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

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

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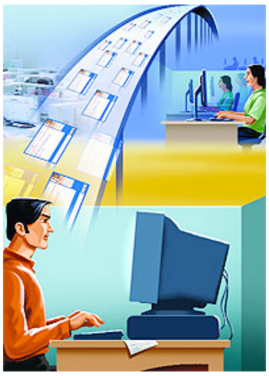

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10.1 Introduction

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

10.2 On the primacy of the body

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

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

More importantly, one's own body is the only "object" in the world that can be freely moved according to one's own will. "[…] Body is an organ of the will, the one and only Object which, […], is moveable immediately and spontaneously and is a means for producing a mediate spontaneous movements in other things […]" [9, §38, pp.152]. The simple fact that we are capable of action with and sensation in our bodies is sufficient to distinguish the relation we have with our bodies from our relations with other objects [10].

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

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

10.3 On motor and sensory signals

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

Efferent signals are the centrally-generated signals that control every voluntary movement. A key concept in the motor control literature is that of an efference copy. The concept of efference copy was first described as an "effort of will" by Helmholtz [11]. In fact, the idea of an "effort of will" was the answer to Helmholtz's question regarding our visual experience of the world. When we move our eyes, the retinal image of a perceived object is displaced. Similarly, in the case where we keep our eyes still, but we perceive a moving object, the retinal image of this object is again displaced. The critical question is how the CNS distinguishes between a sensation that is due to the activity of the organism itself from movement that is due to external activity. Helmholtz initially suggested that whenever we make eye movements, the "effort of will", that is the voluntary effort to produce the eye movement provides critical predictive information about the sensory outcome of the eye movement that will follow. In the 20th century, Helmholtz's idea was further developed into the concept of an efference copy. Whenever a motor command is issued in the motor cortex, a copy of this command is generated in parallel [12,13]. This information can be used for perceptual compensation, and can help identify the source of the movement (i.e. self vs. nonself). Von Holst and Mittelstaedt suggested that during voluntary eye movements, an efference copy can be used by visual or motor areas of the brain to predict the sensory outcome of the descending motor command, and therefore anticipate the self-generated stimulation (i.e. the sensory feedback originating from the eye movement itself). More recently, the idea of an efference copy has been generalised to the operation of the motor system, and it is not restricted only to the operation of the occulomotor system. Thus, an efference copy is thought to be generated whenever a motor command that precedes a self-generated movement is issued. This efference copy can then be used by the internal predictive models of the motor system in order to generate accurate predictions about one's own actions [14].

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

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

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

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

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

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

10.5 Who is the agent?

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

In every inter-action, there are both private and public states and signals represented in the brain of the agent and/or the observer. Private signals refer to centrally generated action representations such as intentions, efferent signals (e.g. efference copy, motor commands), and re-afferent signals such as proprioception. Public signals originate from observable sensory events, both re-afferent and ex-afferent, such as visual and auditory signals that may refer to bodies, objects or complex patterns of motor behaviour. How are these signals used to disambiguate the identity of bodies and the origin of actions? The predictive function of the motor system and the resulting anticipation of sensory inflow have been well documented in the literature across different experimental paradigms [14]. However, the link between the operation of the internal models of the motor system and the conscious awareness of action is still debated [20]. A critical issue in this debate relates to the question of the conscious experience of agency.

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

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

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

With regards to the issue of agency, according to the common coding theory, there are neither quantitative nor qualitative differences in the generation and processing of these common representations that would enable the a priori attribution of the source of the action (i.e. agency), allowing thus a clear-cut distinction between self and other. Knoblich and Flach [27], in an experiment on action prediction, where participants had to predict the outcome of either self- or other-generated actions (e.g. throwing darts), found an authorship effect in correctly predicting the outcome of self-generated actions. In the light of this evidence, they acknowledge that one problem of the common coding theory is that "[…] first-person and third-person information cannot be distinguished on a common-coding level" [27, p. 468]. The authorship effect reported by Knoblich and Flach could be accounted by the fact that the motor system that perceived the action during the prediction task was the same motor system that generated the action. Thus, the matching process between first-person perspective (i.e. producing the effect) and third-person perspective (i.e. observing the effect) was even more complete, leading to more accurate predictions. Nevertheless, according to the common coding theory, it remains unclear what could be the functional role of the first-person perceptive in action generation and perception: "In any case, we see no indication of privileged access to 1st person knowledge, that is, to knowledge referring to the mental preparation of the upcoming action and arising before the fact. Rather, like any other event, both the physical action itself and its mental antecedents appear to be perceived after the fact. The mental representation seems to follow the physical event it represents." [25, p.149].

