) when they triggered an auditory stimulus (operant conditions). An additional sham TMS condition was used as control. Judgment errors were defined as the difference between the actual time of occurrence of the judged event and the perceived time of its occurrence, and they were calculated for each trial and averaged. By subtracting the judgment error for an event in the single-event baseline condition (i.e., only one of the three possible events occurred in each trial) from the perceived time of the same event in a causal, operant context, Haggard and colleagues calculated the perceptual shifts for each context. These perceptual shifts represent the effect of operant context on the perceived time of each event. Moreover, they control for factors such as the sensory transmission and division of attention of each participant, and differences in the salience or perceptual center of judged events. Figure 3 shows the perceptual shifts across conditions.

The analysis of perceptual shifts showed that the perceived times of voluntary actions and their sensory consequences (auditory tones) were attracted together. Participants perceived voluntary movements as occurring *later* and their sensory consequences as occurring *earlier*, when these events occurred together compared to when they occurred in isolation. Approximately comparable *involuntary* movements caused by TMS over the motor cortex reversed this attraction effect between the movement and the auditory tones, producing a perceptual repulsion in the opposite direction. Haggard and colleagues (2002b) concluded that only truly operant intentional actions elicit perceptual attraction or binding effects between the action and its sensory auditory consequence.

Recently, Tsakiris and Haggard (2003) also compared the perceived times of voluntary actions or involuntary movements and of a subsequent somatic effect. The experimental design compared somatic effects of agentic movement to those of nonagentic movement: A voluntary action and its somatic effect were compared with a physically comparable involuntary passive movement and identical somatic effect. A response key positioned under the left index finger was connected to a transcranial magnetic stimulator (TMS) placed over the left motor cortex (see Figure 1). Participants were informed that the key could be pressed either voluntarily or passively by the index finger of their left hand, according to condition. In both cases, the

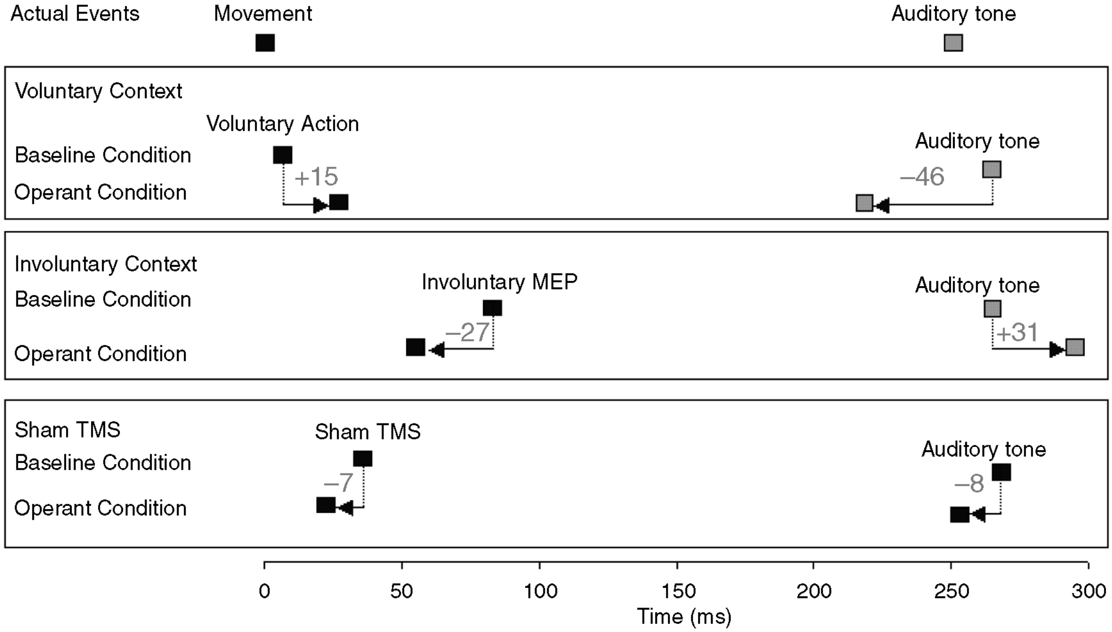

Figure 3. *The pattern of perceptual shifts (in ms) from Haggard et al. (2002b).*

key press would produce a TMS pulse 250 ms later, inducing a twitch of their right index finger approximately 270 ms after the key press. Thus, the key press was defined as the causative action, and TMS-induced twitch was the somatic effect of this action. In the experimental blocks, the same events were arranged in an operant context so that the somatic effect followed either the voluntary action or the passive movement of the left hand. For each operant condition, only one event was judged, either the action or the effect, in separate blocks. In additional single-event baseline conditions participants judged the onset of voluntary key press, involuntary key press, or TMS-induced twitches when only one of these events occurred in each trial. The parameters of movement were identical across conditions, and the spatiotemporal relation between the key press and the TMS pulse was also identical. Only the authorship of the action was different across conditions.

