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REVIEW

The sense of agency and its disturbances in schizophrenia: a reappraisal

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Abstract How it happens that one can recognise oneself as the source of one's own actions? This process of self-recognition is in fact far from trivial: although it operates covertly and effortlessly, it depends upon a set of mechanisms involving the processing of specific neural signals, from sensory as well as from central origin. In this paper, experimental situations where these signals can be dissociated from each other and where self-recognition becomes ambiguous will be used in healthy subjects and in schizophrenic patients. These situations will reveal that there are two levels of self-recognition, an automatic level for action identification, and a conscious level for the sense of agency, which both rely on the same principle of congruence of the action-related signals. The automatic level provides an immediate signal for controlling and adapting actions to their goal, whereas the conscious level provides information about the intentions, plans and desires of the author of these actions. The contribution of schizophrenic patients is to show that these two levels can be dissociated from each other. Whereas the automatic self-identification is functional in these patients, their sense of agency is deeply impaired: the first rank symptoms, which represent one of the major features of the disease, testify to the loss of the ability of schizophrenic patients to attribute their own thoughts, internal speech, covert or overt actions to themselves.

Keywords Action · Self-identification · Sense of agency · Schizophrenia · Parietal lobe

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Introduction

"Know thyself". Is the famous injunction of Greek wisdom a reachable goal? Can one believe what one sees or feels about oneself? Or, are those beliefs pure illusions? In this paper, we will describe how it happens that one can recognise oneself as the source of one's own actions. This process of self-recognition is in fact far from trivial: we will show that, although it operates covertly and effortlessly, it depends upon a set of mechanisms involving the processing of specific neural signals, from sensory as well as from central origin. Using experimental situations where these signals can be dissociated from each other and where self-recognition becomes ambiguous, we will first be able to determine some of the brain areas involved. We will then consider the subjective experience arising from such ambiguous situations, with the aim of determining the factors of conscious knowledge about oneself. Finally, we will show, by exploring pathological conditions, that self-recognition, not unlike any other brain function, may be subject to errors and failure.

Motor simulation as a basic mechanism for action identification

One possible mechanism by which self-recognition is achieved is motor simulation. To illustrate what motor simulation could be, consider the case of undertaking a goal-directed action. A generally accepted theoretical account assumes that, at the same time the brain generates the appropriate motor commands, it simulates the outcome of that action: a copy of the commands (the efference copy) is issued and used for building an internal model of the desired action and its effects on the external world. In turn,

the function of the internal model is to check whether the incoming (reafferent) signals (visual, proprioceptive) resulting from the action itself are congruent with the desired effect. This theoretical mechanism has been assigned a number of purposes according to different authors, such as stabilization of the visual world during eye movements (Sperry 1950; von Holst and Mittelstaedt 1950), or error monitoring during the execution of goal-directed actions (Wolpert et al. 1995). In the context of executing a goal-directed action, it can be considered as well as a way of disentangling the self-produced effects of that action on the external world against incidental changes due to an extraneous cause. As such, simulation of the outcome of an action by the internal model can be a powerful means for action identification: if, and only if the reafferent signals match the expectation of the internal model, can the action be definitely identified as self-generated. Several brain structures have been assigned a role in this automatic mechanism. Among those, the cerebellum appears to be well suited for playing the role of a comparator where the internal model of the action would be confronted with the actual result (Wolpert et al. 1998): indeed, the cerebellum receives, not only abundant dynamic signals (visual and proprioceptive) about movement execution, but also copies of the command signals through collateral branching of the pyramidal tract. Other structures, such as posterior parietal cortical areas might also be involved (see below).

Beyond theoretical modelling, the role of motor simulation in action identification has received abundant confirmation from experiments in normal subjects. These experiments have used now a classical paradigm where what subjects see or feel from their own actions does not correspond from what they actually do. Such situations create a sensory-motor conflict between the efferent and reafferent signals that are generated at the time of an action, and that are normally congruent with each other. However, in spite of the discrepancy between these signals, normal subjects have been found to automatically adapt their movements, when instructed to move their hand toward a visual target, for example. As shown in several experiments, subjects remain unaware of the corrections they have to make to reach the target (Fourneret and Jeannerod 1998; Knoblich and Kircher 2004). It is only when the discrepancy becomes too large to be resolved by the automatic process that subjects become suddenly aware of the systematic distortion of their own motor output they had to produce for achieving the task (Slachevsky et al. 2001).

