Neural Mechanisms of Understanding Rational Actions: Middle Temporal Gyrus Activation by Contextual Violation

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Performing goal-directed actions toward an object in accordance with contextual constraints, such as the presence or absence of an obstacle, has been widely used as a paradigm for assessing the capacity of infants or nonhuman primates to evaluate the rationality of others’ actions. Here, we have used this paradigm in a functional magnetic resonance imaging experiment to visualize the cortical regions involved in the assessment of action rationality while controlling for visual differences in the displays and directly correlating magnetic resonance activity with rationality ratings. Bilateral middle temporal gyrus (MTG) regions, anterior to extrastriate body area and the human middle temporal complex, were involved in the visual evaluation of action rationality. These MTG regions are embedded in the superior temporal sulcus regions processing the kinematics of observed actions. Our results suggest that rationality is assessed initially by purely visual computations, combining the kinematics of the action with the physical constraints of the environmental context. The MTG region seems to be sensitive to the contingent relationship between a goal-directed biological action and its relevant environmental constraints, showing increased activity when the expected pattern of rational goal attainment is violated.

Keywords: extrastriate cortex, functional imaging, human, MTG, vision

Introduction

Assessing the rationality of others’ actions in relation to the situational constraints within which the action unfolds is supposed to be a central mechanism for attributing an intentional state to the actor’s goal (Gergely and Csibra 2003). This capacity is at the core of the early development of a theory of mind in humans (Wellman et al. 2008), which involves the attribution of a variety of other intentional mental states to the actor apart from desired goal states (such as beliefs or intentions). The evaluation of the rationality of an action is further underscored by the fact that even nonhuman primates are able to evaluate the efficiency of others’ goal-directed actions (Buttelmann et al. 2007; Wood et al. 2007; Rochat et al. 2008). This opens up the possibility of studying this cognitive capacity with more direct techniques than those routinely used in humans.

The rationality of an action is evaluated as a joint function of the goal of the action, the action itself, and the relevant constraints imposed by the context in which the action takes place (Gergely and Csibra 2003). Several behavioral studies have shown that human infants are sensitive to the rationality of an action from a very early age (Gergely et al. 1995; Sodian et al. 2004; Phillips and Wellman 2005; Brandone and Wellman 2009). In the standard violation-of-expectation looking time paradigm, infants are habituated to a visual event where the experimenter repeatedly reaches over a barrier to grasp an object (Phillips and Wellman 2005). In subsequent test trials, the barrier is removed, and the experimenter performs 2 different actions in this new context: either a movement identical to that in the habituation trials or else a novel but—given the changed environmental constraints—more rational or efficient movement (reaching directly for the object) is displayed. By 12 months of age, infants look longer at the old, now indirect reach, indicating that they are sensitive to violations of the expected efficiency of the action, depending on the action goal and the environmental constraints. Their increased observation time for the unjustified indirect goal approach indicates that they detect the departure from the expected rational pattern of goal-directed action. Whether the infants see the real-life actions or watch a video display does not matter, but the presence of a goal object seems essential (Phillips and Wellman 2005). Similar findings have been obtained in macaque monkeys (Rochat et al. 2008).

The neural substrates involved in evaluating the rationality of actions are under dispute. Some studies (Gallese and Goldman 1998; Rochat et al. 2008) have suggested that this capacity may involve the mirror system in premotor and parietal cortices. At the other extreme, de Lange et al. (2008) have suggested that observing actions performed with extraordinary means activates visual cortex around the extrastriate body area (EBA) (Downing et al. 2001). It remains to be seen how closely such extraordinary means are related to the notion of rational or efficient behavior. Brass et al. (2007) observed activation in the superior temporal sulcus (STS) and superior temporal gyrus (STG) when rationality of goal-directed action was violated. However, in this study, rationality evaluation did not depend solely on the presence of external contextual constraints that required modification of the movement trajectory for the action to be efficient, as in the barrier paradigm. Rather, the evaluation required reliance on additional knowledge about the typical effector (e.g., hand rather than knee) that is commonly used to execute the instrumental action given the affordance properties of the operandum (such as operating a light switch with the hand to turn on the light). Therefore, the STS activation in the study of Brass et al. (2007) may reflect either the activation of the additional knowledge or the violation of the expectation of rational effector choice by the use of an unusual body part when the environmental constraints do not justify this behavior (using the knee to switch on the light even though the hands are free).

To investigate the functional neuroanatomy of rationality evaluation more directly, our experiments focused on the standard barrier paradigm developed by Gergely et al. (1995)
that does not involve the use of different effectors for comparing rational versus nonrational goal-directed actions. Special care was taken to equalize the kinematics of the actions presented and to minimize the low-level visual differences between conditions, parameters not controlled for in previous studies (Brass et al. 2007; de Lange et al. 2008). Furthermore, we localized EBA and hMT/V5 in individual subjects.