Figure 4 shows the mean perceptual shifts across conditions. As in the experiment of Haggard et al. (2002b), participants perceived voluntary actions as occurring later and their bodily effects as occurring earlier in the agency context, compared to single-event baseline conditions. When the voluntary action was replaced by a passive, involuntary movement this attraction effect reversed. This study adds several additional facts to our knowledge of this binding process. First, we showed that the binding process works with a different, and more ecological, modality of effect (i.e., somatomotor), in addition to auditory tones. Second, it does not work with involuntary movements and their identical somatic effects. The binding mechanism is engaged by intention, but not by mere body movement. In this experiment, the sense of agency was manipulated by design: The key-press could be effected either voluntarily or involuntarily. By contrast, the sense of ownership (e.g., the TMS-induced somatic effect) was maintained constant across conditions. The results suggest that the sense of our body is modulated by the intentional context of a prior action. In particular, intention, or "sense of agency," is necessary for binding, while "sense of ownership" is not.

Consistent results obtained from all these studies suggest that (1) awareness of action depends on central signals, which precede actual bodily movement, and (2) the volitional character of the movement modulates not only the perception of the action, but also the perception of the sensory stimulus following that action. Briefly, voluntary

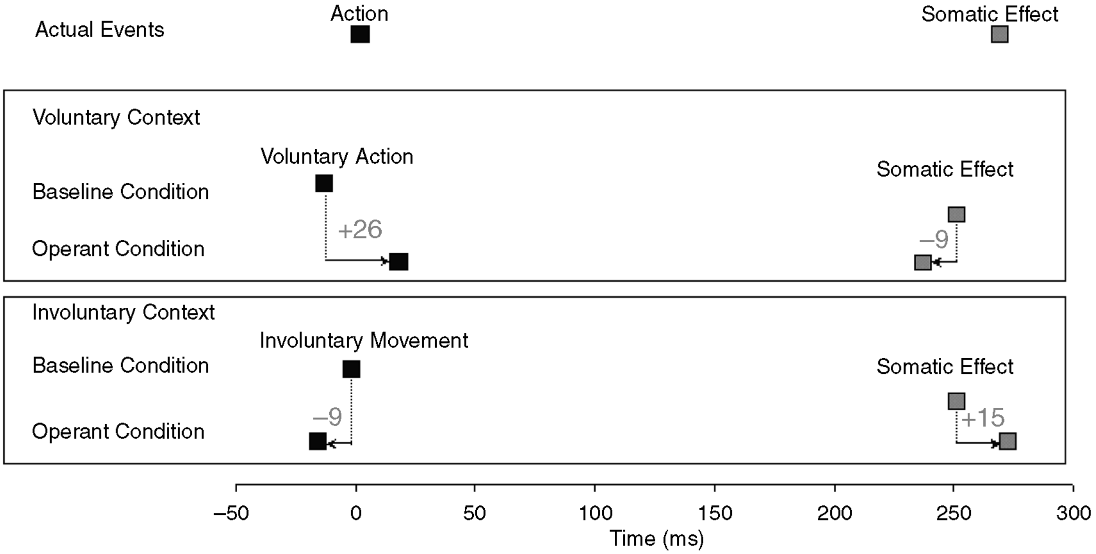

Figure 4. *The pattern of perceptual shifts (in ms) from Tsakiris and Haggard (2003), adapted with permission.*

actions that produced an external effect were perceived to occur *later* than voluntary actions that produced no effect. Conversely, external events produced by one's own voluntary action were perceived to occur *earlier* than comparable events that occurred without agency. Thus, awareness of actions and effects showed an attraction in time towards each other, termed "intentional binding" (Haggard et al., 2002a, 2002b; Tsakiris & Haggard, 2003).

In summary, by manipulating both causality (Haggard et al., 2002b) and agency (Tsakiris & Haggard, 2003), we showed that the perceived times of voluntary actions and their effects are bound together. The results reviewed provide support for the existence of a CNS process that operates only when a subject is the active agent of her actions. This "intentional binding" process integrates the conscious representations of actions and events. A series of experiments have consistently shown that this process is specific to actions, thereby underlying its intentional nature, and does not reflect general perceptual attraction. This "intentional binding" mechanism might underlie the way in which the mind constructs a strong association between intentions, actions, and consequences so as to generate the unique and private phenomenological experience of self-agency.

RECOGNISING WHEN I AM ACTING: THE ROLE OF AFFERENT AND EFFERENT INFORMATION IN SELF-RECOGNITION TASKS

Whereas in the previous sections we reviewed recent experiments that dealt separately with sensory and time perception, self-recognition tasks provide an opportunity of combining these two elements. In most studies of self-recognition, participants are presented with a visual stimulus that may or may not be related to their own body. The task is to judge whether they see themselves or not. The information available to support this judgment is systematically varied across conditions, for example by moving the hand. 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.

Visual stimuli have predominated in this area, because ambiguities regarding visual representations of the body are both fairly convincing phenomenologically and also easy to produce via mirrors or virtual reality. This is the main reason behind the use of mirrors and video monitors in self-recognition experiments on dolphins (Reiss & Marino, 2001), chimpanzees (Kitchen, Denton, & Brent, 1996), infants (for a review, see Rochat & Striano, 2000), and adults (for a review, see Jeannerod, 2003).

