

Motor ontology in representing gaze–object relations

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Abstract

Event-related functional magnetic resonance imaging (fMRI) was used to explore how the human brain models gaze–object relations. During scanning participants observed a human model gazing towards or away a target object presented either in isolation or flanked by a distractor object. In two further conditions the model's gaze was shifted and subsequently maintained away from the stimulus/i. These four conditions were implemented within a factorial design in which the main factors were “type of observed behavior” (gaze vs. gaze-away) and “context” (target alone vs. target flanked by a distractor). Results revealed that premotor, parietal and temporal areas, known to sub-serve the understanding of other people actions, were significantly more activated by the observation of the model gazing towards rather than away from the stimulus/i. In addition, a significant interaction indicated that, when the target was presented in isolation, neural activity within the inferior frontal gyrus, another key area for action understanding, was influenced by gaze–object relations. Our findings suggest that this area is important for the establishment of intentional gaze–object relations and indicate that the presence of a distractor interferes with the representation of such relations.

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The term “motor ontology” has been proposed to describe how the motor system represents observed actions and goals [10]. Empirical evidence demonstrates that the brain models movements and actions in terms of multimodal representation of organism–object relations. Suppose an observer is watching a human-model reaching towards and grasping a target object. Being represented in the observer's brain is not only the agent movement or the target object, but the intentional relation between the effector (e.g., the agent's hand) and the target object [4,9].

The proposal that organism–object relations are one basic constituent of motor ontology was recently supported by a study examining the effect of the presence of multiple potentially graspable objects [22]. Participants observed a human model grasping a target object presented either in isolation or flanked by a distractor object. When grasping occurred in the presence

of a distractor object, a differential level of activation within the premotor cortex and the inferior frontal gyrus was observed. In accordance with the hypothesis that actions are mapped in relation to objects, these findings were interpreted in terms of interference effects due to parallel intentional relations evoked by both the target and the distractor object [22].

Here we test whether interference effect in hand action observation areas, such as premotor cortex and inferior frontal gyrus, may be revealed by the observation of an agent simply gazing at a target in the presence of a distractor object.

Gaze is an important source of information about others intentions and actions [20,21]. Reasons to believe that motor interference effects may arise from gaze observation come from behavioral studies using kinematics (e.g., [3]). Observing a model gazing at a distractor object produced in the observer the same type of motor interference than observing the model executing a grasping action. No transfer of interference was observed when the model was instructed to fixate the target while performing the reach-to-grasp action.

These findings suggest that gaze is necessary and sufficient as to elicit motor interference. To investigate the neural underpinnings of this phenomenon we designed an event-related fMRI

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experiment in which healthy subjects observed a human model gazing towards a target in the presence or in the absence of a distractor object. We reasoned that if a common motor ontology underpins the specification of gaze–object relations and hand–object relations, then observation of a human model gazing at a target should activate – at least in part – the same areas involved in hand action observation. By following this line of reasoning, differential neural activity within action observation areas should be revealed when comparing observation of human model gazing at a target in isolation or flanked by a distractor object.

Twelve healthy adults (mean age, 27 years) were recruited for the present experiment. All participants were naïve as to the purpose of the experiment, they had normal or corrected to normal vision and had no history of neurological problems. The study was approved by the local ethical committee. Informed consent was obtained from all of the participants before the testing session in accordance with the declaration of Helsinki.