Materials and Methods

Participants

Eight volunteers participated in the psychophysical pilot experiment to assess the quality of the stimuli. Fifteen volunteers participated in the main functional magnetic resonance imaging (fMRI) experiment (6 males; mean age 26 years; range 18–35 years). Seven of these 15 volunteers also participated in the control experiment (3 males). All participants were right-handed, had normal or corrected-to-normal visual acuity, and no history of mental illness or neurological diseases. The study was approved by the Institutional Ethical Committee of the Katholieke Universiteit Leuven Medical School, and all volunteers gave their written informed consent in accordance with the Helsinki Declaration before the experiment.

Apparatus

The stimuli were projected with a liquid crystal display projector (Barco Reality 6400i; 1024 × 768, 60 Hz refresh frequency) onto a translucent screen positioned in the bore of the magnet at a distance of 56 cm from the point of observation. Participants viewed the stimuli through a mirror tilted at 0° and attached to the head coil. To reduce the amount of head motion during the scanning sessions, the participants were asked to bite an individually molded bite bar fixed on the scanner table. Throughout the scanning session, the eye movements of the participants were recorded with an Applied Science Laboratories (ASL) eye tracking system 5000 (60 Hz, Applied Science Laboratories).

Stimuli

Main Experiment

The stimuli for our experiment were reach-to-grasp actions. The videos displayed human actors sitting behind a barrier separating them from a piece of fruit on the table. In order to grasp the fruit and bring it to his/her mouth, the actor had to reach over the barrier (analogous to Phillips and Wellman 2005). Four different movement conditions were presented, which were arranged according to a 2 × 2 factorial design by changing either the height of the barrier or the height of the arm trajectory (Fig. 1). The conditions were as follows 1) low barrier with high arm trajectory (lb/ht), 2) high barrier with high arm trajectory (hb/ht), 3) low barrier with low arm trajectory (lb/lt), and 4) high barrier with low arm trajectory (hb/lt). Notice that the low trajectory matched the barrier height in the high-barrier condition (Fig. 1). Hence, in the first 3 conditions, the arm trajectory was not adapted to the height of the barrier, rendering the action nonrational. Videos lasted 2 s (60 Hz). To equate the videos presented in the 4 different conditions, the first frame of the videos in the 2 high-barrier conditions depicted the actor with his hand entirely visible above the barrier. The first frame of the videos for the 2 low-barrier conditions showed the hand at a similar position in space. Approximately midway through the video, the actor grasped the fruit, subsequently bringing it toward his/her mouth. In all conditions, the video ended when the actor was about to bite the fruit. Thus, the reaching component predominated in the reach-to-grasp videos as it was present in the beginning of the videos, in bringing the hand toward the fruit as well as toward the end, in bringing the fruit toward the mouth.

To guarantee that the arm trajectories were similar for the 2 high-trajectory conditions and for the 2 low-trajectory conditions, we manually tracked the elbow and the first articulation of the index finger in each frame of the videos using the MTrackJ (Biomedical Imaging Group Rotterdam) plugin for Image J (NIH). Subsequent statistical analysis revealed no significant differences in the trajectories of the 2 high-trajectory conditions (elbow: \( t_1 = 0.3, P = 0.78 \); hand: \( t_1 = 0.9, P = 0.35 \)) or the 2 low-trajectory conditions (elbow: \( t_1 = 0.1, P = 0.88 \); hand: \( t_1 = 0.5, P = 0.65 \), respectively (Fig. 2A). This analysis insured that the actual movement was very similar in the 2 conditions sharing the same trajectory height. This result was confirmed when we compared the motion energy on a pixel-by-pixel basis across the main effect of barrier height. Adding the motion vectors of the 2 low-barrier conditions over all videos and comparing them to the ones of the 2 high-barrier conditions yielded no difference larger than 1/s on a pixel-by-pixel basis anywhere in the display (Fig. 2B). This analysis shows that the main effect of barrier did not carry any difference in local motion. Naturally, differences in local motion across the main effect of trajectory were more pronounced. The 2 high-trajectory conditions contained much more local motion compared with the 2 low-trajectory conditions (Fig. 2B).

In addition to the 4 movement conditions, 2 static control conditions were presented, showing the actor with his/her hand hidden behind the high barrier or the low barrier, respectively. These 2 static conditions were used to control for the effect of the barrier height. Moreover, an additional movement condition, in which the rational trajectory was presented in the context of the low barrier (Supplementary Fig. 1A), was used for illustration and was not analyzed further. To increase the variety of stimuli, all movements were performed by 4 different actors (2 males/2 females) grasping 3 different fruits (carrot, banana, and apple), leading to 12 videos per condition (Supplementary Fig. 1B).

The stimuli measured 14.8 × 14.8 visual degrees. The edges of the videos were blurred with an elliptical mask, leaving the actor in the center unchanged but gradually blending the periphery into the black background. A small red square (0.2°) was superimposed on all individual stimuli. This fixation dot was presented 0.7° to the upper right or the upper left with respect to the middle of the fruit. These 2 fixation positions were chosen to minimize retinotopic effects.

