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Perceived Animacy Influences the Processing of Human-Like Surface Features in the Fusiform Gyrus

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Abstract

While decades of research have demonstrated that a region of the right fusiform gyrus (FG) responds selectively to faces, a second line of research suggests that the FG responds to a range of animacy cues, including biological motion and goal-directed actions, even in the absence of faces or other human-like surface features. These findings raise the question of whether the FG is indeed sensitive to faces or to the more abstract category of *animate* agents. The current study uses fMRI to examine whether the FG responds to all faces in a category-specific way or whether the FG is especially sensitive to the faces of animate agents. Animate agents are defined here as intentional agents with the capacity for rational goal-directed actions. Specifically, we examine how the FG responds to an entity that looks like an animate agent but that lacks the capacity for goal-directed, rational action. Region-of-interest analyses reveal that the FG activates more strongly to the animate compared with the inanimate entity, even though the surface features of both animate and inanimate entities were identical. These results suggest that the FG does not respond to all faces in a category-specific way, and is instead especially sensitive to whether an entity is animate.

Keywords

animacy detection; face processing; goal-directed actions; fusiform; posterior superior temporal sulcus; fMRI

> The human perceptual system is tuned to rapidly identify animate agents in the environment. This may be an adaptive mechanism to ensure in-depth processing and engagement with social partners, entities that have the capacity for thoughts, feelings, and intentional actions.

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Cues signaling animacy can be grouped into roughly three categories, which include (1) human-like surface features, such as faces and limbs (Baron-Cohen, 1995; Carey & Spelke, 1996; Guajardo & Woodward, 2004); (2) biological motion, such as self-propelled motion (Baron-Cohen, 1995; Leslie, 1994, 1995; Premack, 1990), non-rigid transformation (Gibson, Owsley, & Johnston, 1978), and the ability to react contingently and reciprocally with other entities (Premack, 1990); and (3) rational goal-directed actions - actions that are purposeful and efficient given the constraints of the surrounding environment (Csibra, Bíró, Koós, & Gergely, 2003; Csibra, Gergely, Bíró, Koós & Brockbank, 1999; Gergely & Csibra, 2003).

While these cues typically co-occur in the natural world and are inherently linked (animate agents have a human form, move in biologically plausible ways, and engage in rational goaldirected behavior) they are often studied in isolation in experimental settings. Research examining the neural correlates of animacy perception has typically focused on localizing the processing of specific animacy cues presented in isolation, such as static faces or pointlight displays of biological motion, to particular brain regions. Most notably, faces and biological motion have been localized to the right fusiform gyrus (FG) (Puce, Allison, Gore, & McCarthy, 1995) and right posterior superior temporal sulcus (pSTS) (Allison, Puce, & McCarthy, 2000), respectively. The FG has been found to respond more strongly to faces compared with scrambled faces and other complex objects (Haxby et al., 1994; Kanwisher, McDermott, & Chun, 1997; Puce et al., 1995; Sergent, Ohta, & Macdonald, 1992). The right pSTS is not only sensitive to biological motion but is also involved in reasoning about the intentions underlying actions (Pelphrey, Morris, & McCarthy, 2004; Pelphrey, Singerman, Allison, & McCarthy, 2003; Shultz & McCarthy, 2012). For instance, this region exhibits increased activation when participants observe a human actor perform a reaching motion that is inconsistent with an implied goal or implausible given the structure of the surrounding environment, compared to actions that are consistent with an implied or plausible goal (Pelphrey et al., 2004).

Despite the localization of particular functions, such as processing faces and intentions underlying biological motion, to the FG and pSTS, respectively, there is evidence that *both* brain regions are actually involved in processing both types of information. The clearest demonstration of the functional similarity between the FG and pSTS comes from a recent study that directly compared activation maps from two large data sets, designed to localize face-sensitive and biological motionsensitive regions of cortex (Engell & McCarthy, 2013). This study revealed highly similar patterns of activation, including activation of the fusiform and the pSTS, in response to both classes of stimuli. In addition, both regions activate when animacy is conveyed via a range of cues, including human-like movements (Gobbini et al. 2011), human-like interactions (Schultz et al., 2003; Gobbini et al. 2007; Castelli et al., 2000), contextual cues (Wheatley, Milleville, & Martin, 2007), and goal-directed actions (Shultz & McCarthy, 2012). Critically, FG and pSTS activation in response to these cues can be elicited even in the absence of faces and other human-like surface features (Shultz & McCarthy, 2012; Wheatley, Milleville, & Martin, 2007; Schultz et al., 2003; Gobbini et al., 2007; Castelli, 2000) or biologically-plausible motion (Shultz & McCarthy, 2012). The substantial overlap in the response profiles of the FG and pSTS to faces and biological motion and their sensitivity to a range of animacy cues raises questions about whether these

