Role of the parietal cortex in predicting incoming actions

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ABSTRACT

Animal and human studies have shown that the parietal and the ventral premotor cortices constitute the neural substrate of the so-called mirror system. The word "mirror" originally referred to the discovery of neurons in non-human primates whose visual response echoes their motor response. This account proposes that action understanding and imitation depend on a mechanism which activates directly our own motor system as we observe the actions of other agents (Rizzolatti and Sinigaglia, 2010). Single unit recording experiments have also demonstrated that parietal neurons have predictive activity and discharge well ahead of a planned movement. Interestingly, patients with parietal damage can show impairments in their ability to imitate or understand an observed action, but they have also difficulties in monitoring early phases of their own movement planning, be it simple reaching movements or more complex object-directed actions. The fact that both deficits may co-occur after a parietal lesion raises the question whether this reflects the impairment of a common mechanism. To address this question we examined EEG activity in patients with selective lesions in the inferior parietal lobe (N = 6) who were requested to watch passively a video showing an actor grasping a colored object. The object's color cued the subject that the actor was about to move. We recorded the Readiness Potential (RP), a marker of motor preparation which also arises when preparing to observe an action (Kilner et al., 2004). Parietal patients' performance was compared to that of neurologically normal subjects (n = 9) and patients with a ventral premotor cortex lesion (N = 4). We show that neurologically normal subjects and premotor patients exhibit a significant RP prior to the observed action, whereas no such RP is observed in parietal patients. Our results indicate that parietal cortex injury alters the ability to monitor the early planning phases not only of one's own actions but those of other agents as well. We speculate that parietal activity during action observation does not only or essentially reflect a mirroring process, as recently proposed by mirror neurons' account, but involve instead an anticipatory process which arises through prior learning and predictive mechanisms.

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Introduction

Executing or observing the same goal-directed hand action activates similar cortical areas both in primates and humans (Buccino et al., 2001; Fadiga et al., 1995; Fogassi et al., 2005; Gallese et al., 1996; Kilner et al., 2009; Rizzolatti et al., 1996a). This network of areas employed during action execution and observation has been called the "mirror neuron system" (MNS). First described in primates, the MNS comprises both pre-motor (Gallese et al., 1996; Rizzolatti et al., 1996a) and parietal (Fogassi et al., 2005) areas. In humans, the hypothesized mirror system is supposed to involve a cortical network composed of the rostral part of the inferior parietal lobule and the caudal sector (pars opercularis) of the inferior frontal gyrus (IFG), plus the adjacent part of the premotor cortex (Buccino et al., 2004; Grafton et al., 1996; Grézes and Decety, 2001; Kilner et al., 2009; Rizzolatti et al., 1996b, 2001).

It has been proposed that mirror mechanisms could allow us to directly understand the meaning of the observed actions of others by internally replicating ("simulation-simulating") the action (Gallese et al., 2004; Jeannerod, 2001). In addition, neurons in these frontoparietal regions seem to also monitor the observation of other agents' actions through prediction mechanisms (Blakemore and Frith, 2005; Iacoboni and Dapretto, 2006; Rizzolatti and Sinigaglia, 2010; Wolpert and Flanagan, 2001). This idea is supported by single unit recordings from macaque monkeys. First, a subset of mirror neurons in premotor cortex have been shown to discharge even when the final part of an action is hidden by an occluder and therefore can only be inferred (Umiltà et al., 2001). Second, parietal neurons have been shown to discharge well ahead of a planned movement (Andersen and Buneo, 2002) and to encode the goal of actions during movement observation (Bonini et al., 2010; Fogassi et al., 2005). On the other hand, impairment in gesture recognition has been described both after

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ventral premotor (Pazzaglia et al., 2008) and inferior parietal lobule (Kalénine et al., 2010) lesions.

Thus, both regions, the parietal and the premotor cortices, could potentially play a role in action prediction and action observation. It is interesting to note that in the above studies the concept of movement prediction is used in reference to different phases of movement planning. On one hand premotor cortex activity is thought to reflect prediction processes in a situation where the animal temporarily holds in memory (i.e., during its partial occlusion) the course of an action which has already started (Umiltà et al., 2001). On the other hand, predictive mechanisms in the parietal cortex are suggested to be activated when the animal expects an action that is not initiated.

Direct evidence of a role of the parietal cortex in prediction comes from human studies which suggest that this region creates forward state estimates of impending movements (Andersen and Buneo, 2002; Andersen and Cui, 2009; Blakemore and Sirigu, 2003; Desmurget et al., 1999; Sirigu et al., 1996, 2004; Wolpert et al., 1998; Wolpert and Ghahramani, 2000). In addition, it was recently shown that the electrical stimulation of the parietal cortex induces an intention to move, suggesting that motor intention and awareness are emerging consequences of increased parietal activity before action onset. Thus, the subjective (and potentially illusory) feeling that we are executing a movement would not arise from movement itself, but would instead be generated by prior conscious intention and its predicted consequences (Desmurget et al., 2009; Desmurget and Sirigu, 2009). It may be that similar prediction processes involved during one's own movement intention are at stake also when preparing to observe someone else's intentional action. According to his hypothesis for our motor system being ready to observe a movement may be equivalent to being ready to act. This may be achieved through a mechanism of endowment of others' movement intention. If this is so parietal lesions should alter anticipation and consequently motor preparation to observe actions.

