SHORT COMMUNICATION
Transfer of interfered motor patterns to self from others

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Abstract

Previous behavioural and neuroimaging data on humans demonstrated that kinematics and the level of brain activity vary according to whether participants reach towards and grasp a target object presented in isolation or flanked by a distractor object. Here we seek to explore whether a differential activation can be revealed by the mere observation of another person grasping an object in isolation or alongside a distractor. To this end we used event-related functional magnetic resonance imaging to localize neural activity related to action observation that was influenced by the presence of a distractor object. We found that observing a human model reaching-to-grasp a three-dimensional target alongside a distractor elicits a differential level of activation in a network of areas typically involved during action observation: the dorsal sectors of the premotor cortex and the inferior frontal gyrus. Whereas our previous understanding of the human action observation system has been restricted to actions directed to single objects, we provide compelling evidence that areas within this network modulate with respect to the context in which the observed action takes place. This may prove to be a fundamental process for our understanding of how others' actions can be represented at a neural level.

Introduction

When choosing a piece of fruit from a bowl, many fruits are visible and within reach but only the desired one governs the particular pattern and direction of movement. Kinematics (for reviews see Castiello, 1999; Tipper *et al.*, 1998) and neuroimaging studies (Chapman *et al.*, 2002) investigating this selection-for-action process revealed that motoric aspects of a human agent response are influenced by the presence of distracting information (e.g. the other fruits). Even to-be-ignored objects can be processed in parallel with target objects such that competition between planned-and-executed action towards the target and planned-but-not-executed action towards the to-be-ignored object emerges (for review see Castiello, 1999). For instance, Tipper *et al.* (1997) asked participants to grasp a target presented alongside a distractor and found that kinematic parameters such as wrist trajectory and peak velocity were influenced by the presence of the distractor. At neural level, Chapman *et al.* (2002) revealed differential parietal and premotor activity depending on whether participants were required to reach towards and grasp a target presented in isolation or flanked by a distractor.

An interesting question still to be addressed is whether this interference can also be revealed by the mere observation of an agent grasping an object in the presence of a distractor. Previous attempts to answer this question may be found within the kinematics literature. For example, Castiello (2003) demonstrated that the interference produced by the distracting objects can be transferred from an agent to an observer. In this study, participants observe a model reaching for a target object in the presence or absence of a smaller size distractor. When the observer then reaches for the same target object with no distractor, the motor pattern is as if the distractor were present. The finding that the observer's action is influenced by the observation of a previously affected action may suggest that the interference produced by a distractor is coded not only at a level of action execution but also at a level of action observation.

By using functional magnetic resonance imaging (fMRI) we sought to investigate whether the brain areas activated by action observation (Rizzolatti *et al.*, 1996; Decety *et al.*, 1997; Buccino *et al.*, 2001; Tai *et al.*, 2004; Wheaton *et al.*, 2004) are sensitive to the presence of a distractor during the observation of a reach-to-grasp action. If the interference produced by the distractor extends to observation, then a differential level of activation within this system is expected. Although we do not know exactly what may occur in the brain when performing an object-related action in the presence of a distractor, behavioural evidence shows that the presence of the distractor determines interference effects (e.g. slower movements and delayed kinematics) in the movement of acting (Castiello, 1996; Tipper *et al.*, 1997) and observing agents (Castiello, 2003). Commonly, such interference effects are explained in terms of action-based inhibitory mechanisms that select the target from competing distractors. Thus, it might well be that the target and distractor both evoke motor representations which interact in a mutually suppressive or competitive way. In other words, the inhibitory mechanisms experienced by the model to suppress the planned-but-not-executed competing action representation for the distractor may be transferred to the observer. In line with this prediction our results show that during action observation the level of activation within the precentral gyrus and the inferior frontal gyrus decreased when the distractor object was present.

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Methods and materials

Subjects

Subjects were 14 normal, healthy right-handed volunteers (mean age 28 years). All subjects had normal or corrected-to-normal vision and gave informed consent to participate in the study. All subjects were naive as to the purpose of the experiment and gave informed consent to participate in the study. The experimental procedures were approved by the local ethical committee and were in accordance with the declaration of Helsinki.