Developmental studies suggest that explicit self-awareness in infants comes between the 14th and 18th month: At this period, infants will be embarrassed when they see in a mirror that there is a rouge spot on their face (Bertenthal & Fisher, 1987). However, from the 4th month, infants start playing in front of mirrors and therefore attending to the visuoproprioceptive contingencies that accompany self-generated movements. In numerous studies, visuoproprioceptive incongruence was introduced, and the results suggested that infants were able to discriminate temporal incongruence (Bahrick & Watson, 1985) and that they were also sensitive to spatial calibration of their own body movements (Rochat, 1998; Rochat & Morgan, 1995). More recently, it has been shown that infants as young as 4 months of age were able to discriminate between self- and other's mirror images (Rochat & Striano, 2002). This evidence demonstrates the presence of a preconceptual self-awareness that is bodily in its nature. It is possible that this play with movements, vision, and proprioception contributes to the prereflective awareness of the same self who will be embarrassed some months later, during more explicit self-reflecting situations, like the "rouge task."

In cases of abnormal self-awareness, the ability to correctly recognise intentions, actions and their effects, or even one's own body parts is often disturbed, as shown in cases of "anarchic hand syndrome" (Hari et al., 1998), somatoparaphrenia (Bottini, Bisiach, Sterzi, & Vallar, 2002), and schizophrenia (Daprati et al., 1997; Fourneret, Franck, Slachevsky, & Jeannerod, 2001; Franck et al., 2001). These pathological cases suggest that both action and bodily cues need to be integrated in order to generate the normal experience of will, agency and body-ownership that we entertain in our daily lives.

Schizophrenics and parietal patients were the focus of interest in previous self-recognition experiments, because of the deficits these groups show in action attribution and action recognition. Daprati et al. (1997) and Sirigu, Daprati, Pradat-Diehl, Franck, and Jeannerod (1999) investigated the perception of simple and complex gestures in schizophrenic and in parietal patients respectively. The experimental design was the same in both experiments. Participants were instructed to perform simple or complex self-generated movements (extension of one or two fingers) without direct visual image of their hand. An experimenter, sitting in a similar cabin, performed either the same or a different gesture at the same time. Two cameras were filming the experimenter's and the participant's hands, thus enabling the manipulation of the visual feedback. Participants could see (a) their *own* hand, (b) the experimenter's hand performing the *same* gesture as the participant, or (c) the experimenter's hand performing a *different* gesture. Participants were asked to judge whether the hand they saw was theirs or not.

The pattern of results was the same across the two experiments. 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. However, both schizophrenics and parietal patients were significantly worse, compared to controls, when they saw the experimenter's hand performing the *same* movements as them. In this case, the patients tended to misattribute the experimenter's hand to themselves. Presumably, the patients were less able than normal subjects to detect or interpret small spatiotemporal and kinematic differences between the observed movement and their own actions as represented proprioceptively or via efferent information.

Daprati et al. (1997) suggested that this pattern of results revealed a wide deficit in reading other people's intentions. A defective internal model for action attribution (Fourneret et al., 2001; Franck et al., 2001) may also underlie the impaired performance of schizophrenics. Sirigu et al. (1999) suggested that parietal cortex contains an internal model that compares internal and external feedback about one's own movements, and therefore parietal damage would impair the on-line monitoring of actions. The common point in these two interpretations is that a process of coordinating egocentric and allocentric representations underlies self-recognition.

In these two studies, proprioceptive and efferent information were not dissociated, and therefore the relative contribution of each signal was not directly tested. Efferent and proprioceptive information were the same and present across all conditions, because the movements were self-generated. Only the visual feedback was manipulated. It is debatable whether visual manipulations alone can distinguish if the critical proprioceptive information about one's own action, which is required for the matching process, is afferent or efferent in origin. Subjects might recognise themselves in the visual display using purely afferent information. For example, if the proprioceptive and visual afference that they receive match each other perfectly, they might conclude they are watching themselves. If some mismatch occurs, they might conclude they are watching someone else's hand. Equally, efferent information could make a key contribution to this matching process.