Action identification and the sense of agency

Thus, in everyday life, action identification appears to be a largely automatic process. Subjective awareness does not seem to be involved in "how" actions are performed. Consider the example of two surgeons operating jointly in the same surgical theatre and seeing their respective hands through a magnifying lens, there are several moving gloved hands visible in the scene, which may not appear to be directly connected to the corresponding body; yet, the movements of these hands are correctly identified by the two surgeons. Things change, however, when instead of asking the question of "how", one asks the question of "who" (Georgieff and Jeannerod 1998). One may become aware (though within limits) of how an action is performed while still ignoring who is the author of that action: the question of "how" is a matter of understanding the appropriate motor procedures for obtaining a certain effect, whereas the question of "who" refers to the feeling of being the agent responsible for that action. In other words, notwithstanding the fact that a surgeon makes the appropriate movements during the course of the surgical action, what would be his response if he was asked to consciously judge who owns each of the hands he sees? The question here is to determine what are the cues a subject uses to build his conscious sense of being the author of his own actions (the sense of agency); and, more specifically, to determine to which extent the automatic mechanism can contribute to this sense of agency (Jeannerod and Pacherie 2004). Those may appear bizarre questions indeed, but their justification will become clearly apparent later in this paper.

One way to answer these questions is to examine the responses of subjects placed in experimental situations where an uncertainty is artificially created about the origin of an action, and where they are explicitly requested to make conscious agency judgements. A series of such experiments, which all pertained, in one way or another, to the same "substitution" paradigm (Nielsen 1963), have been reported by our group (see review in Jeannerod 2006). In the first experiment of the series (Daprati et al. 1997), normal subjects were instructed to execute simple finger movements without direct visual control of their hand: instead of seeing their hand during their movements, subjects saw on a TV screen the image of a gloved hand which could be either their own hand or an alien hand (the hand of an experimenter) executing the same or different movements. Their task was to verbally judge whether the hand presented on the screen was their own or not. Precautions were taken to make the situation as ecological as possible, the image of the hand appeared, by way of mirrors, at the true location of the subject's hand, and the movements were displayed in real time. Not surprisingly, subjects made more errors in the most ambiguous condition, i.e. when they were presented an alien hand performing the same movements as their own. The error rate in this condition amounted to 30%, i.e. subjects erroneously attributed to themselves the hand of the experimenter in about one-third of the trials.

Due to the experimental condition (only one hand was visible at a time), only one type of error could be made: subjects self-attributed the experimenter's hand.

One may wonder, however, what would happen if the subjects were provided an alternative choice. In a follow up experiment, van den Bos and Jeannerod (2002) used a display where both the subject's hand and the experimenter's hand were simultaneously presented during a brief period of time over successive trials. Trials involved different degrees of conflict between the seen and the felt position of the subject's hand, and between the seen and the actually executed finger movements: the two hands could either make the same movements, different movements, or no movement at all. At the end of each trial, after the two hands had disappeared, a pointer was placed at the location of one of the two hands and the subject was asked to judge whether that hand was his own or that of the experimenter. In this condition, the subject's errors could be in two different directions: in the other-to-self direction when the subject attributed to himself the hand of the experimenter (over-attribution errors) and in the self-to-other direction when he attributed his own hand to the experimenter (under-attribution errors). The overall pattern of results was that the subjects tended to make more over-attribution errors. This pattern was particularly striking in the condition where all the cues for discriminating between the two hands had been suppressed: in spite of responding at chance on average, the subjects still made significantly more errors by over-attribution than by under-attribution.