A computer-controlled projector was used to deliver 2 s-long movies (AVI format, 25 frames per second, 720×540 pixel array) presented in color. Each movie represented a human model (a 27 years old male naïve as to the purpose of the experiment) 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 located at a distance of 30 cm from the model at 20° either to the right or to the left of the model's midline. We adopted a 2×2 factorial event-related design [24] in which factors were “type of observed behavior” (gaze vs. gaze away) and “context” (target alone vs. target flanked by a distractor). There were four resulting conditions (Fig. 1): (1) the model initially has the eyes fixed and forward away from the scene containing the target object presented in isolation. Subsequently, the human model gazes towards the target object (condition GT); (2) the model initially has the eyes fixed and forward away from the scene containing the target object flanked by the distractor. Subsequently, the human model signals through gaze the presence of both the target and the distractor and then maintains the eyes on the target (condition GTD); (3) the model initially has the eyes fixed and forward away from the scene containing the target object presented in isolation. Subsequently, the model gazes upwards and maintains the eyes fixed on that location (condition GAT); (4) the model initially has the eyes fixed and forward away from the scene containing the target object flanked by the distractor. Subsequently, the model gazes upwards and maintains the eyes fixed on that location (condition GATD). For conditions GT and GTD the target for the model was always the large object. We adopted this configuration (large target flanked by a smaller size distractor) because as previously demonstrated it is the most effective in triggering distractor interference effects from the observation of gaze patterns (e.g., [3]). The observers were not explicitly informed that the target object remained the same. The time course for the presentation of the videos relatively to all conditions was as follows: the initial frames showed the human model with the eyes fixed and forward, then the model naturally shifted eye gaze towards or away from the object(s) and at the end of the trial the eyes were returned to their original starting position. For

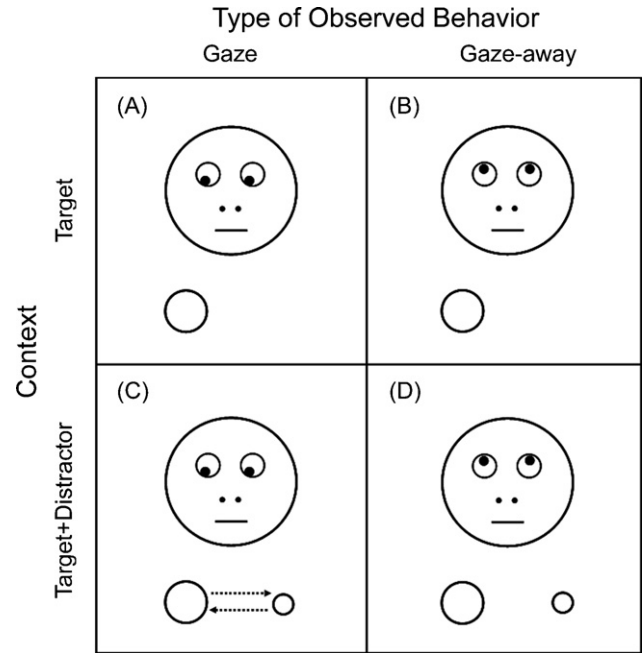


Fig. 1. Schematic representation of the experimental design depicting the 4 experimental conditions. (A) Gaze target (GT) condition: the human model initially has the eyes fixed and forward away from the scene containing the target object presented in isolation. Subsequently, the model gazes towards the target object; (B) gaze-away target condition (GAT): the model initially has the eyes fixed and forward away from the scene containing the target object presented in isolation. Subsequently, the model gazes upwards and maintains the eyes fixed on that location; (C) gaze target + distractor condition (GTD): the model initially has the eyes fixed and forward away from the scene containing the target object flanked by the distractor. Subsequently, the human model signals through gaze the presence of both the target and the distractor and then maintains the eyes on the target; (D) gaze-away target + distractor condition (GATD): the model initially has the eyes fixed and forward away from the scene containing the target object flanked by the distractor. Subsequently, the model gazes upwards and maintains the eyes fixed on that location. Dotted arrows in panel ‘C’ indicate that the model’s gaze shifted from the target to the distractor and viceversa.

each condition three different video clips representing different trials performed by the model were presented. Please note that when constructing the stimuli we took great care in selecting only those trials in which both the target and the distractor were signalled through gaze and there was an equal amount of shifts from the target to the distractor and viceversa.

All stimuli were delivered by means of a PC that ensured synchronization with the MR scanner. An LCD computer-controlled projector was employed to present the stimuli on a screen positioned within the bore of the magnet which was viewed by the participants through a mirror mounted on the head coil (visual angle $15^\circ \times 20^\circ$ approximately).

