A specific role for efferent information in self-recognition

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Abstract

We investigated the specific contribution of efferent information in a self-recognition task. Subjects experienced a passive extension of the right index finger, either as an effect of moving their left hand via a lever ('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') during the passive extension of the index finger. Both hands were covered with identical gloves, so that discrimination on the basis of morphological differences was not possible. Participants judged whether the right hand they saw was theirs or not. Self-recognition was significantly more accurate when subjects were themselves the authors of the action, even though visual and proprioceptive information always specified the same posture, and despite the fact that subjects judged the effect and not the action per se. When the passive displacement of the participants right index finger was externally generated, and only afferent information was available, self-recognition performance dropped to near-chance levels. Differences in performance across conditions reflect the distinctive contribution of efferent information to self-recognition, and argue against a dominant role of proprioception in self-recognition.
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1. Introduction

Imagine that you are entering into a hall, where a mirror, large enough to reflect many people, is just in front of you. It is not easy to locate the reflection of your own-self among those of others. Most people would make a gesture and try to visually locate it in the reflection. In other words, they would produce a movement and compare it against the visual feedback in order to detect themselves. This example illustrates the interplay between central (i.e. efferent) information related to the motor command, and peripheral (i.e. afferent) information related to the sensory feedback.

Efferent and afferent information jointly constitute the core of our bodily self-awareness (Bermúdez, Marcel, & Eilan, 1998). However, for more than a century (see for example the 'Williams debate' in Petit, 1999), their respective contribution has been debated. Efference has been usually implicated in the unconscious function of internal models of the motor system, responsible for motor learning, motor prediction and motor correction (for a review see Wolpert, 1997). Afference, and especially proprioception, provides us with the specific content of our bodily self-awareness (Gibson, 1979). In effect, proprioception is usually conceptualised as the modality of the self *par excellence*, because no one else can feel my hand moving, the way I feel it from the inside (Bermúdez, 1998). However, afference can be the result of either self-generated actions or externally-generated sensory stimulation. As a result, the meaning of afferent information for perception and behaviour is ambiguous. Recent theories of motor control have shown how an interaction between efferent commands and sensory inflow may reduce this ambiguity. In the case of a self-generated action, intentions and efferent information not only predict the consequent multisensory signals produced by our own movements (Helmholtz, 1995; Sperry, 1950; von Holst & Mittelstaedt, 1950; Wolpert, 1997), but also modulate their perception and underlie the sense of agency (for a review see Tsakiris & Haggard, 2005a).

We distinguish 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. Self-recognition, in the current context, involves deciding whether a visual stimulus shows one's own body or not. Action recognition may involve unconscious operation of internal predictive models, while self-recognition appears to be a specific cognitive process typically involving conscious experience. As the example with which we started this paper shows, 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 resulting body movements were caused by one's own voluntary action. The action–recognition problem has been studied largely in the sensorimotor control literature (Blakemore, Frith, & Wolpert, 2002; Wolpert, 1997). Only a few studies have explicitly investigated the link between action–recognition and self-recognition (van den Bos and Jeannerod, 2003, and for a review see Jeannerod, 2003). We focus here on the contribution of voluntary action to the self-recognition problem.

Daprati et al. (1997) and Sirigu et al. (1999) investigated the perception of simple and complex gestures in schizophrenic patients and in parietal patients respectively, using the same experimental design. In both studies, participants were instructed to perform simple or complex gestures (extension of one or two fingers), without direct vision of the hand. An experimenter, sitting in a similar cabin, performed either the same or different gesture at the same time. Two cameras filmed the experimenter's and the participant's hands, enabling thus the manipulation of the visual feedback, by switching the video source that the participant saw. Thus participants saw either their own hand, or the experimenter's hand performing the same gesture as the participant, or the experimenter's hand performing a different gesture. Both the experimenter's hand and the participant's hand were covered with identical gloves. Participants were asked to judge whether the hand they saw was theirs or not. They could do this by comparing the gesture they saw via the video feedback with combined efferent and proprioceptive information about the gesture they made. The pattern of results was the same for both experiments. Patients and normal controls performed almost perfectly both when they saw their own hand, and also 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 relatively easy task, even for the patients. However, both schizophrenics and apraxics were significantly worse than normals when they saw the experimenter's hand performing the *same* movements as them. In this case, they tended to misattribute the experimenters's hand to themselves.

In a recent self-recognition study with normal subjects, both the participant's and the experimenter's hands were presented on a monitor simultaneously (Van den Bos & Jeannerod, 2002). *Visual* afferent information was operationalized by rotating the hand image (0, 90, −90, 180°) on the screen and the efferent information was manipulated by creating three action conditions: (i) participant and experimenter performed the same movement, (ii) participant and experimenter performed a different movement, and (iii) participant and experimenter made no movement. Subjects performed perfectly when the experimenter made a different movement, across all rotation conditions, suggesting, "when distinctive movements are available, subjects tend to recognize actions, and not just hands" (van den Bos and Jeannerod, 2003, p. 185). When the movements of both hands were the same, performance was influenced by the rotation factor: reflecting the "sense of body", according to the authors. The main conclusion of the authors is that 'action cues' are used when distinctive movements are made (i.e. different movement condition), and that 'bodily cues' are used when action cues are ambiguous (i.e. same movement condition).