The conclusion that can be drawn from the above results is twofold. First, conscious judgements about the origin of an action do not necessarily match the action identification process or can even be in contradiction with the available evidence. False attribution judgements may coexist with accurate functioning of action identification. A similar difference between the automatic and conscious modalities of processing of the same event can also be found in other domains, like visual perception. Take for example the visual illusion where two identical discs are surrounded by different visual contexts: one is surrounded by a crown of small circles, the other one by a crown of large circles: the disc surrounded by the small circles is perceived as larger than the disc surrounded by large circles (the Ebbinghaus illusion). Yet, when one of the discs is grasped by hand, the finger grip automatically adjusts to the real size of the disc, not to its illusory size (Aglioti et al. 1995). Like the perception of the visual array, the sense of agency can be subjected to misinterpretation and illusions (and possibly even to delusions, as we will see below). The second conclusion is that attribution judgements are biased: a subject placed in ambiguous situations like those created by the substitution experiments experiences alien actions as his own. This is indeed an illustration of an illusion of agency: faced with an action of an uncertain origin, this subject will tend to believe that he is the agent who caused that action to appear.

The dissociation, in normal subjects, between automatic processing and conscious responses raises the question of the relationship between their respective underlying mechanisms. Is action identification a cue for the sense of agency? Would the sense of agency be affected by a perturbation of the automatic process? Indications in the literature are very scarce on this point. It has been observed that normal subjects placed in experimental substitutions like those described above may experience bizarre feelings: Nielsen (1963) reported that his subjects, when misattributing the alien hand to themselves, felt as if they had lost control of their movements, "as if driving on ice". Leube et al. (2003) reported that subjects observing a delayed presentation of their motor performance experienced the bizarre sensation of having an "anarchic" hand. In both the examples, subjects experienced the illusion of a disturbed sense of agency when the feedback from their actions did not correspond to the expected effect. These observations seem to suggest a causal relationship between the action identification mechanism and the sense of agency. This relationship, however, will not be fully confirmed when we examine the disturbances of the sense of agency in patients with schizophrenia.

The role of parietal cortex in the sense of agency

Another set of experiments in normal subjects has been undertaken in order to determine the functional anatomy of the sense of agency. These experiments have disclosed the role of posterior parietal cortex as a critical link within the simulation network for self-recognition. Indeed, the primate posterior parietal cortex integrates information about self-generated action from different origins, efferent as well as reafferent. Studies in monkeys have revealed the existence within the intraparietal sulcus of neurons coding for visually goal directed movements (eye movements as well as arm movements). Neurons in this area also respond to kinaesthetic and visual spatial stimuli. In humans, posterior parietal lesions, especially on the right side, impairs the ability of recognizing one's own body parts and self-attributing one's own movements (Daprati et al. 2000).

Studying the functional anatomy of the sense of agency required experiments where the normal correlation between the signals which arise at the time of a self-generated movement could be disrupted. Fink et al. (1999) studied the effect of a conflict between self-produced finger movements and the visual feedback given to the subjects about their movements: when the finger movements shown to the subjects no longer correlated with those that they had executed, an increased activity was observed in the posterior parietal

cortex (areas 40 and 7) bilaterally (Fink et al. 1999). In a subsequent experiment by Farrer et al. (2003), the visual feedback provided to the subjects about their own movements could be either congruent with the execution, or distorted to a variable degree. The degree of distortion went up to the point where the seen movements were completely unrelated to the executed ones. Subjects were instructed to concentrate on their own feelings of whether they felt in control of the movements they saw. The task of observing one's own movements in this unusual situation activated the posterior parietal lobe, predominantly in the right hemisphere. The peak activation was located in the inferior parietal lobule, in Brodmann area 39. Furthermore, the less the subjects felt in control of their own movements, due to larger and larger degrees of distortion, the more the right inferior parietal lobule was activated. This suggests that the process underlying self-recognition is not an all or none process: rather, self-recognition relies on a continuous monitoring of the different movement related signals, from sensory and central origin. Any mismatch between these normally congruent signals should require an increased level of processing, as shown by the progressive increase in activity observed by Farrer et al. (2003).

