

Investigating Action Understanding: Inferential Processes versus Action Simulation

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Summary

In our daily life, we continuously monitor others' behaviors and interpret them in terms of goals, intentions, and reasons. Despite their central importance for predicting and interpreting each other's actions, the functional mechanisms and neural circuits involved in action understanding remain highly controversial [1, 2]. Two alternative accounts have been advanced. Simulation theory [3] assumes that we understand actions by simulating the observed behavior through a direct matching process that activates the mirror-neuron circuit [4]. The alternative interpretive account [5] assumes that action understanding is based on specialized inferential processes activating brain areas with no mirror properties [1]. Although both approaches recognize the central role of contextual information in specifying action intentions, their respective accounts of this process differ in significant respects [1, 5–7]. Here, we investigated the role of context in action understanding by using functional brain imaging while participants observed an unusual action in implausible versus plausible contexts. We show that brain areas that are part of a network involved in inferential interpretive processes of rationalization and mentalization but that lack mirror properties are more active when the action occurs in an implausible context. However, no differential activation was found in the mirror network. Our findings support the assumption that action understanding in novel situations is primarily mediated by an inferential interpretive system rather than the mirror system.

Results

Remarkably, humans and even young infants [4, 5] not only can attribute goals to familiar behaviors, but—relying on situational cues—can also understand even novel or improbable actions as intentional and goal directed [8]. Using contextual information to identify intentions and reasons behind observed behaviors is ubiquitous and seems to be especially necessary when interpreting unusual or novel actions. Imagine seeing a man at the gate leaning toward a bell button with his forehead. If his hands were occupied with heavy nylon sacks filled with breakable china, we easily interpret his forehead action as a rational means for realizing the stereotypic goal of ringing the bell. However, if the man's hands were free, this differential context leads us to infer other intentions or reasons to justify his unusual behavior. We might attribute a different goal: He might be trying to read the name tag under the bell. We infer further intentions: Maybe he wants to entertain his on-looking child by ringing the bell in this funny way. Alternatively, we might infer further constraints: Maybe the man's hands are paralyzed. So what mechanisms and neural processes mediate our remarkable capacity to so flexibly interpret observed behaviors as intentional actions in terms of goals and reasons in a variety of contexts?

One dominant approach assumes that we understand others' actions by internally simulating their behaviors [4, 9, 10]. Recently, simulation theory has received new support by the finding of mirror neurons in the premotor cortex of the macaque monkey [11, 12]. Mirror neurons are active when the monkey observes or executes the same action. It has been argued that mirror neurons provide the neural basis for action understanding through motor simulation [4, 13]. In this view, action goals are recognized by direct mapping of the observed behavior onto a corresponding action scheme in the observer's motor repertoire, whose goal is already known. Recent fMRI and TMS research indicates that areas assumed to constitute the human mirror system (inferior frontal gyrus and inferior parietal cortex) are involved in tasks requiring action understanding [6, 14]. Clearly, direct matching provides a plausible mechanism for the quick and effortless recognition of goals of actions that are highly familiar to the observer. More recently, however, it has been proposed that the premotor mirror-neuron areas are sensitive to context effects on intention recognition and are “also involved in understanding the [“global”] intentions of others” in which “intention” is interpreted “to indicate the ‘why’ of an action” [6, 7]. The alternative to the motor-simulation account assumes that action understanding is at its core an inferential process that assigns a goal to an action by evaluating its efficiency as an optimal means of obtaining the goal within the specific constraints of the situation [5, 8, 15]. This model assumes that the neural mechanisms of action understanding involve context-sensitive inferential processes of rationalization or mentalizing that are

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Figure 1. Experimental Design and Evaluation of Mean Plausibility

The top panel illustrates an example for the implausible action (operating a light switch with the knee) in three different contexts (hands free, hands implausibly occupied, and hands plausibly occupied). On the bottom panel, the mean plausibility rating for the three different action contexts on a five-point rating scale (1 completely implausible, 5 completely plausible) is displayed. These ratings were provided by a different group of 15 subjects.

based on the visual processing of the stimuli [1, 2, 16, 17]. Such mechanisms have been consistently related to regions along the superior temporal sulcus (STS), the temporoparietal junction (TPJ), the anterior frontomedian cortex, and the posterior cingulate cortex [16–19], which are brain areas lacking mirror properties. Clearly, the inference-based model provides a plausible mechanism of action interpretation when the observed behavior in a given context is unfamiliar or improbable and when intention recognition must rely on interpreting the action in relation to its situational constraints (as in our examples above).

