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Familiarity Modulates Mirror Neuron and Mentalizing Regions During Intention Understanding

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Abstract: Recent research suggests that the inference of others' intentions from their observed actions is supported by two neural systems that perform complementary roles. The human putative mirror neuron system (pMNS) is thought to support automatic motor simulations of observed actions, with increased activity for previously experienced actions, whereas the mentalizing system provides reflective, non-intuitive rea-

INTRODUCTION

How do we efficiently infer other's intentions by observing their actions? Recent research indicates that intention understanding engages two complementary systems: the putative human mirror neuron system (pMNS) and the mentalizing system [de Lange et al., 2008; Hesse et al., 2009; Keysers and Gazzola, 2007; Uddin et al., 2007]. The pMNS, composed of motor-related brain regions in the inferior frontal gyrus (IFG) and inferior parietal lobule (IPL), is activated both when an individual makes an action and when he or she observes another person make the same action [Aziz-Zadeh et al., 2006; Gallese et al., 1996; Rizzolatti and Craighero, 2004]. It has been proposed that mapping observed actions onto one's own motor representations supports motor simulations of an observed action, allowing the observer to then predict others' intentions [Gallese et al., 2004; Iacoboni et al., 2005; Rizzolatti and Craighero, 2004]. In contrast, the mentalizing system is composed of regions in the medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), and the bilateral temporal-parietal junctions (TPJ), and is thought to be involved in non-intuitive reflections of others' mental states [Fletcher et al., 1995; Frith and Frith, 2006; Saxe and Powell, 2006; Saxe, 2006]. These regions have been linked to perspective-taking and tend to be activated by a conscious effort to infer others' intentions, across a variety of stimuli including stories, cartoons, and images of others [Frith and Frith, 2006; Gallagher et al., 2000; Saxe and Kanwisher, 2003].

A recent meta-analysis [Van Overwalle and Baetens, 2009] revealed that pMNS regions tend to be active when observing biological movement, with stronger activity when observing familiar actions for which one has a pre-existing motor representation [Calvo-Merino et al., 2005; Cross et al., 2006; Van Overwalle and Baetens, 2009]. In contrast, mentalizing regions are activated for higher level goal inferences, regardless of the presence of visual biological stimuli, and tend to be active in the absence of existing motor representations, such as during observation of movements that are unplanned, out-of-context, or biomechanically impossible [Brass et al., 2007; Kilner and Frith, 2008; Liepelt et al., 2008; Van Overwalle and Baetens, 2009]. Thus, the existing body of research suggests that these systems serve complementary roles, with mentalizing regions more active during novel contexts and pMNS regions more active during familiar contexts [Van Overwalle and Baetens, 2009].

Although the task of understanding others' actions is heavily social in nature, little is known about how social factors affect the contributions and interactions of pMNS and mentalizing regions. Prior research has demonstrated that one's race, culture, religion, and even political affiliation can modulate cognitive and sensorimotor processing during passive observation [Han and Northoff, 2008; Serino et al., 2009; Xu et al., 2009]. However, to date, no studies have explored how these powerful factors modulate neural activity when asked to infer intentions from observed human movements.

The current functional magnetic resonance imaging (fMRI) study manipulated two critical factors related to familiarity (perceptual familiarity with the race of the actor, motor familiarity from experience with the action) during the task of inferring an actor's intentions. The aim was to understand the specific contributions of individual regions within the pMNS and mentalizing systems when perceptual and motor familiarity with the stimuli are manipulated. In order to explore the social influences on action understanding in these two neural systems, the current study utilized symbolic, or intransitive, gestures (e.g., thumbs up), which are learned and familiarized through one's cultural experiences [Archer, 1997]. As these gestures require an integration of visuomotor representations with abstract intentions, they have been shown in separate studies to activate regions of both pMNS [Skipper et al., 2009; Straube et al., 2009; Villarreal et al., 2008] and mentalizing networks [Gallagher and Frith, 2004].