Stimuli and experimental design

A computer-controlled projector was used to deliver 4-s-long movies (Audio Video Interleave format, 25 frames/s) presented in colour. Each movie represented a human model seated at a table on top of which one or two spherical plastic objects of different size (diameter 6 and 2.5 cm) were positioned. The two objects were of different size so as to evoke different types of grasping action. They were located at a distance of 30 cm from the hand starting position at 20° either to the right or left of the model's midline. We employed a 2×2 factorial design in which one factor was type of observed behaviour (action vs. static) and the other was distractor (absence vs. presence). There were four resulting conditions (36 trials for each condition pseudorandomly presented): (1) the human model reaching towards and grasping the target object presented alone; (2) the human model reaching towards and grasping the target object flanked by a distractor object; (3) the human model without performing any action seated behind the working surface on which the target object was presented alone or (4) the human model without performing any action seated behind the working surface on which the target object flanked by a distractor object was presented. In conditions 1 and 2 the model always grasped the large object. We adopted this configuration because, as previously demonstrated, it is the most effective in triggering distractor effects on grasping kinematics (for review see Castiello, 1999). Although it could be argued that grasping the same object over and over again may lead to habituation effects, such effects have never been found in previous kinematical studies or in the kinematics of the model used in the present study (please refer to 'Kinematical analysis of the human model's action' below). Further it should be noted that the observers were not explicitly informed that the target object was always the same. Videos for conditions 1 and 2 started with the human model reaching towards the target object, i.e. there was no delay from the video onset and the movement onset. The time course for these 'action' videos was as follows: the model started the reaching action towards the target object and the object was then grasped, lifted and repositioned on the working surface. Finally, the hand was relocated on the starting position. One single movement was presented per video. For each condition three different video clips representing different trials performed by the same model were presented.

An event-related design (Rosen *et al.*, 1998) was used to sample the functional imaging data. The video clips were presented on a variable schedule, the interstimulus interval being determined by a 'long exponential' probability distribution (Hagberg *et al.*, 2001) with a mean interstimulus interval of 6 s and a range of 2–10 s.

Task

Throughout the experiment, subjects performed the same explicit task, which was to watch the video clips back-projected onto a screen (rectangular frame in a 720×540 pixel array) visible in a mirror mounted on the magnetic resonance imaging head coil (visual angle $15 \times 20°$ approx.).

Functional imaging and data analysis

Whole-brain fMRI data were acquired on a 3T scanner (Siemens Magnetom Trio) equipped with an eight-channel head array RF coil. The GRAPPA algorithm (Griswold *et al.*, 2002) for integrated parallel acquisition technique was used with an acceleration factor of 2. Functional images were obtained with a gradient echo-planar (echo-planar imaging) T2*-weighted sequence in order to measure blood oxygenation level-dependent contrast throughout the whole brain (42 contiguous axial slices, 3 mm isotropic voxel size, in-plane resolution 64×64 voxels, field of view 192×192 mm, flip angle 90°, TE 30 ms, bandwidth 752 Hz/pixel). Volumes were acquired continuously with a repetition time of 3 s. A total of 114 scans were acquired for each participant in a single scanning run (5 min 42 s; six runs). In addition, high-resolution T1-weighted images (anatomical scans) were also acquired for each participant (MP-RAGE, 176 axial slices, in-plane resolution 256×256, 1 mm isotropic voxels, repetition time 1830 ms, TE 4.43 ms, flip angle 11°, bandwidth 130 Hz/pixel).

The fMRI data were analysed using statistical parametric mapping software (SPM2, Wellcome Department of Cognitive Neurology, London, UK). Individual scans were realigned to the first functional volume of each series in order to correct for any head movement occurring within the run. The images were then spatially normalized (Friston *et al.*, 1995b) using a template originally supplied by the Montreal Neurological Institute (the MNI152 template) and distributed with SPM2. Finally, the data were spatially smoothed using a 6-mm full width at half maximum Gaussian kernel. A high-pass temporal filter (cut-off 120 s) was also applied to the time series.

Statistical analysis

Analysis was carried out by the application of the general linear model for analysis of fMRI time series (Friston *et al.*, 1995a) as implemented in SPM2. Regressors were defined based on the timing of presentation of each of the four conditions and these functions were convolved with a canonical, synthetic haemodynamic response function in order to produce the model. Individual models were generated for each subject and contrasts were defined in order to pick out the main effects of the two main factors (type of observed behaviour and distractor) and their interactions. These contrasts were then entered into several second-order random-effects analyses. The alpha level for these second-level analyses was set at $P < 0.001$ (uncorrected).

