Report

Complementary Systems for Understanding Action Intentions

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Summary

How humans understand the intention of others' actions remains controversial. Some authors have suggested that intentions are recognized by means of a motor simulation of the observed action with the mirror-neuron system [1–3]. Others emphasize that intention recognition is an inferential process, often called "mentalizing" or employing a "theory of mind," which activates areas well outside the motor system [4–6]. Here, we assessed the contribution of brain regions involved in motor simulation and mentalizing for understanding action intentions via functional brain imaging. Results show that the inferior frontal gyrus (part of the mirror-neuron system) processes the intentionality of an observed action on the basis of the visual properties of the action, irrespective of whether the subject paid attention to the intention or not. Conversely, brain areas that are part of a "mentalizing" network become active when subjects reflect about the intentionality of an observed action, but they are largely insensitive to the visual properties of the observed action. This supports the hypothesis that motor simulation and mentalizing have distinct but complementary functions for the recognition of others' intentions.

Results

Understanding the intentions of others is the basis of social cognition and is of crucial importance for any species living in groups. The ability to understand intentions has been demonstrated in 14-month-old human infants [7], as well as in other social animals [8, 9]. The mechanisms behind the ability to understand intentions are, however, poorly understood. On the one hand, it has been proposed that understanding the intention of others' actions is accomplished by means of an automatic motoric simulation [1]. This simulation is thought to be carried out by neurons in the parietal and premotor cortex that are active during both observation and execution of action—the mirror-neuron system (MNS) [2, 3]. On the other hand, others assert that intention understanding cannot be purely motoric in nature. Rather, mental states like beliefs and desires are attributed to other people in order to understand the intentions of their actions—the formation of a so-called theory of mind (ToM) [4, 5]. This mentalizing process recruits a network of cerebral regions that are well outside the motor system, namely superior temporal cortex, the temporoparietal junction, and the midline structures posterior cingulate and medial prefrontal cortex [4, 6, 10, 11].

These different accounts of intention understanding have often been considered mutually exclusive, but recently the hypothesis has been coined that these two systems may have a complementary role in understanding action intentions [12, 13]. For instance, motor-simulation mechanisms may provide a "prereflective" or automatic representation of an action based on the visual state of the other, whereas inferential mechanisms may then elaborate on this initial hypothesis by using conceptual knowledge of the other's mental state [12]. We tested this hypothesis by recording neural activity while participants observed an actor performing an ordinary or extraordinary goal-directed action, in terms of its intention or in terms of its motoric manner (see Figure 1A for examples). Moreover, we varied the task of the participant: On some trials, participants had to judge whether the intention of the action was ordinary, whereas on other trials, subjects had to judge whether the action was carried out in an ordinary manner (Figure 1B). By means of this design, we could pry apart regions that encode the intentionality of an action in an automatic stimulus-driven manner and regions that are activated when we actively reflect about the intentionality of an action. Areas driven automatically by the intention conveyed by the visual information should be modulated by the stimulus, irrespective of the task for the participants. On the other hand, areas sensitive to mentalizing should be modulated by the task, irrespective of the stimulus.

Behavioral data indicate that both the intentionality and means of the observed actions were processed, irrespective of the task in which subjects were engaged (Supplemental Experimental Procedures and Figure S1, available online).
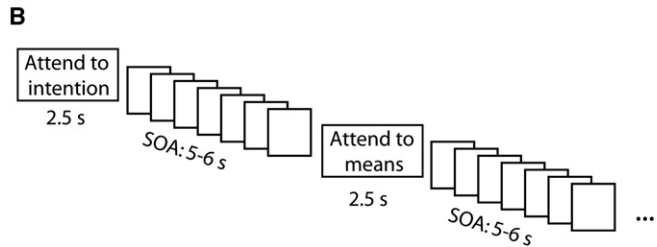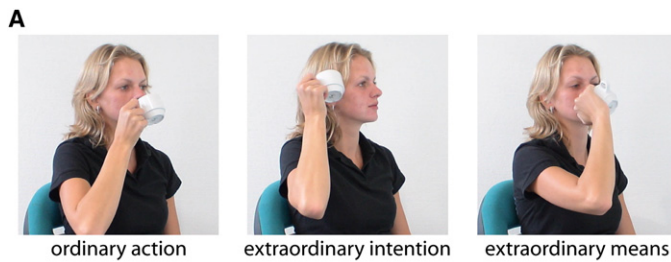
Observing actions with extraordinary intentions was associated with increased activation (compared to ordinary actions) in the inferior frontal gyrus (Figure 2A, left column). Activity in this region was independent of whether the participants attended to the intention or to the manner of the action (Figure S2A). Observing actions that were carried out in an extraordinary manner was associated with higher activity (compared to ordinary actions) in the lateral occipitotemporal cortex, around the "extrastriate body area" (Figure 2A, right column) [14].

