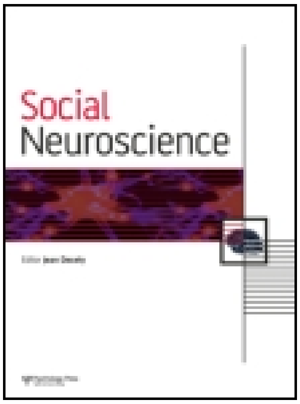

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Getting a grip on other minds: Mirror neurons, intention understanding, and cognitive empathy

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Getting a grip on other minds: Mirror neurons, intention understanding, and cognitive empathy

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We have previously shown that a right inferior frontal mirror neuron area for grasping responds differently to observed grasping actions embedded in contexts that suggest different intentions, such as drinking and cleaning (Iacoboni, Molnar-Szakacs, Gallese, Buccino, Mazziotta, & Rizzolatti, 2005). Information about intentions, however, may be conveyed also by the grasping action itself: for instance, people typically drink by grasping the handle of a cup with a precision grip. In this fMRI experiment, subjects watched precision grips and whole-hand prehensions embedded in a drinking or an eating context. Indeed, in the right inferior frontal mirror neuron area there was higher activity for observed precision grips in the drinking context. Signal changes in the right inferior frontal mirror neuron area were also significantly correlated with scores on Empathic Concern subscale of the Interpersonal Reactivity Index, a measure of emotional empathy. These data suggest that human mirror neuron areas use both contextual and grasping type information to predict the intentions of others. They also suggest that mirror neuron activity is strongly linked to social competence.

The ability to understand the intentions of others is an important aspect of human social interaction. We are just beginning to acquire knowledge on the neural circuitry that allows us to understand the actions of others. The discovery of mirror neurons, neurons that fire when an action is performed or when the same action is observed, have stimulated research on the topic. Mirror neurons were first described with single-unit recordings in the ventral premotor cortex of the monkey brain (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti & Craighero, 2004; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), and now mirror neuron activity has also been shown with fMRI in humans (Grezes, Armony, Rowe, & Passingham, 2003; Iacoboni, Woods, Brass, Bekkering, Mazziotta, & Rizzolatti, 1999; Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005). Mirror neurons provide a mechanism by which we can understand the actions of others by mapping the actions of other people onto our own motor system, thus allowing a shared representation of actions. Activating our own motor representation could allow us also to activate motivations and intentions that are associated with those actions. This ‘‘resonance’’ with another individual can also be viewed as a form of empathy. Not only do we understand what are the goals of another person, but we experience their intention and therefore their emotion when we watch them behave.

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However, understanding intention involves more than simply identifying a movement. Actions are embedded in a context that provides clues to the actor's goal. For instance, a man reaching for a chocolate bar probably intends to eat it. However, if the man reaching for the chocolate bar is in front of a conveyor belt at a chocolate bar factory, it may be obvious that his intention is not to eat. If mirror neurons are involved in assigning intention, they should be sensitive to the context in which an action occurs.

Recently, Iacoboni et al. (2005) found that at least some human mirror neuron areas do seem to take context into account. In an fMRI study, subjects were shown videos of a hand grasping a teacup. The backdrop of the scene provided the context: either a breakfast scene ready to be eaten or an already eaten breakfast asking to be cleaned up. In other conditions the grasp occurred with no backdrop, i.e., no context, or a context was shown with no action. In a comparison of the ''intention'' conditions (when an action was embedded in context that cued a specific intention) compared with the others (action out of context or context alone) revealed significantly greater signal changes in the right inferior frontal gyrus, specifically in the dorsal part of the pars opercularis. This area is well known for its mirror neuron properties (Iacoboni et al., 1999; Molnar-Szakacs et al., 2005) The mirror neurons in this area then, seem to be sensitive to the presence of information about intention.