In these three studies, proprioceptive and efferent information were not dissociated, and therefore the relative contribution of efferent and afferent signals to self-recognition was not directly tested. Across all conditions, subjects performed self-generated movements, and therefore both efferent and proprioceptive signals were always present.

The critical condition for all the experiments was the one where both experimenter and participant performed the same movement, and subjects saw the experimenter's hand. In this condition, patients were significantly impaired compared to normal participants. What can account for this pattern? Were normal subjects more accurate in detecting small differences between visual and proprioceptive information, or in detecting differences

between visual and efferent information? Alternatively, did they use fine efferent information to improve the comparison between proprioception and vision?

In the present study, we attempted to answer this question, apparently for the first time. We examined the specific role of efferent information in the self-recognition task used in previous experiments (see Daprati et al., 1997; Sirigu et al., 1999). However, unlike previous studies, we manipulated the availability of efferent information for self-recognition judgements, by spatially dissociating an action from its bodily effect (cf. Tsakiris & Haggard, 2003). Separating the action in space from its somatic effect allows 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 this somatic effect. Subjects made voluntary actions with their left hand, which were transmitted by a lever to the passive right hand. Self-recognition judgements were based on vision of the right hand, which was either the subject's own hand, or someone else's hand. More importantly, we manipulated efferent information. The action could be either self-generated (the subject moved their right hand by an active movement of their own left hand, in which case afference and efference were available) or externally generated. In the externally-generated condition, the experimenter used the same lever to move the subject's right hand. In that case only afferent information was available to the subject. Therefore, we were able to manipulate efference, while maintaining both proprioceptive and visual input constant. This design enabled us to assess the specific role of efferent information in the self-recognition task.

2. Experimental design

The experimental design was 2×2 factorial. The factors were the authorship of action (self-generated/externally-generated) made on the left of the lever, and the identity of the viewed hand (own hand/other's hand).

The action was to press with the left index finger on a lever (length 15 cm, angle 45°). This action lifted the subject's right index finger, which rested on the right end of a lever (see Fig. 1). The lever could be pressed either by the subject ('self-generated' condition) or by the experimenter ('externally-generated' condition).

Subjects viewed either their right hand ('view own hand' condition) or someone else's right hand ('view other's hand' condition) on a video display. They saw only the right hand and right side of the lever. The left hand, which performed the action, was never seen.

To prevent self-recognition based on purely morphological characteristics, both the subject's hand and the other person's hand were covered with identical woollen gloves, positioned on identical levers.

Subjects performed four blocks in total. The "authorship of action" factor was blocked, whereas the visual feedback was manipulated randomly within blocks. Two blocks for the 'self-generated' condition were performed, followed by two blocks for the 'externally-generated' condition or vice versa. The order of blocks was counterbalanced across subjects. Each block contained 30 trials, with 15 trials for each visual feedback condition occurring in a random order. After each block there was a short break.
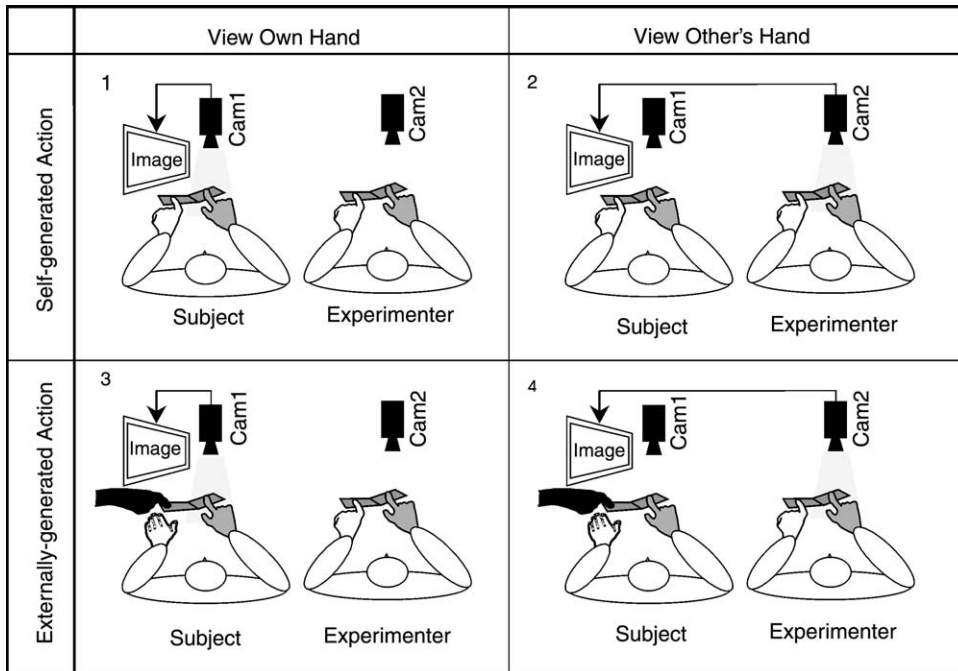
Fig. 1. A schematic representation of the apparatus and the 4 experimental conditions. The conditions were arranged as a 2×2 factorial design with factors of the authorship of action (self-generated vs. externally-generated), and the source of the visual feedback available to the subject (the subject's own right hand vs. the experimenter's right hand). The participant and the experimenter sat in similar cabins. The participant did not have direct view of her hands. The displacement of the right index finger was always passive. In condition 1, the subject herself generated the right hand movement, and saw her own right hand. In condition 2, the displacement of the right index finger was again self-generated, but the participant saw the experimenter's right hand. In condition 3, the displacement of the right index finger was externally-generated by another experimenter, and the participant saw her own right hand. Finally, in condition 4, the displacement of the right index finger was externally-generated by another experimenter, and the participant saw the experimenter's right hand.

