

Individuals' and groups' intentions in the medial prefrontal cortex

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Functional MRI signal was recorded while participants perceived stimuli presented using moving dots. In two conditions of interest, the motion of dots depicted intentions: dots representing the joints of an agent performing an action, and dots representing individual agents behaving contingently. The finding of a common cluster in the posterior part of the medial frontal cortex involved in intentional action representation validates the hypothesis that perception of these two conditions requires a similar internal representation. A cluster responding to the behaving group only is found in the anterior medial frontal cortex. These results support a division of the medial frontal cortex according to social stimuli attributes, with anterior areas responding to higher-order group behaviours integrating the action of multiple individual agents.

Introduction

Humans naturally perceive others' behaviours not in terms of their appearance but in terms of the intentions causing them [1]. When people view videos of an actor lifting a box with the attempt to deceive the viewer about the real weight of the box, there is a high probability that they recognize the intention to deceive the observer [2]. Impoverished point-light displays formed by moving dots representing the moving joints of an individual performing an action (Johansson's point-light displays [3]) are recognized as action, and can also convey emotional states [4]. In contrast, Heider and Simmel animations [5], showing three triangles moving contingently around a rectangle, are perceived irresistibly as agents having intentions (e.g. one triangle is chasing the other) and personality traits like shyness [6]. Even simpler displays showing the contingent motion of simple geometrical shapes at a distance [7–9], such as those used originally by Michotte [10], are perceived as depicting interactions between intentional agents. In most cases, perception of intentionality relies on contingent movements of at least two elements displaying flexibility in adapting their behaviour to changing circumstances to reach a goal, for example when one element is chasing another.

A growing literature of neuroimaging studies has identified two brain regions involved in perceiving intentions: the temporoparietal junction and the medial frontal cortex. Although the temporoparietal junction responds particularly

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to intentional motion [11], the medial frontal cortex responds to a variety of stimuli depicting intentional interactions (see [12] for a review), from intentional animations using simple geometrical shapes [8,11,13] to real people acting [2,14]. The medial frontal cortex is proposed to be involved in the '*integration of complex representations of possible actions and anticipated outcomes*' [15], and may be subdivided into three functional parts along an rostrocaudal axis (15; illustrated in Fig. 2): a posterior part involved in *representing action*, a middle part involved in *monitoring the outcome of action* and an anterior part involved in *monitoring of the value of action outcomes* [15].

Experiments investigating the perception of different types of intentional actions are useful to better characterize this subdivision. In both Johansson point-light displays and Michotte contingent displays, the motion of simple geometrical shapes are perceived as intentional actions, the action of an individual agent in the former, the behaviour of more than one agent in the latter. The two types of stimuli thus differ in terms of the processes giving rise to the perception of an intentional action, human form elicited by biological motion in point-light displays versus our tendency to attribute intentions when a scenario presents contingent interactions between elements. The goal of the present functional MRI (fMRI) experiment is to investigate whether the perception of intentions from individuals' actions and from multiple agents' behaviours utilize the same neural mechanisms in the medial frontal cortex, by using similar low-level visual stimulations for presenting the two types of intentions. Our hypotheses stem from the fact that group behaviours are the result of contingent actions of

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individual agents. Therefore both stimuli should engage the posterior part of the medial frontal cortex, involved in representing simple actions, whereas only group stimuli, in which the perception of intention results from the contingent motion of multiple agents, would engage the more anterior part of the medial frontal cortex required to integrate the outcome of multiple agents' actions.

Methods

Stimuli

Stimuli consisted of 20 dots moving randomly for 9 s. After 1.5–4 s and for 3.5 s, 13 of the dots moved contingently to depict:

- (1) Human action: dots represent the main joints (e.g. running, walking, cartwheel; <http://astro.temple.edu/~tshipley/pltarchive.html>);
- (2) Group behaviour: functional relations between the dots lead to the perception of a coherent behaviour (e.g. follow the leader, forming a group, chasing one dot). Stimuli are formed by biasing the random motion towards a specific target, for example one of the dots;
- (3) Polygon: a simple geometrical form (e.g. square, triangle, line) displayed with dots located at the angles or equally distributed on the shape is rotated around the centre of the screen;
- (4) Polyhedron: a three-dimensional solid (e.g. cube, pyramid) with dots located at the angles or vertices is rotated in three dimensions around the centre of the screen.

The motions, scaled to the centre ($\sim 14\text{--}16^\circ$ of visual angle) of the stimulus ($\sim 18\text{--}20^\circ$), were played at 20 frames per second. 1.5 s after the end of the stimulus, a five-choice response screen ('Action', 'Group', '2D', '3D', 'Don't Know', in randomized order) allowed participants to select their response and was followed by a 2.5 s intertrial interval. A central fixation cross was present throughout the course of the experiment.

