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The role of proprioception in action recognition

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Abstract

This study aimed at evaluating the role of proprioception in the process of matching the final position of one's limbs with an intentional movement. Two experiments were realised with the same paradigm of conscious recognition of one's own limb position from a distorted position. In the first experiment, 22 healthy subjects performed the task in an active and in a passive condition. In the latter condition, proprioception was the only available information since the central signals related to the motor command were likely to be absent. The second experiment was realised with a deafferented patient who suffers from a complete haptic deafferentation, including loss of proprioception. The results first argue in favour of a dominant role of proprioception in action recognition, but they also stress the possible role of central signals. The process of matching the final position of one's limbs with an intended movement and thus of action recognition would be achieved through a comparison process between the predicted sensory consequences of the action, which are stored in its internal model, and the actual sensory consequences of that action.

Keywords: Action recognition; Agency; Proprioception; Deafferented patient; Internal model

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1. Introduction

When we perform a goal oriented arm movement, we anticipate seeing and feeling changes in our arm position and configuration that should correspond to the intention and to the motor

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commands that we have generated to get to the goal. This function of matching limb position with an intended movement is a key condition for keeping the central representation of our body in register with its actual position. Indeed, an artificial mismatch between the two (e.g., created by an optical device, like seeing one's arm through a laterally displacing prism) triggers a quick compensation so as to restore the correspondence.

Although most of this matching process is likely to remain at the automatic level, it must also have a conscious counterpart: we normally are able to consciously monitor our own movements and to recognise them as ours. The problem raised in this paper is thus twofold. First, we asked the question of how sensitive is this ability to match the final position of our limbs with an intended action? Second, we tried to disentangle the respective contributions of peripheral (sensory) signals and central (efferent) signals to this process. We define central signals as ones that have an endogenous origin (Sperry, 1950; Von Holst & Mittelstaedt, 1950) and are issued from internal models (see Kawato, 1999 for review). These models mimic aspects of one's own body and the external world and are divided into two main categories: the inverse internal model and the forward internal model. The first model provides the feedforward motor commands necessary to achieve the desired outcome. The latter models aspects of the external world and of the motor system in order to capture the forward or causal relationships between actions and their outcomes. When a subject undertakes an action the internal inverse model first provides the feedforward motor commands necessary to achieve the desired outcome. A copy of this motor command, also called efference copy (Von Holst & Mittelstaedt, 1950) or corollary discharge (Sperry, 1950), is then sent to the forward model that estimates the sensory consequences (i.e., predicted sensory consequences) of the ensuing movements (see Desmurget & Grafton, 2000; Wolpert & Ghahramani, 2000 for reviews). When we refer to central signals, we refer to the feedforward motor command issued from the inverse model and to the predicted sensory consequences issued from the forward model. The interplay between the peripheral and the central signals is considered as a key factor for the *sense of agency* by which a subject will feel that he/she is the initiator of the action, or is causally involved in the production of that action (Gallagher, 2000). To determine the different signals involved in recognising one's own actions would allow a better understanding of the mechanisms required for the sense of agency.

Among the sensory signals which are currently available to the conscious subject, vision and proprioception are likely to play a role in action monitoring. Proprioception, the integrated signal arising from cutaneous, muscular and joint receptors, should be of peculiar relevance: it arises directly from the moving limb and is the only source of 'first person' information, e.g., information that unambiguously pertains to the subject. We considered that, if we could either maximise or eliminate proprioception during a change in limb position, we could provide a direct answer to the above questions. To this aim, we designed two experiments using the same paradigm of conscious recognition of one's own limb position from a distorted position. Experiment 1 was run in normal subjects: in this experiment, proprioception was the only available, as visual input was controlled and the change in limb position was produced by a passive displacement. Conversely, because the subject did not produce any active movement, the central signals related to the motor command were likely to be absent. For Experiment 2, we took advantage of the condition of a patient who suffers from a complete loss of kinaesthetic input and position sense from most of her body, following a sensory neuropathy. When this subject voluntarily moved her arm, central signals were present whereas, by contrast, no reafferent input from the limb movement and/or position was available. The comparison between the results of these two experiments stresses the role of proprioception in action recognition.