There is sparse existing research on how perceptual familiarity modulates action understanding. In the current study, we examined the effect of perceptual familiarity on action understanding by manipulating the race of the actors used in the stimuli (Chinese, Caucasian). To this end, we recruited Chinese individuals living in mainland China who have limited exposure to, and thus less perceptual familiarity with, Caucasian individuals compared to Chinese individuals. For the sake of clarity, in this article, we refer to this factor related to perceptual familiarity specifically as "race," while experience with an action (motor familiarity) will be referred to simply as "familiarity." However, we acknowledge that the construct of race may also include many other factors not explored here, most notably, in-group/out-group effects, and that these larger constructs related to race should be further studied using a design comparing participants from two or more racial groups.

Previous studies on the effects of race on the pMNS demonstrate conflicting evidence, with two transcranial magnetic stimulation (TMS) studies revealing opposite results: one demonstrated increased corticospinal excitability during observation of actors of one's own race versus a different race [Molnar-Szakacs et al., 2007], whereas the other found a reverse pattern [Desy and Theoret, 2007]. In support of the former results, an fMRI study showed greater activation in regions associated with the pMNS for more physically similar others than physically dissimilar others [Buccino et al., 2004a]. In addition, there is increased activity in mentalizing regions when observing the eyes of one's own race versus the eyes of another race, suggesting increased higher level processing of one's own race [Adams et al., 2009]. Notably, these same-race effects may also be due to one's increased perceptual familiarity with one's own race compared to another race. We thus hypothesized that observation of same-race individuals, who are more perceptually familiar than different-race individuals, ought to evoke stronger activity in regions

Figure 1.
Examples of still images of the stimuli. Participants observed 2-s videos of familiar gestures (left panel), unfamiliar gestures (middle panel), and control still images (right panel). Each gesture and still image was performed by an actor of the participants' own race (Chinese) and an actor of a different race (Caucasian). Original videos were presented in full color.

associated with both motor simulation and mentalizing than observation of different-race individuals.

Furthermore, research on passive observation of familiar or unfamiliar actions suggests that experience with the action increases pMNS activity for one's own expert skilled actions, such as expert dancers watching their own dance form versus an unfamiliar dance form [Calvo-Merino et al., 2005; Cross et al., 2006]. On the other hand, passive observation of actions that are biomechanically impossible or that do not make sense within a context has been associated with increased activation in mentalizing regions [e.g., turning on a light-switch with one's knee when one's hands are free versus when one's hands are occupied; Brass et al., 2007; Kilner and Frith, 2008; Liepelt et al., 2008]. Thus, we hypothesized that observations of familiar gestures, which are within one's own motor repertoire, would be easier to simulate and thus more strongly involve pMNS regions, while observations of unfamiliar gestures, which lack an existing motor representation and may require additional reasoning capabilities, would more strongly involve mentalizing regions.

MATERIALS AND METHODS

Participants

Eighteen healthy Chinese adults (10 males and 8 females, 18–30 years of age, mean ± SD = 23.0 ± 2.28), born in and living in China, were recruited in this study. Participants were scanned while observing familiar and unfamiliar gestures performed identically by two actors, one Caucasian and one Chinese. All participants were right-handed, had normal or corrected-to-normal vision, and had no neurological or psychiatric history. Written informed consent was obtained from all participants before inclusion in the study. This study was approved by a local ethics committee and the University of Southern California Institutional Review Board and was performed in accordance with the 1964 Declaration of Helsinki.

Stimuli

Action observation

The visual stimuli consisted of 2-s movie clips. Half of the clips depicted a Caucasian performing expressive hand gestures that were either familiar (i.e., thumbs up) or unfamiliar (i.e., "quail" in American Sign Language) with his right hand. The other half depicted a Chinese actor making identical gestures. Both actors were male, in their mid-20s, right-handed and of similar physical build. While performing gestures, actors maintained a neutral affect with gaze held directly forward and no additional eye movements to prevent provision of additional social cues. In addition, both actors were equally familiar or unfamiliar with the gestures they were asked to perform and rehearsed all gestures prior to filming. To assess the potential differences in familiarity with gestures performed by Chinese and Caucasian actors, in a separate behavioral study, we asked 64 Chinese participants to rate how familiar they were with the gestures performed by the actors using a 3-point Likert scale (1 = familiar, 3 = unfamiliar). We found that there were no significant differences between the gestures performed by Chinese and Caucasian actors; familiar gestures performed by the two actors were judged as being equally familiar (Chinese: 1.35 ± 0.24, Caucasian: 1.38 ± 0.28, $P = 0.43$) while unfamiliar gestures performed by both actors were judged as being equally unfamiliar (Chinese: 2.80 ± 0.09, Caucasian: 2.77 ± 0.11, $P = 0.51$). Still photos of some of the different stimuli are illustrated in Figure 1. Each actor was filmed completing six different familiar gestures and six different unfamiliar gestures, resulting in 12 clips per actor and 24 different clips total. A control for action observation consisted of a 2-s presentation of a still photo made from the first frame of the video clips (six stills per actor and 12 different stills total).