When participants selectively attended to the intentionality of the action, three regions showed an enhanced response (compared to when they attended to the means): The medial prefrontal cortex, posterior cingulate cortex, and right posterior superior temporal sulcus (Figure 2B). These three regions are all part of a network that is involved in inferential, interpretive processes, such as mentalizing [10, 15] and introspection [16].

Discussion

A recent hypothesis states that motor simulation and inferential nonmotoric mechanisms may play complementary roles in understanding action intentions [12, 13]. Our results provide empirical support for a specific type of division of labor between mirroring and mentalizing networks during action

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Figure 1. Stimulus Material and Experimental Design

(A) Examples of the stimuli. Subjects observed pictures of normal actions (left column), actions of which the intention was unusual (middle column), and actions that were carried out in an unusual manner (right column).

(B) Task setup. Participants were instructed to attend either the intention or the means of the action. They subsequently had to judge a series of stimuli. The stimulus-onset asynchrony (SOA) between subsequent stimuli within one block was 5–6 s. We used a mixed blocked and event-related design to isolate both stimulus- and task-related effects.

understanding: Whereas the inferior frontal gyrus, part of the MNS, automatically encodes the intentionality of an action on the basis of its visual properties, brain regions that are part of a "mentalizing network" are specifically engaged when we reflect about its intention.

Previous studies have shown the involvement of the MNS in action understanding [17, 18]. Consistent with these observations, we found activation of the inferior frontal gyrus related to action understanding. The inferior frontal gyrus was not modulated by the task of the observer, but its contribution was nevertheless specific to intention extraction. Actions that had an ordinary intention but were carried out in an unusual manner did not modulate the MNS, but rather the extrastriate body area (EBA) [14]. This area selectively responds to body parts [14], and disruption of the region results in impaired identification of body parts [18]. Our data show that EBA activity is further influenced by the motoric context in which the body part is presented. Although we found distinct brain regions involved in processing the means and the intention of an action, these aspects of action understanding do

appear intricately linked and exhibit a hierarchical relationship [19]: Only after an actor's intention is recognized can the means of an action be usefully interpreted. This hierarchical and distributed organization of goal-directed action fits well with neuropsychological [20, 21] and brain-imaging [22–24] dissociations found between different levels of the hierarchy of motor control.

When participants attended to the intentionality of the action, there was an increase in activation in the medial prefrontal cortex, the posterior cingulate, and the right posterior superior temporal sulcus (compared to when the participants attended to the means). All these regions have been involved in several aspects of social cognition, such as the interpretation of human motion, attribution of agency, and inference of the mental state of an observed actor [10, 11, 15]. This network also showed intrinsic (non-task-related) activity (Figure S2), in line with earlier studies showing a link between these regions and stimulus-independent thought and introspection [16, 25]. Here we show that activity in this network is driven by the reflective state of the participant but is largely insensitive to the visual properties of the observed action.

To infer another person's intentions, we need to complement sensorimotor knowledge with conceptual information about mental states and attitudes [26]. Therefore, motor simulation and mentalizing are not mutually exclusive. Rather, our data underscore the notion that mirroring mechanisms and reflective, inferential mechanisms play distinct but
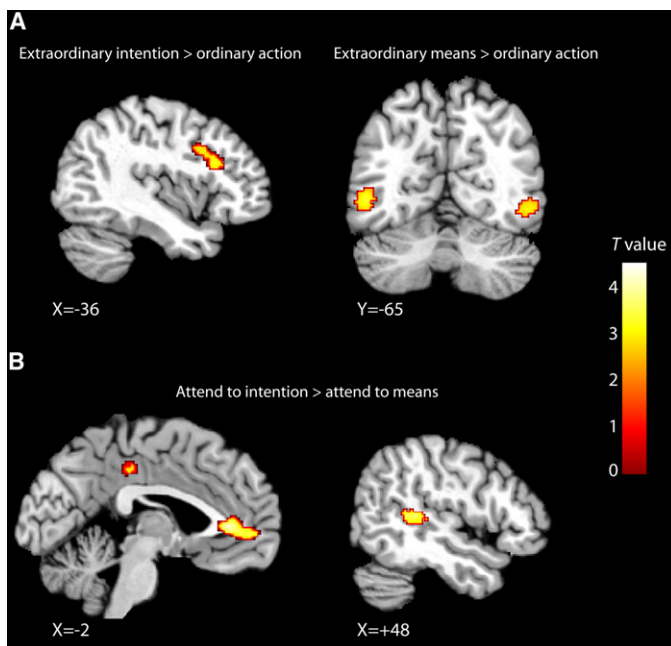

Figure 2. Stimulus-Driven and Task-Driven Brain Reponses

(A) Stimulus effects. Unusual intentions evoked greater activity bilaterally in the inferior frontal gyrus (IFG; left column), part of the MNS. Actions that were carried out in an unusual manner evoked greater activity bilaterally in the lateral occipitotemporal cortex, around the putative extrastriate body area (EBA; right column).