2. Experiment 1: Comparison of action recognition following active and passive arm displacement

2.1. Subjects

Twenty-two subjects (11 men, 11 women, mean age 28.18 years ± 7.14) performed the task. Their educational level was 16 years ± 2.49 and their laterality score was 84.1 ± 38.13 according to the Edinburgh questionnaire (Oldfield, 1971). All subjects were naïve to the purpose of the experiment.

2.2. Materials

During the experiment, the image of an electronically reconstructed hand was presented to the subjects on a high refresh rate computer screen. A specially designed program displayed the picture of a hand holding a joystick seen at the same position as that of a real joystick actually held by the subject and connected to the computer (Franck et al., 2001). This design allowed the dynamic representation of the movements of the joystick held by the subject with an intrinsic delay less than 30 ms. Angular biases could be introduced in this representation (see below), modifying the apparent direction of the movement actually performed by the subject with respect to the movement displayed on the computer screen.

The computer screen was placed face down on a support. A mirror was placed horizontally 18 cm below the screen and the joystick was placed below the mirror on the table supporting the apparatus (Fig. 1). The distance between the table and the mirror was 31 cm, so that the subject's hand holding the joystick was located approximately 18 cm below the mirror. Thus, when subjects looked at the mirror, they saw the image of a virtual hand moving a joystick just above their own (invisible) hand actually doing that.

2.3. Procedure

Subjects sat in front of the apparatus with their forehead leaning on a foam cushion. They held the joystick with their right hand, with their elbow resting on the table. The position of their forearm was adjusted so as to coincide with the direction of the virtual forearm seen in the mirror. Subjects were instructed to maintain their fingers in a fixed position on the joystick and to restrict their movements to the wrist joint.

In the active condition, the task consisted in executing a series of simple movements with the joystick. Each trial started with a dark screen. A green spot (1 cm diameter) was displayed for 1 s on the top of the screen. The image of the virtual hand then appeared for 2 s during which the subjects had to execute a movement of the joystick in the direction indicated by the position of the

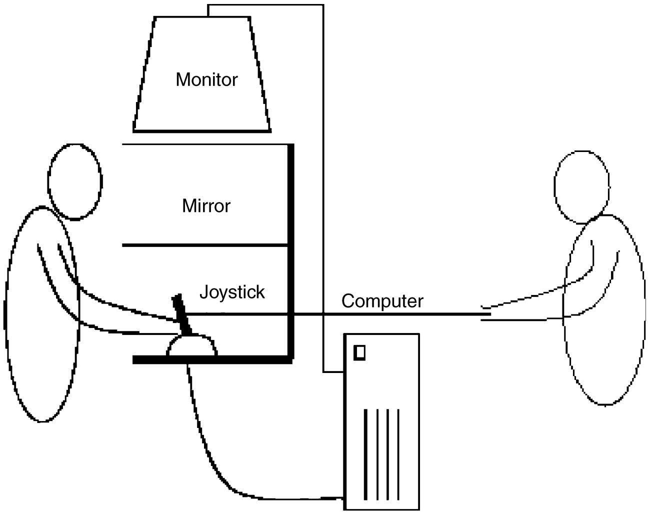

Fig. 1. Experimental set-up. The dynamic parameters of the subject's hand moving the joystick were fed into a virtual hand holding a joystick. This image was represented on a monitor and projected on a mirror overlying the subject's hand. Angular biases could be introduced in this representation, modifying the apparent direction of the movement actually performed by the subject with respect to the movement displayed on the monitor. In the passive condition a metallic rod was hung at the top of the joystick. An experimenter (on the right) pulled the rod toward him and the joystick moved toward the top.

green spot. At the end of the trial the subjects had to verbally report whether the movement they saw on the mirror was concordant with the movement they performed. They had to answer YES or NO.