During the experiment participants laid supine in the scanner. While being scanned they were simply requested to carefully observe the presented videos (implicit task). Each participant underwent six experimental functional runs each lasting 5 min approximately. Within each functional run 28 trials (7 repetitions of each condition) were pseudo-randomly distributed along the run length. In order to optimize the sampling of the hemodynamic responses trials were presented on a variable schedule, the inter-stimulus interval (ISI) being determined by a ‘long

exponential' probability distribution [14], with a mean ISI of 6 s and a range of 2–10 s.

Whole-brain functional volumes were acquired on a 3T scanner (Siemens Magnetom Trio) equipped with an eight-channel headcoil. Functional images were obtained with a gradient echo-planar (EPI) T2*-weighted sequence in order to measure blood oxygenation level-dependent (BOLD) contrast throughout the whole brain (42 contiguous axial slices, 3 mm isotropic voxel size, inplane resolution of 64×64 voxels, Field of View = 192×192 mm, flip angle = 90° , TR = 3000 ms, TE = 30 ms). A total of 600 scans were acquired for each participant in six scanning runs. In addition, high-resolution T1-weighted images (anatomical scans) were also acquired for each participant (MP-RAGE Siemens, 176 axial slices, in-plane resolution 256×256 , 1 mm isotropic voxels, TR = 1830 ms, TE = 4.43 ms, flip angle = 11° , bandwidth = 130 Hz/pixel).

Functional MRI data were analyzed using Statistical Parametric Mapping software (SPM2, Wellcome Department of Cognitive Neurology, London). Image volumes were pre-processed using SPM2 (www.fil.ion.ucl.ac.uk/spm). Scans from the six sessions were spatially realigned [8] to remove variance attributable to movement-by-susceptibility interactions ("realign and unwarped" option). The images were then normalized [1] to the standard space defined by the Montreal Neurological Institute template [19]. Lastly, a 6 mm full-width at half-maximum isotropic Gaussian kernel was applied to spatially smooth all volumes. High-pass filtering was also applied to remove low-frequency drifts in signal.

A random effects analysis was conducted on the data. The four different types of video stimuli corresponding to the four experimental conditions were modeled as four separate event types. Regressors were defined based on the timing of presentation of each experimental condition, and these functions were convolved with a canonical, synthetic HRF (haemodynamic response function) in order to produce the individual models. For each participant, all regressors were incorporated into General Linear Models (GLM). Individual models were separately estimated and contrasts were defined in order to pick out the main effects of each experimental condition. These contrasts were then entered into a second level analysis in which participants served as a random effect in a within-subjects ANOVA allowing for non-sphericity. The main effects (i.e. main effect of 'type of observed behavior', main effect of 'distractor') and the interactions between conditions were then specified by appropriately weighted linear contrasts. The alpha level for these second-level contrasts was set at $p < 0.01$ (FDR corrected) [11]; the extent threshold was of at least 10 contiguous voxels. The resulting SPM{t} maps reflected areas in which variance related to the experimental manipulation was captured by the canonical HRF.

Anatomical details of significant signal changes were obtained by superimposing the SPM{t} maps on the T1 canonical MNI (Montreal Neurological Institute) template image. Results were also checked against structural images of each subject. We used two atlases as a general neuroanatomical reference [5,18]. Further, the SPM Anatomy Toolbox [6] based on three-

dimensional probabilistic cytoarchitectonic maps was used to determine the cytoarchitectonic probability (when available; see Table 1) of the peak activity voxels.

The main effect of type of observed behavior [(GT + GTD) – (GAT + GATD)] was conducted to localize differences in haemodynamic activity between those conditions in which participants observed gazing actions performed by the model (GT and GTD) and those conditions in which no overt gazing actions towards the objects were executed by the model (GAT and GATD). Differential haemodynamic activity was present in a network of areas including the right posterior superior temporal sulcus (STS), the precentral gyrus bilaterally and the inferior parietal lobule bilaterally (see Table 1).