While context provides information about intention, it is not the only source of such information. Additional clues as to what a person intends to do can be found in *how* they do it. For example, the type of grip one uses to grasp a cup when drinking may be different from the type of grip used to remove the cup from the table for cleaning purposes. Early work on mirror neurons in monkeys found that many neurons responded to specific types of grasps (Gallese et al., 1996). In fact, the stimuli used in the Iacoboni et al. study did include two grips: a precision grip where the fingers grasp the handle of the teacup and a whole-hand prehension where the hand reaches around the whole cup. Due to the blocked design used in that study, however, it was not possible to discern how the type of grip used interacted with the specific context.

The present study uses the same stimuli in a single-trial design to investigate how the two types of information affect activity in mirror neuron areas. We focus our analysis on the right inferior frontal gyrus. If mirror neurons here are sensitive to intention, their activity should be modulated by whether the grip type and context point to the same intention. For example, when a precision grip is made in a drinking context, both sources of information point to the person intending to drink. When a whole-hand grasp is made in a drinking context, there is conflicting information. We predicted that mirror neurons in the inferior frontal gyrus would be sensitive to the congruency between intention cues. Furthermore, if mirror neuron activity in this region reflects the degree to which we identify and understand the intentions of others, then the activity may reflect an individual's ability to empathically resonate with others. To investigate this, we administered an empathy scale to each of our subjects.

METHOD

Subjects

Twenty-two subjects participated in this experiment (9 men, 13 women), mean age 26 ± 6 years. All participants were right-handed and were screened to rule out medication use, head trauma, history of neurological or psychiatric disorders, substance abuse, or other serious medical conditions. Subjects gave informed consent according to the guidelines of the UCLA Institutional Review Board.

Stimuli and procedure

The stimuli consisted of a series of 3-second video clips. Each video clip began with a set of three-dimensional objects against a blue background. The ''context'' of the clip consisted of a background scene in one of three configurations. The ''drinking context'' showed a breakfast scene with a plate of cookies, a teapot, and some jars. In the center of the scene is a full, steaming cup of tea. In the ''cleaning context'', the breakfast has clearly been eaten already, leaving a dirty scene of crumbled cookies, crumpled napkins, and an empty cup of tea. In the ''no context'' clips, the mug of tea appears alone against the blue background. After 1 second, the action portion of the clip begins when a hand reaches in and grasps the cup. This portion of the clip had two variations: a ''precision grip'' condition in which the hand grasps the cup by its handle, using a precision grip and a "whole-hand prehension" condition in which the hand grasps the cup around its body using the whole hand. In two additional video clips the context was shown for a full 3 seconds with no hand appearing at all ("context only" condition). Examples are shown in Figure 1.

There was a total of eight video types: drinking context only, cleaning context only, precision grip only, whole-hand prehension only, precision grip in drinking context, whole-hand prehension in drinking context, precision grip in cleaning context, whole-hand prehension in cleaning context. The precision grip in drinking context and whole-hand prehension in cleaning context conditions are the congruent action–context conditions, since people tend to grasp the cup by its handle with a precision grip when they drink and also tend to grasp the cup by its body with a whole-hand prehension when they clean up, although less consistently in the latter case. Following this logic, the whole-hand prehension in drinking