Experiment

Eleven right-handed volunteers (five men; 25 ± 3 years old) with no history of neurological nor psychiatric disorders and normal vision were scanned in the experiment, which was approved by the ethics committees of the Advanced Telecommunications Research Institute. They gave their written informed consent to the experimental procedure and signed a participation agreement. They underwent a full session outside of the scanner before the fMRI experiment to ensure that they had understood the task and were able to recognize stimuli, followed by 4 fMRI sessions. One session consisted of six repetitions of the four experimental conditions in a pseudo-randomized order such as the intentional and geometric stimuli alternated.

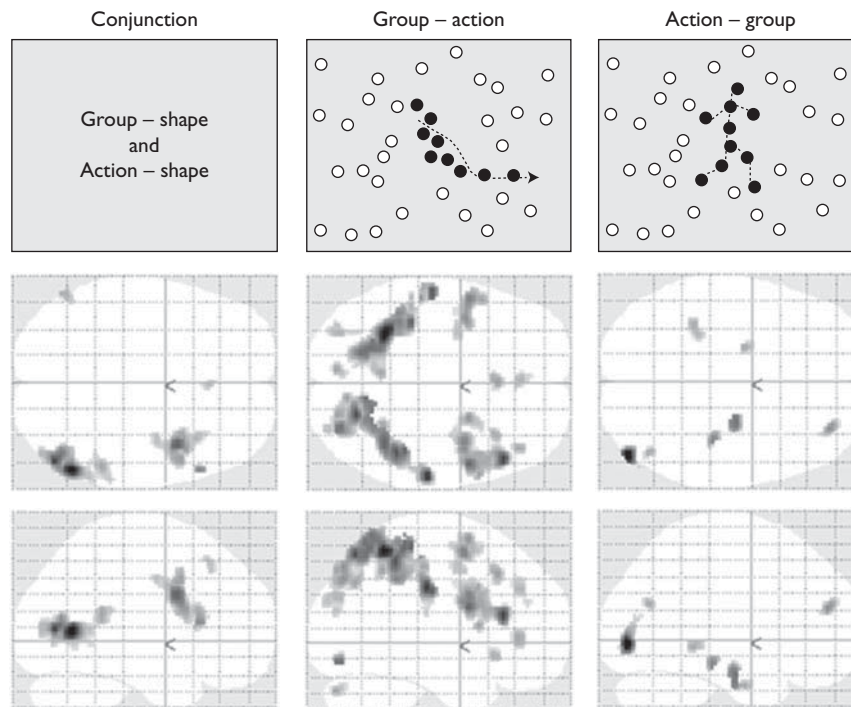
The 1.5 T MRI scanner (Shimadzu-Marconi Magnex ECLIPSE 1.5 T, Shimadzu Medical Systems, Kyoto, Japan) of the Advanced Telecommunications Research Institute Brain Activity Imaging Center was used to obtain blood oxygen level dependant contrast functional images. Images weighted with the apparent transverse relaxation time (T^*_2) were obtained with an echo-planar imaging sequence (repetition time = 2.5 s, echo time = 50 ms, flip angle = 90°). Voxel size was $3.5 \times 3.5 \times 3.5$ mm with 1.5 mm gap between slices ($64 \times 64 \times 25$ voxels), which gave a total field of view $192 \times 192 \times 125$ mm³. A total of 150 image volumes were acquired in each session. In a separate session, high-resolution ($1 \times 1 \times 1$ mm) whole-brain anatomical images were acquired from each participant using a T1-weighted three-dimensional radio frequency spoiled Fourier-acquired steady-state technique.

Analysis

We used SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/>) for statistical analysis. For each participant, the first four volumes of each session were discarded whereas the remaining 146 functional image volumes were realigned to the first volume. The mean image created during realignment was coregistered with the anatomical image, which was used to normalize all functional data and smoothed with a Gaussian kernel of 6 mm full width at half maximum.

At the individual participants' level, β was estimated for the four conditions of interest (3.5 s), the Random motion mask (9 s) and the Motor response (0 s). These boxcar regressors were convolved with the hemodynamic response function and high-pass filtered (cut-off frequency = 128 ms).