In a recent study, Van den Bos and Jeannerod (2002) attempted to separate the contribution of afferent and efferent information to self-recognition. In this study, both the participant's and the experimenter's hands were presented on a monitor simultaneously. *Visual* afferent information was operationalised by rotating the hand image (0°, 90°, −90°, 180°) on the screen and the efferent information was manipulated by creating three action conditions: (1) participant and experimenter performed the *same* movement, (2) participant and experimenter performed a *different*

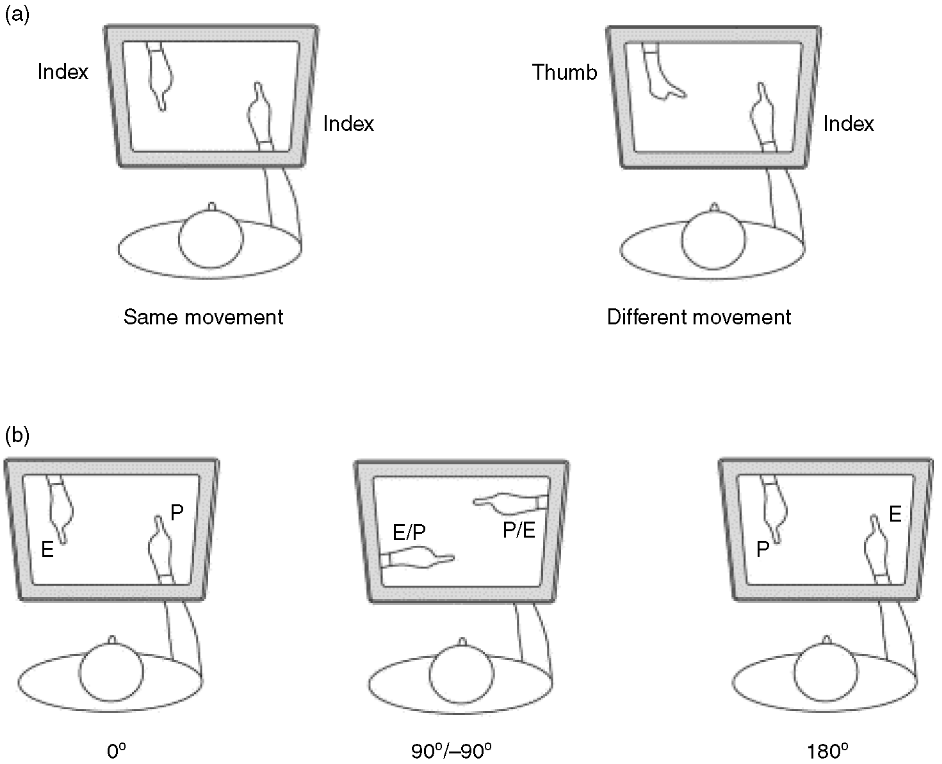

Figure 5. *The experimental set-up used in Van den Bos and Jeannerod (2002), adapted from Knoblich (2002) with permission.*

movement, and (3) participant and experimenter made *no movement* (see Figure 5).

As in previous studies (Daprati et al., 1997; Sirigu et al., 1999), participants performed perfectly when the experimenter made a different movement, across all rotation conditions. The authors suggested that "when distinctive movements are available, subjects tend to recognize actions, and not just hands" (Van den Bos & Jeannerod, 2002, p. 185). When, the movements of both hands were the same, performance was influenced by the rotation factor. The main conclusion of the authors is that action cues are used when distinctive movements are made, and that bodily cues are used when action cues are ambiguous.

But still, in this study, efferent information was not dissociated from proprioceptive afferent information because movements were self-generated, and therefore their relative contributions were not clarified. As shown in the studies of schizophrenic (Daprati et al., 1997) and parietal patients (Sirigu et al., 1999), it is relatively easy to detect the kind of mismatch produced when experimenter and participant perform *different* movements. Furthermore, it is questionable whether the manipulation of visual afference was an appropriate way to operationalise the "sense of body," because proprioceptive afference may be more important for self-consciousness (Bermúdez, 1998). Only in the "same movement" condition can the role of efference and proprioceptive afference be properly addressed. By implementing a situation where proprioceptive information is constant, whereas efference is manipulated, we can clarify the distinctive contribution of central signals. In the design used by Van den Bos and Jeannerod, differences in performance across conditions are not informative for the respective contribution of central and peripheral signals, since "in the same movement condition" efference was always present, proprioception was the same, and only the visual orientation of the hand image was manipulated.

An alternative way of investigating the distinctive role of efferent and afferent signals in action awareness and body awareness is to examine patients who are deprived of afferent signals. Deafferented patients, such as GL, have been extensively tested in a variety of experimental designs. GL was tested in the "action conflict task" developed by Fourneret and Jeannerod (1998). In this experimental paradigm, participants are asked to trace a continuous line, as straight as possible, with a stylus on a surface hidden from direct view. The visual feedback, manipulated by the experimenters who introduce angular biases, is presented on a monitor screen. There are two issues under investigation. The first one refers to the motor performance: Will the participants be able to compensate for the angular biases after a certain number of trials? The second issue refers to the content of motor awareness. Normal participants are able to compensate after some trials and therefore to produce the desired straight line (Fourneret & Jeannerod, 1998), and they do become aware of their actual behaviour only when the biases are large. When GL was tested in the same paradigm (Fourneret, Paillard, Lamarre, Cole, & Jeannerod, 2002), she was able to compensate for the angular biases in a similar way as the control participants, suggesting that her motor performance was intact. However, "GL never became aware of the bias and, consequently, of any strategy of correction she had to apply to correct" (Fourneret et al., 2002, p. 545), suggesting that the *content* of awareness of one's own movements is derived not from the efferent signals, but from the comparison of the predicted to the real sensory consequences of the executed movement. In a deafferented patient like GL, this process never takes place, since she is deprived of any afferent signals. GL was also tested in a self-recognition task developed by Farrer and colleagues (Farrer, Franck, Paillard, & Jeannerod, 2003). The results were consistent with GL's performance in the action conflict task. Her motor performance was not significantly different compared to controls, but her motor awareness was significantly impaired. GL was also tested in a "sense of effort" task (Lafargue, Paillard, Lamarre, & Sirigu, 2003). Controls and GL were asked to produce and judge isometric forces: The force was produced with one hand and, 3 s later, participants were asked to match the force with the other hand. Again, GL's motor performance was not significantly different compared to controls, suggesting that she did have a sense of muscular effort derived from efferent signals, even though she reported been unaware of any fatigue or of how hard she tried to match the produced forces. These consistent results seem to suggest that the *content* of body awareness is largely dependent on afferent signals. However, the fact that GL's performance was accurate, and that she did have a sense of effort, suggest that the sense of agency may be crucially dependent on efferent, rather than afferent, signals (for a similar argument, see Marcel, 2003).