Among visual areas, activations were evident within the medial surface of the right lingual gyrus and within the bilateral middle occipital gyrus (see Table 1). This latter area is known to be activated during motion tracking and corresponds to the putative motion area V5 identified in the human brain [27]. Tentatively we suggest that this differential activation might be due to a possible difference in the amount of gaze shift between the gaze and the gaze-away conditions. The reverse contrast [(GAT + GATD) – (GT + GTD)] did not reveal differential activation.

The main effect of type of context [(GTD + GATD) – (GT + GAT)] revealed no differences in brain activity between those conditions in which participants observed the target flanked by the distractor (GTD and GATD) and those conditions in which the target was presented alone (GT and GAT) were revealed. When explored at a more liberal threshold ($p < .001$ uncorrected) differential activity was found only within the right lingual gyrus (MNI coordinates: $-9, -69, -3$). The reverse contrast [(GT + GAT) – (GTD + GATD)] did not reveal differential activation.

In order to determine whether responses to gaze shifts were modulated by the context, we analyzed the interaction between type of observed behavior and presence of a distractor object. The interaction [(GT – GTD) – (GAT – GATD)] was associated with activation of the pars triangularis of the right inferior frontal gyrus at the border between Brodmann areas 45 and 44 (see Table 1 and Fig. 2). The reverse interaction [(-GT + GTD) + (GAT – GATD)] was not significant.

The central advance of this study is the demonstration that gaze-object relations are represented within action observation areas. Two key results support this conclusion. First, the observation of gaze shifts directed towards a target object yielded activation within areas which are commonly known to be involved in coding hand-object interactions (main effect of type of observed behavior). In this connection, the present results demonstrate that activity within dorsal premotor, inferior parietal and right superior temporal areas can be evoked by the mere observation of gaze shifts towards an object. This is in line with previous evidence suggesting that monitoring of gaze shifts activates regions of inferior parietal and superior temporal cortex—regions associated with action understanding, motor intention understanding, and with shifts in spatial attention [28,20,12,17].

Table 1

Local maxima of the activation foci for the main effect of ‘type of observed behavior’ and for the interaction ‘type of observed behavior’ by ‘context’, $p < 0.01$ FDR corrected

Brain region	Probabilistic cytoarchitecture	<i>T</i>	<i>Z</i>	MNI Coordinates (<i>x</i> , <i>y</i> , <i>z</i>) (mm)		
Main effect of type of observed behavior						
Prefrontal cortex						
Precentral gyrus	Area 6 (20%)	5.68	4.71	−36	0	45
Precentral gyrus	Area 6 (50%)	4.64	4.04	48	−3	51
Precentral gyrus	Area 6 (30%)	4.80	4.15	27	−6	51
Precentral gyrus	Area 6 (50%)	5.43	4.56	−27	−12	60
Temporal cortex						
Superior temporal gyrus (STS)		5.98	4.89	60	−36	15
Parietal cortex						
Inferior parietal lobule	Area 2 (70%) hIP1 (10%)	4.95	4.25	36	−42	51
Postcentral gyrus	Area 2 (50%) Area 1 (50%) Area 3b (20%)	5.16	4.39	−30	−42	60
Inferior parietal lobule	Area 2 (20%) Area 1 (20%)	4.69	4.08	−24	−51	51
Visual cortex						
Fusiform gyrus		5.35	4.50	42	−48	−18
Lingual gyrus	Area 18 (90%) Area 17 (60%)	5.72	4.73	6	−63	3
Middle occipital gyrus (MT/V5)	hOC5 (30%)	7.35	5.62	−39	−69	9
Middle occipital gyrus (MT/V5)	hOC5 (40%)	6.41	5.13	54	−66	3
Interaction						
Frontal cortex						
Inferior frontal gyrus (pars triangularis)	Area 45 (40%)	6.12	4.97	50	24	21
Visual cortex						
Lingual gyrus	Area 18 (80%) Area 17 (20%)	6.09	4.95	9	−78	−3
Lingual gyrus	Area 17 (90%) Area 18 (50%)	5.93	4.85	−3	−75	−3

Positive coordinates values on the *x* axis indicate right lateralization, negative values indicate left lateralization.