By using a task where the onset time of an observed action was predictable, Kilner et al. (2004) have shown that the readiness potential (RP), a marker of motor preparation, increases just before the observed movement begins. They recorded EEG from healthy subjects while they watched a series of short video clips showing an actor's right hand and a colored object indicating whether the hand would subsequently move or not. They also performed a prediction Control condition to distinguish a negative going potential that was related to the observed movement from one (the contingent negative variation, CNV) related to a predictable stimulus change. It was shown that the observation-related RP occurred only in trials in which there was a predictable movement. This movement observation-related RP did not simply reflect prediction per se as it was significantly different from the negativity that preceded a predictable stimulus change. Thus, it was proposed that the rise of the RP precedes the observed movement's onset each time the nature and onset time of the upcoming action is predictable, suggesting that knowledge of a coming action automatically activates the motor system (Kilner et al., 2004).

In another line of evidence, Aglioti et al. (2008) applied transcranial magnetic stimulation (TMS) in the primary motor cortex (M1) to investigate the dynamics of action anticipation and its underlying neural correlates in professional basketball players. They found an increase of motor excitability in elite athletes when they performed an observational task that tapped the ability to predict the fate of shots at a basket, indicating that high levels of motor expertise are linked to the fine-tuning of specific anticipatory resonance mechanisms.

There is a large agreement on the recruitment of premotor and parietal areas during the observation of actions (Buccino et al., 2001; Fadiga et al., 1995). However, it is less clear if and how these regions contribute to predict actions when performed by other agents. In the present study we investigated the contribution of parietal and premotor areas in action prediction. We examined whether patients with focal lesions in the parietal or in the premotor areas generated a RP when expecting to observe a hand movement (grasping an object).

Methods

Subjects

We tested three groups of subjects: (i) nine neurologically normal subjects (S; three women/six men; mean age 54.8 years, range 47–72; mean education level 14 years, range 11–16) (ii) six patients suffering from a selective lesion in the parietal cortex (P; 1 female, 5 males; mean age 54.7 years, range 40–66; mean education level 12.5 years, range 11–15) (iii) four patients suffering from a selective lesion in the premotor region (PM; 4 males; mean age 62.5 years, range 48–75; mean education level 12 years, range 10–15). In both groups of patients, lesions resulted from stroke and testing occurred in the chronic phase after the injury (mean time from lesion in months:

Table 1
Personal features and clinical signs of Neurologically normal subjects, Parietal and Pre-motor patients.

Subjects	Sex (F/M)	Age years; mean (range)	Education level years; mean (range)	Hand laterality (R Right, L Left)	Lesion's site (BA)	Lesion's volume (mm3); mean (SD)	Damaged Hemisphere (R Right, L Left)	Months post Stroke mean (range)	Motor/sensory impairments (chronic phase)	Ideomotor Apraxia (acute/chronic phase)
Parietal (P) n = 6	1F/5M	54.7 (40-66)	12.5 (11-15)			8.78 (4.56)		17.5 (9-32)		
P1	M	61	15	R	BA 21/39/40	10.76	R	9	none/mild	none/none
P2	M	66	15	R	BA 39/40	6.19	R	9	none/mild	mild/none
P3	M	49	11	R	BA 40	2.08	R	18	none	moderate/mild
P4	M	54	12	R	BA 39/40	11.13	R	9	none	mild/mild
P5	F	58	11	R	BA 39/40	7.35	L	28	none/mild	moderate/mild
P6	M	40	11	R	BA 39/40	15.17	L	32	none	mild/mild
Pre-motor (PM) n = 4	4M	62.5 (48-75)	12 (10-15)			14.82 (14.21)		20.5 (9-36)		
PM1	M	55	12	R	BA 6/44	22.42	R	9	none	mild/none
PM2	M	72	11	R	BA 6/44	2.13	L	28	none	mild/none
PM3	M	48	15	R	BA 44/45/46	31.05	L	36	none	mild/none
PM4	M	75	10	R	BA 6/44	3.71	L	9	none	mild/none
Neurologically normal subjects (S) n = 9	3F/6M	54.8 (47-72)	14 (11-16)	R						

BA (Brodmann area), BA 21 middle temporal cortex, BA 39 (angular gyrus), BA 40 (supramarginal gyrus), BA 6 (premotor area), BA 44 (inferior frontal gyrus), BA 45/46 frontal medial gyrus.