Localization

Anatomical localization and visualization of significant signal changes were obtained by superimposing the SPM$\{T\}$ maps on the T1 canonical Montreal Neurological Institute template image, using the visualization software suite MRI3DX (version 5.50; http://www.aston.ac.uk/lhs/staff/singhkd/mri3dX/). MRI3DX incorporates the Talairach Daemon Database (Lancaster *et al.*, 2000) and this was our primary neuroanatomical reference. We also used the designations of Brodmann as a rough guide to the location of cytoarchitectonic areas of the cortex.

Kinematical analysis of the human model's action

To identify differential brain responses related to the presence or absence of a distractor, the stimulus configuration must evoke a kinematic pattern of interference. We therefore analysed the human model kinematic data to test whether the presence of a distractor object resulted in an altered kinematical pattern. A 27-year-old right-handed male reporting normal vision acted as a model. The model was seated at a table in a room illuminated so that the experimental set-up could be seen clearly. The working surface measured 100×100 cm and was smooth and homogeneous. Prior to each trial the model put his right wrist on the starting position (diameter 0.5 cm) positioned 25 cm in front of his mid-line. A 'go' signal indicated to the model to reach towards and grasp the target indicated by the experimenter before the beginning of the trial. The target and the distractor (when present) remained visible throughout the duration of the trial. Trials were of two types: (i) 'distractor', where the target was flanked by a distractor and (ii) 'no distractor', where the target was presented in isolation. For all trial types the model was required to reach and grasp the target at a leisurely pace. Trials were recorded with a digital video camera. A digitizing technique was used to extract the kinematics of the model from the videos that were presented to the subjects during the fMRI experiment. For each dependent variable paired t-tests were performed to compare the no-distractor with the distractor conditions. The dependent variables that were thought to be specifically relevant to the scientific hypothesis were movement duration, the velocity profile of the arm and the time of maximum grip aperture. These variables were chosen because consistent results within the reach-to-grasp literature have shown that the reach-to-grasp movement is dependent upon the size of the stimuli. In particular, movement duration is longer, deceleration time (the time from the moment of peak velocity to the end of the movement) is prolonged and the amplitude of the maximum grip aperture is reached earlier for smaller than for larger stimuli (Castiello, 1999). Thus, in a movement towards a large target, if the results showed either a longer movement duration, a prolonged deceleration time or an anticipated time of maximum grip aperture in the presence of a smaller distractor, inferences regarding the influence of the small distractor on the kinematics of both the model and the observer for movements towards the larger target could be advanced (Jakobson & Goodale, 1991). The dependent measures that were investigated showed a significant change in the direction of the experimental hypothesis, i.e. the classic kinematic patterning that characterizes the reach-to-grasp for large objects (target) was modified according to the classic kinematic pattern that characterizes smaller objects (small distractor). Movement duration was longer for movements directed to the target in the presence of the small distractor than in the no-distractor condition ($t = 9.55$; $P = 0.001$). Deceleration time was longer for the distractor condition than for the no-distractor condition ($t = 5.04$; $P = 0.007$). The time of maximum grip aperture was reached earlier for the target presented together with the smaller sized distractor than when the target was presented in isolation ($t = 6.43$; $P = 0.003$).

Results

The t-contrast comparisons used in our study were: (i) action vs. no-action (1 1 −1 −1); (ii) target alone vs. target and distractor (1 −1 1 −1) and (iii) interaction (1 −1 −1 1).

Main effect of type of observed behaviour

Table 1 shows differences in activity between those conditions in which subjects observed reach-to-grasp actions performed by the model and those conditions in which no overt actions were executed by the model.