Action execution

A cue for action execution trials consisted of a stimulus with 500 ms of a black box outlined in red, followed by 1500 ms of the red outline around the still images used in control trials.

Task Design and Procedure

Action observation

Prior to scanning, to try to engage both the pMNS and mentalizing regions [de Lange et al., 2008], participants were instructed to observe the video clips as though the actors were performing the gestures directly to them and were asked to think about the actor's intentions in doing each gesture. Also, prior to scanning, they were shown still photos of both actors for 30 s each to become familiar with the actors' faces. They were finally instructed to actively infer the actor's intentions by attending to the actor's hand movements, rather than the actor's face, for the duration of the clips shown during the scanning session and were informed that they would be asked the meaning of each gesture immediately after the scanning session, as an additional motivation to actively think about the intentions of each gesture clip.

Action execution

Participants were instructed to rest their right hand next to, but not on, a button box. When cued by the red-outlined action execution stimuli, participants moved their hand to the button box, using their index fingers to repeatedly press the button for the duration of the clip.

General procedure and design

The video clips were presented through a projector onto a rear-projection screen located at the subject's head. Each movie clip subtended a visual angle of 21.4° × 17.1° at a viewing distance of 80 cm. Each condition was shown for 18 trials per run for three runs, for a total of 54 trials per condition, with the exception of the action execution condition, which was shown for nine trials per run for a total of 27 trials. All conditions, including action observation and action execution conditions, were combined and evenly distributed across three functional runs of 340 s (170 TRs) each. Following an event-related design, each run used an optimized random sequence generated in Optseq (http://surfer.nmr.mgh.harvard.edu/optseq/) with an interstimulus interval between successive clips that was jittered between 0 and 5 s, with a mean of 2 s. A schemata of the general design can be found in Figure S1.

Behavioral methods

Following scanning, subjects were shown the gesture stimuli on a computer outside the scanner and were asked to rate how familiar they were with each gesture, using a Likert-type scale where 1 indicated extremely unfamiliar and 10 indicated extremely familiar. They were also asked how positive/negative they felt each gesture was and what they thought each gesture meant, using a 3-point scale for positive, negative, or neutral for the former and an open response for the latter. Finally, they were asked to rate how much they liked each actor on a Likert-type scale where 1 indicated not liking the actor at all and 10 indicated liking the actor very much. These scores were later computed to ensure the stimuli were accurately perceived as either familiar or unfamiliar and positive or negative and to ensure both actors were similarly perceived. In addition, participants were given the Multigroup Ethnic Identity Measure (MEIM), a self-report measure designed to examine one's sense of ethnic identity [Roberts et al., 1999, modified from Phinney, 1992].

fMRI Image Acquisition and Analysis

Scanning was performed at Peking University First Hospital on a GE 3-T scanner with a standard head coil. Thirty-two transverse slices of functional images covering the whole brain were acquired using a gradient-echo echo-planar pulse sequence (64 × 64 × 32 matrix with a spatial resolution of 3.4 × 3.4 × 4.4 mm, repetition time = 2000 ms, echo time = 30 ms, FOV = 24 × 24 cm, flip angle = 90°). Anatomical images were obtained using a 3D FSPGR T1 sequence (256 × 256 × 128 matrix with a spatial resolution of 0.938 × 0.938 × 1.4 mm, TR = 7.4 ms, TI = 450 ms, TE = 3.0 ms, flip angle = 20°).