Second-level random effect analyses were performed using flexible factorial design with sessions as a repeated measure, and results are presented with a threshold of $P < 0.001$ and extent superior to 25 voxels. To identify responses to the intentional motions, a two-way repeated-measure ANOVA using single participant contrast images Group-Polygon and Action-Polygon in each of the four experimental sessions was performed. Global null conjunction [16] between (Group-Polygon) and (Action-Polygon) was used to identify common resources used for the perception of both intentional stimuli, whereas the differences between the contrasts were used to isolate specific responses to both intentional stimuli. For example, specific response to Group Behaviour conditions was calculated at the second level as [(Group-Polygon)–(Action-Polygon) inclusively masked with (Group-Polygon) at $P < 0.05$]. Whole brain results are illustrated in Fig. 1 and given in Supplementary Table 1 (Supplemental digital content 1, <http://links.lww.com/WNR/A150>), whereas medial frontal cortex responses are provided in Fig. 2. In addition, brain correlates of random motion perception and of action execution were calculated using the main effect of Random motion mask and the main

Fig. 1

Transverse glass-brain renders (bottom) of whole-brain contrasts (see Methods) for the conjunction between the two intentional stimuli (illustrated above), specific response to Group Behaviour (middle) and to human action (right).

effect of Motor response with two one-way ANOVAs using sessions as repeated measures.

Results

Participants' responses were correct more than 90% of the time for all stimuli but the Polyhedron (Group: 92%, Action 93%, Polygon 92%, Polyhedron 81%), as Polyhedron were often confused with Polygon (12%) in the fMRI environment. As no specific hypotheses pertained to the Polyhedron, it was excluded from subsequent analyses.

Action execution resulted in responses of the left primary motor cortex ($x, y, z = -34, -16, 66$; Z -score Inf), the right cerebellum, two clusters in the medial premotor cortex (posterior: $-2, -18, 44$; 9.94 ; anterior: $0, 6, 42$; 12.01), and a region of the ventral extrastriate cortex. Perception of the motion mask resulted in responses of the motor cortex, right cerebellum and medial premotor cortex, as well as lateral extrastriate areas bilaterally ($-36, -90, 0$; 8.46 and $26, -98, 0$; 8.32) and the posterior frontal cortex bilaterally ($42, -4, 60$; 6.94 ; $-40, 2, 58$; 11.30) at the location of frontal eye fields [17]. The finding of the medial premotor region in both action execution and perception of the motion mask suggests they correspond to the presupplementary motor area caudally ($y < 0$), associated with motor response preparation and execution, and the supplementary

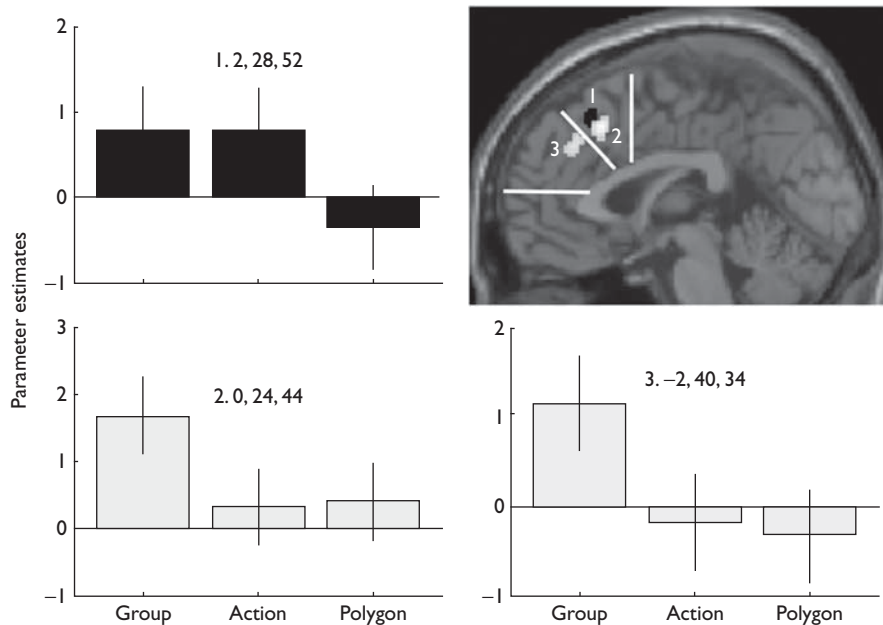
eye field ($y > 0$ [18]) associated with control of eye movements.

Figure 1 presents the main result of the experiment: conjunction of Group-Polygon and Action-Polygon was associated with bilateral posterior middle temporal gyrus, dorsal to the middle temporal/V5 complex according to probability maps [19], the right inferior frontal gyrus and the medial frontal cortex anterior to the medial motor areas characterized above ($y = 28$). Specific response to Group behaviour was found spanning the entire parietal cortex along the intraparietal sulcus, in the ventral premotor cortex, inferior frontal gyrus and posterior middle frontal gyrus, all bilaterally (Supplementary Table 1 and Fig. 1), as well as in two clusters in the medial frontal cortex. Specific response to human action was found in the amygdala and hippocampus bilaterally, as well as in posterior superior temporal gyrus region that could correspond to the temporoparietal junction [20]. Parameter estimates from the three medial prefrontal clusters are presented in Fig. 2.