Parietal mechanisms thus appear to be superimposed on other mechanisms using the same principle of comparing a desired output and its predicted effects. We discussed earlier the possible role of the cerebellum for achieving this task at the automatic level, with the function of providing the nervous system with an identification signal for self-generated actions. If this mechanism is duplicated at the cortical (parietal) level, this should be for fulfilling a different function. Indeed, parietal cortex, in addition to receiving action related signals, is connected with many other cortical areas, including in prefrontal cortex, involved in the cognitive aspects of action representation. It is likely that this cortical level is open to conscious interpretation (and misinterpretation) about the goal of actions and their author, which is not the case for the automatic level. It can therefore be proposed that the same information about action execution contributes to the two levels, but that, at the upper level, parietal cortex integrates this information with top–down influences arising from prefrontal cortex. This interpretation will be supported by the data obtained about the disturbances of the sense of agency in patients with schizophrenia.

Pathological misattribution of actions: failure of automatic action identification or delusional sense of agency?

The above results on the factors of the sense of agency and their anatomical substrate stress the subtlety of the involved mechanisms. It is therefore not surprising that pathology shows many examples of a disturbed sense of self: delusional belief about one's own body or actions is a frequently observed pathology (Berlucchi and Aglioti 1997; Coltheart 2007; Blanke et al. 2008). A typical case of such disturbances is schizophrenia. Schizophrenic patients typically exhibit symptoms which testify to an impairment in self-attributing their own thoughts or actions: symptoms like acoustic-verbal hallucinations, thought insertion or withdrawal, and delusions of alien control (the so-called "first rank symptoms" according to Schneider 1955), all refer to feelings or experiences of loosing control of oneself, and being controlled or influenced by other agents. These symptoms clearly correspond to what we categorised earlier as attribution errors. Although the most frequently observed pattern in schizophrenic patients is that of errors in the other-to-self direction (under-attribution), the opposite pattern (over-attribution) may also be observed, e.g. when patients believe that they can control the thoughts and the behaviour of other people (the so-called megalomania). The current explanation for the first rank symptoms, as proposed by Feinberg (1978) and by Frith (1992) is that schizophrenic patients loose the normal ability to monitor one's self-willed intentions and actions. Frith proposed the hypothesis that intended actions and thoughts are self-monitored or, in other words, that they would be labelled by central neural signals that are issued at the time of their generation: the efference copy, which is part of the internal model described earlier in this paper, could be one example of such signals. Self-monitored actions and thoughts would thus be recognised as self-produced when the execution matches the efference copy. Correlatively, a deficient self-monitoring would result in nonattributed or misattributed actions or thoughts, and give rise to symptoms like hallucination, thought insertion or delusion of influence (Frith et al. 2000).

However, the notion of a deficient self-monitoring, which is now frequently used for explaining schizophrenic disorders (Farrer and Franck. 2007 for review) is confusing, because it collapses into one single entity two processes, which are clearly distinct from one another: automatic identification of self-generated actions and conscious sense of agency. How can this interpretation be reconciled with the fact that the two processes can be experimentally dissociated? One possibility is to examine schizophrenic patients using the same set of substitution experiments as in healthy subjects, namely, to examine their behaviour and their brain activity in situations where the origin of an action is rendered uncertain (Jeannerod et al. 2003). Remember that, is such situations, a conflict is created between the set of signals (central commands, visual and proprioceptive reafferences) that are generated at the time of a movement, and which are normally congruent with each other.

The first set of experiments refers to action identification and action awareness. Fourneret et al. (2001, 2002) found that schizophrenic patients, like healthy subjects, can automatically adapt their movements to a visuomotor conflict and can reach a visual target in spite of a distorted visual feedback. When the degree of distortion becomes too large to be automatically compensated, the same patients also become aware of their own strategy and can comment about it, but with a higher threshold than healthy subjects. According to the distinction we made earlier between "how" to make an action and "who" made it, it appears that schizophrenic patients are relatively unimpaired in mastering the former problem: in other words, their system for automatic action identification is functional. When the automatic compensation of the visuomotor conflict breaks down, however, they have difficulties shifting to a conscious strategy. This is remindful of the behaviour in the same test of patients with focal lesions in the frontal lobes, who can automatically compensate for small conflicts but also fail to shift to a conscious strategy when the conflict becomes larger (Slachevsky et al. 2003).