In the passive condition, a metallic rod was hung at the top of the joystick. An experimenter pulled the rod toward him and the joystick moved toward the top of the screen (see Fig. 1). The movements of the joystick, driven by the experimenter, were modeled on a screen near the support in order to control the linearity and the straight direction of these movements. The same series of trials as in the active condition were run. At the end of each trial the subjects had to verbally report whether the movement they saw in the mirror was concordant with the movement made by the joystick. They had to answer YES or NO.

Two types of trials were used for each condition.

1. Neutral trials: movements of the virtual hand exactly replicated those made by the joystick.
2. Trials with angular biases: movements of the virtual hand were deviated either to the right or to the left by a given angular value with respect to those made by the joystick. Seven angular values (5°, 10°, 15°, 20°, 30°, 40°, and 50°) were used.

Each trial was run four times ($N = 64$). The order of processing of the trials was randomised and a different randomisation was realised for each subject.

The subjects were familiarised with the device before the beginning of the session. The subjects ran a trial without bias, and another trial with a bias of 30° of 15 s each. At the end of each trial subjects were asked if the movements they visualised on the mirror were concordant with the ones they executed. Each subject performed two familiarisation tasks; one in the active condition and one in the passive condition.

A control of the passive nature of the movements was made in two subjects (not included in the experiment). They performed the active and passive tasks in the same conditions as the other subjects. EMG was recorded with two electrodes placed on the arm at the level of the triceps and the biceps muscles, and the reference electrode placed on the leg. The EMG recordings showed that there was no systematic motor response in the passive condition.

2.4. Data analysis

The YES responses, which reflect the subjects' ability to recognise a movement as his/her own, were used for the analyses. A YES response was considered as a correct response in neutral trials and as an error in biased trials.

Two scores were taken into account for describing and analysing the performances of the subjects.

1. The threshold value from which the subjects gave 50% of correct responses.
2. The correlation score of Pearson between the number of YES responses and the value of the bias.

Comparisons between the two conditions (active and passive) were realised a *t* test for pairwise comparisons.

2.5. Results

The threshold value below which the subjects gave more than 50% of correct (NO) responses was found to be located between biases of 10° and 15° in the two conditions (Fig. 2). These results showed that the subjects tend to become aware of the discordance for the same bias whether they executed the movements or not.

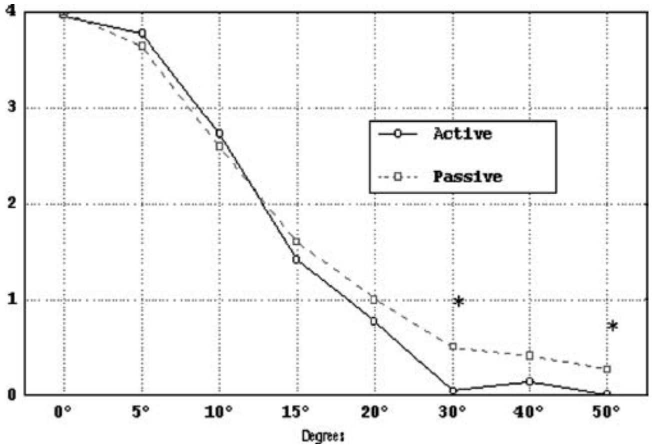

Fig. 2. Number of "YES" responses as a function of angular bias in the active and in the passive conditions.

We considered that the subjects correctly performed the task if the Pearson correlation score was negative and significant. Indeed, the greater the bias value, the lesser the number of YES responses should have been reported if the subjects did recognise the discordance between the movements they executed and the movements they saw in the mirror. In the active condition, the bias value was negatively and significantly correlated to the number of YES responses ($r = -.87$; $p < .05$). In the passive condition, the Pearson correlation score was $r = -.80$; $p < .05$.

To compare more accurately the difference in recognition of one's own movements between active and passive conditions, a t test for pairwise comparisons was realised for each bias. The results showed significant differences in the number of correct responses only for the biases of 30° ($t = -2.663$; $p = .014$) and 50° ($t = -2.324$; $p = .03$). Thus, for biases below 30°, the subjects tended to perform equally in the two conditions whereas for larger biases they tended to perform better in the active than in the passive condition.