regions actually respond to faces and biological motion in a category-specific way, or whether these regions may be sensitive to the more abstract category of animate agents.

One study has provided direct evidence indicating that the FG prioritizes the detection of *animate* faces over global facial form (Looser, Guntupalli, & Wheatley, 2012). Multivariate pattern analysis revealed that while the configuration of a face was sufficient to activate the FG, this region was especially sensitive to faces perceived as 'alive' or animate. Specifically, the FG prioritized the detection of animate faces (real human and dog faces) compared to inanimate faces (life-like mannequin and toy dog faces).

In the present study we further examine whether the FG is especially sensitive to the faces of animate agents or whether the FG responds to all faces in a category-specific way. While previous work has examined this question by manipulating the animacy of a face via perceptual features (i.e. real life human face versus a life-like face) (Looser et al., 2012; Looser & Wheatley, 2010; Wheatley, et al., 2011), we chose to manipulate a different cue for animacy – the ability to act in a way that is purposeful and rational given the constraints of the surrounding environment. Specifically, we examine how the FG responds when the actions of an entity suggest that they are inanimate, *despite* the presence of human-like facial features. If the FG responds to faces in a category-specific way then the FG should activate to an entity with facial features, regardless of whether that entity demonstrates the capacity for rational, goal-directed behavior. However, if the FG is especially sensitive to the faces of animate agents then the FG should respond more strongly to entities that engage in rational, goal-directed behavior.

Materials and Methods

2.1 Participants

Twenty participants (7 female, 13 male, average age = 25.2 years, all right-handed) with normal vision and no history of neurological or psychiatric illness participated in this study. All participants gave written and informed consent and the Yale Human Investigations Committee approved the protocol.

2.2 Stimuli

Stimuli consisted of movie clips of two computer-animated avatar characters. Both avatars had human-like surface features (faces and body limbs) and moved in biologically plausible ways. The key manipulation was whether the avatar performed purposeful and rational actions (characteristics diagnostic of a minded agent), referred to henceforth as the 'rational' avatar, or whether the avatar demonstrated an inability to behave rationally and purposefully (characteristics diagnostic of an inanimate entity), referred to henceforth as the 'irrational' avatar. Each avatar was shown in two scenarios for a total of 4 movie clips. In both scenarios, the implied goal of the rational and irrational avatars was the same but the avatars differed in their capacity for rational action. In the first scenario the rational avatar walked toward a brick wall, turned towards an opening in the wall, and walked through the opening. By contrast, the irrational avatar walked into the wall repeatedly without adjusting its trajectory (see Figure 1a for example still frames). In the second scenario, the rational avatar

walked towards a cardboard box, bent down, and picked up the box. By contrast, the irrational avatar walked directly to the left of the box, bent down, and performed a lifting motion as though they were lifting up the box (see Figure 1b for example still frames). These scenarios were chosen to convey that the irrational avatar lacked a mind or the capacity to behave intentionally. Critically, the important distinction between the rational and irrational avatar is not simply that the irrational avatar failed to complete an implied goal but rather that the types of actions or errors that were made are not of the type that we would expect from an animate agent. For instance, if an animate agent attempted to pick up an object but missed, we might expect them to adjust their reach or simply stop making a lifting motion. Similarly, if an animate agent approached an obstacle in their path we might expect them to move around it, move the object, stop, or turn around. The actions of the irrational avatar (performing a lifting motion to completion even though they were not holding an object and repeatedly walking into a wall without changing their trajectory) were designed to be inconsistent with our expectations about how a minded agent should behave.