In the second set of experiments, schizophrenic patients had to make conscious agency judgments. When shown moving hands of uncertain origin, they were consistently worse than healthy subjects in judging whether the movement they saw was theirs or not. Furthermore, among patient groups, those with first rank symptoms were worse than those without (Franck et al. 2001). In the experiment of Daprati et al. (1997) described earlier, the rate of attribution errors in patients with first rank symptoms went up to 80%, as opposed to 50% in patients without such symptoms (and 30% in healthy subjects). The issue of the direction of these errors, e.g. over-attribution or under-attribution, has not yet been fully investigated: one experiment by Haggard et al. (2003) suggests a possible bias in favour of over-attribution.

The main problem met by schizophrenic patients is therefore an impairment of their mechanism for the conscious sense of agency: they lack the cues for firmly attributing their own actions and thoughts to themselves. As a consequence, they tend to misinterpret these nonattributed actions and thoughts as originating from external sources. This impairment contrasts with the preserved automatic system for action identification. Such a clear dissociation between the two mechanisms was already suggested by experiments in healthy subjects. The condition of these patients offers a further opportunity for answering the question of the respective anatomical substrate of automatic and conscious processing. As we saw above, experimentally decorrelating these signals from each other, produces, in healthy subjects, an increased activity in the right inferior parietal lobule (Farrer et al. 2003). This is also the case in schizophrenic patients, but with a different pattern: firstly, the spontaneous resting activity of their inferior parietal lobule is higher than that in healthy subjects (Spence et al. 1997; Whalley et al. 2004); secondly, this activity is poorly modulated by changing the degree of congruence between the movement related signals, contrary to what is observed in healthy subjects (Farrer et al. 2004). This result suggests, first that the deficient parietal mechanism should be responsible for the impaired sense of agency observed in schizophrenic patients, and second that parietal cortex would have only little impact at the level of the automatic processing, which is largely preserved in such patients. Although it remains true, as suggested by Frith (1992), that schizophrenic patients can no longer properly link their intentions to their actions, the disconnection between intentions and actions should not be looked for at the sensorimotor level. This disconnection is more likely to occur within the cortical network responsible for the representation of actions, a network which includes strong interconnections between parietal areas and prefrontal cortex.

The comparison with patients with frontal lobe lesions is interesting to consider under this respect. Frontal patients, like schizophrenic patients, have a preserved automatic sensorimotor control, contrasting with a difficulty for shifting from automatic corrections to a conscious strategy (Slachevsky et al. 2003). Although the involvement of prefrontal cortex in the genesis of schizophrenic symptoms is still an open question, it is tempting to push this comparison one step further. The two types of patients have in common a disturbance of what can be called "belief evaluation": as a consequence, they may present delusional beliefs (i.e. beliefs that they are unable to reject) about external reality or about themselves. A typical case in patients with frontal lobe lesion is anosognosia, a persistent denial of their impairment: for example, a patient with left hemiplegia may be convinced that she would be able to move her paralysed arm if she decided so, despite contradictory evidence. In his recent meta-analysis of clinical cases with different sorts of delusional beliefs, Coltheart (2007) pointed to the fact that these beliefs are associated with frontal lobe lesions, more frequently in the right hemisphere. It is therefore plausible that a right frontal lobe dysfunction might be responsible for delusions in schizophrenic patients. It would be when this dysfunction is associated with a posterior parietal dysfunction that the delusion would affect the sense of agency and produce the false belief of alien control.

Conclusion

Thus, there are two levels of self-recognition, a "subpersonal" automatic level for action identification, and a "personal" conscious level for the sense of agency, which both

rely on the same principle of congruence of a simulated output and the actual feedback. Yet, the outcome of the two levels is different: the subpersonal level provides an immediate signal for controlling and adapting actions to their goal, whereas the personal level provides information about the intentions, plans and desires of the author of these actions.

The condition of schizophrenic patients dramatically contributes to our knowledge of these mechanisms for self-recognition. The core of the problem met by these patients is a disturbance of their sense of agency: the first rank symptoms, which represent one of the major features of the disease, are nothing but a loss of the ability to attribute their own thoughts, internal speech, covert or overt actions to themselves. Nonattributed or misattributed thoughts and actions then become a material for delusional interpretation and delirium.

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