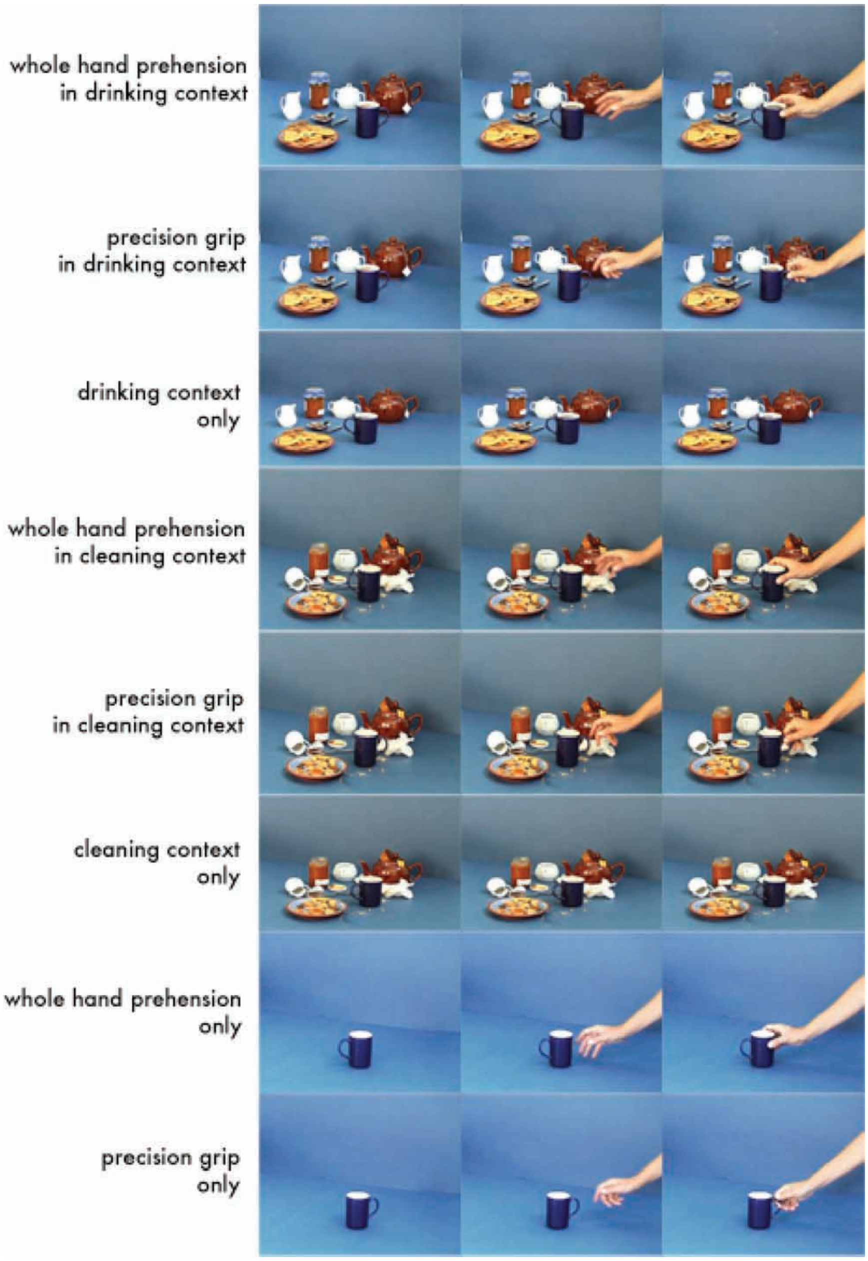

Figure 1. The video stimuli. Eight types of video clips were shown, each lasting three seconds.

context and the precision grip in cleaning context conditions are the incongruent action–context conditions.

After an initial rest period of 12 seconds, each clip was shown three times during a functional scan in random order, with a random interval between 12 and 14 seconds between each clip. During the rest periods a fixation cross appeared on the screen. Subjects were instructed simply to watch and pay attention to the video clips, and each subject completed three functional runs which lasted 7 minutes and 4 seconds. Thus, this was a passive viewing design with no behavioral response required.

Image acquisition

Images were acquired using a Siemens Allegra 3.0 T MRI scanner. For each functional scan we acquired 210 EPI volumes (gradient-echo, TR = 2000, TE = 25, flip angle = 90°), each with 36 transverse slices, 3 mm thick, 1 mm gap, and a 64 × 64 matrix yielding an in-plane resolution of 3 × 3 mm. Two sets of high-resolution anatomical images were also acquired for registration purposes. We acquired an MP-RAGE structural volume (TR = 2300, TE = 2.93, flip angle = 8°) with 160 sagittal slices, each 1 mm thick with 0.5 mm gap and 1.33 × 1.33 mm in-plane resolution. We also acquired a T2-weighted co-planar volume (TR = 5000, TE = 33, flip angle = 90°) with 36 transverse slices covering the whole brain, each 3 mm thick with 1 mm gap, a 128 × 128 matrix and an in-plane resolution of 1.5 × 1.5 mm.