Control Experiment

To eliminate potential confounds due to differences between local motion energies in the 4 conditions, we analyzed the motion vectors of each original video (Fig. 2C). The local motion vector for each pixel in the image was computed on a frame-by-frame basis (Pauwels and Van Hulle 2009). Subsequently, these vectors were used to animate a random dot texture pattern. The resulting videos contained exactly the same amount of local motion as the original ones but no configural information. Each 120-frame video was split into 4 segments of 30 frames each, and during scanning, these 4 segments were presented in random order to further reduce any perceptual similarity with the original movies and thereby any possible priming effects.

Psychophysical Assessment of the Stimuli

In a psychophysical pilot experiment, a different set of subjects (n = 8) rated the stimuli with respect to their rationality. Subjects sat in dim lighting conditions in front of a computer screen (Iiyama Vision Master pro151, 1280 × 1024 pixels, 60 Hz) watching 2 videos presented side by side for 4 cycles. During an intertrial interval (2 s), subjects had to rate the difference between the 2 videos with respect to nonrationality on a scale from 1 to 4, with 4 being the most different. The videos were selected from the 4 different movement conditions shown in the main experiment (Fig. 1) with 4 videos per condition (all 4 actors; the fruit was selected randomly). The conditions were paired in all possible combinations leading to 380 trials per subject, lasting about 1 h. During the experiment, subjects were free to move their eyes. The resulting dissimilarity matrix, with all pairwise distances, was analyzed using the ISOMAP algorithm for nonlinear dimensionality reduction (Tenenbaum et al. 2000) (K nearest neighbor, \( k = 4 \)).

Scanning Procedure

Main Experiment

All subjects were naïve with regard to the underlying research question, and none of them participated in the psychophysical pilot experiment. Prior to scanning, participants were familiarized with the different stimuli (movements as well as controls) outside the scanner and instructed to maintain their gaze on the red fixation dot throughout the experiment.
A single run of the experiment included the 4 different movement conditions, the 2 static control conditions, and a baseline fixation condition (Fig. 1). These 7 conditions were presented in blocks of 24 s each (12 different 2-s stimuli), except the baseline condition, which was shown for 18 s. During the first presentation of the conditions, an additional condition was included showing a rational movement (very low trajectory) in the context of the low barrier (Supplementary Fig. 1A) for 18 s. This condition was shown only once per run in order to pair also the low barrier with a rational action, which was impossible in the factorial design. This condition was not included in any further analysis, however. The other 7 conditions were shown 3 times within any given run, yielding 22 (3 × 7 + 1) blocks per time series. The order of conditions was randomized and counterbalanced across runs and subjects. Every run started with the acquisition of 4 dummy volumes to assure that the magnetic resonance (MR) signal had reached its steady state. Every subject took part in 1 scanning session consisting of 6 individual runs: 3 with leftward and 3 with rightward fixation, presented in alternation.

Following the scanning, subjects participated in a psychophysical test session inside the scanner analogous to the psychophysical pilot experiment. To reduce the length of this test, only 2 videos per condition (Fig. 1) were randomly selected and paired in all possible combinations. This test was repeated 3 times, and ratings were averaged to define the contrast values for the general linear model (GLM). During this test, subjects were free to move their eyes.

**Control Experiment**

This experiment was designed to control for the influence of local motion energy differences between the conditions. The design was identical to the main experiment, but each run was accompanied by...
a complementary motion control run, showing exactly the same order of conditions (except the static stimuli). In these control runs, the original stimuli were substituted by the random dot motion control stimuli. Thus, each subject participated in 2 sessions, in which original and control runs were presented in alternation, yielding 12 runs, 6 of each type.

Localizer Runs
In addition to the experimental runs, 7 subjects participated in 2 different standard localizer experiments to individually identify the location of the human MT complex (hMT/V5+) and the EBA. hMT/V5+ was localized by contrasting moving and static random dot texture patterns (Sunaert et al. 1999) in 2 time series. EBA was localized by contrasting human bodies with chairs in 2 additional time series, following Downing et al. (2001). The stimulus set can be obtained from http://www.bangor.ac.uk/~pss811/page7/page7.html.

Data Collection
Scanning was performed with a 3-T MR scanner (Intera, Philips Medical Systems) located at the University Hospital of the Catholic University Leuven. Functional images were acquired using gradient echo-planar
imaging with the following parameters: 50 horizontal slices (2.5 mm slice thickness, 0.25 mm gap), repetition time (TR) = 3 s, time of echo (TE) = 30 ms, flip angle = 90°, 80 x 80 matrix with 2.5 x 2.5 mm in plane resolution, SENSE reduction factor of 2. The 50 slices of a volume covered the entire brain from the cerebellum to the vertex. Additionally, a 3D high-resolution T1-weighted image covering the entire brain was acquired and used for anatomical reference (TE/TR 4.6/9.7 ms; inversion time 900 ms, slice thickness 1.2 mm; 256 x 256 matrix; 182 coronal slices; SENSE reduction factor 2.5). A single scanning session lasted about 90 min.