An equally critical issue is what would happen if, instead of being deprived of afferent information, subjects were deprived of efferent information. To that extent, efferent information was systematically manipulated in a recent study, where the self-recognition task developed by Daprati and colleagues was used (Tsakiris et al., in press). We manipulated the efference by dissociating an action from its effect, using the same logic as in Tsakiris and Haggard (2003). Separating the action in space and/or time from its somatic effect allowed us to investigate whether the recognition of the somatic effect depends primarily on the afferent information generated during the body movement itself, or whether it also depends on efferent information from the spatially remote action that produced the somatic effect.

In a 2 × 2 factorial design, an action performed with the left hand produced a passive displacement of the right hand. There were two experimental factors. The first factor was the authorship of action that caused the passive displacement of the right hand (self-generated vs. externally generated), and the second factor was the visual feedback of the right hand (view participant's hand vs. view other's hand).

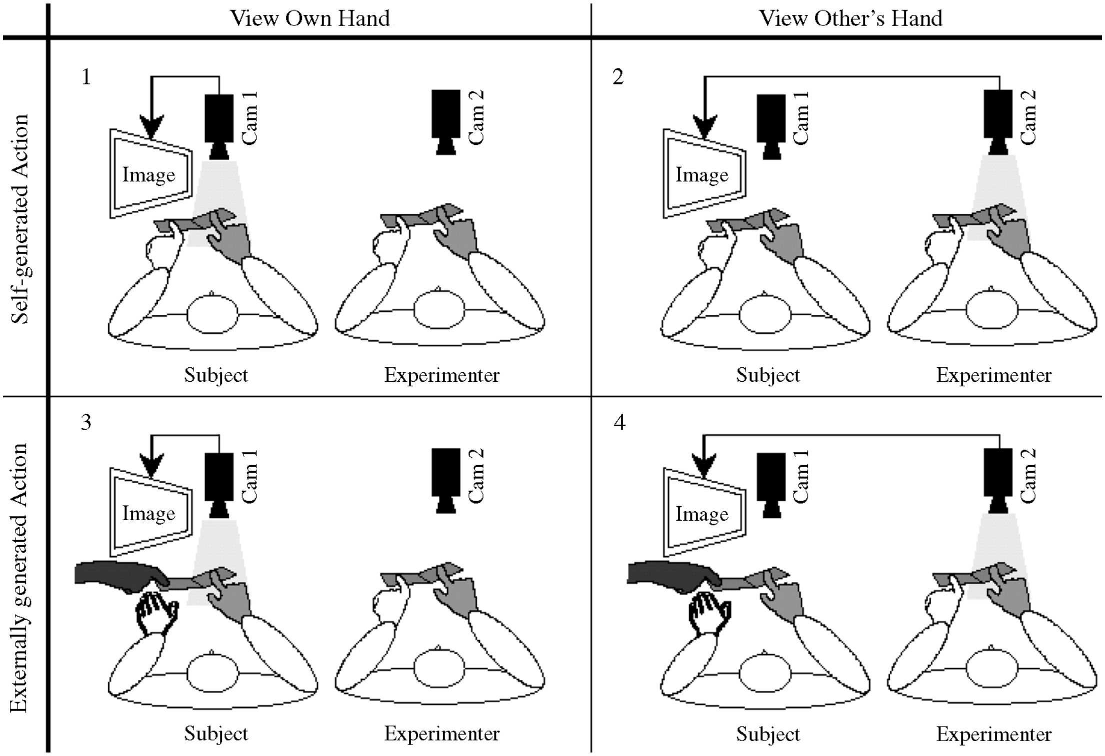

Figure 6. *The experimental set-up and design used in Tsakiris et al. (in press). The participant and the experimenter are sitting in similar cabins. The task was to produce a passive displacement of the right index finger by pressing on a lever (length 15 cm, angle 45°), and consequently to recognise the identity of the viewed hand. The movement of the right hand was always effected passively, and can therefore be seen as a somatic effect of the left hand action. The lever could be pressed either by the subject's left hand (self-generated condition) or by the experimenter (externally generated condition). Each box represents a different condition. The displacement of the right index finger was self-generated by the participant herself, and she saw her own right hand (condition 1). The displacement of the right index finger was self-generated, but the participant saw the experimenter's right hand (condition 2). The displacement of the right index finger was externally generated by another experimenter, and the participant saw her own right hand (condition 3). Finally, the displacement of the right index finger was externally generated by another experimenter, and the participant saw the experimenter's right hand (condition 4). Both hands were covered with identical gloves in order to eliminate morphological differences.*