Before the experiment, each subject performed two training blocks of 10 trials each, one for the self-generated movement and one for the externally-generated movement.

The subject sat with their hands on a table, while an experimenter sat at a separate but similar table. Two video cameras filmed the subject's and the experimenter's right hands. Black and white video images from one of the cameras were routed via a computer to a video display, which the subject could view by a mirror on the table in front of them. The delay in relaying the image was less than 20 ms. Thus, the subject could see either her right hand or the experimenter's right hand at the centre of the mirror. A further experimenter was continually checking 2 TV monitors, connected to the two cameras respectively. This experimenter could check that the subject and the other experimenter made comparable movements at similar times. This discouraged the subjects from deliberately making slow or otherwise idiosyncratic, and highly recognisable movements. Trials in which the experimenter clearly detected a difference between the onset times of the subject's movement and the other experimenter's movement were noted and excluded from

analysis. The image was shown for 2000 ms in order to minimize the time available to study any morphological differences. 500 ms after the onset of the image, an auditory tone gave the signal for the execution of the action, and the hand remained on the screen for 1500 ms more. At the end of each trial, the forced choice options (Yes/No) appeared on the mirror. Subjects had to respond 'Yes' if they thought they saw their right hand, and 'No' if they thought they saw someone else's hand. Subjects were instructed to respond promptly.

Eighteen naïve volunteers, with normal or corrected to normal vision, took part (10 female, 8 male, mean age 24.1, range 22–32). All participants were right-handed. Mean laterality coefficient, as assessed by the Edinburgh Inventory (Oldfield, 1971), was $+0.87$ (SD$=0.13$). None of the subjects suffered from neurological or psychiatric pathologies. All participants gave their informed consent to participate in this study.

To summarize, there were 4 conditions that differed according to the authorship of the action (Self-generated/Externally-generated) and the visual feedback of the effect of action (Own hand/Other's hand). Note that across all conditions and trials what the subject sees and feels is a displacement of the right index finger. Their task is to match what they see against the proprioceptive and efferent information about their movement. Across conditions and trials, the afferent information originating from their right hand was held constant, but efferent information was available only in the self-generated condition.

3. Results

Due to unsuccessful performance in the execution of the action, such as a gross asynchrony in the initiation of the subject and the experimenter's action, 3.1% of trials were excluded from analysis. Performance was 79% correct in the self-generated condition, and 68% correct in the externally-generated condition. Because we are interested in the visual, proprioceptive and efferent contributions in self-recognition, we further break down the data according to whether the subjects saw themselves or another person. Fig. 2 shows the mean proportion of correct responses across the four conditions.
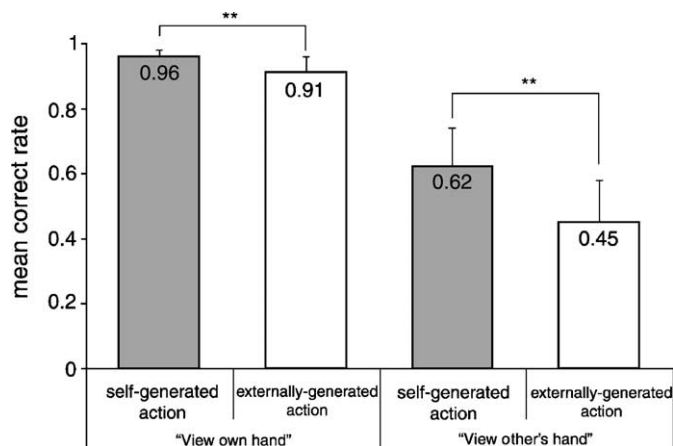

Fig. 2. Mean correct rates per condition. The error bars represent 95% confidence intervals. Asterisks indicate significant differences in self-recognition between self- and externally-generated movements.