**Data Analysis**

Data analysis was performed using the SPM5 software package (Wellcome Department of Cognitive Neurology) running under MATLAB (The Mathworks, Inc.). The preprocessing steps involved the following: 1) realignment of the images, 2) coregistration of the anatomical image and the mean functional image, and 3) spatial normalization of all images to a standard stereotaxic space (Montreal Neurological Institute) with a voxel size of 2 x 2 x 2 mm. Before further analysis, the functional data were smoothed with an isotropic Gaussian kernel of 8 mm.

For every participant, the onset and duration of each condition were modeled by a GLM. The design matrix was composed of 8 regressors modeling the 8 conditions (7 experimental conditions plus the illustrative condition) plus 6 regressors obtained from the motion correction during the realignment process. The latter were included to account for voxel intensity variations due to head movement. All regressors were convolved with the canonical hemodynamic response function. For the main experiment, a second-level random effects analysis was performed on the contrasts obtained from the first-level analyses (Holmes and Friston 1998). Except when contrasts were used for masking, threshold was set at $P < 0.05$ false discovery rate (FDR) corrected.

The "main rationality" contrast used the participants’ own non-rationality ratings from the psychophysical test conducted immediately after scanning. The contrast values were derived by subtracting the average nonrationality score over all 4 movement conditions from the rationality score for the individual condition. Thus, conditions rated highly nonrational received positive values, while the most rational condition received negative values, fixing the mean across contrasts at zero. Four additional contrasts were defined. The "action observation network" was defined by contrasting all action conditions with all static conditions for each subject. The main effect of "barrier height" compared the 2 low-barrier action conditions with the 2 high-barrier action conditions, and the main effect of "trajectory" contrasted the 2 high-trajectory action conditions with the 2 low-trajectory action conditions. Finally, we computed the effect of the barrier height also for the 2 static conditions, contrasting the low- and high-barrier conditions. This subtraction was used as an exclusive mask ($P < 0.05$ uncorrected) for the main rationality contrast to control for the differences in the amount of body information present in the different conditions.

The procedure for the control experiment was identical, except that all subjects were combined in a fixed-effects model. Threshold for the rationality contrast in the original runs was set at $P < 0.05$ FDR corrected. The contrast values assigned to the different conditions in this rationality contrast were also assigned to the corresponding random dot motion control conditions. The resulting statistical parameter map (SPM) from the dot motion condition was thresholded at $P < 0.05$ uncorrected and used as an exclusive mask to discard regions, which were activated by differences in local motion between the stimulus conditions. As a second exclusive mask, we used the contrast static low barrier versus static high barrier ($P < 0.05$ uncorrected), like in the main experiment.

**Definition of EBA for Individual Subjects**

De Lange et al. (2008) proposed the involvement of area EBA in the processing of the motoric context in which an action is situated. However, this conclusion was based on anatomical location rather than on the specific localization of area EBA in their population of subjects. To investigate the specific involvement of area EBA in the analysis of nonrationality, we performed a region of interest (ROI) analysis on the individual non-smoothed data, carefully avoiding overlap between activations for EBA and for hMT/V5+ as described earlier (Jastorff and Orban 2009).

**Activity Profiles**

To compute the activity profiles for the main rationality contrasts, the data were split into even and odd runs. Using the local maxima defined on the basis of all runs as guides, we defined new local maxima exclusively for the odd runs. All new local maxima were located within less than 6 mm distance away from the original local maxima. Activity profiles show the fMRI activation of the even runs, averaged across the 27 voxels surrounding the new local maxima. For all experiments, the activity profiles were first computed for each subject individually and subsequently averaged across subjects. They represent the percent MR signal change relative to fixation baseline in the different conditions. For the EBA ROI analysis, activity profiles were generated by averaging the responses of all voxels included in the ROI using the nonsmoothed data.

**Visualization**

For visualization purposes, a more lenient threshold of $P < 0.0001$ uncorrected for multiple comparisons was applied to the contrasts, and the resulting activations were projected (enclosing voxel projection) onto the PALS atlas surface (Van Essen 2005) using the Caret software package (Van Essen et al. 2001).

**Results**

The experiment was designed to investigate the neural substrates involved in the detection of rational actions. To this end, stimuli depicted a human actor reaching over a barrier to bring a fruit to his/her mouth. In only 1 of the 4 stimulus conditions, which were arranged according to a 2 x 2 factorial design (Fig. 1), was the height of the arm trajectory adapted to the height of the barrier, resulting in a rational or efficient action. In the remaining 3 conditions, the arm trajectory was too high with respect to the barrier, thus violating the expectation of efficient goal attainment.