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

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

The "who system" seems to be strongly committed to a representational model of agency and self-consciousness, and thus, the problem is no more that of *being* the agent, but it is rather that of *knowing* who the agent is. In this sense, the model ignores all the processes that precede the execution of intentional actions, and instead focuses on the perception of action as an objective manifestation of "naked intentions" [31]. On a strong view of the attributional perspective on agency, conscious agency could only be "the mind's best trick" [32]; an "after the fact", perhaps illusory, ownership of the intention to move. If "shared representations" is the brain's basic model, then the "who system" is needed in order to reconstruct the representation of an agentic self. In effect, the "shared representations" model and the "who system" raise an epistemological problem, because they leave no room for a phenomenally or epistemologically special self.

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

10.6 A working example: self-recognition

A working example that may be used to elucidate this tension between private and public signals, between shared and self-specific representations, and provide some critical insights for the self-other distinction is the self-recognition of bodily movement. Recent research on self-recognition distinguishes between two related computational problems: the problem of action recognition and the problem of self-recognition. In action-recognition, the brain must distinguish between afferent information generated by our own movements, and afferent information that is externally imposed. Action-recognition may involve unconscious operation of internal predictive models of the motor system [34], while self-recognition appears to be a specific cognitive process typically involving conscious experience [36]. Self-recognition, in the current context, involves deciding whether a visual stimulus shows one's own body or not. Thus, self-recognition is also possible in the absence of any movement or action, for example by purely morphological features. However, we often use voluntary movements as a means of self-recognition. This fact by itself suggests a hierarchical relation between action-recognition and self-recognition: voluntary action can aid self-recognition only if one can be sure that the viewed resulting body movements were caused by one's own voluntary action. In most studies of self-recognition, participants see a body-part, which may or may not be related to their own body. The task is to judge whether what they see is their own body or not. The information available to support this judgment is systematically varied across conditions, for example by moving the hand [36, 37], by introducing delays between the movement and the visual feedback [38], or by rotating the hand image [39]. Self-recognition requires the monitoring and integration of various sources of information such as intention, motor command and somatic perception in a short time-window. Only a few studies have explicitly investigated the link between voluntary movement and action-recognition [40, 41], while the specific contribution of efferent signals for self-recognition has been under-investigated (see Table 1).

Summary of Action-Recognition Studies

	Fourneret & Jeannerod, 1998	**Farrer et al., 2003b**	**MacDonald & Paus, 2003**
Participants	Normal Subjects	Normal Subjects & Deafferented Patient GL	Normal Subjects
Experimental Manipulation	Angular Bias	Angular Bias	Temporal Delays
Visual Feedback	Display of the line drawn by the subjects	Computer-reconstructed image of a hand	CyberGlove
Manipulation of Efference	No	Yes	Yes
Results	Subjects automatically compensate for the introduced bias, but they are unaware of these corrections when bias<15º.	Normal subjects: differences between active and passive movement were significant only for bias >30º. GL was significantly more impaired.	rTMS over left superior parietal lobule impaired the detection of asynchrony for active but not for passive movement.

Summary of Self-recognition Studies

	Daprati et al., 1997	**Sirigu et al., 1999**	**Van den Bos & Jeannerod, 2003**
Participants	Schizophrenics & Controls	Parietal Patients & Controls	Normal Subjects
Experimental Manipulation	Visual Feedback: 1.Own hand 2.Other's hand/same movement 3.Other's Hand/different movement	Visual Feedback: 1.Own hand 2.Other's hand/same movement 3.Other's hand/different movement	Visual Feedback : 1. Rotation of Hand-Location on screen (0º, 90º, -90º, 180º) 2.Movement (same, different, no movement)
Visual Feedback	Video display of 1 hand	Video display of 1 hand	Video Display of 2 hands (performing same / different / no movement)
Manipulation of Efference	No	No	No
Results	Schizophrenics were significantly impaired in condition 2	Parietal patients were significantly impaired in condition 2	For same movements, self-recognition performance was influenced by the rotation of the hand image.