3. Experiment 2: Action recognition in a haptically deafferented patient

This second experiment is complementary to the previous experiment, although it differs from it in some aspects that will be discussed later. A comparison between these two experiments is thus interesting for discussing the role of proprioception in action recognition.

3.1. Subjects

A deafferented patient (GL, aged 52 years) and five control subjects (three women, two men, mean age 34 years) participated in the study. Four of the control subjects were right-handed; one subject was left-handed according to the Edinburgh questionnaire (Oldfield, 1971). All subjects were naïve to the purpose of the experiment.

Patient GL suffered a permanent and specific loss of the large sensory myelinated fibres in all four limbs, following two episodes of sensory polyneuropathy which affected her whole body below the nose level. The illness resulted in a total loss of the senses of touch, vibration, pressure and kinaesthesia as well as a total absence of tendon reflexes in the four limbs. Motor nerve conduction velocities were found to be normal (Cooke, Brown, Forget, & Lamarre, 1985).

3.2. Material and procedure

The device described for Experiment 1 was also used in Experiment 2 (Franck et al., 2001). However, the procedure had to be changed, in order to adapt to the patient's condition. The position of the mirror was lowered to adjust to the height of her wheelchair. Her right hand was attached to the joystick to maintain a stable hand position.

Each trial started with a dark screen. The image of the virtual hand then appeared for 5 s and the subject had to execute a simple movement with the joystick in the direction given previously by the experimenter (toward the top, the left or the right of the screen). The screen returned dark and the subject had to answer the question: "Did the movement you saw on the screen exactly correspond to that you have made with your hand?" The subject had to answer YES or NO.

A training session realised before each block showed that the patient could not execute the movement with an angular bias. To succeed she had to close her eyes, to position the joystick at its start position and execute the movement. Then she opened her eyes and answered the question. The same procedure was applied for the control subjects.

Two categories of trials were used:

1. Neutral trials: movements of the virtual hand exactly replicated those made by the joystick.
2. Trials with angular biases: movements of the virtual hand were deviated to the right by a given angular value with respect to those made by the joystick. Six values of angular bias (40°, 50°, 60°, 70°, 80°, and 90°) were used.

The bias values were increased in this experiment because patient GL did not recognise a deviation of her movements with the bias values used in the first experiment. Each trial was run four times for each of the three directions of movement, each trial was thus repeated 12 times ($N = 84$). Because the patient had difficulties performing the task when a deviation was introduced, the trials were made in three different blocks:

1. Movements towards the top with neutral and angular biases.
2. Movements towards the left with neutral and angular biases.
3. Movements towards the right with neutral and angular biases.

In each block, the order of presentation of the trials was randomised before the participation the subject. Identical trials could not be presented twice in a row. Missed trials were repeated if necessary.

This second experiment differs from the previous experiment in two points concerning the procedure. First, the subjects were requested to close their eyes during the execution of the movements; thus they did not have visual feedback of their movements but of the final position of their arm. Second, the values of the biases employed were far more important in this second experiment than in the first one.

3.3. Data analysis

The "YES" responses were used for the analyses. Performances between the different experimental conditions for both groups were analysed with the Spearman correlation score. The differences between the control group and the deafferented patient were assessed with an ANOVA with repeated measures since such analysis is considered as valid for comparing the mean score of an individual with that of a group of controls (Mycroft, Mitchell, & Kay, 2002). The factors were: "group" (two levels: control group and patient GL), "bias" (seven levels: 40°, 50°, 60°, 70°, 80°, and 90°). Post-hoc analyses were realised with the test of Schefféin order to precise the differences between the types of responses.

4. Results

Fig. 3 shows that the control subjects' responses were clearly below the threshold of 50% (correct) NO responses for the smallest bias (40°) used in this experiment and that the level of 100% correct responses was for higher biases (70°–80°). To understand this difference with respect to the results of Experiment 1, one has to keep in mind the differences in experimental procedure between the two experiments (see Section 5).

