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Short Report

The Well-Tempered Social Brain

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Philosophers defined empathy as the process of understanding another by placing ourselves into another person's place for a "shared experience" (Gallese, 2003). Mirror neurons, which respond during the observation and execution of actions, have been linked to empathy because understanding another often begins with understanding the actions of another (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Gallese, 2003). Functional magnetic resonance imaging (fMRI) studies of humans have found that the inferior parietal lobe and frontal operculum are activated during the observation and execution of actions and, thus, form a putative human mirror neuron system (hMNS; Iacoboni et al., 1999; Montgomery & Haxby, 2008). Although a relationship between empathy and hMNS activity has been suggested (Gazzola, Aziz-Zadeh, & Keysers, 2006; Shulte-Rüther, Markowitsch, Fink, & Piefke, 2007), it is unclear whether the hMNS is more active in individuals with higher empathy in general or whether the hMNS is more selectively tuned to social actions that convey information important for perspective-taking as compared to actions that have little social relevance. We decided to test, using fMRI, whether the hMNS is selectively tuned to socially relevant actions and whether empathic ability rests on a well-tuned hMNS, rather than on an hMNS that is simply more responsive.

EXPERIMENT

To find the distribution of empathy scores in our sample of undergraduate students at Princeton University, we gave the Interpersonal Reactivity Index (Davis, 1983) to 208 participants. The average perspective-taking score for women was 18.14 (SD = 1.57) and for men was 17.14 (SD = 1.95). Because perspective-taking scores for women were significantly higher than those for men ($p < .01$), the scores were divided based on gender. We defined low and high perspective taking as more than 1.5 standard deviations lower or higher than the average score, respectively. A total of 42 participants, 14 each (7 female, 7 male) with low, average, and high perspective-taking scores, participated in the experiment.

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During the fMRI experiment, participants viewed, imitated, and produced social facial expressions or nonsocial facial movements. Social facial expressions are expressions used during social interactions (e.g., happiness, anger, surprise), whereas nonsocial facial movements are typically overlooked in social interactions (e.g., blinking, chewing, sneezing). For each participant, we obtained five time series for social facial expressions and nonsocial facial movements. During each time series, there were three conditions. In the viewing condition, participants passively viewed the video clips. During the imitation condition, participants imitated the expressions or facial movements that they saw in the video clip. Finally, during the production condition, participants saw a word or phrase describing the expressions or facial movements and produced the action described. Participants practiced the task outside the scanner to ensure accurate performance.

MRI scanning was performed using a 3-T head scanner (Allegra, Siemens, Erlangen, Germany) with a standard bird-cage head coil. Functional images were taken with a gradient echo echoplanar imaging (EPI) sequence (repetition time = 1,500 ms; echo time = 30 ms; field of view = 192 mm; flip angle = 80°; 64 × 64 matrix). Twenty-five contiguous, axial slices that covered most of the brain were used (thickness = 3 mm; gap = 1 mm; in-plane resolution = 3 × 3 mm). For each time series, a total of 184 EPI volume images were acquired. A high-resolution anatomical scan of the whole brain (T1-MPRAGE; repetition time = 2,500 ms; echo time = 4.3 ms; flip angle = 8°; 256 × 256 matrix) was acquired in the same session for anatomical localization and spatial normalization.

A random-effects analysis of variance was performed using AFNI to obtain group results (Cox, 1996). We identified regions that were activated significantly by the perception and production of actions based on the response during imitation, using a threshold of $p < .001$ (uncorrected) and a cluster size of 540 mm^3. For the analyses of time course of responses, anatomically defined volumes of interest (VOI) were drawn on high-resolution structural images to identify the inferior parietal lobe and frontal operculum. Within these VOIs, voxels that were significantly responsive to any of the experimental conditions, as determined by an omnibus general linear test ($p < .0001$), were identified in each individual.

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In the full group, we found significant activation in the hMNS for socially meaningful facial expressions and nonsocial face movements (Fig. 1). Among participants with average and high perspective-taking scores, passive viewing of socially relevant facial expressions evoked significantly greater activation in the frontal operculum than did viewing of nonsocial facial movements (Fig. 1). By contrast, passive viewing of facial expressions and nonsocial facial movements evoked equivalent frontal opercular activation in participants with low perspective-taking scores (Fig. 1). We did not observe this same pattern in the imitation and production conditions, which involve the execution of the actions.