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

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

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

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

Moreover, the paradigm of the rubber hand illusion [42, 43] suggests that if only afferent information were present or used for self-recognition, then the viewed hand would always be attributed to the self, provided that vision and proprioception were synchronised. In such cases, a dominance of vision which is based on the perception of public “states” would be the main cue for self-recognition. Thus, it may be hypothesized that for highly reliable self–other discrimination, visuo-proprioceptive congruence may not be sufficient. The specific contribution of efference to self-recognition can only be addressed by implementing a situation where visuo-proprioceptive information is kept congruent and maintained constant, while efference is systematically manipulated. This manipulation was implemented in a recent self-recognition experiment. Tsakiris et al. [44] investigated the specific role of efferent information for self-recognition. Subjects experienced a passive extension of the right index finger via a lever, either as an effect of moving their left hand (‘self-generated action’), or imposed externally by the experimenter (‘externally generated action’). The visual feedback was manipulated so that subjects saw either their own right hand (‘view own hand’ condition) or someone else’s right hand (‘view other’s hand condition) undergoing the same passive displacement of the right index finger. Thus, across all trials, subjects experienced a passive displacement of their right index finger. In one block, this passive displacement was self-generated, and in another block, the same passive displacement was externally generated. In half of the trials, subjects saw their own right hand, and in the other half, subjects saw someone else’s hand. Participants judged whether the right hand they saw was theirs or not. In that experiment, unlike other self-recognition studies [36, 37, 39], efferent information was selectively manipulated because the right hand’s displacement could be effected either by the participant or by the experimenter. In the former case, participants had two kinds of information about the passive displacement of the right hand: efferent information from the left hand that caused the displacement of the right hand, and also afferent information from the right hand itself.

Overall, performance was significantly better when the passive displacement of the right index finger was self-generated across both viewing conditions (i.e., viewing ‘‘self’’ and ‘‘other’’). Self-recognition was significantly more accurate when subjects themselves were the authors of the action, even though visual and proprioceptive information always specified the same posture, and despite the fact that subjects judged the somatic effect of an action and not the action per se. In fact, even when subjects saw their own hand, they were significantly better at correctly recognizing it as their own when they produced the passive displacement themselves, than when the passive displacement was externally generated. This significant difference suggests that efference can also improve the comparison and integration of private (e.g. proprioception) and public (e.g. vision) signals, because these were the same in both the self-generated and externally-generated conditions while participants were looking at their own hand. In the critical condition where participants saw someone else’s right hand and the displacement of their right hand was externally generated, they incorrectly attributed the viewed hand to themselves in 55% of the trials. When the passive displacement was self-generated and they saw someone else’s hand, incorrect attribution to self occurred in only 38% of the trials. The difference between these two conditions shows the specific role of efferent information in the accuracy of self-recognition. Therefore, efferent information clearly contributes to the ability to match proprioceptive and visual representations of a remote bodily effect. The observed efferent advantage could occur for two reasons. First, efferent information might provide an advantage in monitoring the timing of sensory events. In the case of a self-generated action, forward models of the motor system use the efferent information so as to generate a prediction about the anticipated sensory feedback [14]. Second, efference might modulate the on-line comparison between vision and proprioception by providing detailed temporal and kinematic information, and integrating these signals in posterior parietal areas [37, 41].

The results suggest that afferent-driven body-awareness alone may not be sufficient for reliable explicit self-recognition. Similarly, even when there is a perfect match between proprioception and vision, efference does provide a significant advantage for their integration. Self-recognition, in the sense of correctly recognizing a visual object or event as ''me'' or ''mine'' seems to depend largely on efference and agency. This is consistent with recent experiments on action recognition and prediction, where an agentive effect was observed in recognizing and predicting actions that were performed by the participants themselves, when compared to actions performed by other agents (for a review, see [45]). This finding also suggests that efferent information is important for self-recognition, and the self-other distinction, and not only for motor control. The distinctive role of efference in self-recognition suggests that central efferent signals have a highly predictive power allowing the correct detection of appropriate afferent signals that pertain to one's self, and can therefore be used to distinguish between the self and others. It has been suggested [46] that a basic computational mechanism that implements this function may also underpin higher cognitive abilities such as perspective taking and mental states attribution, and that right temporo-parietal areas may underpin this basic computation.

10.7 Towards an implicit self-recognition measure?

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

10.8 Conclusions

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

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10.10 References

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