Differential haemodynamic activity was present in a network including the left dorsal premotor cortex (precentral gyrus Brodmann area 6; Table 1), postcentral gyrus bilaterally (see Table 1), dorsal part of the pars opercularis of the right inferior frontal gyrus (see Table 1), superior parietal cortex, posterior superior temporal sulcus and supramarginal gyrus bilaterally (see Table 1). This anatomical profile has been broadly identified in previous action observation studies (Rizzolatti *et al.*, 1996; Decety *et al.*, 1997; Hari *et al.*, 1998; Buccino *et al.*, 2001; Grezes & Decety, 2001; Saxe *et al.*, 2004; Iacoboni *et al.*, 2005). Furthermore, a point worth mentioning is that activity in the left premotor cortex has also been ascribed to the deployment of attention to objects in connection with motor output (Rees *et al.*, 1997). Along these lines, the reported activation of the left premotor cortex may signify that attention acts distinctly when an overt action rather than static objects is observed. In this connection a left

TABLE 1. Main effects of type of observed behaviour (action vs. no-action; $P < 0.001$)

Brain regions	T-value	Equivalent Z-value	Coordinates (Montreal Neurological Institute)		
			x	y	z
Left dorsal premotor cortex, BA 6	5.53	3.9	−40	−12	62
Left postcentral gyrus, BA 4	3.9	3.11	−48	−10	36
Right postcentral gyrus, BA 4	4.53	3.45	42	−8	34
Right inferior frontal gyrus, BA 45	4.05	3.2	56	28	28
Left posterior superior temporal sulcus, BA 22	3.89	3.11	−54	−44	12
Right posterior superior temporal sulcus, BA 22	4.46	3.42	54	−32	8
Left superior parietal lobule, BA 1	6.2	4.16	−28	−44	64
Right superior parietal lobule, BA 1	6.18	4.15	26	−42	58
Left supramarginal gyrus, BA 40	8.70	4.92	−48	−36	26
Right supramarginal gyrus, BA 40	4.99	3.67	50	−27	26
Left middle occipital gyrus, BA 37	9.93	5.2	−50	−74	6
Right middle occipital gyrus, BA 37	9.67	5.15	48	−74	8
Right superior occipital gyrus, BA 19	11.2	5.46	28	−82	30

BA, Brodmann area.

hemisphere dominance has been proposed for motor tasks or at least for tasks that require greater attention to action (Rushworth *et al.*, 1997, 2001).

Among visual areas, activations were evident within the middle occipital gyrus bilaterally (see Table 1). These areas are known to be activated during motion tracking and correspond to the putative motion area V5 identified in the human brain (Watson *et al.*, 1993). Further, similar visual areas were found to be active in a study comparing the observation of a static vs. a moving arm (Tai *et al.*, 2004). Furthermore, the stereotaxic coordinates for these areas closely resemble those reported by Downing *et al.* (2001) for the extrastriate body area which is activated by passive viewing images of the human body. As proposed by these authors extrastriate body area may be part of a broader system for inferring the action of others. In this respect, the activation of extrastriate body area together with the activation of areas involved in action observation in the present study may confirm this view.

Main effect of distractor

No differences in brain activity between those conditions in which subjects observed the target alone and those conditions in which the target was presented together with the distractor were revealed.

Interaction between type of observed behaviour and distractor

The primary purpose of the present study was to localize haemodynamic changes due to the presence of the distractor during action observation (see Fig. 1). We found that the presence of the distractor determined changes in activation within the pars triangularis of the left inferior frontal gyrus (Brodmann area 45; see Table 2 and Fig. 2a) and the left frontal inferior operculum (Brodmann area 44; see Table 2 and Fig. 2b). Several functional neuroimaging investigations have shown activation within the left inferior frontal gyrus when humans observe dynamic hand movements (Buccino *et al.*, 2001; Grezes *et al.*, 2003; Johnson-Frey *et al.*, 2003). Furthermore, the right dorsal sectors of the premotor cortex (see Table 2 and Fig. 2c) were activated. As previously reported, these loci are activated by the observation of hand actions (e.g. Buccino *et al.*, 2001; Grezes *et al.*, 2003). Finally, the right ventral precentral gyrus was also activated (see Table 2 and Fig. 2d).