Empathy questionnaire

After scanning, each subject completed the Interpersonal Reactivity Index (IRI; Davis, 1983). This questionnaire is a commonly used empathy scale, which measures both "cognitive" and "emotional" empathy. There are 28 items which are broken down into four subscales of 7 items each. Cognitive empathy is measured by the Perspective Taking (PT) scale, which measures the ability to imagine another person's perspective, and the Fantasy scale (FS) which measures the tendency to imagine oneself in the place of fictional characters in books or movies. The two emotional scales are the Empathic Concern (EC) scale for the emotions of others and the Personal Distress (PD) scale, which measures the emotional response one experiences when watching someone else experience strong emotion. The IRI is a well-tested scale showing high convergent and discriminant validity (Yarnold, Bryant, Nightingale, & Martin, 1996).

Data processing and statistical analysis

Analysis was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.1, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). After motion correction (Jenkinson, Bannister, Brady, & Smith, 2002), images were temporally high-pass filtered with Gaussian-weighted LSF straight line fitting (sigma = 25.0 s) and smoothed using an 8 mm Gaussian FHWM algorithm in three dimensions.

We modeled the BOLD response using a separate explanatory variable (EV) for each of the eight categories of video. For each stimulus type, the presentation design was convolved with a gamma function to produce an expected BOLD response. The temporal derivative of this time course was also included in the model for each EV. Functional data were then fitted to the model using FSL's implementation of the general linear model.

Each subject's statistical data were then warped into a standard space based on the MNI-152 atlas. We used FLIRT to register the functional data to the atlas space in three stages (Jenkinson et al., 2002; Jenkinson & Smith, 2001). First, functional images were aligned with the high-resolution co-planar T2-weighted image using a 6 degrees of freedom rigid-body warping procedure. Next, the co-planar volume was registered to the T1-weighted MP-RAGE using a 6 degrees of freedom rigid-body warp. Finally, the MP-RAGE was registered to the standard MNI atlas with a 12 degrees of freedom affine transformation.

After analyzing the functional runs for each subject in a fixed-effects model, data for each subject were passed into a higher-level random effects analysis. Higher-level analysis was carried out using FLAME (FMRIB's Local Analysis of Mixed Effects; Behrens, Woolrich, & Smith, 2003). Z (Gaussianized T/F) statistic images were thresholded using clusters determined by $Z > 2.3$ and a (corrected) cluster significance threshold of $p = .05$ (Forman, Cohen, Fitzgerald, Eddy, Mintun, & Noll, 1995; Friston, Worsley, Frakowiak, Mazziotta, & Evans, 1994; Worsley, Evans, Marrett, & Neelin, 1992).

Since our hypotheses involved specific questions about the right posterior inferior frontal mirror neuron area, we performed further analysis of this region. Using the voxels that were significant in the Iacoboni et al. (2005) paper, we created a region of interest (ROI) in the right posterior inferior mirror neuron area and computed percent signal change from baseline within this ROI for each of the eight video types for each subject. The location of this ROI is depicted in Figure 2. It is centered in the dorsal section of the pars opercularis of the inferior frontal gyrus, and extends posteriorly into the ventral premotor cortex. The peak voxel activated in the previous study was located at (46, 20, 22).

RESULTS

While subjects completed three functional scans each, they reported experiencing fatigue and distraction by the third run due to the repetitive nature of the experimental procedure. Many of these third runs also showed unacceptable levels of motion. As a result, we restricted our analysis to the first two functional runs for each subject.

Whole brain analysis

Task versus rest. This analysis looked at overall activity while watching the video clips compared to resting baseline. Results revealed widespread signal changes throughout the brain, including the occipital cortex, parietal and frontal premotor regions, and the posterior inferior frontal gyrus on the right side. This pattern of activity was also observed in our previous study (Iacoboni et al., 2005). The location of the right posterior inferior frontal gyrus activation also overlapped completely with the activation observed in the previous study (Iacoboni et al., 2005). Significant signal changes in inferior frontal cortex are shown in Figure 2.