Behavioral ratings of the perceived animacy of the rational and irrational avatars obtained from an independent sample of adults confirmed that the rational avatar was perceived as more animate than the irrational avatar (Z=-4.39, *p*<.001; please see Supplemental Materials for details). Further, eye-tracking data collected from the independent sample of adults revealed no difference in overall percent fixation on the rational and irrational avatar clips and no difference in percent fixation on the face of the rational and irrational avatar $(F_{1,15}=$. 029, $p=.87$ and $F_{1,15}=1.5$, $p=.24$, respectively). Percent time spent fixating on the body of the rational compared with the irrational avatar was marginally significant ($F_{1,15}=4.0$, $p =$. 06; please see Supplemental Materials for additional details and for a discussion of these results).

2.3 Experimental Design

The four movies (2 per condition) were presented over the course of 2 runs. The movie depicting avatars walking towards the wall was 5 seconds long, while the movie depicting avatars walking towards to the box was 3 seconds long. The presentation of successive movies was separated by a randomly chosen 2, 4, or 6 second rest period. Movies were presented in pseudorandom order such that participants always viewed the 'rational' version of each scenario at least one time before viewing the 'irrational' version to ensure that the implied goal was clear. Importantly, the identity of the rational and irrational avatar was counterbalanced across participants. For half of the participants the female avatar was rational and the male avatar was irrational. For the other half of the participants the male avatar was rational and the female avatar was irrational. As such, any difference in brain activation to the rational and irrational avatars cannot be due to surface features alone. Sixteen movies per condition were played in each run. Participants were instructed to pay attention to the stimuli at all times.

A secondary aim of this study was to examine whether any differential brain response to the rational and irrational avatar movie clips persisted when participants later viewed static faces of these same avatars. To address this question, participants viewed the static faces of the avatars both before and after viewing the movie clips. Each face was presented 30 times

for 1 second and was separated by a 2, 4, or 6 second rest period. We predicted no difference in brain response to the rational and irrational avatar static faces prior to viewing the movie clips. However, we predicted that brain regions involved in animacy detection, such as the FG, would respond more strongly to the rational compared with the irrational avatar static faces after viewing the movie clips.

2.4 Image Acquisition and Preprocessing

Brain images were acquired at the Magnetic Resonance Research Center at Yale University using a 3.0T TIM Trio Siemens scanner with a 12-channel head coil. Functional images were acquired using an echo planar pulse sequence (repetition time $|TR| = 2$ s, echo time [TE] = 25 ms, flip angle = 90° , matrix = 64^2 , field of view [FOV] = 224 mm, slice thickness $= 3.5$ mm, 36 slices). Two sets of structural images were acquired for registration: coplanar images, acquired using a T_1 Flash sequence (TR = 300 ms, TE = 2.47 ms, flip angle = 60°, $FOV = 224$ mm, matrix = 256^2 , slice thickness = 3.5mm, 36 slices); and high-resolution images acquired using a 3D MPRAGE sequence (TR = 2530, TE = 2.4 ms, flip angle = 9° , FOV = 256 mm, matrix = 256^2 , slice thickness = 1mm, 176 slices).

Analyses were performed using the FMRIB Software Library (FSL, [http://](http://www.fmrib.ox.ac.uk/fsl) [www.fmrib.ox.ac.uk/fsl\)](http://www.fmrib.ox.ac.uk/fsl). All images were skull-stripped using FSL's brain extraction tool. The first 4 volumes (8 seconds) of each functional data set were discarded to diminish MR equilibration effects. Data were temporally realigned to correct for interleaved slice acquisition and spatially realigned to correct for head motion using FSL's MCFLIRT realignment tool. Images were spatially smoothed with a 5mm full-width-half-maximum isotropic Gaussian kernel. Each time series was high-pass filtered (0.01 Hz cutoff) to eliminate low-frequency drift. Functional images were registered to structural coplanar images, which were then registered to high-resolution anatomical images and then normalized to the Montreal Neurological Institute's MNI152 template.

2.5 fMRI Data Analysis

Whole-brain voxelwise regression analyses were performed using FSL's fMRI expert analysis tool (FEAT). Each condition within each preprocessed run was modeled with a boxcar function convolved with a single-gamma hemodynamic response function. The model included explanatory variables for the factor of interest: animacy (rational, irrational).