One possibility is that the basic default mechanism of action understanding both in humans and nonhuman primates is indeed motor simulation as it is implemented through direct matching by the mirror-neuron system [4]. It could be that context-sensitive inferences to rationalize actions are involved only under atypical circumstances and, even then, only in humans. However, recent converging evidence from studying action understanding under variable contextual constraints in a variety of nonhuman primate species (M.J. Rochat, E. Serra, L. Fadiga, and V. Gallese, personal communication, and [20–22]) and domestic dogs [23] suggests that context-sensitive efficiency-based teleological inferences [5] to assign goals to actions might in fact constitute the basic mechanism of action understanding shared by both human and nonhuman species.

Up till now, the brain areas and mechanisms of action understanding in novel situations have rarely been investigated. Most previous studies presented highly familiar actions performed in stereotypic contexts [6]. In contrast, the present study aimed at investigating the neural processes underlying action understanding by presenting subjects with unusual actions in variable

contexts in which identifying the purpose or reason for why the particular action is performed was not obvious but required context-based inferencing. Presenting identical target behaviors under different situational constraints allowed us testing differential predictions of the mirror-neuron-based motor-simulation account on the one hand and the inference-based model of action understanding on the other.

Contextual effects on inferential processes involved in action understanding have been successfully demonstrated already in preverbal infants [5] by violation-of-expectation paradigms [15]. Recently, Gergely, Bekkering, and Király [24] developed an experimental paradigm to isolate the relevant component processes of action understanding by varying the contextual constraints of the same action demonstrating selective inferential imitation of a novel-means action in 14 month olds. Here, we adapted the basic design structure of this study for a brain imaging paradigm to investigate in adult human subjects whether action understanding in novel situations involves the mirror network or the inferential reasoning network. Participants saw unusual actions (e.g., operating a light switch with the knee) in three different contexts. In the “plausible-constraint” context (hands plausibly occupied), the model’s hands were occupied (she was carrying a stack of heavy folders, Figure 1), thus making it plausible why she had to use her knee to operate the switch. In the “implausible-constraint” context (hands implausibly occupied), the model’s hands were also occupied but in a way that provided no plausible reason for why she used her knee instead of her hands (carrying only one light folder she could have easily liberated one hand to operate the switch). In the “no-constraint” context (hands free), the model’s hands were

Table 1. Experimental Stimuli and Frequency of Presentation

	Hands Free	Hands Im-plausibly Occupied	Hands Plausibly Occupied
Opening a door	4	4	4
Switching on a light	4	4	4
Operating an elevator	4	4	4
Closing a drawer	4	4	4
Closing a cabinet door	4	4	4
Adjusting a pin board	4	4	4
Moving aside a chair	4	4	4
Moving a file in a shelf	4	4	4
Closing a box	4	4	4
Moving aside a package	4	4	4

unoccupied (so she was free to use them to switch on the light). In each condition, ten different actions (Table 1) were presented four times each. Participants were instructed to identify catch trials in which the observed movement was interrupted. We predicted that areas involved in understanding intentional actions in a novel situation should be more strongly activated in the “no-constraint” (hands free) condition than in the “plausible-constraint” (hands fully occupied) condition. For the “implausible-constraint” (hands partially occupied)

condition, we predicted activation levels to lie in between the hands free and the hands occupied condition.