Discussion

Assuming that medial frontal cortices have a special role in social cognition, we investigated how its responses to individual actions, such as walking and running, and to group behaviours [15] overlap, using the fact that both

Fig. 2



Midsagittal brain section depicting medial frontal activated regions (conjunction: dark; Group Behaviour: light). Plot presents parameter estimates for the conditions Group, Action and Shape in the three activated clusters labelled 1, 2 and 3 on the section.

intentional conditions were rendered using motions of dots. In contrast to the posterior temporal cortex [21], the medial frontal cortex is not a canonical region for the perception of point-light displays of human actions, but has repeatedly been shown to respond to animated shapes' contingent motions, which are irresistibly perceived as biological agents [13].

Conjunction between the two conditions depicting intentions, compared with the control condition, was associated with bilateral response in the posterior middle temporal gyrus and in the right posterior temporal cortex. These regions thus respond not to the specific aspects of the stimuli eliciting perception of intention (human form-from-motion for Action, functional relationship between dots representing single agents for Group) but to a factor common to both stimuli. The bilateral posterior middle temporal cluster falls partly into the human motion sensitive area (according to the probability map in [22]), and extends dorsally to the putative human homologue of primates' medial superior temporal area, characterized as more responsive than the ventral middle temporal to complex coherent motions [23], common to both Action and Group conditions.

The perception of intention induced by contingent movements has been associated with the right posterior temporal cortex in experiments using simple displays, such as distance interaction (60, -52, 15 in [7]) and chasing behaviours (48, -44, 12 in [8]). The region found here (54, -42, 18) thus likely responds to the

perception of simple aspects of both conditions, here non-rigid breaches of randomness in the motion. Altogether, this region is involved when the perceived motion is not random and cannot be interpreted with simple physical explanations such as collision [7]. It is therefore a good candidate to play a central role in the perception of animacy, that is, recognition that the agent is alive, using its will and energy to move in ways that cannot be explained solely by physical laws.

The last region responding to both intentional displays lies within the posterior part of the medial frontal cortex (2, 28, 54; cluster 1 on Fig. 2). In this experiment, motor response selection is separated in time from stimulus presentation; the supplementary frontal eye field is clearly identified as more posterior by the analysis of responses to perception of the motion mask and the execution of the motor response. The medial frontal cortex response is thus associated with the intentional content of stimuli, not with the participants' motor control. This result corroborates our hypothesis that, as making sense of group behaviour implies perceiving each dot as an autonomous acting agent, an overlap in the posterior part of the medial frontal cortex, involved in representing actions in a broad sense, is also expected to respond to group behaviours, in which each agent moves intentionally. For example, when 'follow the leader' was shown during a Group condition, each dot represented an individual agent moving according to a common rule. The absence of significant increase of response between

Action and Group, that could be expected considering that a group has $n > 1$ agents, can be interpreted as a regional response to the category 'intentional action' (or 'animate agent'), not to the number of agents engaged in the action.

In contrast, a response in the more anterior medial frontal cortex, postulated to respond to the monitoring of action outcomes, was found activated in response to Group behaviour, but not Action (Fig. 2, cluster 3). Coordination between agents requires individuals' actions to be contingent in a flexible manner reflecting the coordination rule. For example, in the conditions in which individuals followed a leader (see Fig. 1, top centre) all followers biased their movement towards the leader, which can be described as each individual changing his motor intentions (direction of move) to reach a higher order goal (following the leader). In contrast, when action stimuli show a running motion, there is no higher goal, such as 'where is the person going?' involved. Thus, results support our second hypothesis that higher goals depicted in group interactions activate more anterior subregions of the medial prefrontal cortex associated with higher mentalizing tasks such as monitoring action outcomes.

Finally, a second response specific to Group behaviour is found ventral to the common cluster, dorsal to the cingulate sulcus. It is particularly interesting to find such contrasting patterns in the dorsal and ventral areas in the same part of the frontal medial cortex. It argues in favour of additional distinctions between functions of medial frontal areas more important than the putative gradient from visceral to cognitive functions [15]. Further experiments, using the same experimental approach of depicting different content using comparable visual stimulation, could contribute to a better understanding of the parcellation of the functions of the medial frontal cortex in social cognition.

Conclusion

Our results support the idea that neural resources in the medial frontal cortex are shared when we perceive single individuals' intentional actions or group intentional behaviours, possibly in response to the intentions underlying perceived actions. In contrast, a more anterior region responds specifically to group behaviour, corroborating the hypothesis of an anteroposterior division of the medial frontal cortex in relation to the complexity of intentional content of perceived events.

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Conflicts of interest

There are no conflicts of interest.

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