Discussion

The aim of the present study was to ascertain whether brain areas concerned with action observation modulate according to the presence or absence of a distractor object. Our core findings indicate that, regardless of the presence or absence of a distractor, the observation of a hand action yields activation within areas which are commonly thought to be responsive to hand action observation (main effect of type of behaviour). Further, the mere presence of an object presented in isolation or flanked by a distractor does not determine any changes in brain activation (main factor of distractor). Importantly, the results obtained from the interaction revealed a set of brain regions in which
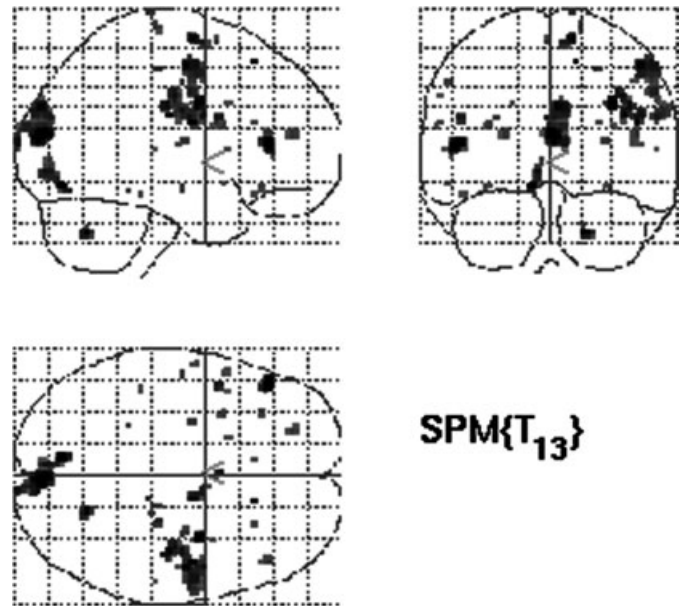

FIG. 1. Statistical parametric mapping (SPM) glass brain representing the interaction between type of observed behaviour and distractor.

TABLE 2. Areas significantly activated by the interaction of type of observed behaviour and distractor ($P < 0.001$)

| Brain regions	T-value	Equivalent Z-value	Coordinates (Montreal Neurological Institute)		
			x	y	z
Left inferior frontal gyrus, BA 45	5.42	3.85	−49	34	11
Left inferior frontal operculum, BA 44	4.17	3.27	−47	7	25
Right dorsal premotor cortex, BA 6	4.69	3.52	54	−6	52
Right ventral precentral gyrus, BA 6	4.15	3.25	58	−7	27

BA, Brodmann area.

the main effect of type of observed behaviour is significantly modulated by the presence of the distractor.

In general, the results of our event-related fMRI investigation confirm previous evidence suggesting that in humans there are brain areas which respond when subjects passively observe hand actions (Grafton *et al.*, 1996; Rizzolatti *et al.*, 1996; Buccino *et al.*, 2001; Grezes *et al.*, 2003; Tai *et al.*, 2004). In line with what has been previously reported we found activations within the premotor network together with the inferior frontal gyrus (Brodmann area 45).

Critically, we demonstrate that these responses are sensitive to the context in which an action takes place. This is in line with recent findings suggesting that actions embedded in contexts elicited a significant signal increase in the inferior frontal gyrus and the adjacent sector of the premotor cortex where hand actions are represented (Iacoboni *et al.*, 2005).