The mean correct rates per subject were submitted to the non-parametric Wilcoxon matched-pairs-tests. First of all, the differences between the 'viewing own hand' and 'viewing other's hand' were significant for both the 'self-generated action' ($Z=-3.68$, $P<0.001$) and the 'externally-generated action' ($Z=-3.68$, $P<0.001$) conditions.

In general, the participants performed extremely well in the 'view own hand' condition. This replicates previously reported data (Daprati et al., 1997; Sirigu et al., 1999). Despite this, correct recognition of one's own hand was significantly better when subjects generated the hand movement themselves, than when the experimenter generated it (96% vs. 91%; $Z=-2.062$, $P<0.05$). This suggests that even when participants saw their hand, efferent information contributed to a significant degree.

Performance in the 'view other's hand' condition was dramatically worse than in the 'view own hand' condition. This difference reflects a bias to attribute the viewed hand to oneself (see also Sirigu et al., 1999; Van den Bos & Jeannerod, 2002). Moreover, the mean correct rates for the 'self-generated action' and the 'externally-generated action' conditions when subjects saw the experimenter's hand were also significantly different ($Z=-2.635$, $P<0.01$). That is, the active movement of the left hand had a significant effect on self-recognition judgments. When the action was externally-generated, subjects scored only 45% correct, which is worse than chance level. In contrast, for the self-generated action correct performance amounted to 62%.

We also performed a signal detection analysis for the self-generated condition vs. the externally-generation condition, as an informational measure of self-recognition, which would be independent of the response bias. We used the hits and the false alarms to calculate the d'prime.

The data shown in Fig. 2 were used to calculate d' prime measures for self-detection, for each subject and in each action condition. The mean d' prime value was 3.15 in the self-generated condition and 1.85 in the externally-generated condition. They were submitted to the non-parametric Wilcoxon matched-pairs-tests. Differences between self-generated and externally-generated conditions were significant ($Z=2.635$, $P<0.005$, 1-tailed), suggesting that subjects had access to more discriminative information for self-recognition in the self-generated condition.

3.1. Control experiments 1 and 2: identifying self- and externally-generated actions

Could the visual stimulus carry other information that is confounded with efference? In particular, if subjects could see that the imposed movement of the right hand was actively generated by the left hand, rather than externally applied, and if they also knew that they did not make any active movement of their left hand themselves, it would follow that the visual stimulus showed another person (see condition 4, Fig. 1). The low accuracy in self-recognition when viewing another person's hand in the externally-generated condition (45%) suggests that subjects did not in fact have access to purely visual information about efference. However, we formally tested this possibility in a control experiment. This control cannot be embedded in the main experiment, since the direct instruction to judge efference might well lead subjects to exaggerate or idiosyncratically pattern their active movements in all trials. This strategy would artificially boost the role of efference in self-recognition, thus altering the phenomenon under investigation.

Two actors were used to produce a total of 80 video clips of 2 sec duration, 40 for each actor. We used the same logic and apparatus as in the self-recognition experiment. The actors could either press the left side of the lever themselves so as to produce a passive displacement of their right index finger, or the lever could be pressed by someone else. Only the movement of the right hand was filmed. 40 of the clips showed self-generated movements and 40 showed externally-generated movements. Eighteen volunteers with normal or corrected to normal vision, all right-handed took part in the experiment (mean age 28, 10 females). Note that the volunteers were viewing the movements made by actors rather than their own movements. This ensured that they judged purely the *visual* character of the actions that they observed, and could not rely on stored efferent or proprioceptive memories gained when making the movements. We return to this point in the discussion. We first trained subjects in visual recognition of the active movements by explaining to them how a movement of the right hand could be self-generated or externally-generated. We then showed them 2 training movies in which both hands of the actors were shown, so that subjects could clearly see whether the movement of the right hand was generated by the actors themselves or by another person. Following the training, subjects viewed movies in which only the passive displacement of the right hand was seen. They were asked to judge whether the actors had themselves generated the movement using the lever, or whether it had been externally applied. Each subject saw 40 movies, 20 for each condition, in a random order. Half of the subjects saw 40 movies of actor 1, and the other half 40 movies of actor 2.

The mean correct rates were 59% for the self-generated movies and 54% for the externally-generated movies. The mean correct rates per subject were submitted to the non-parametric Wilcoxon matched-pairs-tests. Differences in accuracy between the two conditions were not significant ($Z = -1.45, P > 0.1$), suggesting that the visual differences between the kinematics of a self-generated displacement vs. an externally-generated displacement were minimal. In other words, there were no clear differences between self- and externally-generated movements in the visual stimulus that could be used by the subjects as a basis for self-recognition judgments in the original experiment. Moreover, the chance level of performance in the "externally-generated/view other's hand" condition of the original experiment suggests that subjects did not base their judgments on such information. Therefore, the use of lever was an appropriate method to separate efference from afference, because it minimized the visual differences in the kinematics of the passive displacement between conditions.