Efferent information was manipulated because the right hand's displacement could be effected either by the participant or by the experimenter. In the former case, participants had two kinds of information about the passive displacement of the right hand: efferent information from the left hand that caused the displacement of the right hand, and also afferent information from the right hand itself. When the displacement of the right hand was externally generated, the afferent information was similar, but efferent information was absent. Participants viewed only the effect of the action in visual display of the right hand, and never saw the left hand or left side of the lever. As in previous experiments, they saw either their *own* right hand or *someone else's* right hand undergoing the *same* passive displacement (see Figure 6). Participants were asked to judge whether the right hand they saw was theirs or not, as a measurement of self-recognition.

Figure 7 shows the mean correct rates across conditions. Overall, performance was significantly better when the passive displacement of the right index finger was self-generated across both viewing conditions. Authorship of action had a significant effect on self-recognition judgments,enabling the subjects to better recognise 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 38% of the trials. The difference between these two conditions shows the specific role of efferent information in self-recognition.

Therefore, efferent information clearly contributed to the ability to match proprioceptive and visual representations of a remote bodily effect. This significant contribution of efferent information was present in both the "view own hand" and "view other's hand" conditions. This could occur for two reasons. First, efferent information might provide an advantage in monitoring the timing of sensory events. In the case of a self-generated action, forward models of the motor system use the efferent information so as to generate a prediction about the anticipated sensory feedback (Wolpert, 1997). Second, efference might modulate the on-line comparison between vision and proprioception by providing detailed temporal and kinematic information, and integrating these signals in posterior parietal areas (MacDonald & Paus, 2003; Sirigu et al., 1999).

Interestingly, efferent information has a significant contribution not only in the conscious and/or unconscious processing of various aspects of action per se, but also in the perception of the effects of the action. Thus, in this experiment, the movements of the right hand, which subjects used to recognise themselves, were not actions but rather the effects of an action performed by either the subject or the experimenter on the other end of the lever. This is consistent with recent experiments on action recognition and prediction, where an authorship effect

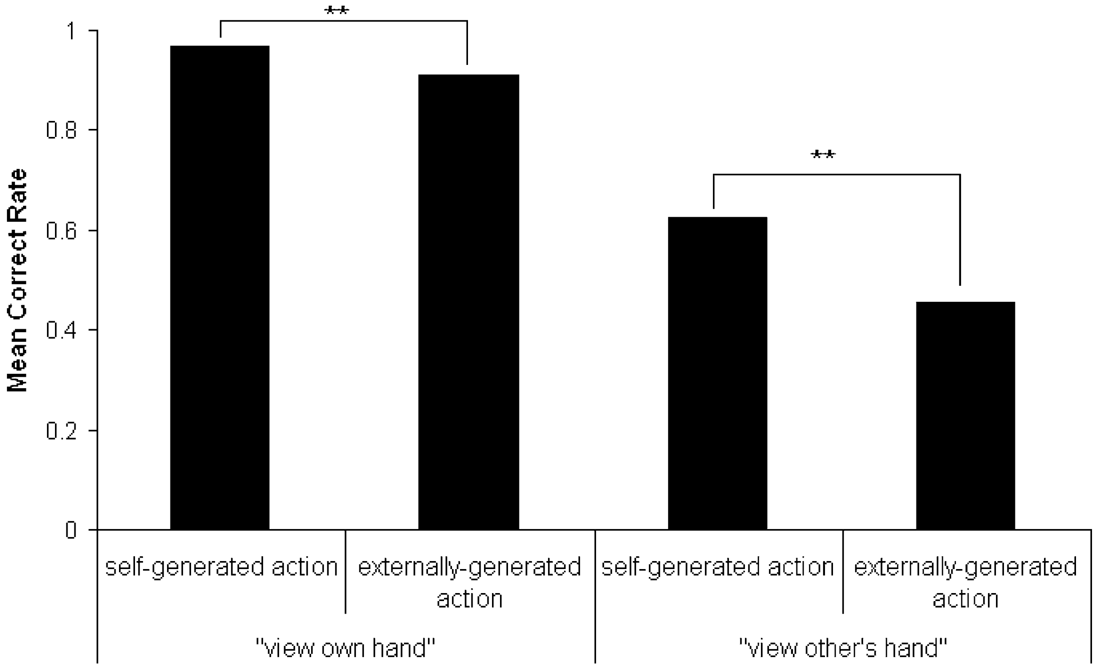

Figure 7. *Mean correct responses across conditions in Tsakiris et al. (in press). Asterisks indicate significant differences across conditions.*