When contrasting the “no-constraint” with the “plausible-constraint” condition we found significant activation ($p < .05$, corrected for multiple comparisons) along the STS with one local maximum in the STS (Talairach coordinates: $x: 43, y: -27, z: 0$) and a local maximum in the posterior STS (Talairach coordinates: $x: 43, y: -35, z: 15$). To investigate whether any part of the mirror system showed an activation when no correction for multiple comparisons was carried out, we applied an uncorrected threshold of $p < .001$. Even with this liberalized significance criterion, no differential activation in the mirror system (inferior frontal cortex or inferior parietal cortex) was observed. Instead, the anterior fronto-medial cortex (aFMC, Talairach coordinates: $x: 7, y: 48, z: 30$) showed activity when not correcting for multiple comparisons. To better understand the activation pattern across conditions, we carried out signal-strength analysis in the STS, the pSTS, and aFMC (Figure 2B). The beta-value diagrams indicate that the implausible-constraint condition shows an intermediate activation level in all three regions of interest. Because we did not find any significant activation in the mirror system even when using a significance threshold uncorrected for multiple comparisons, we carried out an additional

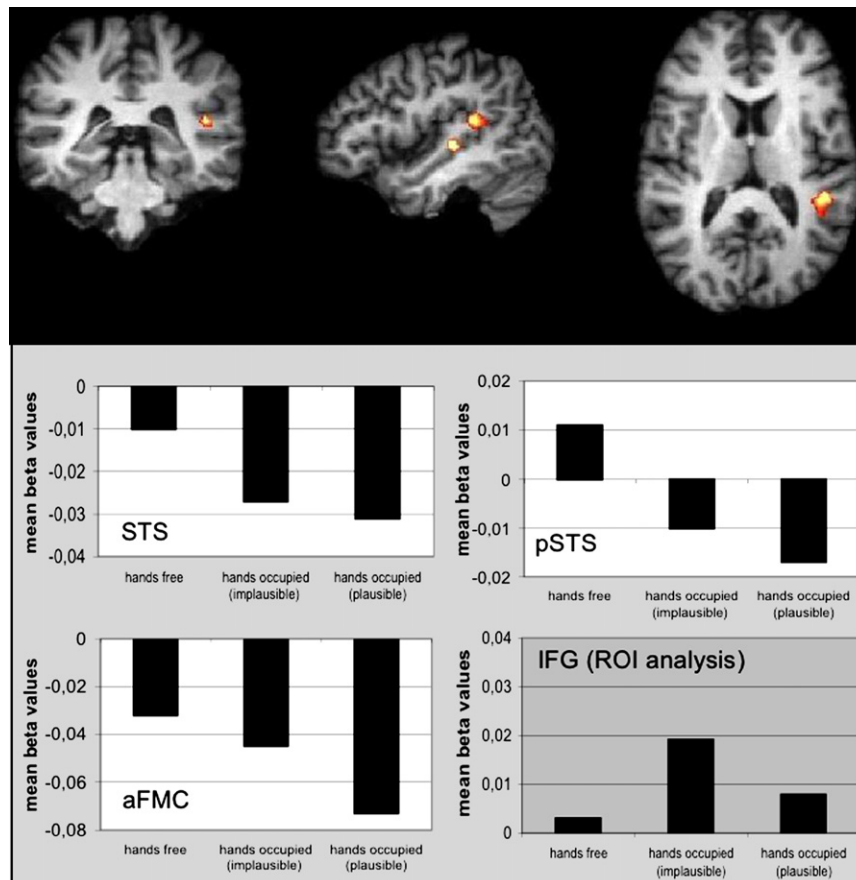


Figure 2. Brain Response for the Comparison of Implausible versus Plausible Actions

The top panel shows the activation foci in the superior temporal sulcus (STS) and the posterior STS. On the bottom panel, the mean beta values for the STS, the pSTS, and the anterior fronto-medial cortex are listed as a function of plausibility. Furthermore, the region-of-interest analysis for the inferior frontal gyrus (IFG) is displayed.