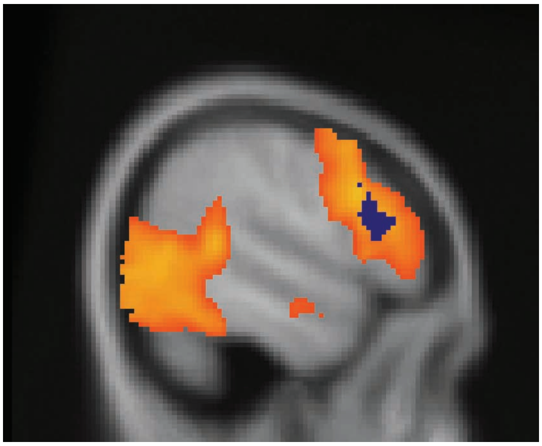

Figure 2. Brain regions with significant signal changes watching all videos compared with rest in the present study are shown in yellow/orange. In blue is the right inferior frontal gyrus ROI from the Iacoboni et al. (2005) study, which showed intention-related activity in that study. All of the voxels in this ROI were also active in the present study.

Region of interest (ROI) analysis

Intention versus action. This analysis (shown in Figure 3) compared clips that contained an action in context with clips showing actions without any context. Comparing percent signal change from baseline in our right inferior frontal ROI from the previous experiment we found significantly greater signal for the action in context clips ($p < .05$), replicating the effect observed in our previous study (Iacoboni et al., 2005).

Congruent versus incongruent action-context clips. This analysis (see Figure 4) compared the clips with a grip that is congruent with the context (precision grip in drinking context and whole-hand prehension in cleaning context) versus clips with a grip that is incongruent with the context (whole-hand prehension in drinking context and precision grip in eating context). Comparing percent signal change from baseline in our ROI from the previous experiment (Iacoboni et al., 2005) we did not find any statistical differences when we collapsed across the two contexts. However, we did find significantly greater signal in the congruent condition in the drinking context, where a precision grip produced a higher signal change than whole-hand prehension ($p < .05$ in a paired sample t-test). This pattern was not present in the cleaning context. This may be due to the overall higher signal change for precision grip compared to whole-hand prehension. Such higher signal for observed precision grips compared to observed whole-hand prehensions mimics the higher signal observed in right inferior frontal gyrus for executed precision grips compared to executed whole-hand prehensions in right-handers (Ehrsson, Fagergren, Jonsson, Westling, Johansson, & Forssberg, 2000).

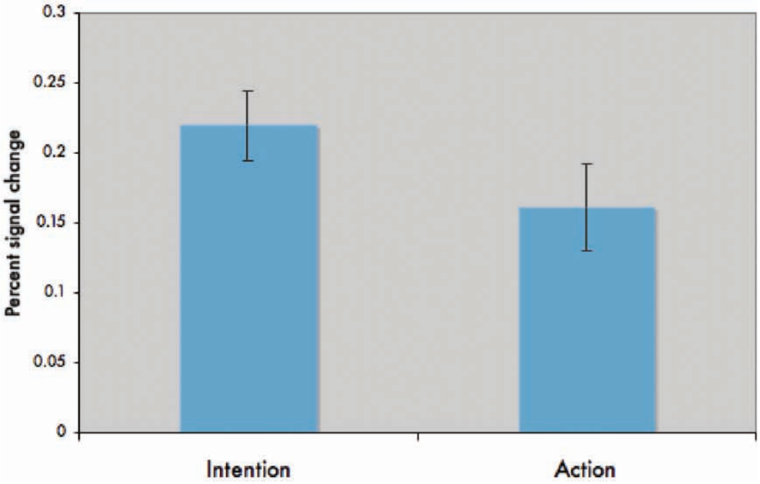

Figure 3. Percent signal change in right inferior frontal gyrus was significantly greater for the intention clips (actions seen in context) compared to the action clips (actions seen without a context). Signal changes shown here were calculated within the region of interest derived from Iacoboni et al., 2005.