Second, results from the interaction type of observed behavior \times context reveal that activity within the inferior frontal gyrus modulates depending on the relationship between the model’s gaze and the objects. Previous understanding of the neural basis underlying action recognition have revealed IFG activation (amongst other areas) restricted to the observation of overt hand-object interactions (e.g. [2,15,23,26]). Here we extend this literature by demonstrating that that the inferior frontal gyrus is not only important for representing hand-object (e.g., [2,13,16]), but also gaze-object interactions.

A close inspection of the pattern characterizing the interaction revealed that the observation of a human model gazing towards a target flanked by a distractor evoked a decrease in signal change with respect to the observation of a model gazing towards the target presented in isolation. This pattern of activation within the pars triangularis of the inferior frontal gyrus closely resembles the signal change modulation previously reported during the observation of hand action [22]. When grasping occurred in the presence of a distractor object, a decrease of activation was observed in a network of areas including the pars triangularis of the right inferior frontal gyrus.

A possible explanation for this effect is concerned with the role of inhibition. When gazing occurs in the presence of a distractor object, competing gaze-object relations may be evoked in the observer’s brain. One for the target and one for the distractor object. The decrease in signal change noticed when multiple stimuli are simultaneously present may reflect inhibitory mechanism necessary to suppress the competing gaze-distractor relation.

An alternative explanation is that the presence of the distractor may have prevented the establishment of an intentional relation between gaze and target. When the distractor object was present the model naturally gazed towards both objects before engaging the target. This may have interfered with the encoding of the gaze-target relation. In this interpretation, no substantial difference is expected in terms of right inferior frontal gyrus activation between the gaze and the gaze away conditions when both the target and the distractor are present. This is because the level of ambiguity characterizing the gaze target and distractor condition prevents the observer from understanding the intentional relation between the model’s gaze and the target. Similarly, due to the nature of the adopted stimuli, such intentional relationship