Group-level analyses were performed using a mixed-effects model with the random effects component of variance estimated using FSL's FLAME stage 1+2 procedure. For both first and higher level analyses, clusters of active voxels were identified using FSL's 2-stage procedure to correct for multiple comparisons. Voxels were first thresholded at an entry level of $z = 2.3$ and the significance of the resulting clusters were then evaluated at a corrected $P < .05$ using a Gaussian random field (GRF) approach.

2.6 Region of Interest Analyses

Additional analyses were conducted to study the time course of activation differences between the rational and irrational condition during the movie clips in an independently localized region of the FG. The region of interest (ROI) was defined in a two-stage process.

First an anatomical region of interest was created for the right FG on the cortical surface of a standard brain, as in Engell & McCarthy (2013). Next, we used a probabilistic atlas for face perception, developed from a large-scale ($n = 124$) fMRI localizer task designed to isolate regions of functional selectivity for faces, to further constrain the ROI using functional criteria (Engell & McCarthy, 2013). The probabilistic atlas represents, at each voxel, the percentage of participants who show a category-specific response to faces (defined by a zscore of $\,$ 1.65 for the face localizer contrast). Within the anatomical ROI we selected all voxels with P (the probability that a participant shows a category-specific response to faces at that specific voxel) > .55, which yielded a cluster of 81 $2 \times 2 \times 2$ mm voxels (peak coordinates: $x = 44$, $y = -48$, $z = -22$). A P of .55 was chosen to maximize the spatial extent of the ROI corresponding to the FG without merging with more posterior ventral face areas corresponding to the occipital face area (Gauthier et al., 2000). The mean signal-averaged time course for each condition (rational and irrational) was then calculated for the FG ROI for each participant and was statistically compared by conducting a paired-samples t-test on the peak percent signal change.

Results

3.1 Brain Activation During Viewing of the Movie Clips

The whole-brain contrast for rational > irrational revealed activation in the right precentral gyrus, bilateral postcentral gyrus and superior parietal lobule, bilateral lateral occipital cortex, bilateral occipital fusiform cortex, lingual gyrus, and temporal fusiform cortex (see Figure 2). Active clusters in temporal fusiform cortex did not overlap with face-sensitive portions of fusiform cortex. Peak coordinates of significant clusters from the rational > irrational contrast are given in Table 1.

The whole-brain contrast for irrational > rational revealed an expansive cluster of activation in right temporoccipital cortex (see Figure 3). This region extended dorsally to the supramarginal gyrus, and the posterior continuation and ascending limb of the pSTS and ventrally to the middle temporal gyrus and lateral occipital cortex. Activation was also observed in the left supramarginal gyrus, superior temporal sulcus, superior and middle temporal gyrus, and lateral occipital cortex. Peak coordinates of significant clusters from the irrational > rational contrast are given in Table 2.

Given our a priori prediction that the FG would respond more strongly to the rational compared to the irrational avatar, we examined the time course of the fMRI signal averaged for each voxel within the FG ROI for each condition. A paired-samples t-test conducted on peak percent signal change within the FG ROI revealed a significant main effect of condition ($t(19)=3.3, P<.01$), indicating that the FG responded more strongly to the rational (animate) compared with the irrational (inanimate) avatar (see Figure 4).

3.2 Brain Activation During Viewing of Static Faces

We did not expect to find any active clusters for any contrast of static faces seen prior to viewing the movie clips, given that the identity of faces as rational or irrational was not revealed during this portion of the experiment. Further, which face would later be conveyed

as rational or irrational in the movie clips was counterbalanced across participants. Unexpectedly, the irrational > rational contrast revealed activation in bilateral precuneus cortex, a finding that we interpret as being a Type 1 error.

No significantly active clusters were observed for the rational > irrational contrast of static faces presented after the movie clips. Given our a priori prediction that the FG would respond more strongly to the rational compared to the irrational avatar, we examined the time course of the fMRI signal averaged for each voxel within the FG ROI for each condition. A paired-samples t-test conducted on peak percent signal change within the FG ROI revealed a significant main effect of condition (t $(19)=$ -2.85, $P < .05$), indicating that the FG responded more strongly to the irrational (inanimate) compared with the rational (animate) static avatar face (see Figure 5).

The inanimate > animate contrast revealed activation in the right frontal pole and middle frontal gyrus. No activation was observed in the pSTS or FG for either whole-brain contrast.