Correlations with empathy scale. When we looked at signal changes within the right inferior frontal gyrus in our a priori ROI, we found that percent signal change correlated with some subscales of the empathy scale during certain conditions. The Fantasy scale (FS) correlated with signal changes during the incongruent clips ($r = .42$, $p < .05$) and during the context alone clips ($r = .44$, $p < .05$). The Empathic Concern (EC) scale correlated with signal changes in the incongruent conditions ($r = .43$, $p < .05$), the contexts alone ($r = .40$, $p < .05$), the actions out of context ($r = .36$, $p < .05$) and with average signal across all clips ($r = .45$, $p < .05$). The relationship between EC scores and overall activity during the video clips is shown in Figure 5. The Personal Distress scale (PD) correlated negatively with congruent action clips ($r = -.60$, $p < .01$), and with actions in context ($r = -.41$, $p < .05$).

DISCUSSION

The current study replicates with a different experimental design the results of our previous study (Iacoboni et al., 2005). A purely visual task of observing grasping actions and graspable objects activate ventral premotor regions, including a right posterior inferior frontal mirror neuron area that responds differently to the

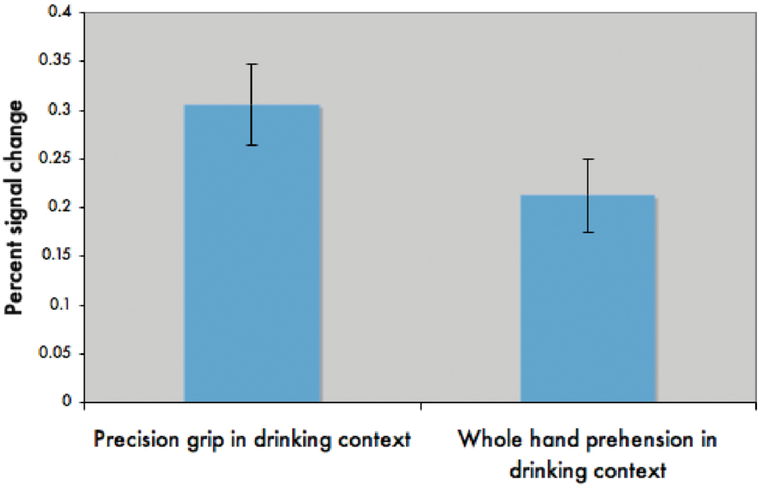

Figure 4. Percent signal change in the right inferior frontal gyrus was significantly greater watching clips with a precision grip in the drinking context compared to watching the whole-hand prehension in the drinking context. Signal changes shown here were calculated within the region of interest derived from Iacoboni et al., 2005.

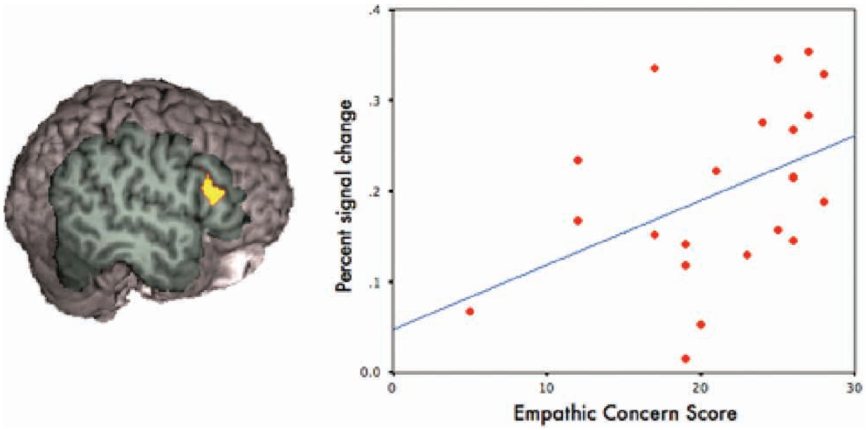

Figure 5. Scores on the empathic concern subscale of the Interpersonal Reactivity Index significantly correlated with activity in right inferior frontal gyrus. Shown here is the relationship between EC score and average signal change across all video clips in our a priori region of interest.

same grasping action embedded in contexts suggesting different intentions. The two novel results shown by this study are the synergy between the type of grasp observed and the type of context in which the action occurs, and the correlation between empathy ratings in our subjects and inferior frontal mirror neuron activity.