FIG. 2. Interaction effects in the pars triangularis of the (a) left inferior frontal gyrus [Brodmann area (BA) 45; −49 34 11], (b) left inferior frontal operculum (BA 44; −47 7 25), (c) right dorsal premotor cortex (BA 6; 54 −6 52) and (d) right ventral precentral gyrus (BA 6; 58 −7 27). The statistical parametric mapping {*T*} maps are overlaid on the canonical T1 image from the Montreal Neurological Institute series (the right side of the brain is represented on the right of the figure for transverse sections; for d the saggital section shows the right side of the brain whereas for a and b the saggital sections show the left side of the brain). Crossbars represent the local maxima within the clusters. The graphs presented adjacent to each activation panel represent the contrast estimates of one representative subject for each experimental condition.
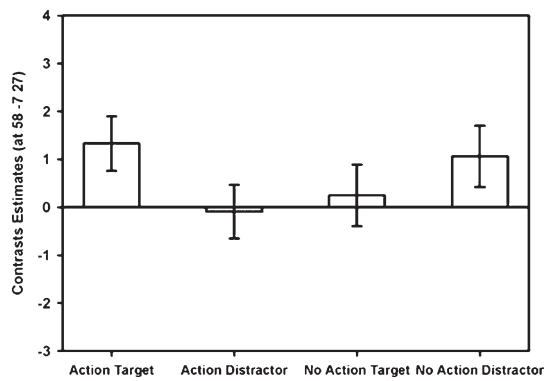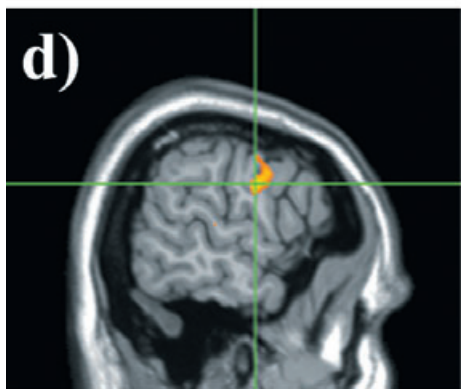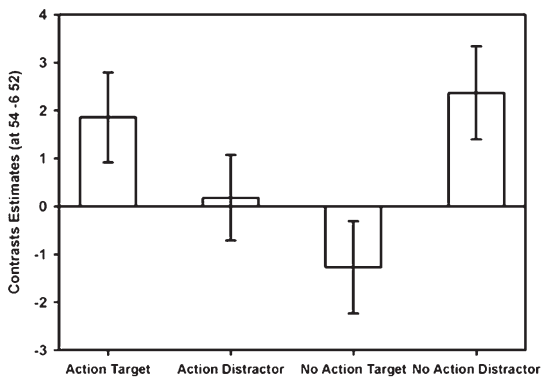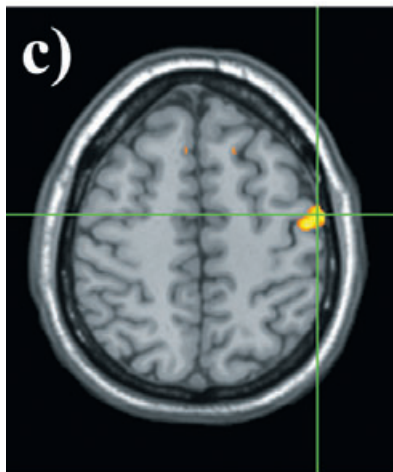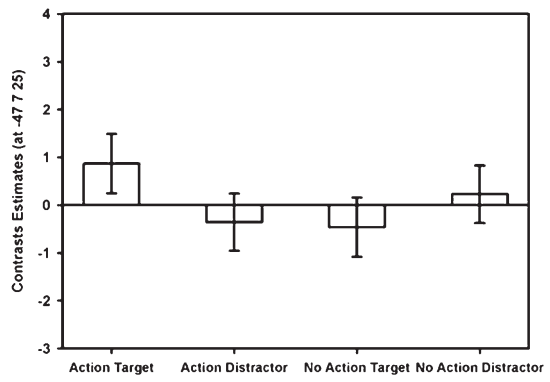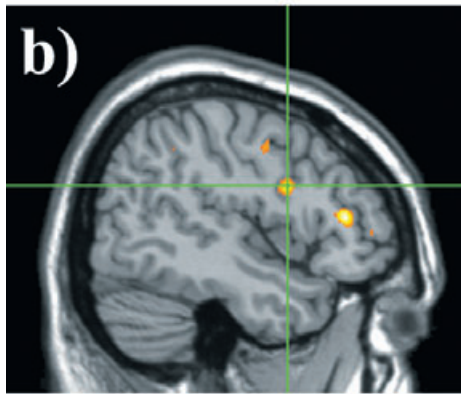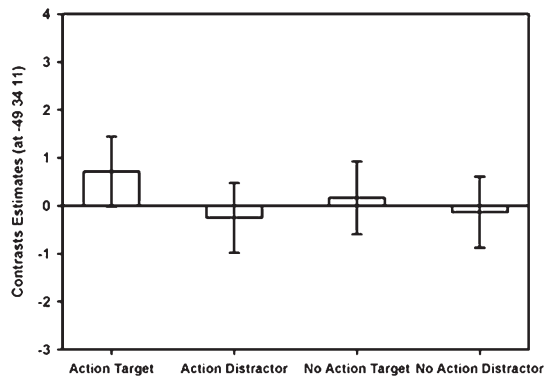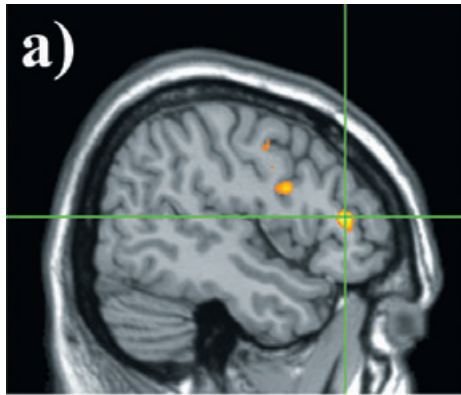
Whereas our previous understanding of the human hand action observation system has been restricted to actions directed to single objects, we now show that this network represents not only to-be-executed actions but also potential actions that are not executed. In particular, the results obtained from the interaction indicate that the action evoked by the distractor object may modulate activation in the hand action observation areas. In other words, both target and distractor evoke parallel actions, and differences in cortical activity might be due to competition between planned simultaneous responses (Tipper *et al.*, 1998; Castiello, 1999). Thus, parallel computations for the observed actions towards the target and the potential action towards the distractor may contribute to the changes in the level of neural activation. However, it might well be that this system not only 'reads' the action in terms of effector/object interactions but also 'reads' in the model's action the process of target selection and activates accordingly. Importantly, this suggests that this system is not a mere hand action observation system but also a system which operates in connection with the observer's action strategies. In other words, this may signify that simulation of another person's brain processes is a mechanism which is not solely related to visuomotor processes. It might well be that higher-level processes (e.g. selection) which control visuomotor processes can also be simulated.