Conclusions

These results suggest that the FG and the pSTS do not respond to all faces or biological motion in a category-specific way, and are instead especially sensitive to whether an entity is animate. A region of interest analysis revealed that the FG responded more strongly to human-like stimuli whose actions were purposeful and rational given the constraints of the surrounding environment compared to humanlike stimuli that acted in an irrational, nonintentional manner. Consistent with previous studies, the pSTS showed the opposite pattern, responding more strongly to the avatar that behaved irrationally compared with the avatar that behaved rationally.

These findings are consistent with those reported by Looser et al. (2011) demonstrating that the FG prioritizes the processing of animate over inanimate entities. The present study corroborates and extends these findings by demonstrating that the FG activates more strongly to animate compared with inanimate entities, even when the surface features of both animate and inanimate faces are identical. Despite these consistencies, Looser et al. (2011) found increased sensitivity to animate faces in the FG when using multivariate pattern analysis but not when examining differences in average magnitude levels within an FG ROI using standard GLM. By contrast, the present study found a differential response to animate and inanimate entities using standard GLM region-of-interest analysis. This difference may have been partially driven by the way ROIs were defined. In Looser et al. (2011) the FG ROI included voxels that were more active for at least one class of faces (human, doll, real dog, or toy dog) compared with clocks, whereas the present study defined the FG ROI on the basis of a large-scale probabilistic atlas defined by a contrast of human faces versus scenes. Given that voxels within ventral temporal cortex ROIs may contain distinct but spatially proximate or even overlapping representations, different approaches for defining ROIs may yield different results (Looser et al., 2011).

The present results also suggest that the capacity for rational action plays a critical role in modulating activation in brain regions involved in detecting and reasoning about animate

agents and their intentions. While perceptual cues alone, such as human-like surface features or biological motion, are sufficient to activate regions involved in animacy detection (Shultz & McCarthy, 2012; Engell & McCarthy, 2013), the current results indicate that FG activation to these cues is attenuated when accompanied by clear evidence that the entity lacks the capacity for rational action. By contrast, previous work has shown that the FG and pSTS activate in response to entities that engage in rational goal-directed actions, even when these entities clearly do not have human-like surface features or act in biomechanically impossible ways (Shultz & McCarthy, 2012; Gobbini et al., 2007; Castelli et al., 2000; Schultz et al., 2003; Wheatley, Milleville, & Martin, 2007). Thus, while human-like surface features, biological motion, and rational goal-directed actions may all be sufficient to engage brain regions involved in animacy detection, the potential for rational action may be a *necessary* cue for strongly activating the FG. Prioritizing the capacity for rational action as a cue for animacy may confer an advantage, as rational actions are likely to be a more stable diagnostic marker of animacy compared to featural or motion cues which can be distorted, altered or perhaps even unfamiliar.

Like the FG, the pSTS also differentiated between the animate and inanimate avatar movie clips. However the pattern of differential activation was reversed with the pSTS responding more strongly to the irrational compared with the rational avatar. This result is consistent with previous research indicating that the pSTS activates more strongly to actions that are incongruent with an implied goal or implausible given the context within which the action occurs (Brass, Schmitt, Spengler, & Gergely, 2007; Pelphrey et al., 2004). While this is a well-replicated finding, questions remain regarding the mechanism underlying the increase in response to actions that violate expectations about how an entity should behave. One interpretation is that the human-like surface features of the avatar establish an expectation that the avatar is animate and should therefore behave rationally and intentionally. When these expectations are violated, the observer must revise or reconcile their expectations, a process which demands continued processing of the observed action sequence. While this may be a plausible explanation, it is important to note that the FG did not respond to these conflicting cues in the same manner. Rather, region of interest analyses indicated that the FG actually responded more strongly to the rational avatar whose surface features and actions provided converging evidence for animacy. What then, might account for the dissociation in the response of the FG and the pSTS?

The relationship between the response of the FG and the pSTS is interesting to consider in the context of a neural model for animacy detection recently proposed by our laboratory (Shultz & McCarthy, 2012; Shultz et al., 2014). The model posits that three processing streams are initially differentially sensitive to cues signaling animacy (human-like surface features, biological motion, and rational goal-directed action) but that information about animate agents is then shared across streams for further processing. As a consequence of such sharing, any one cue signaling animacy is sufficient to activate all nodes of the proposed network. According to the model, the FG is part of the processing stream that is specialized for detecting human-like surface features, while the pSTS is part of a processing stream for detecting biological motion and integrating information about underlying

intentions. A third stream, involving parietal areas such as the supramarginal gyrus and superior parietal lobule, is posited to play a role in detecting intentions.