was observed in recognising and predicting actions that were performed by the participants themselves, when compared to actions performed by other agents (for a review, see Knoblich & Flach, 2003). This finding suggests that efferent information might also be important for self-recognition and self-awareness, and not only for motor control (see also Blakemore et al., 2002; Tsakiris & Haggard, 2003). This distinctive role of efference in self-recognition experiments suggests that central signals are highly accurate in detecting the appropriate afferent signals that pertain to one's self, and that even though the content of our body awareness is mostly afferent in its origin, it is nevertheless modulated by efferent-driven processes.

A MODEL OF EMBODIED AGENCY

The task of a cognitive neuroscience of the embodied self is to explain the sense in which percepts of action and bodily effects are so clearly and inexorably "mine." There are two methodological issues that need to be carefully treated, if research on action is meant to be informative not only for the underlying brain processes, but also for the phenomenology of "acting." Not only is the very concept of intention problematic in the neuroscientific field (see Breitmeyer, 1985; Haggard & Libet, 2001; Libet, 1985), but so is the investigation of the interplay between motor and sensory neural processes, which accompany every voluntary action.

In this review, we highlighted the importance of experimental designs that separate efferent and afferent information. Of course both awareness of one's own actions and one's own body are indispensable for the experience of agency and selfhood. But it is also true that one can have afferent information without efferent information, as in the case of externally generated stimulation. The empirical question that we have addressed is whether the presence of efferent information modulates the perception of afference (especially proprioception) and, if so, in what way. Is the presence of efferent information indispensable only for the prediction of sensory stimulation, or is it linked to the sense of self in an intrinsic way, even before afference arrives? We have investigated this possible role of efference in three different aspects: somato-sensory perception, time awareness, and self-recognition.

In "sensing when I am acting," the aim was to examine whether an intentional modulation of sensory perception occurs whenever an effect is self-generated. To that extent, an artificial situation was created (Tsakiris & Haggard, 2003), where the motor system was not able to accurately predict the sensory consequences of a self-generated action. By using the TMS and randomly varying its output, participants could only have a vague idea about the intensity of the twitch (a typical MEP). The fact that the perceived intensity of the TMS twitches was attenuated when actively generated by the subject, compared to when similar TMS-twitches were generated passively by an identical movement of the subject's left hand, indicates that there is a "sensory bias" in the perception of the somatosensory system. This bias is present even when the motor system cannot accurately predict the sensory consequences. It is as if the system tags the forthcoming event as being "mine", before the motor system starts predicting and correcting the various sensory-motor parameters of the movement. This sensory bias is expected to be present whenever a sensory consequence can unambiguously be attributed to oneself. It was also suggested that the mere presence of intention and "raw" efferent information suffice for this sensory bias to be generated. This finding is not contradictory to the functional role of the forward model. It simply suggests that in the case of self-generated actions, the movement is tagged as "mine" by virtue of the presence of efference. If there is more information available for processing the sensory outcome, then the forward model will produce accurate predictions. The discrepancy between predicted and actual outcome will function in a proportional manner in the resulting perceptual attenuation, whereas the sensory bias derived from efference seems to function as general contextual modulation, because in Tsakiris and Haggard (2003) the perceived intensity of all subsequent somatic effects shifted by a fixed amount.

In "timing when I am acting," the review focused on the neuroscientific investigation of time-awareness. The results showed the operation of a temporal attraction process between the perceived time of voluntary actions and their sensory effects, called "intentional binding." Because intentional binding is specific to intentional operant actions (Haggard et al., 2002b) and it operates independently of whether the produced sensory effects of the action can be predicted by the motor system (Tsakiris & Haggard, 2003), it seems that the sense of agency is generated as part of the process of "translating" the intention to the efferent copy of the motor command. Intention to act also influences the awareness of non-operant voluntary actions (for a review, see Haggard, 2003). More recently, it has been shown that the mere presence of preceding but uncompleted intentions (i.e., intentions that did not lead to voluntary movements, but that were interrupted by TMS-induced movements) does not suffice for the operation of intentional binding (Haggard & Clark, 2003). If the intentional binding was a by-product of a reconstructive self-ascription of agency (Wegner, 2003), then some form of intentional binding should be evident in the case of a preceding, but interrupted, intention. The sense of agency, which generates our experience of actions, seems to be efferent driven, and it can be thought of as the first crucial step towards the realisation of intentions.

In "recognising when I am acting," the main focus was on the role of efference in self-recognition (Tsakiris et al., in press). While proprioception is considered to be intrinsically linked to the constitution of bodily self-awareness (Bermúdez, 1998), we suggest that the role of efference in self-awareness has not been properly addressed in previous studies of self-recognition. The main reason is the methodological difficulties encountered in the attempt to dissociate these two sources of information in experimental designs. However, when proprioceptive afference was separated from efference in a self-recognition task, self-recognition was significantly more accurate when participants were the authors of the action, even though the felt and seen movements had comparable forms in both conditions and despite the fact that it was the effect and not the action *per se* that the subjects were watching. Efferent information therefore played a key role in self-recognition, most probably by improving the visuoproprioceptive comparison.