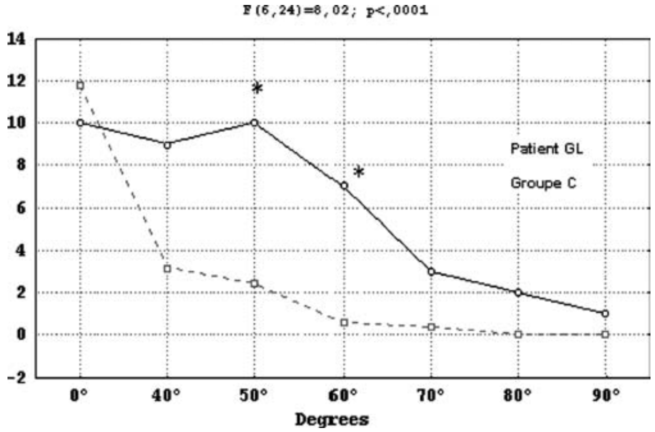

Fig. 3. Number of “YES” responses as a function of angular bias for control subjects (C - - - -) and the deafferented patient GL (GL).

Patient GL correctly recognised her movements in the neutral trials with no bias. Her error rate based on the number of YES responses was higher than in control subjects. When an angular bias was introduced, GL became impaired in executing the movement: she reported impressions of not controlling her movements, and not being aware of what she was doing. However, as illustrated by Fig. 3, the curve of GL’s responses as a function of the value of the bias showed that she tended to give less YES responses as the bias became larger. Indeed, the number of YES responses was negatively and significantly correlated to the value of the bias ($R = -.936$; $p = .002$, Spearman correlation coefficient). This result gave evidence that the patient GL correctly performed the task and could thus recognise the distortion of her movement for high bias. The slope of the curve, however, strongly differed from that of control subjects. The patient reached the threshold of more than 50% of NO responses only for a bias between 60° and 70°.

Although GL recognised a distortion of her movements, the ANOVA indicated that her number of “YES” responses was significantly greater than the control group ($F(1,4) = 24,05$, $p = .008$). This analysis also revealed a significant effect of the factor “bias” ($F(6,24) = 39.16$, $p < .0001$) and a significant interaction between “bias” and “group” factors ($F(6,24) = 8.02$, $p < .0001$). These differences were observed for the biases of 50° ($p = .007$) and 60° ($p = .04$) as revealed by the post-hoc analysis with the test of Scheffé.

5. Discussion

This study aimed at evaluating the role of proprioception in the process of matching the final position of one’s limb with an intended movement, which, we consider as a key component of action recognition. Although the two experiments presented here differed in some aspects, they clearly showed convergent results in favour of a dominant role of proprioception in action recognition. In Experiment 1, the subjects could recognise the distortions of their own movements when they actively produced them, but also when the movements were generated by passive displacements. In the latter condition, only proprioceptive signals were available to the subjects for action recognition since the central signals related to the motor command (Sperry, 1950; Von Holst & Mittelstaedt, 1950; Wolpert, Ghahramani, & Jordan, 1995) were likely to be absent. The slight but significant advantage shown by the subjects in the active condition for the large rotations may relate to the contribution of a gamma command linked to the alpha command, via a contraction of intrafusal muscles. Obviously, this contribution was absent in the passive condition. Paillard and Brouchon (1974) reported that experimental block of the gamma loop suppressed the advantage of active movements in spatial encoding of limb position.

In Experiment 2, we found the haptically deafferented patient GL to be massively impaired with respect to the control subjects. Whereas the control subjects reached the value of 100% of correct responses for a bias between 70° and 80°, GL was still at 50% of correct responses for biases around 60°–70°.