A key prediction of this model is that the directional flow of activation between these processing streams initially depends on the characteristics of the particular stimulus presented. In a recent study (Shultz et al., 2014) we provided evidence for this key prediction using Dynamic Causal Modeling, a measure of effective connectivity. We demonstrated that viewing static faces activates the FG, which then drives activation in the pSTS. By contrast, viewing point-light displays of biological motion activates the pSTS, which then drives activation in the FG. Importantly, while the FG is initially differentially sensitive to faces and drives activation in the pSTS, its activity then becomes influenced by feedback from the pSTS. Similarly, while the pSTS is initially differentially sensitive to biological motion and drives activation in the FG, its activity then becomes influenced by feedback from the FG. Thus, although these regions are initially functionally selective for either faces or biological motion, this selectivity is transient as information is shared bidirectionally across processing streams.

Extending this model to the context of the current experiment offers a potential explanation for the differential response of the FG and pSTS to rational and irrational avatars. According to the model, viewing the face of the rational avatar may have initially driven activation in the FG. Activation in the pSTS, driven by both feedforward connections from the FG and by the presence of biological motion and goal-directed actions, may have fed back into the FG, resulting in greater FG activation. This hypothesized causal flow of activation may have been delayed or disrupted in the case of processing the irrational avatar. The unexpected actions of the irrational avatar may have required additional processing by the pSTS thereby disrupting or delaying feedback into the FG and resulting in less FG activation. Future studies using measures of effective connectivity are required to test these claims.

Finally, counter to our initial predictions, when static faces of the avatars were presented following the movie clips the FG responded more strongly to the irrational compared with the rational avatar. While this finding requires further replication, one possibility may be that the current pattern of results reflects neural adaptation or carry-over effects from the movie clips that differentially influenced the processing of the rational and irrational avatar static faces. For instance, the stronger response in the FG to the rational compared with the irrational avatar movie clips may reflect greater encoding of the rational avatar by the FG. The decreased response in the FG during subsequent viewing of the static face of the rational avatar may reflect adaptation to the rational avatar's face. By contrast, the increased response in the FG during subsequent viewing of the static face of the irrational avatar may reflect the lack of encoding of the irrational avatar by the FG during the movie clips. One implication of these findings is that the experience of viewing conflicting information about the animacy of an entity does not subsequently influence how that agent is processed when later viewed in the absence of conflicting cues. However, the findings during viewing of the static faces were not predicted and require further replication.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

- FG and pSTS do not show a category-specific response to faces or biological motion

- ROI analysis reveals increased FG activation to entities that look *and* act animate

- The pSTS shows the reverse pattern, activating more to conflicting animacy cues

Figure 1. Example still frames from movie clips

(A) The rational character (on left) walked towards the wall, turned towards the opening, and continued walking. The irrational character (on right) repeatedly walked into the wall without adjusting his motion trajectory. (B) The rational character (on left) walked towards the box, bent down, and picked it up. The irrational character (on right) walked to the left of the box, bent down, and performed a lifting motion as though they were lifting the box. The identity of the rational and irrational characters was counterbalanced across participants.

Activation is displayed on a cortical surface representation. The color ranges from *z* = 2.3 to *z* = 5.0.

Figure 3. Activation map for the Irrational versus Rational contrast

Activation is displayed on a cortical surface representation. The color ranges from *z* = 2.3 to $z = 4.1$.

Figure 5. ROI analysis results for the FG: percent signal change during static presentation of faces shown after the movie clips

Percent signal change averaged across voxels in the independently identified FG ROI (pictured in top right) for the rational (blue) and irrational (red) conditions. There is a significant difference in the peak percent signal change in response to the rational (animate) compared with the irrational (inanimate) condition. Stimulus presentation begins at 0s.

Table 1

Peak Coordinates (in MNI space) from the Rational versus Irrational contrast.

Table 2

Peak Coordinates (in MNI space) from the Irrational versus Rational contrast.