In the current study we found that in the drinking context, the activity of the right inferior frontal mirror neuron area was greater when the type of grasp suggested the same intention as the context. This finding, albeit novel, is also in line with the previous study (Iacoboni et al., 2005). Indeed, we argued that the increased activation in the right posterior inferior frontal mirror neuron area in the intention condition was not simply due to the action being seen in *any* context, but rather to a specific context that conveyed a specific intention. In the present data, the effect of grip was present for the drinking context but not for the cleaning context, confirming that the right inferior frontal mirror neuron activity depends upon the presence of a specific, meaningful context. It is also no surprise that the expected effect was observed in the drinking context. The intention ‘‘to drink’’ may be easier to recognize as it is tied to basic motivations and specific sensory experiences. The cleaning action is also different from drinking in that it is not necessarily always performed in the same way. Cleaning is not always a direct consequence of grasping a cup with a whole-hand prehension, whereas grasping the handle of a teacup with a precision grip almost always indicates drinking. It could be argued that the congruency effect we observed is not specific to action observation, but reflects a response to the congruency information in general. Since our experiment only used action stimuli we can not rule out this possibility, but given the role of this brain region in action observation, we believe that the modulation by context reflects a process specific to action understanding.

We also found a relationship between signal changes in the right posterior inferior frontal mirror neuron area and several measures of empathy across our subject population. The FS scale measures the tendency of subjects to identify with characters in fictional situations. Along with the PT scale, it is considered a measure of cognitive empathy. For example, one representative item in this scale reads: ‘‘When I watch a good movie, I can very easily put myself in the place of a leading character.’’ The ability to take the perspective of a character in a movie is clearly relevant to the experience of watching the grasping actions in our experiment. Interestingly, higher scores on this scale were associated with increased activity during the incongruent intention clips. If activity in this region is indeed reflective of processing intentions, this result may suggest that more empathic individuals spend more effort to determine the intention of the actor in the clip when it is not clearly suggested by the context.

The EC scale showed correlations with IFG activity overall. This scale measures emotional empathy, the tendency to feel the emotions of another. A representative statement from the scale is: ‘‘Sometimes I feel very sorry for other people when they are having problems.’’ The positive relationship between emotional empathy and IFG activity makes sense if information about someone's intentions is also informative about their emotional state. In other words, one way to access the emotional state of another person may be through analysis of their intentions. These correlational data are consistent with data from a study on imitation and observation of facial emotional expression in children (Pfeifer, Iacoboni, Mazziotta, & Dapretto, 2006), where all the subscales of the Interpersonal Reactivity Index except the PT correlated with mirror neuron activity during observation of facial emotional expressions. The fact that the same neural system maps well on emotional and cognitive forms of intention understanding in different tasks and different age groups suggests a central role of the human mirror neuron system in social competence. The only difference between the current experiment's results and the study of facial emotions in children is that we found a negative relationship between personal distress (PD) and signal changes while watching the action clips. The PD scale measures how distressed people become when facing emotional situations. For example, one item says: ''When I see someone who badly needs help in an emergency, I go to pieces.'' We found that lower PD scores were associated with increased signal in the IFG while watching action clips. It may be that people who are sophisticated in understanding the intentions of others also feel confident in their ability to handle situations that require empathy.

The laterality of the posterior inferior frontal activation observed here and in our previous study mimics the laterality of posterior inferior frontal activity during executed grasping actions in right-handers (Ehrsson et al., 2000). When right-handers grasp three-dimensional objects with their dominant hand, the ipsilateral inferior frontal cortex is activated (Ehrsson et al., 2000). Similarly, when right-handers imitate finger movements in a controlled lateralized study (Aziz-Zadeh, Koski, Zaidel, Mazziotta, & Iacoboni, 2006), the ipsilateral inferior frontal cortex is activated for right and for left fingers movements. In the current study, right-handed subjects are simply watching grasping actions performed with the right hand and they activate the right inferior frontal area they would activate if they were actually performing those actions with their own right hand. These data clearly seem to map well onto a simulation model of intention understanding.