(B) Task effects. When subjects watched ordinary actions but selectively attended the intention of the action, there was greater activity in the posterior cingulate and medial prefrontal cortex (left column) and in the right superior temporal sulcus (right column). These are three core nodes of the "mentalizing" network.

complementary roles in understanding the intentions of other agents around us. The exact nature of this interaction should be the focus of future research.

Experimental Procedures

Subjects

The study was approved by the local ethics committee and in accordance with the Helsinki declaration. Subjects were screened for the following exclusion criteria: left handedness, regular taking of drugs or medication, history of psychiatric or neurological illnesses, and contraindications to MRI scanning (pregnancy, claustrophobia, metallic implants). All subjects gave informed consent prior to taking part. A total of 19 subjects were scanned: 10 females (mean age 21.5 ± 2.3 yr; Edinburgh Handedness Inventory 92 ± 11) and 9 males (mean age 24.2 ± 3.3 yr; Edinburgh Handedness Inventory 91 ± 14).

Behavioral Task and Analysis

Subjects were shown pictures of an actor who was engaged in an interaction with an object. The scene could depict a normal action (e.g., an actor bringing a coffee cup to her mouth), an action with an unusual intention (e.g., an actor bringing a coffee cup to her ear), or an action with an unusual means (e.g., an actor bringing a coffee cup to her mouth while holding the cup with a power grip; see Figure 1A for examples and Supplemental Data for a full list of stimuli). Scenes with both unusual intention and means were also included in order to balance all the possible combinations of usual and extraordinary means and intentions. We have used the term "intention" to refer to the global intention of the actor performing a given motor act, or the "why" of an action, as defined by Iacoboni et al. [17]. Note that this distinction between intentions and means coincides with the distinction between "prior intentions" and "motor intentions" [27]. The picture was shown for a duration of 3 s. Subjects had to judge either the intentionality of the action or whether the means of the action was normal or unusual by pressing one of two buttons with the index or middle finger of their right hand. The instruction for the intention task was, "For the following set of pictures, decide whether the intention of the action is ordinary or unusual." The instruction for the means task was, "For the following set of pictures, decide whether the action is carried out in an ordinary or unusual manner." Before scanning, subjects were familiarized with the tasks by practicing 36 trials per task. For the scanning session, we grouped the different task conditions in separate blocks. Each block consisted of 6–7 stimuli. The stimulus-onset asynchrony (SOA) ranged from 5 to 6 s. Each stimulus type was replicated 20 times for each task, leading to an experimental duration of ~21 min, spaced over a total of 26 task blocks. Stimulus presentation was controlled with Presentation software (Neurobehavioral Systems, Albany, NY, USA). Reaction times (RTs) and error rates (ERs) were recorded for subsequent behavioral analysis. We assessed the influence of Task (two levels: attend to intention, attend to means) and Stimulus (three levels: normal action, unusual intention, unusual means) on RT and ER with a multivariate repeated-measures ANOVA.

Image Acquisition and Analysis

Whole brain T2*-weighted echo-planar imaging blood-oxygenation-level-dependent (EPI-BOLD) fMRI data were acquired with a Siemens Trio 3T magnetic resonance scanner using the CP head array coil, with ascending slice ordering, a volume repetition time of 2.13 s, an echo time of 30 ms, a 80° flip angle, and isotropic voxel size of 3.5 mm. The fMRI data were preprocessed and analyzed in an event-related manner, within the general linear model, with SPM5 software (Wellcome Department of Imaging Neuroscience, London, UK). The first five volumes of each session were discarded, to allow for T1 equilibration effects. Preprocessing consisted of spatial realignment, slice-timing correction, normalization, and spatial smoothing with a Gaussian kernel with a full width at half-maximum of 10 mm. We used a single statistical linear regression model for all our analyses, as follows. Each trial was modeled as a boxcar, of which the onset corresponded to stimulus onset and the duration corresponded with the average reaction time of the subject. Two control analyses were carried out to exclude the possibility that reaction-time differences between tasks were driving the observed task differences (see Supplemental Data). Separate regressors were created for the six conditions (two tasks × three stimulus types). Separate regressors that modeled the instruction epochs, erroneous trials, and missed trials were included in the model. All regressors were convolved with a canonical hemodynamic response function (HRF). To correct for motion-related artifacts, we modeled subject-specific realignment parameters as covariates of no interest. Linear contrasts of regression coefficients were computed at the individual subject level and then taken to a group-level random-effects analysis. To avoid any priors on brain localization, we applied whole-brain family-wise error (FWE) correction for multiple comparisons on the basis of random field theory. We used a corrected cluster threshold of p < 0.05, on the basis of a voxel-wise threshold of p < 0.001.

The contrasts isolating stimulus-related effects (unusual intention > normal action and unusual means > normal action) considered stimuli in both task blocks. The contrast isolating task-related effects considered only normal actions, in order to avoid any confounding effects of stimulus type on this comparison.

Supplemental Data

Additional Experimental Procedures, two figures, and two tables are available at http://www.current-biology.com/cgi/content/full/18/6/454/DC1/.

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