CONCLUSION

Our results suggest that the predisposition and capacity to take the perspective of others is associated with preferential tuning of

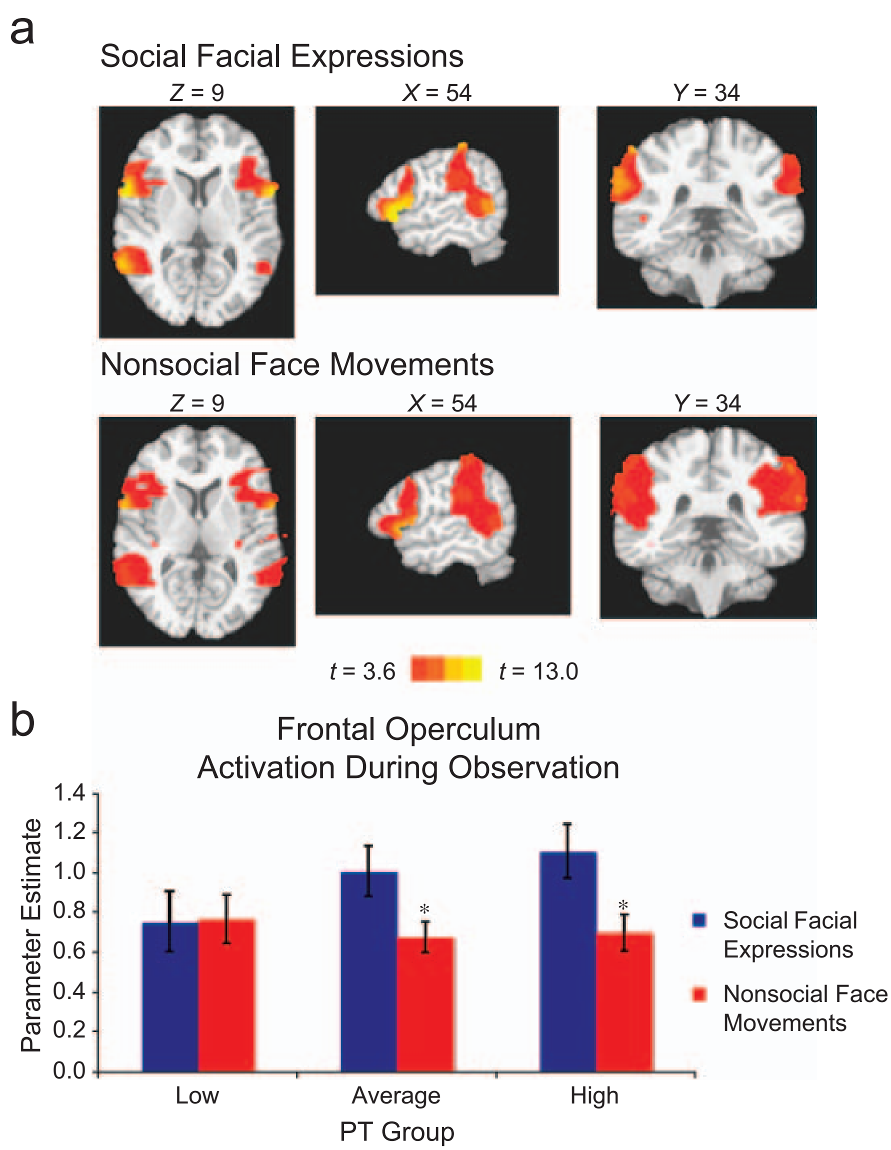

Fig. 1. Areas of significant activity in the human mirror neuron system and parameter estimates for frontal operculum activation as a function of perspective-taking (PT) group and facial expression. The images (a) show areas of significant activation during the observation, imitation, and production of social facial expressions (upper row) and nonsocial face movements (lower row) as compared to baseline activity ($p < .001$, uncorrected for multiple comparisons; cluster size = 540 mm^3). Group data ($N = 42$) from a mixed-effects analysis of variance have been overlaid on a single participant's high-resolution anatomical scan. The bar graph (b) shows the average peak parameter estimates of activity in the frontal operculum during observation for the three perspective-taking groups. The error bars show standard errors of the mean. Asterisks indicate a significant difference in activity between observation of social facial expressions and observation of nonsocial face movements ($p < .01$).

the hMNS for socially informative actions. Empathy was not associated with differential recruitment of the hMNS for the perception of nonsocial facial movements. Interestingly, empathy also was not associated with differential recruitment of the hMNS in conditions in which participants produced facial movements. Rather, empathy was associated with socially tuned spontaneous activation of motor representations only during perception, when such activation was not explicitly required.

Our results suggest that the predisposition to take the perspective of others is associated with selective tuning of the hMNS to simulate socially informative facial movements. It is possible that this tuning reflects greater selective attention to movements that are socially interesting. The effect of attention, however, would also modulate activity in perceptual regions, such as the superior temporal sulcus, and in regions associated with attention, especially the intraparietal sulcus. Empathy was not associated with greater response to facial expressions in these regions, suggesting that attention cannot account for our results. Rather, empathy appears to be related to the development of an hMNS that is engaged selectively to simulate actions that are most informative for understanding the mental states of others.

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