**Behavioral Results**

In a behavioral pilot experiment, 8 subjects were asked to compare pairs of videos testing all experimental conditions with respect to the rationality of the action (Fig. 3A). The resulting dissimilarity matrix with all pairwise distances was analyzed using the ISOMAP algorithm for nonlinear reduction of dimensionality (Tenenbaum et al. 2000). The result of this analysis showed that 2 dimensions sufficed to explain 91% of the variance. Plotting these 2 dimensions clearly demonstrates strong separation between the individual conditions, with the low-barrier/high-trajectory and the high-barrier/low-trajectory conditions furthest apart along the first dimension (Fig. 3B). Subsequent statistical analysis along the first dimension using a factorial analysis of variance (ANOVA) showed a significant effect for condition ($F_{1,9} = 15.2, P < 0.001$) but not for actor ($F_{1,9} = 0.6, P = 0.60$). For the second dimension, none of these factors were significant. This analysis revealed that the videos indeed differed with respect to perceived rationality and that this effect was not influenced by the identity of the actor performing the movement. The pilot subjects did not take part in the main experiment.

During scanning, subjects averaged $8 \pm 0.55$ saccades per minute, and the number of saccades did not differ significantly between conditions (1-way ANOVA: $F_{1,9} = 1.2, P = 0.30$). Directly after the scanning session, subjects were asked to rate the degree of dissimilarity between pairs of videos, and these ratings confirmed the results of the pilot experiment (Fig. 4A). The condition showing the low barrier combined with the high trajectory and the condition showing the high barrier combined with the low trajectory were judged as being most
dissimilar with respect to rationality. The other 2 conditions received intermediate ratings.

**Action Rationality**

The dissimilarity ratings from a given subject were directly used to model the contrasts for that subject. The resulting SPM (random effect), projected onto the inflated left and right hemispheres of the PALS atlas (Fig. 4B), thus highlights areas where the activation pattern followed the perceived rationality of the subjects. The red spheres give the location of the 5 local maxima that reached significance at corrected level ($P < 0.05$, FDR correction; see Table 1). Two local maxima (numbers 1 and 2) were located at symmetrical coordinates in the posterior inferior temporal sulcus (ITS) and gyrus of the 2 hemispheres (LH / RH). One additional maximum (number 3), located in the posterior middle temporal gyrus (MTG), was

![Figure 3](image1.png)

**Figure 3.** Psychophysical pilot experiment. Panel (A) shows the dissimilarity matrix obtained during the psychophysical pilot experiment. Panel (B) illustrates the results of the multidimensional scaling analysis. The most rational (red) and the most nonrational condition (black) are located furthest apart, and different actors belonging to the same condition are grouped together. Same color code in (A and B).

![Figure 4](image2.png)

**Figure 4.** Results of the main experiment. Panel (A) shows the average dissimilarity rating across the 15 volunteers participating in the main experiment. Panel (B) displays the results of a random effects analysis where the contrast images for each subject were modeled individually based on the dissimilarity ratings of that subject—colored voxels: $P < 0.0001$ uncorrected; red spheres: $P < 0.05$, FDR corrected. The activation was exclusively masked with the contrast static low barrier versus static high barrier ($P < 0.05$ uncorrected) to exclude regions primarily sensitive to the amount of body information present in the different videos. Black outlines define the borders of the action observation network, contrasting all action conditions with all static conditions at $P < 0.0001$. Panel (C) shows the fMRI activation for the even runs as percent MR signal change from fixation baseline ($\pm$ standard error of the mean) for the local maxima defined on the odd runs. These were located in close proximity to the 5 local maxima of the whole 6 runs indicated in (B) (red spheres).
present only in the left hemisphere. All local maxima were located within the network of areas involved in action observation indicated by the black outlines (see also Fig. 6). Even by lowering the threshold to \(P < 0.01\) uncorrected, we did not observe any frontal activation.

Figure 4C shows the activity profiles for the even runs only, expressed as percent MR signal change from the baseline fixation condition of the 5 local maxima defined on the odd runs and located in close proximity to the ones indicated in B (see Materials and methods). Clearly, the most nonrational condition elicited the strongest response in all local maxima, whereas the most rational condition resulted in the lowest activation. Even in this split data analysis, rationality ratings and runs and located in close proximity to the ones indicated in B showed an unspecific effect of barrier height and thus the visibility of the actor’s body. This was confirmed in a 2-way repeated measures ANOVA with the factors movement (high trajectory, low trajectory, and static) and barrier height (low and high), where we obtained a main effect of barrier height (\(F_{1,6} = 36.2, P < 0.001\)) but no interaction (\(F_{2,12} = 0.6, P = 0.57\)).