A counterintuitive issue relates to the fact that the identified network was more active during the presentation of the hand action not involving the distractor object. One might wonder why the cortical activity related to hand action observation decreases in the presence of the distractor. We propose two non-mutually exclusive hypotheses to explain this effect. The first concerns the role of inhibition. In this respect, inhibitory control in general is the basis for goal-directed behaviour, such as selecting and responding to the appropriate object. If simulation is a basic mechanism underlying action understanding then one would expect that such inhibitory processes might also be simulated. Along these lines we suggest that the inhibition process acts on the action representation of a potential distractor. On theoretical grounds this possible explanation fits with the notion of 'contention scheduling' (Cooper & Shallice, 2000; Norman & Shallice, 1986). This notion refers to a basic biased competition mechanism that allows routine actions such as grasping to be produced without conflict by activating relevant and inhibiting irrelevant schemata. Within this framework the amount of competition between any pair of schemas depends upon the degree of overlap in their effector systems requirements. This is in line with the evidence of inhibitory mechanisms usually found in kinematics studies when observed grasping actions in the presence of distractors evoking competing grasping schemata (e.g. precision grip vs. whole hand prehension) correspond to a prolongation of movement duration and delayed kinematics in the subsequent action performed by an observer (Castiello *et al.*, 2002; Castiello, 2003). In the present study the kinematics of the model's grasping action towards the target (whole hand prehension) was affected by the presence of the distractor evoking in principle a different grasping action (precision grip). Thus, it could be hypothesized that the model put in place inhibitory mechanisms to suppress the competing grasping schemata. Along these lines, if the observer experienced similar inhibitory mechanisms as the model then it is plausible to assume that the observation of the 'interfered' action evoked inhibitory control within the action observation areas which resulted in a lower level of activation.

Finally, this hypothesis might be consistent with fMRI evidence suggesting that when multiple stimuli are simultaneously presented in the visual field their cortical representations interact in a mutually suppressive or competitive way (Kastner *et al.*, 1998). As a result, the level of activation decreases when multiple visual stimuli are simultaneously presented as compared with when the same stimuli are individually presented.

The second hypothesis concerns the uncertainty dictated by the observed actions. In trials in which the model did perform a movement and both distractor and target were present, no information was given to the subject with respect to which object the model would grasp. Thus, whereas in the distractor condition they do not know what target will be grasped, in the target-alone condition the observer can anticipate the model's action. Consequently, the more ambiguous situation for the distractor condition and the resulting division of attention on the two objects may have rendered the action preparatory process looser leading to a less active action observation network.

In summary, we have demonstrated a new property of the action observation system, i.e. its sensitivity to the context in which the action takes place. Observing a model grasping an object in the presence of a distractor object produces differences at the level of activation within a network of areas including the premotor cortex and the inferior frontal gyrus, a neuroimaging marker of action observation.

Acknowledgements

Abbreviation

fMRI, functional magnetic resonance imaging.

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