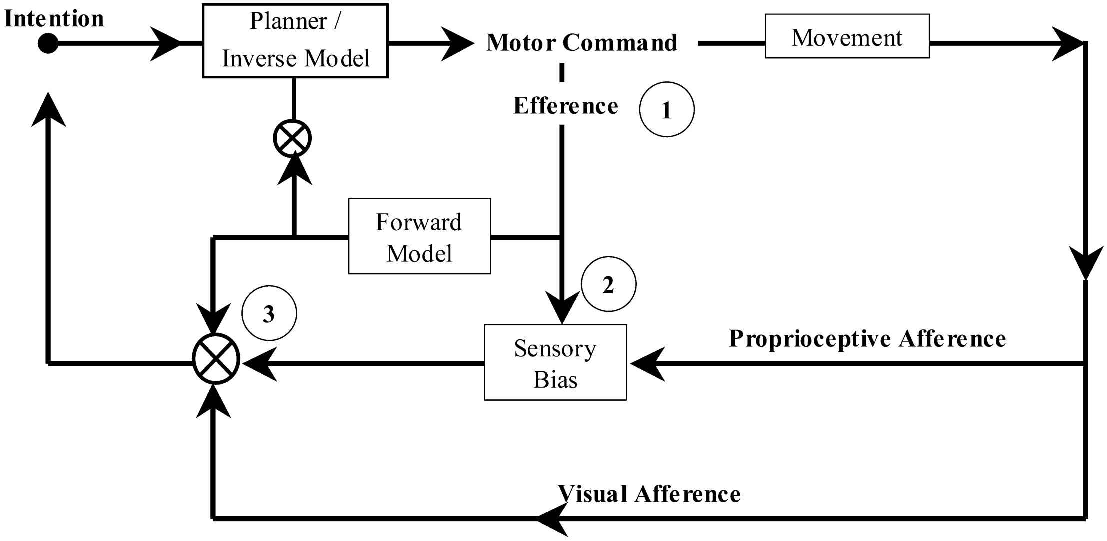

Figure 8. *A schematic model of the embodied agent.*

Taken overall, the results across these three sections are consistent and can be used to create a preliminary model of embodied agency. Figure 8 represents this model.

Intention refers to the desired state of the system's motor behaviour, which is translated into a motor command through the inverse model. When the motor command is generated, an efferent copy of this command is generated in parallel. This efferent copy seems to be sufficient condition for the raw sense of agency (point 1), as suggested by the experiment on time-perception of voluntary actions and their sensory consequences (Haggard et al., 2002a, 2002b; Tsakiris & Haggard, 2003). The experiment by Tsakiris and Haggard on sensory suppression showed that even when the motor system cannot actually predict the final state, the sensory consequences are still attenuated. This suggest that a sensory bias is introduced in the system, and that possibly the generation of efference is sufficient for this bias to occur (point 2). This bias might reflect the knowledge of the system that "it is me who is acting" as a direct consequence of an efferent-driven sense of agency, and does not need specifications of the actual motor parameters. The experiment on self-recognition (Tsakiris et al., in press) highlighted the critical role of efference in correctly attributing a visual representation to oneself. We suggest that efference modulates the comparison between proprioception and visual afference (point 3). An alternative possibility, that efference directly improves the quality of the proprioceptive signals, is rejected on the grounds of inconsistency with the established efferent down-regulation of proprioceptive afference (point 2). Whereas it seems that efference provides an intrinsic sense of agency, it is suggested that the contents of body awareness are derived from the multisensory on-line comparisons between efferent and afferent signals. The better the integration of these signals, the more accurate the self-recognition performance will be.

Overall, the "agentic self" seems to be constituted by voluntary movement, and it is experienced as a "perspectival source" (Gallagher & Marcel, 1999; Marcel, 2003) that modulates the phenomenal experience of peripheral and central signals. Our results suggest that this sense of agency is efferent-driven, whereas the contents of body awareness may be predominantly afferent in their origins. At the beginning of this paper we argued for a methodological separation between "acting" and "sensory" self. This distinction can be implemented by dissociating efferent and afferent information in order to investigate the interplay between these two sources in self-awareness. Efference intrinsically modulated the perception of afferent events. This is not surprising since normally we actively explore our environment, rather than passively perceiving it. The body is only rarely an object of perception; it is normally a subject. In that sense, body awareness is not simply another form of object consciousness (Zahavi, 2002). Models of self-awareness based on the privileged nature of proprioception as the "sense of the self" (Bermúdez, 1998) 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; it is my being-in-the-world (Merleau-Ponty, 1962). And this might be so because, in both phylogenetic and ontogenetic terms, perception and cognition begin with movement.

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