**Main Effect of Barrier and Trajectory**

Analyzing the main effect of the barrier for the action conditions showed that not only EBA but also several other brain regions carry information about barrier height (Fig. 6, green regions). Included among these were the retinotopically organized early visual areas because the low-barrier conditions revealed more detail about texture (e.g., actor’s clothes) in the upper visual field. Also higher level visual areas around the posterior MTG/STS showed significantly stronger activation for the low-barrier conditions. This effect was more prominent in the left hemisphere, possibly reflecting a preference for contralateral effector movement as has been proposed earlier (Pelphrey, Morris, McCarthy 2004; Jastorff et al. 2010; Peeters et al. 2009).

The main effect of trajectory resulted in very localized activation in early visual areas and bilateral activation of the posterior MTG. The early visual activations match the more peripheral location in the upper field of the moving arm in the high-trajectory conditions. The MTG activation in the left hemisphere partially overlapped with the main effect of the barrier (Fig. 6, red areas). In our design, the rationality of an action was defined as a combination of the height of the barrier and the height of the trajectory. The overlap of these 2 main effects in the posterior MTG supports our interpretation that this site is sensitive to rationality of an action, which implies the combination of these 2 factors.

**Control Experiment**

During stimulus production, we carefully controlled our videos in order to ensure that the effects described cannot simply be attributed to either the height of the movement trajectory or the height of the barrier but that rationality emerges as a combination of both factors. However, the conditions inevitably differed with respect to the amount of local motion information present, with the low-barrier/high-trajectory condition containing the most local motion summed over the whole video and the high-barrier/low-trajectory condition containing the least local motion. It could therefore be possible that some areas correlating with perceptual rationality (Fig. 4B) are not actually sensitive to the rationality of the action but to the amount of local motion present in the different conditions.

To address this possible confound, we devised a control experiment, for which we rescanned 7 subjects who had already participated in the main experiment. The stimuli for the control runs consisted of random dot texture patterns, solely animated with the optic flow of the original action stimuli (Fig. 2C, see Materials and methods). Thus, the control stimuli contained exactly the same amount of motion at exactly the same location as the original movies but lacked any kind of configural information.

Figure 7A presents the results of a fixed-effects analysis over the 7 subjects who took part in the control experiment. As for the main experiment, the model was defined by the individual dissimilarity ratings given by the subjects. In parallel, the same
model was applied to the optic flow control runs, and any common activation between the 2 resulting SPMs was masked out (black outline in Fig. 7A). The 2 red spheres, located on the posterior MTG, indicate the positions of 2 local maxima where activation reached significance at corrected level (° < 0.05 FDR correction, Table 1). For comparison, the white asterisks highlight the location of the 5 local maxima obtained from the main experiment (Fig. 4B). Figure 7B shows the activity profiles of the even runs for the 2 local maxima of the odd runs located in close proximity to the 2 local maxima obtained across all runs (Fig. 7A). Importantly, also in the control experiment, rationality ratings and fMRI activation were still correlated in the split data analysis, thereby ruling out any possible circular reasoning (LH: R = 0.55, ° < 0.01; RH: R = 0.47, ° < 0.01).

The results of this control experiment indicate that the more posterior activations found in the main experiment, those within the ITS, were actually related to motion energy instead of perceived rationality. In contrast, the bilateral activation sites in the posterior MTG were not affected by the motion control, which supports our interpretation that this region is participating in the integration of the observed action with the context in which the action is performed. Thus, we have obtained converging evidence that neural processes within the posterior MTG site are involved in evaluating the rationality of the action as a function of its goal and given environmental constraints.

Discussion
In a series of experiments, we have shown that activation of the posterior MTG correlates significantly with the subjective evaluation of the rationality of an action. These experiments were the first to directly link behavioral judgments about the rationality of an action with fMRI responses on a subject-by-subject basis. In agreement with other studies (Saxe et al. 2004; Brass et al. 2007; de Lange et al. 2008), the activation levels were higher for the observation of nonrational than for rational actions. Moreover, we demonstrate that this differential activation cannot be accounted for by potential differences in the
local motion energy present in the stimuli or differences in the kinematics of the actions presented.

In our study, the rationality of goal-directed manual actions could be derived from a combination of kinematic (trajectory) and contextual (barrier height) elements. As indicated by the main effect of trajectory, the kinematic information was most likely evaluated in the region surrounding the posterior part of the STS, generally referred to as STS or pSTS, which is involved in the processing of biological motion (Grossman et al. 2000), as well as being activated by the observation of a wide range of actions, such as walking, grasping, eye and mouth movements, and even animations of abstract shapes providing an impression of goal-directed interactions of agents (Allison et al. 2000; Castelli et al. 2000; Pelphrey, Mitchell, et al. 2003; Puce and Perrett 2003; Schultz et al. 2004; Pelphrey et al. 2005). Recently, Jastorff and Orban (2009) showed that this sequence of areas, originating at the hMT/V5+ complex and crossing the posterior part of ITS, MTG, and STS to reach the STG, is activated not only by the perception of human movements per se but also by the processing of the movement kinematics (Fig. 8). These regions, proposed to correspond to the anterior part of the upper bank of monkey STS by Jastorff and Orban (2009), process not only action kinematics but also barrier height, as shown by their respective main effects. Hence, the finding that an area in posterior MTG is sensitive to the rationality of human actions is consistent with the view that rationality results from the integration of action kinematics with contextual elements, insofar as all information needed to determine rationality are coded in nearby regions. It remains to be seen whether MTG integrates only the kinematics of the action with the contextual elements or is also concerned with other aspects, such as the effort needed to perform the action (Gergely 2005). Given the present findings, the lack of any activation in frontal cortex for this very elementary form of rationality understanding that simply follows the laws of physics might not come as a surprise. We cannot exclude the possibility, however, that other cerebral regions are involved in the evaluation of rationality, especially when the assessment involves extraction of more complex visual aspects of the action, such as effort or more cognitive elaboration of the visual information.