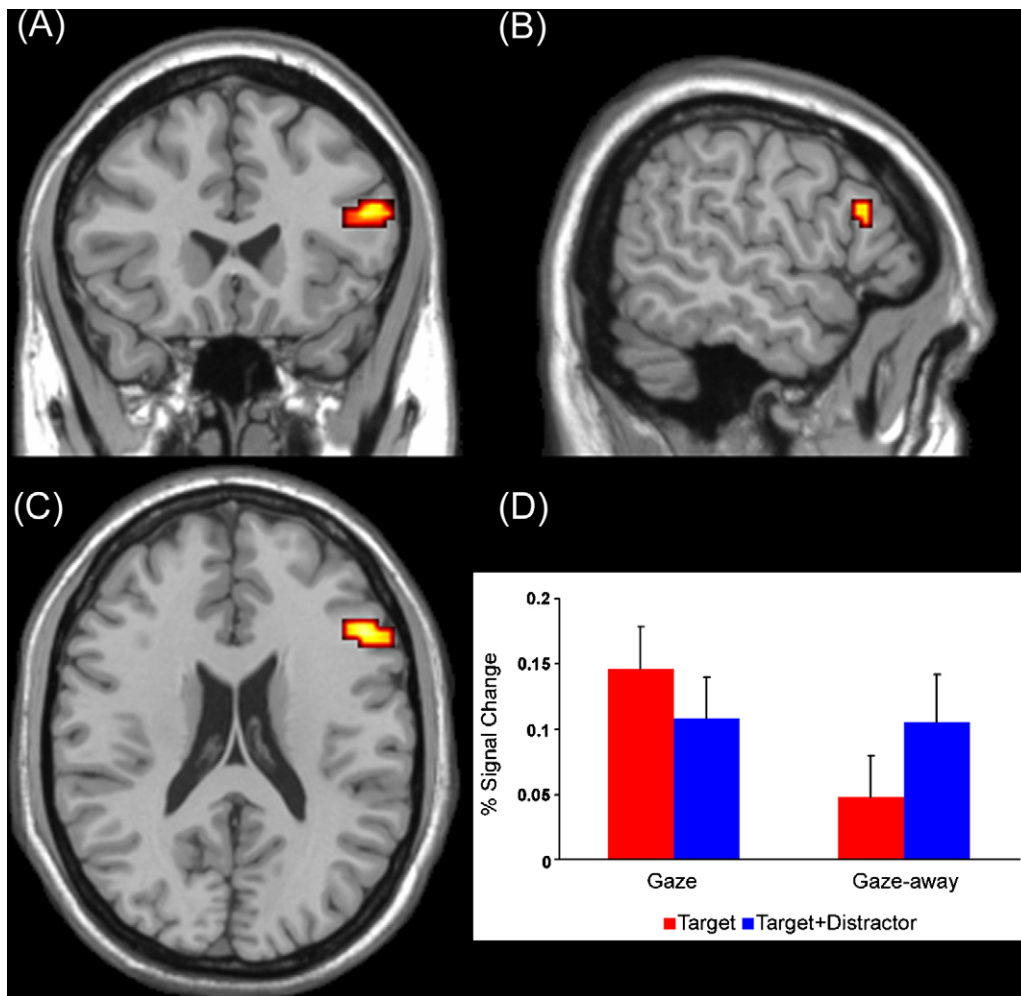


Fig. 2. Right inferior frontal cortex activation emerged from the interaction [(GT – GTD) – (GAT – GATD)]. Activation map superimposed on the canonical brain of the MNI series show significant differential activity ($p < 0.01$, FDR corrected) in coronal (A), sagittal (B), and transverse (C) sections. Mean percent signal change for the local maxima of the right inferior frontal gyrus cluster is shown (D). Bars represent standard errors.

cannot be inferred by the observer in the gaze-away target and distractor condition.

When the model did not gaze towards the objects the effect concerned with an increase of right inferior frontal gyrus activation for the gaze target condition disappeared and almost reversed. This partial inversion was chiefly due to a consistent decrease in signal change for the condition in which the gaze was away from the scene and the target was presented in isolation. This finding can be accounted for by the above mentioned interpretation concerned with the establishment of an intentional relation between gaze and target. It might well be that, when the target is presented in isolation and its presence is signalled through the model's gaze, the increase in signal change observed within the right inferior frontal gyrus reflects the understanding of an intentional gaze–target relationship. Conversely, when the model's gaze does not signal the presence of the target (gaze-away target condition), the observers understand that this condition does not entail the establishment of any gaze–target relationships. This would fit with the observed decrease in signal change.

A final issue is concerned with the laterality of the inferior frontal gyrus activation. Whereas observation of grasping

actions generally activates the inferior frontal gyrus bilaterally, here we report that the understanding of gaze–objects relationship reliably activates only the right inferior frontal gyrus (although some sub-threshold activity was also observed for the same area within the left hemisphere). This lateralized pattern of activation has been previously reported and ascribed to the understanding of intentions behind the action of others (e.g., [15]). In this vein, it might be advanced that understanding gaze objects relations is likely to entail an intentional component which might be responsible for the lateralization of the observed inferior frontal activation.

Altogether these results suggest that during the observation of gaze shifts participants implemented motor representations within brain areas similar to those identified for the observation of hand actions. Evidence of a tight linkage between hand action representations and gaze representation has been provided by previous behavioral studies. For example, it has been demonstrated that observation of manual action influences the observer's eye movements. When people watch an actor performing a visually guided object manipulation, the coordination between their gaze and the actor's hand is very

similar to the gaze–hand coordination adopted when they perform the task themselves [7,25]. This suggests that hand action observation influences gaze patterns. The opposite interaction, i.e. observation of gaze patterns influences hand action has also been revealed [3]. The present findings provide a parsimonious explanation for these effects: if the same functional ontology is employed to represent both hand-object relations and gaze–object relations, then this might explain why there is a robust coupling between gaze and hand motor programs.

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