The two actors that were used to produce the movies, were also tested later in the same task (control experiment 2). Each actor saw 40 movies of their own hand. In half of the movies, the displacement of the right index finger was self-generated, and in the other half it was externally-generated. The task was to judge whether the passive displacement of the right index finger was self- or externally generated.

Actor A scored 60% correct at detecting self-generated movements and 60% correct at detecting externally-generated movements. Actor B scored 55% correct at detecting self-generated movements, and 50% correct at detecting externally-generated movements. This pattern of results suggests that even the authors of an action did not show enhanced visual classification of these same movements. Taken together, the results from these 2

control experiments suggest that subjects could not use visual information alone to judge whether a movement was self-generated or externally-generated.

3.2. Control experiment 3: visual discriminability

A second possible explanation of our main result relates to another potential visual difference between conditions. In principle, self-generated movements might carry more visual information than externally-generated movements, for example if subjects deliberately made "exaggerated" or unusual patterns of movement in the self-generated condition. This might involve a motor strategy to produce particular movement patterns that are highly visually identifiable. On this hypothesis, individual exemplars of self-generated movements should have higher visual discriminability than individual exemplars of externally-generated movements. Therefore, we performed a second control experiment. Eighteen new participants watched pairs of movies. As with the first control experiment, we could not embed this control within the main self-recognition experiment, because doing so might have introduced motor strategies that would artificially boost the efferent contribution to self-recognition. Each pair consisted of either (a) two repeats of the same movie in which the passive displacement was externally-generated, or (b) two different movies in both of which the passive displacement was externally-generated, or (c) two repeats of the same movie in which the passive displacement was self-generated, or (d) two different movies in both of which the passive displacement was self-generated. If in the self-generated actions, participants used a motor strategy of exaggerating their movements, so that they would be more easily recognizable, then discrimination between movies should be better for the self-generated than for externally-generated movements.

Eighteen volunteers with normal or corrected to normal vision, all right-handed (mean age 27, 8 males) took part in the experiment. Each participant watched a total of 80 pairs of movies (20 pairs of movies for each category) in a random order. The task was to judge whether the two movies in each pair were the same or different. In that control experiment we used the same movies as in control experiment 1. These movies were made by two actors in a similar context employing similar task demands as in the original experiment. The task demands in this control experiment differed to the extent that focus of interest was not self-recognition per se, but the visual discriminability of movement exemplars. During the making of the movies, the actors did not have direct view of their hand, they were asked to press with their left index finger the left end of the lever as soon as they heard an auditory tone (go-signal). The length of the movies was the same as in the original experiment (2 s).

When participants watched a repetition of the same movie, they correctly detected the repetition on 66% of trials in the self-generated condition, and 66% in the externally generated condition. When, participants watched a pair consisting of 2 different movies, they correctly discriminated them on 45% of trials in which two self-generated movements were shown, and 46% of trials in which two externally-generated movements were shown.

We then performed a signal detection analysis, in which the signal was defined as the detection of a difference between the two movies in a pair. We calculated the d'primes per condition and per subject, and we submitted them to the non-parametric Wilcoxon matched-pairs-tests. Differences in performance for detecting visual differences between

self-generated and externally-generated movements were not significant ($Z = -.710$, $P > 0.4$). Visual discriminability was no higher for self-generated than for externally-generated movements. Therefore, we cannot straightforwardly explain the pattern of results presented in the original experiment by arguing that subjects deliberately exaggerated or modified the pattern of the left hand movement in the self-generated condition with the aim of increasing the visual information available when viewing their right hand.

Overall, the results of the present study support a differential contribution of afferent and efferent information in self-recognition. In the case of self-generated action, when efferent information is present, self-recognition judgments are significantly more accurate, even though the action itself was "invisible". That was true when subjects saw someone else's hand, but also when they saw their own hand. Moreover, in the absence of efferent information, performance in the critical condition where participants saw someone else's hand was below chance.

4. Discussion

Self-recognition judgments were more accurate when subjects made a voluntary action, even if this action was unseen and spatially remote from the part of the body that had to be recognized. The efferent information clearly contributed to the match between proprioceptive and visual representations that underlies the self-recognition task. Before discussing precisely how efferent information contributed, we briefly consider possible artifactual explanations of our results.

There could be a mean difference in movement latency between the self-generated and externally-generated conditions. However, several features of the design suggest that this did not occur. First, when the experimenter clearly detected a difference between the subject's and the second experimenter's reactions, the trial was excluded. Second, our use of a single motor action, and an auditory go-signal at fixed 500 ms latency after the image appeared was designed to allow rapid reaction times and stereotyped movement patterns. Third, if there were major differences in movement onset times, one would expect that correct rejections when subjects saw the experimenter's hand in the self-generated condition would be as high as hits when they saw their own hand. In fact correct rejections were significantly less frequent than hits ($Z = -3.68$, $P < 0.01$). Finally, we observed a significant difference between "self-generated" and "externally-generated" conditions even when subjects were looking at their own hand. In this condition, visual and proprioceptive information are perfectly synchronised, and therefore there can be no temporal mismatch to detect. In this case, the benefit of efference could not be an artefact due to an increase in the difference in movement onset or movement kinematics between visual and proprioceptive signals. Therefore, this significant difference reflects a genuine contribution of efferent information per se.