region of interest (ROI) analysis to investigate the activation pattern in the mirror system (Figure 2B, last panel). We selected a coordinate from Iacoboni and colleagues' study [6] that was related to understanding the intention of others. This coordinate is located in the right inferior frontal gyrus (IFG, x: 46, y: 20, z: 22), an area that was assumed to be part of the mirror system. A paired-samples t test did not reveal a statistically reliable difference between the plausible-constraint condition and the no-constraint condition ($t = .27$, $p = .79$) nor between any other condition. In order to demonstrate that the inferential network is more strongly involved in action understanding than the mirror system, we carried out region (STS, pSTS, or aFMC versus IFG) by condition (hands free, hands partially occupied, and hands fully occupied) interactions. A significant interaction was found when comparing the STS with the IFG ($F = 5.18$, $p < .05$) and when comparing the pSTS with the IFG ($F = 3.44$, $p < .05$). A marginally significant interaction was found when comparing the aFMC with the IFG ($F = 2.73$, $p = .08$).

Discussion

Our data strongly support the inference-based account of action understanding in novel situations, which involves rationalization as a function of contextual constraints. When comparing a situation where an unusual action was highly implausible with one where the same action was very plausible, we found strong and reliable activations along the STS and a less reliable activation in the aFMC. The posterior STS and the aFMC have been previously related to perception of social stimuli, mentalizing, and action understanding [16, 25]. In contrast, no differential activation was found in the mirror network as a function of context-based plausibility of the observed action.

At first sight, these findings seem to contradict recent studies showing an involvement of the mirror circuit in action understanding [4, 6, 14]. However, a crucial difference in the types of stimuli presented in these studies might be responsible for their differential findings. Whereas the former studies always depicted highly familiar actions in their stereotypic contexts, all the actions shown in the present study were unusual and were performed in nonstereotypic contexts of varying plausibility. We assume that the action-understanding processes triggered by these two types of actions are qualitatively different. Identifying the goal of a familiar action observed in its stereotypic context can be easily and automatically achieved by mapping it onto the corresponding motor representations already present in the observer's action schemes. In contrast, inferring the purpose of an unusual action and the reason why it is performed in an implausible context necessitates a great deal of active inferencing to evaluate the efficiency of the action in relation to its situational constraints. Our finding that the degree of context plausibility of the same action predicted differential activation of brain areas with no mirror properties, which are normally involved in inferential processing during rationalization and mentalization tasks, supports the above hypothesis. In the hands-free condition, participants must have been working hard to infer an acceptable reason to

justify why the model used her knee rather than her free hands to switch on the light. The low plausibility ratings support this interpretation. We suggest that in contrast to most previous studies, the present experiment captures a crucial type of context-sensitive inferential activity (rationalization) that is necessary for a generative understanding of intentional actions across variable contexts [5]. The data are also consistent with recent demonstrations that an incongruent relation of action and context leads to activation in the posterior STS [18].

Interestingly, the same experimental design we adapted here to fMRI has been used recently to investigate understanding rational action in preverbal infants [24] as well as in several nonhuman species (M.J. Rochat, E. Serra, L. Fadiga, and V. Gallese, personal communication, and [20–23]). These studies indicate that context-sensitive action-interpretation processes that involve evaluating efficiency of goal attainment as a function of situational constraints are not restricted to human adults but occur already in preverbal infants and seem present in other species as well. Whether the neural circuit identified here overlaps with that involved in action understanding in preverbal infants or in nonhuman animals remains an open question.

Finally, we wish to stress that our results in accordance with a recent study by de Lange and colleagues (F.P. de Lange, M. Spronk, R.M. Willems, I. Toni, and H. Bekkering, personal communication) do not exclude the possibility that the mirror network is involved in action understanding. However, the mirror network seems to play a role only in situations in which no active inferential processing is required to identify the goal of the observed behavior because both the action and its stereotypic context are highly familiar and map onto corresponding motor schemes already represented in the observer's action repertoire. This limits the explanatory value of simulation theory to a specific subclass of behaviors, namely to familiar actions performed in stereotypic contexts.