The MTG activation sites were part of the main action observation network. That network, as revealed in the present study, differs in several aspects from the networks described in previous studies ( Buccino et al. 2001; Jastorff et al. 2010; Peeters et al. 2009), in that we did not obtain significant activation in ventral temporal cortex, the anterior intraparietal sulcus, or ventral premotor cortex. The reason for this difference might be that the reaching component in our reach-to-grasp videos was much more pronounced than the grasping component. This interpretation is consistent with studies by Filimon et al. (2007), showing that frontoparietal activations for observed reaching were more dorsal than activations typically reported for the observation of grasping. It is also consistent with the results of monkey anatomical studies (Borra et al. 2008), indicating that lower bank of STS, which we have proposed to correspond to ventral temporal cortex in the human (Jastorff and Orban 2009), is connected with anterior intraparietal cortex and ventral premotor cortex (F5a) and may constitute a functional circuit.

Brass et al. (2007) have described 2 sites in the STS and STG, located several centimeters rostroventrally from our MTG activation, as being involved in the evaluation of rationality (Fig. 8). However, in contrast to our study, their stimuli depicted human actors performing well-known instrumental actions (switching on a light switch) in a highly unfamiliar way that involved the use of an unusual body effector, such as operating a light switch with the knee. In some of the videos, however, the hands of the actor were occupied in a plausible manner (by holding folders) that justified the agent’s unusual choice of effector turning the behavior into a rational means action for achieving the goal. In contrast, in other videos, the hands were free, which rendered the knee action nonrational given the stereotyped expectation that one should use one’s hands to operate a switch. Thus, the observed behavior was assessed as nonrational on a more cognitive level by detecting the mismatch between the observed (but unmotivated) choice of effector and the subject’s stored expectation about the stereotypic effector to be used. The detection of this mismatch requires the activation and reliance on stored knowledge about the particular effector and its stereotypic use given the affordance properties of the manipulandum (the light switch). In contrast, in the present study, the inference to the rationality of the goal-directed reaching action did not involve prior knowledge-based expectations of this kind but was more directly perceptually driven by assessing whether the height of the arm trajectory was adequate given the height of the barrier.

Neither the study of Brass et al. (2007) nor our own provides any support for the view that assessment of rational actions involves the mirror system in premotor and parietal cortices (Rochat et al. 2008). However, this does not preclude the involvement of the mirror neuron system in assessing the intentions of the actor (Cattaneo and Rizzolatti 2009). Furthermore, Moro et al. (2008) have provided evidence for a causal relationship between ventral premotor cortex and action discrimination. These 2 studies (Brass et al. 2007 and ours) similarly provide no support for any role by EBA in assessing the rationality of actions, in agreement with the recent study of Kontaris et al. (2009). There are several differences between our study and that of de Lange et al. (2008), including differences in controls for lower level visual

Figure 8. Comparison with related studies. Regions responding to human kinematics in yellow (modified from Jastorff and Orban 2009). Spheres indicate local maxima reported in related studies—pink: EBA (this study); orange: temporoparietal junction (Saxe 2006); green: pSTS-A (Saxe et al. 2004); blue: STS (Brass et al. 2007); and purple: posterior STG (Corbetta et al. 2002, 2005). Another local maximum reported in Brass et al. (2007) was located on the dorsal bank of the STG and is not indicated.
factors as well as in the stimuli themselves. “Extraordinary means” as defined by the study of de Lange et al. (2008) involved an abnormal or inefficient relationship between the action and the target object of the action, while our paradigm involved a contextual element, the barrier. Thus, our study is the first one to point to a specific role of visual areas in the understanding of rational actions.