Before we can get into the interpretation of these results, we have to discuss the differences in performance of the control groups in the two experiments. In Experiment 1, the level of 100% of correct responses was comprised between 20° and 30° whereas in Experiment 2, this level was reached for larger bias values. This difference may be explained by different experimental conditions since the procedure was changed in Experiment 2 in order to adapt to the patient's condition. In this experiment, the subjects had to close their eyes while they executed their movements. Thus they did not have a visual feedback from their own movement. They could only see the final position of the virtual hand on the screen. It is well known that visual signals can be selectively used as kinesthetic cues for controlling limb movements and positions. These visual cues can be provided by vision of a moving body segment in relation to other body parts (Gibson, 1979; Lee & Lishman, 1997). Indeed "proprioception" at large should not be restricted to signals arising from muscles, but could also include other sensory cues. Paillard and Stelmach (1999) have shown that both visual and tactile cues contribute to the evaluation of one's own limb position in a pointing task. Furthermore, neurophysiological studies in monkey showed that neurones in the cortical areas of convergence of visual and somesthetic inputs (e.g., at the level of the intraparietal sulcus) respond to both visually guided movements and passive limb displacements (Duhamel, Colby, & Goldberg, 1998). It is thus likely that visual and proprioceptive cues potentiate each other in signaling limb position. The lack of visual motion cues in Experiment 2 could explain why subjects were less accurate in recognizing their movements.

The present results also stress the possible role of other non sensory, cues for conscious position sense and action recognition. Compelling evidence supports the existence of internal models that can mimic the input/output characteristics, or their inverse, of the motor apparatus (see Kawato, 1999 for review). One of these models, the internal forward model, estimates the sensory consequences (i.e. predicted sensory consequences) of the ensuing movements based on the copy of this motor command (Desmurget & Grafton, 2000; Wolpert & Ghahramani, 2000 for reviews). We propose that these centrally produced sensory signals play an additional role to proprioceptive and visual signals in action recognition. It has been shown that the predicted sensory signals can be used for different purposes. For example, it is needed to distinguish the sensory consequences of our own actions from externally produced sensory stimuli. When the movement comes to execution, the actual sensory consequences inferred from the proprioceptive and visual signals arising from the moving segments are compared with the predicted sensory consequences of that action. If the sensory perceived changes are correlated with the predicted sensory feedback, they are registered as consequences of one's own action. If not, by contrast, they are registered as originating from an external source (Blakemore, Frith, & Wolpert, 1999, 2001; Frith, 1992; Sperry, 1950; Von Holst, 1954). This comparison process also plays a critical role in the estimation of the current state of the system (Wolpert et al., 1995). We propose that conscious monitoring of the outcome of the comparison process between the prediction of the sensory consequences of an action and the actual consequences of such an action could also represent a possible basis for knowledge about the movement. The results from Experiment 1, where normal subjects performed better in the active than in the passive condition, and which replicate previous results (Eklund, 1972; Paillard & Brouchon, 1968), can be interpreted along this line. It can be postulated that in the passive condition, where no efferent signals existed and no internal model was generated, the comparison process could not take place. The only possibility for judging whether the final position corresponded to the actual movement or not was the degree of match between the proprioceptive signal and the visual signal. Can a similar reasoning explain the results obtained with the patient GL? Although GL showed some evidence of recognition of her movements (the Spearman correlation score calculated between her number of YES responses and the value of the bias was significant), this was mostly true for very high bias values. In the absence of proprioceptive cues, GL might have relied on the comparison between the predicted visual consequence and the actual visual consequence to recognise the deviation. The mismatch between the two was only detected for large discrepancies.

It remains that efferent signals cannot by themselves provide information for conscious knowledge of limb movements and/or position. We know from another study with GL that, when visual control from her movements was prevented, she lost every possibility to make any report on her movements, in spite of the fact that she was able to correctly perform complex motor tasks (Fourneret, Paillard, Lamarre, Cole, & Jeannerod, 2002). Fleury et al. (1995) also showed that GL was not able to discriminate heavier weights in a weight judgement task in the absence of vision.

The present paper carries strong arguments as to the respective role played by proprioceptive and visual signals in the process of matching the final position of our limbs with an intended movement and thus in action recognition. This function is achieved through a comparison process between the predicted sensory consequences of the action, which are stored in its internal model, and the actual sensory consequences of that action. These results also shed some light on the mechanisms involved in the sense of agency (i.e., the feeling that we cause an action) since the recognition of one's own actions is a key component of this feeling. It has been proposed that the sense of agency only relies on central signals (Gallagher, 2000). However, this study provides evidence that this is not the case but that in fact sensory feedback from the action itself also plays a role in our sense of agency.

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