Experimental Procedures

Participants

Sixteen participants (eight males, eight females, mean age: 25.5) participated in the experiment. One participant (female) was excluded because of the high number of errors in catch trials. The remaining fifteen participants had normal or corrected-to-normal vision. None of the subjects had a history of neurological, major medical, or psychiatric disorders. All were right handed, as assessed by the Edinburgh Inventory.

Design

Participants were lying in the MRI scanner while watching short video clips on TFT goggles (VisuaStim XGA, Magnetic Resonance Technologies, Northridge, USA). Each video clip was approximately 7 s long. The relevant leg action started approximately after 2.5 s. The video clips depicted ten different situations in three different contexts (see Table 1). Each video clip was presented four times. Hence, the absolute number of experimental trials was 120 (ten situations \times three conditions \times four repetitions). In addition, 12 catch trials were inserted randomly. Catch trials consisted of videos that were interrupted before the movement ended. Finally, 40 null events, which consisted of a blank screen presented for the whole trial length, were inserted. The trial length was 10 s, starting with a variable jitter interval of 0 ms, 500 ms, 1000 ms, or 1500 ms. Trials were presented randomly.

MRI-Scanning Procedure

The experiment was carried out on a 3T scanner (Siemens TRIO, Erlangen, Germany). Twenty axial slices (19.2 cm FOV, 64 × 64 matrix, 4 mm thickness, 1 mm spacing), parallel to the AC-PC plane and covering the whole brain, were acquired with a single-shot, gradient-recalled EPI sequence (TR 2000 ms, TE 30 ms, 90 flip angle). Prior to the functional runs, 20 corresponding anatomical MDEFT slices and 20 EPI-T1 slices were acquired. Slice thickness was 4 mm with a 1 mm gap.

fMRI Analysis

Analysis of fMRI data was performed with the LIPSIA software package. Data were filtered with a spatial Gaussian filter with $\sigma = 0.8$. A temporal high-pass filter with a cutoff frequency of 1/80 Hz was used for baseline correction. In addition, a global scaling was carried out. All functional data sets were individually registered into 3D space with the participants' individual high-resolution anatomical images. The 2D anatomical MDEFT slices, geometrically aligned with the functional slices, were used for computing a transformation matrix containing rotational and translational parameters that register the anatomical slices with the 3D reference T1 data set. These transformation matrices were normalized to the standard Talairach brain size by linear scaling and finally applied to the individual functional data. The statistical evaluation was carried out with the general linear model for serially autocorrelated observations. The design matrix for event-related analysis was created with a model of the hemodynamic response with a variable temporal delay. The onset of the hemodynamic response was placed on the onset of the video clip (we tested also a model in which the onset of the hemodynamic response was modeled from the onset of the leg movement; however, the results revealed the same activation pattern). The model equation was convolved with a Gaussian kernel with a dispersion of 4 s FWHM. Contrast maps were generated for each participant. We computed a one-sample *t* test of contrast maps across participants (random-effects model) to ascertain whether observed differences between conditions were significantly different. Subsequently, *t* values were transformed into *z* scores. To protect against false positive activations, we used a double-threshold approach, that is, combining a voxel-based threshold with a minimum cluster size [26]. This nonarbitrary voxel cluster size was determined with the program AlphaSim (<http://afni.nimh.nih.gov/afni/doc/manual/AlphaSim>). On the basis of a Monte Carlo simulation (1000 iterations), with our brain volume and an individual voxel height threshold of $Z > 2.57$ ($p < 0.005$, uncorrected), it could be determined that a cluster size of 1674 mm³ (62 contiguous voxels) ensured an overall image-wise false-positive rate of 5%. Activations exceeding this double threshold are therefore considered to be activated at an experiment-wise threshold of $p < .05$, corrected for multiple comparisons. We carried out the signal-strength analysis by extracting the mean beta value from the most activated voxel and determined the six adjacent voxels from the mean contrast across participants (superior temporal sulcus, posterior superior temporal sulcus, and anterior frontomedian cortex). Furthermore, we did the same signal-strength analysis in a ROI taken from Iacoboni and colleagues [6].

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