Finally, could there be differences in the detailed kinematics of the passive displacement of the right index finger between the self-generated and externally-generated conditions? The thrust of this argument is that self-generated movements might be recognisable through their specific visual form, without the subject needing to use efferent

information in the visual-proprioceptive matching process. We performed two control experiments to compare the information available in the visual stimulus between self-generated and externally-generated conditions. The first two control experiments showed that subjects could not use visual information alone to judge whether a movement was self-generated or externally-generated. In the third control experiment, we investigated whether the levels of visual information in exemplars of self-generated movements were higher than in exemplars of externally-generated movements, using a visual discrimination task. Discrimination performance did not differ between conditions, suggesting that subjects could not have used purely visual information for self-recognition. Both the control experiments involved the subjects viewing movements of another person's hand in all the trials. Such control experiments could not be interleaved with the main self-recognition experiment, because the question asked in the control experiments has a "leading" quality, which would encourage subjects to make precisely the exaggerated or idiosyncratic styles of movement that our main experiment sought to avoid. However, there is no reason to suppose that the purely visual detectability of efference (control experiments 1 and 2), or the visual discriminability of movements (control experiment 3) would be any higher for judgements performed in real-time vs. offline, or for one's own movement vs. that of others. Indeed, the control experiments with new subjects provide a strong way of studying the purely visual component of these movements. The null findings show that visual differences cannot explain the efferent contribution to self-recognition in the main experiment. Therefore, the improved self-recognition performance in the self-generated condition of the main experiment must reflect a specific contribution of efferent information to the process of visual-proprioceptive matching, rather than a difference in the visual stimuli alone.

Previous studies of the self-recognition task have identified the critical condition as the one in which subjects watch someone else's hand performing the same movement (Daprati et al., 1997; Sirigu et al., 1999). In our study, subjects were significantly more accurate in correctly recognizing their own hand when the passive displacement was self-generated compared to when it was externally-generated. In fact, when the displacement was externally-generated, just by comparing visual and proprioceptive signals, subjects were unable to accurately discriminate between self and other, and performed at chance. When the action was externally-generated, subjects incorrectly attributed the experimenter's hand to themselves in 55% of the trials, whereas for the self-generated action incorrect attribution to self occurred in 38% of the trials. The difference between these two conditions shows that efferent information makes a specific contribution to self-recognition. Moreover, we show for the first time that even when subjects were looking at their own hand, their performance was significantly improved when efference was present.

Our results also show that afferent information is not sufficient for self-recognition. Other studies confirm that proprioceptive information can be over-ridden or altered to produce an anomalous sense of self. For example, during the rubber hand illusion, when tactile stimulation is applied simultaneously on a rubber hand and a real hand, subjects mislocalize the position of their own unseen hand as being closer to the rubber hand that it really is (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005b). They tend to feel the touch at the locus where they see the rubber hand is touched, rather than on their real

hidden hand. It seems that the phenomenology of a matching between proprioception and visual feedback is strong enough so as to attribute alien body parts to one's self. It is surprising however, that in the absence of efference, normal participants performed so poorly. This poor performance is particularly surprising since many physiological studies have shown that proprioceptive afferent information about passive movement is highly precise, and includes considerable temporal detail (Prochazka, 1999). Instead, we suggest that the brain centres responsible for self-recognition do not have access to this level of detailed proprioceptive information.

Another interesting finding is the direction of misattribution. In general, subjects tended to misattribute the experimenter's hand to themselves, and not the opposite. The same pattern has been reported in several studies (Daprati et al., 1997; Sirigu et al., 1999; Van den Bos & Jeannerod, 2002). The explanation put forward is that self-attribution might be a default mode of attribution, when no clear cues for self-recognition are available (Van den Bos & Jeannerod). In our view, the direction of this effect can also be explained by the nature of the experimental task used and by the prevalent role of vision over proprioception. Several studies have shown that synchronous visual and proprioceptive stimulation is a powerful cue for self-attribution. In the rubber hand illusion discussed above, synchronicity induces a feeling that a rubber hand is one's own, despite clear morphological differences between the rubber hand and the subject's hand.

We now consider how efference may have facilitated self-recognition. Clearly, subjects must base their self-recognition judgements on detection of very small differences in either the onset latency and/or kinematic pattern between what they see, and what they do and feel. If the timing and kinematic details provided by viewing the subject's hand and the experimenter's hand were exactly identical, no information would be available to support self-recognition. How, then, could efferent information improve detection of such small timing and/or kinematic differences?