It has been argued that if one looks at the type of behavioral errors made by children when they reason about others' beliefs, a simulation account cannot readily explain the behavioral data (Saxe, 2005). Unfortunately, the lack of neural data correlating with the behavioral errors made while reasoning about others' beliefs makes it difficult to compare our results with those behavioral errors. At any rate, we do not intend to make sweeping claims about the role of the mirror neuron system in all forms of understanding of the mental states of others. However, we believe that the data presented here suggest that the mirror neuron system supports a simulation-based form of the intentions of others while they perform everyday goal-oriented actions. Moreover, the functions of the mirror neuron system seem to map well onto important forms of social competence in adulthood, such as cognitive empathy.

REFERENCES

Aziz-Zadeh, L., Koski, L., Zaidel, E., Mazziotta, J., & Iacoboni, M. (2006). Lateralization of the human mirror neuron system. *Journal of Neuroscience*, *26*(11), 2964–2970.

Davis, M. (1983). Measuring individual differences in empathy: Evidence for a multidimensional approach. *Journal of Personality and Social Psychology*, *44*, 113–126.

Ehrsson, H., Fagergren, A., Jonsson, T., Westling, G., Johansson, R. S., & Forssberg, H. (2000). Cortical activity in precision- versus power-grip tasks: An fMRI study. *Journal of Neurophysiology*, *83*, 528–536.

Forman, S. D., Cohen, J. D., Fitzgerald, M., Eddy, W. F., Mintun, M. A., & Noll, D. C. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magnetic Resonance Medicine*, *33*(5), 636–647.

Friston, K. J., Worsley, K. J., Frakowiak, R. S. J., Mazziotta, J. C., & Evans, A. C. (1994). Assessing the significance of focal activations using their spatial extent. *Human Brain Mapping*, *1*, 214–220.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*(2), 593–609.

Grezes, J., Armony, J. L., Rowe, J., & Passingham, R. E. (2003). Activations related to ''mirror'' and ''canonical'' neurones in the human brain: An fMRI study. *Neuroimage*, *18*(4), 928–937.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology*, *3*(3), e79.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, *286*(5449), 2526–2528.

Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved optimization for the robust and accurate linear registration and motion correction of brain images. *Neuroimage*, *17*(2), 825–841.

Jenkinson, M., & Smith, S. (2001). A global optimisation method for robust affine registration of brain images. *Medical Image Analysis*, *5*(2), 143–156.

Molnar-Szakacs, I., Iacoboni, M., Koski, L., & Mazziotta, J. C. (2005). Functional segregation within pars opercularis of the inferior frontal gyrus: Evidence from fMRI studies of imitation and action observation. *Cerebral Cortex*, *15*(7), 986–994.

Pfeifer, J., Iacoboni, M., Mazziotta, J. C., & Dapretto, M. (2006). *Mirror neuron system activity correlates with empathy and interpersonal competence in children.* Manuscript submitted for publication.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Reviews of Neuroscience*, *27*, 169–192.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Research: Cognitive Brain Research*, *3*(2), 131–141.

Saxe, R. (2005). Against simulation: The argument from error. *Trends in Cognitive Sciences*, *9*(4), 174–179.

Woolrich, M. W., Behrens, T., Beckmann, C. F., Jenkinson, M., & Smith, S. M. (2004). Multilevel linear modelling for FMRI group analysis using Bayesian inference. *NeuroImage*, *21*, 1732–1747.

Worsley, K. J., Evans, A. C., Marrett, S., & Neelin, P. (1992). A three-dimensional statistical analysis for CBF activation studies in human brain. *Journal of Cerebral Blood Flow and Metabolism*, *12*(6), 900–918.

Yarnold, P., Bryant, F. B., Nightingale, S. D., & Martin, G. J. (1996). Assessing physician empathy using the interpersonal reactivity index: A measurement mode and cross-sectional analysis. *Psychological Health Medicine*, *1*, 207–221.