One might argue that the most nonrational condition, which elicited the strongest fMRI response in the present study as in other studies (Saxe et al. 2004; Brass et al. 2007; de Lange et al. 2008), would also be the condition most affected in terms of attention. In the beginning of a nonrational block, the first videos might be unexpected and therefore attract more attention. This effect should weaken as the block continues, but attention could be recruited to find some alternative justification for the apparent nonrationality of the observed action. While we cannot exclude the possibility that attention may have contributed to the level of activation we observed, we believe for several reasons that our results are not driven primarily by attention. First, subjects were naive as to the goal of the experiment and only passively fixated the stimuli thus minimizing top–down influences. Second, the posterior MTG site was the only region across the whole brain where the activation followed the subjects’ perception, whereas attentional mechanisms modulate activity throughout the visual cortex (O’Craven et al. 1999; Ress et al. 2000). Third, the posterior MTG is distinct from occipitotemporal regions involved in the control of attention (Gitelman et al. 1999; Corbetta and Shulman 2002), nor is it a component of the right temporoparietal network involved in reorienting attention (Corbetta et al. 2002) (Fig. 8). Both the dorsal and the ventral attention networks involve several additional cortical regions (Corbetta and Shulman 2002), which were not activated in the present study. The lack of activation in the dorsal control system fits with the passive conditions, as pointed out above. The lack of activation in the ventral control system suggests that reorienting of attention was also not required, probably because our conditions were presented in a block design, and the reaching occurred at similar locations in space.

Finally, the pSTS regions are clearly distinct from the temporoparietal junction, which has been proposed to be specifically involved in theory of mind (for review, see Saxe 2006). Although evaluating the rationality of an action may be necessary to attribute intentional states such as goals or desires to others (and developmental studies also suggest this to be the case, Wellman and Brandone 2009), the regions involved in rationality evaluation and in theory of mind are quite distinct from one another (Fig. 8). Thus, the main cognitive component underlying the MTG activation in our study is the evaluation of action rationality.

Our MTG site is located in close proximity to the pSTS-A site described by Saxe et al. (2004) as activated by the observation of intentional actions (Fig. 8). This site was identified in a paradigm in which a walker disappeared behind a screen and either reemerged immediately or remained hidden for a longer period of time. As in our study, intentionality arose as a combination of a kinematic element (speed of walking) with a contextual element (duration of disappearance behind the screen), and, like our MTG activation, their focus is located well within the regions responsive to human kinematics (Fig. 8). Thus, both sites reflect a visual computation, integrating the kinematics of an observed action with another visual element in the display or scene that physically constrains the action. Both sites were also very specific: each was the sole activation in the entire brain for the contrast of interest and both were shown to be involved in the integration of kinematics and context in a series of control experiments. In both our and the study of Saxe et al. (2004), there was an explicit contextual element in the display, different from the object goal of the action or from the observer: the barrier and the occluder. There is, however, one important difference between the 2 studies: we did manipulate the barrier height, while only one occluder width was used in the Saxe study. Therefore, our study provides more compelling evidence that nonrational behavior arises from the integration of kinematics and physical constraints.

In a number of studies, it has been shown that context modulates the activity of STS regions (Allison et al. 2000; Pelphrey and Morris 2006), but context was an object that was a possible target of the action (Pelphrey, Singerman, et al. 2003; Pelphrey, Morris, McCarthy 2004), an observer (Pelphrey, Viola, et al. 2004), or was an emotional context provided by the facial expression of the actor (Vander Wyk et al. 2009). These studies are using the notion of relevant context in a broader sense, which allows us to generalize our findings: in all these studies, the context, whether in a broader or narrower sense, is relevant in so far as it contributes to build up a prediction about which action is appropriate for goal attainment. The pSTS regions are activated when these predictions are violated. Thus, these STS regions do not only analyze the kinematics of the body and body part movements (Grezes et al. 2004; Jastorff and Orban 2009) but also integrate these biological motion cues with the relevant context in the visual display. This integration provides information about the actors’ intention, both socially and in terms of goal directness, as previously pointed out (Pelphrey and Morris 2006). Our study indicates that the integration also provides information about the mental characteristics of the actor: whether he/she acts rationally, as a normal human being would do, or nonrationally as a demented patient might do. In the previous studies, goal-directed action and rational goal-directed actions were confounded because there was no situational constraint in the display. These aspects were disentangled in our study by the introduction of the barrier. That the STS signals the characteristics not only of the action but also of the actor fits nicely with other studies showing that STS regions also signal the emotions of the actor (Pichon et al. 2008).

Conclusion
Our results, together with those of Saxe et al. (2004), clearly indicate that the initial assessment of the rationality or efficiency of an observed action is a purely visual computation. Processing in the STS is only a first step toward a full understanding of an observed action (Woodward and Sommerville 2000), and the signals related to actions of the subjects’ own repertoire (Buccino et al. 2004; Calvo-Merino et al. 2006) may be further processed in the inferior parietal lobule, particularly for the chaining of motor acts into a more global action (Fogassi et al. 2005) or for the distinction between different types of actions (Jastorff et al. 2010). By demonstrating, however, that rationality of others’ behavior is initially assessed in a visual MTG region, we open up the possibility of exploring this cognitive function in single-cell studies since fMRI studies in the monkey using a similar paradigm (Vanduffel et al. 2001) could indicate the equivalent visual cortical area from which to record.
Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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References