First, efferent information might not be used directly, but could provide an indirect benefit by improving the quality of information in either the proprioceptive or visual feedback pathways. For example, internal predictive models within the motor system may use efferent information so as to generate a prediction about the anticipated sensory feedback (Wolpert, 1997). In such cases, the subject may know exactly when to expect visual and proprioceptive information about the movement. This efferent prediction could improve sensory processing, perhaps by enhancing detection of small timing differences. Equally, the spatial precision of proprioception can be enhanced by active positioning of the limb (Paillard & Brouchon, 1968). However, in our experiment, the active movement of the left hand would additionally need to transfer to improved proprioception of the right hand.

Moreover, recent models of sensorimotor control suggest that such effects may not be sufficient to explain our results. First, one major effect of motor commands on sensory information is to suppress the magnitude of sensations (Blakemore, Wolpert, & Frith, 2000). Although the effects on temporal discriminability have not been specifically studied, the combination of decreased sensory magnitudes with increased temporal resolution seems unlikely. Second, studies on the relation between voluntary movement and time perception have generally reported that voluntary motor commands bias time perception by a constant amount, without altering the variability of temporal judgement

(Haggard, Clark, & Kalogeras, 2002; Tsakiris & Haggard, 2003). Therefore, the hypothesis that efferent signals influence self-recognition indirectly, by altering the processing of proprioceptive information seems unlikely, though it cannot be ruled out.

Could efference improve the visual representation by similar means? A recent self-recognition experiment with a deafferented patient (Farrer, Franck, Paillard, & Jeannerod, 2003b) suggests not. Deafferented patient GL could only perform the task by comparing efferent information with visual information. GL detected differences only when the discrepancies were large ($>70°$ angular bias, whereas for normal subjects it was $>40°$)". This suggests that efferent information cannot improve the prediction of visual information. We draw the same conclusion from our control experiment 2.

We put forward two possible accounts for the role of efferent information in self-recognition, which are not mutually exclusive. Our discussion is based on a simple model of self-recognition, shown in Fig. 3.

The efferent information available in the self-generated action condition could be directly used in the matching process. For example, efferent information could provide an additional input to the comparison process. The efferent signal could either be a "raw" motor command (path 1 in Fig. 3), or could be situated after the motor command has been processed by the forward predictive model (path 2 in Fig. 3). A raw motor command would provide only timing information to the comparator, while a signal processed by the forward model could provide a full kinematic description of the movement, suitable for detailed comparison with the proprioceptive or visual signals. Our results showed a poor level of self-recognition performance when proprioceptive signals alone were available, and a significant enhancement when efferent signals were used, even when subjects were looking at their own hand. This pattern suggests that the efferent input to the comparator is at least as important as the proprioceptive input. Indeed, the fact that performance was at chance when subjects viewed the experimenter's hand in the externally-generated condition, suggests that proprioceptive inputs to the comparator may be insufficient for correct self-recognition.

The experimental design used in the present study cannot exactly quantify the individual contributions of raw efference and forward model output to self-recognition. However, since the movements were simple finger flexions, we suspect pathway 1 may
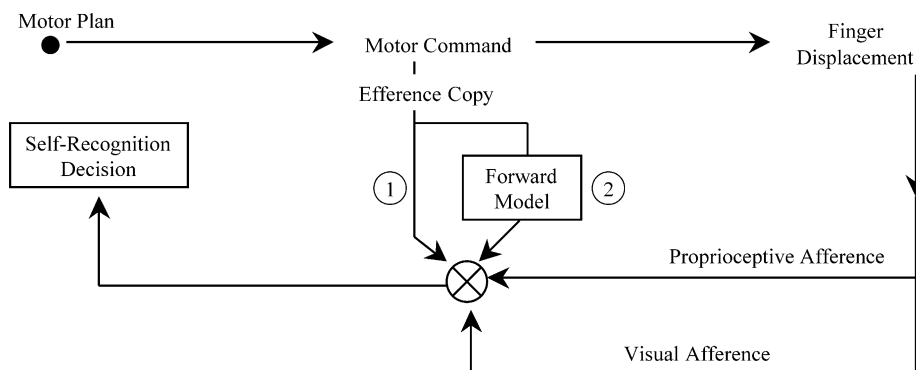

Fig. 3. A cognitive architecture for self-recognition.

have played an important role in the present study. Comparison between the time of this efferent signal and the time of the visual movement onset may be sufficient for self-recognition. Recently, in a bimanual unloading task, Diedrichsen, Verstynen, Hon, Lehman, and Ivry (2003) showed that efference produces an accurate anticipatory feedforward signal, which enhances the movement representation of the loaded hand. This signal need not detail the full motor parameters of the movement, because the same effect was found when the subjects unloaded the weight with their other hand, but also when they pressed a button that initiated the unloading. The occurrence of a voluntary action appeared to be more important than its precise kinematic form.

Nevertheless, in the present study, efference significantly improved self-recognition even when participants were looking at their own hand. This suggests that the role of efference cannot be strictly limited to the generation of an accurate temporal-signal. When participants were looking at their own hand, proprioceptive and visual signals were precisely synchronous. In this case, an additional efferent temporal signal adds no new information and should not improve self-recognition performance. The fact that performance does improve suggests that efferent information must contribute via another route, such as the forward model output (Pathway 2 in Fig. 3). Therefore, we suggest that over and above the generation of accurate temporal predictions, efference may also provide predictions of current kinematics which improve the detection of kinematic errors.

The comparator underlying self-recognition judgements may be located in the parietal cortex (Farrer et al., 2003a; Leube, Knoblich, Erb, & Grodd, et al., 2003a; Leube, Knoblich, Erb, & Kircher, 2003b; Sirigu et al., 1999). Previous studies have shown that parietal cortex is an important integration site for multi-modal information including visual and proprioceptive signals (for a review see Graziano & Botvinick, 2002). In addition, recent neuropsychological (Sirigu et al., 2004) and imaging studies (Lau, Rogers, Haggard, & Passingham, 2004) suggest that efferent information is also processed in these same regions. The neural substrates of perception of self-generated movements were also assessed in two recent imaging studies. Farrer et al. (2003a), following the paradigm first reported by Franck et al (2001), introduced spatial distortions (i.e. angular deviations) in the visual feedback of the subject's voluntary movement. Activation in the right inferior parietal lobe was positively correlated with the degree of the spatial distortion. Similarly, Leube and colleagues (2003b) identified a right fronto-parietal network activated when subjects observed a mismatch between the performed movement and the visual feedback.

An anterior–posterior functional differentiation within the parietal cortex for the processing of peripheral and centrally generated signals has been suggested by various research groups (Burbaud, Doegle, Gross, & Bioulac, 1991; Graziano & Botvinick, 2002; Schwoebel, Boronat & Coslett, 2002). The anterior region of parietal cortex forms the somatosensory areas that are responsible for the processing of unimodal and multimodal sensory signals. Posterior parietal cortex has been linked to the planning of movements (for a review see Cohen & Andersen, 2002) of any body-part (Gemba, Matsuura-Nakao, & Matsuzaki, 2004). One recent review emphasises the role of the parietal cortex in multisensory integration and in the generation of intentions (Andersen, & Buneo, 2002), while other authors emphasise its role in the on-line control of actions (Gréa et al., 2002). The impaired performance of parietal patients in a self-recognition task quite similar to that used here may be explained by an impaired ability to compare on-line the sensory

feedback with an internally generated representation of the planned movement (Sirigu et al., 1999). Human neuroimaging studies have consistently showed activation in the parietal cortex linked to the sense of agency (Farrer & Frith, 2002; Lau et al., 2004; Ruby & Decety, 2001). One recent study points to a specific role of parietal cortex in self-recognition tasks like that used here. MacDonald and Paus (2003) reported impaired self-recognition performance following rTMS over superior parietal lobule (SPL) only for active, but not for passive movements. According to those authors, SPL is specifically engaged in detecting temporal congruencies between efferent and afferent signals.

The authorship effects observed in the present study are in accordance with previous research on the perception (Tsakiris & Haggard, 2003), recognition (Knoblich & Flach, 2001; Knoblich, Seigerschmidt, Flach, & Prinz, 2002) and prediction (Blakemore, Frith, & Wolpert, 1998) of effects following voluntary actions. Knoblich and colleagues have shown that efference provides a significant advantage in predicting and recognizing self-generated events. In these studies, the action and the effect took place on the same body part. Our study extends this evidence by emphasizing the role of efference in recognizing afferent events that occurred to a different body part from the one that performed the action. This significant contribution of efferent signals provides evidence for an authorship effect on self-recognition. This position contrasts with recent philosophical concepts of the "bodily self". In that literature, proprioception is often held to be the modality of the self par excellence, it is often conceptualised as a basic form of self-consciousness (Bermúdez, 1998; Gibson, 1979). The present results challenge this view and argue against a dominant role of proprioception in action recognition (Farrer et al., 2003b). Our data suggest that self-recognition in the presence of only afferent information, and without action, is quite limited.

To conclude, we studied the efferent and afferent contributions to self-recognition. We kept afferent information constant across conditions, while manipulating efference by separating the action from its bodily effect. Thus, we showed that voluntary action significantly improved self-recognition judgments. Importantly, the movement seen was always the effect of an unseen action. This 'remote' informational power of efferent processes in the perception of bodily effects has important implications for the concept of the "embodied self". The results of the present study suggest that proprioceptive self-consciousness may not be the kind of self-consciousness required for infallible self-recognition. Attribution, in the sense of correctly recognizing an external visual object or event as related to "me" seems to depend very largely on agency (Tsakiris & Haggard, 2005a).

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