Imaging data was analyzed using SPM2 (Statistical Parametric Mapping 2; the Wellcome Department of Cognitive Neurology, London, United Kingdom) implemented in MATLAB (Mathworks, Sherborn, MA). The functional data were first time-corrected to compensate for delays associated with acquisition time differences between slices during the sequential imaging. The functional images were then realigned to the first scan to correct for head motion between scans. All six movement parameters (translation: x, y, z and rotation: pitch, roll, yaw) were included in the statistical model. The anatomical image was co-registered with the mean functional image produced during the process of realignment. All images were normalized to a 2 × 2 × 2 mm^3 Montreal Neurological Institute (MNI) template. Functional images were spatially smoothed using a Gaussian filter with the full-width/half-maximum parameter (FWHM) set to 8 mm. In addition, high pass temporal filtering with a cut-off of 180 s was applied. The event-related neural activity was modeled using a canonical hemodynamic response function (HRF) with temporal

TABLE I. Localization of brain activations from random effects analysis

Anatomical region	BA	*T*-Value	Cluster size	Coordinates [x, y, z]
		All Gestures > Still Photo		
L Inferior parietal lobule	**40**	**4.80**	**515**	**[−52, −32, 34]**
L Inferior frontal gyrus	**44**	**4.09**	**336**	**[−48, 10, 38]**
L V5/MT	18	11.86	1747	[−48, −70, 0]
R Fusiform gyrus	37	8.89	1867	[50, −58, −18]
R Superior parietal lobule	7	5.22	106	[32, −56, 60]
L Superior parietal lobule	7	5.17	156	[−26, −56, 64]
L Precentral gyrus	6	4.73	21	[−46, 2, 50]
R Posterior cingulate cortex	30/31	4.10	15	[6, −38, 12]
L Inferior frontal gyrus	44	4.09	26	[−48, 10, 38]
R Posterior superior temporal gyrus	22	3.93	10	[68, −34, 14]
		Same Race > Different Race		
R Insula		4.387	20	[38, −2, −6]
L Inferior parietal lobule	2	4.20	37	[−58, −22, 32]
		Different Race > Same Race		
L Middle occipital gyrus	19	5.64	57	[−28, −86, 2]
L Fusiform gyrus	37	4.61	95	[−32, −66, −16]
R Fusiform gyrus	37	4.36	20	[30, −78, −10]
		Familiar Gestures > Unfamiliar Gestures		
R Posterior cingulate cortex	**23**	**5.38**	**498**	**[6, −38, 32]**
L Temporoparietal junction	**39**	**4.85**	**334**	**[−50, −66, 38]**
L Dorsal medial prefrontal cortex	**32/9**	**4.09**	**421**	**[−4, 44, 26]**
R Temporoparietal junction	**39**	**3.56**	**267**	**[52, −68, 40]**
R Posterior cingulate cortex	23	7.39	178	[6, −34, 36]
L Lingual gyrus	17/18	6.02	505	[−4, −82, 2]
L Posterior cingulate cortex	31	5.38	113	[−4, −16, 48]
L Temporoparietal junction	39	4.85	101	[−50, −66, 38]
R Angular gyrus	40	4.36	33	[62, −54, 34]
L Middle frontal gyrus	10	4.30	35	[−28, 48, 26]
R Posterior cingulate cortex	23	4.17	19	[10, −4, 48]
L Dorsal medial prefrontal cortex	9	4.09	35	[−4, 44, 26]
R Calcarine gyrus	17	4.01	40	[14, −80, 14]
		Unfamiliar Gestures > Familiar Gestures		
L Inferior parietal lobule	**40**	**6.90**	**515**	**[−52, −30, 36]**
L Superior parietal lobule	7	10.25	1817	[−20, −70, 60]
L Middle occipital gyrus	19/18	9.09	484	[−38, −78, 4]
R V5/MT	18	7.75	671	[50, −72, 2]
L Thalamus		4.50	13	[−14, −28, 0]
L Superior frontal gyrus	6	4.23	9	[−20, −6, 68]
R Superior parietal lobule	7	4.16	54	[18, −66, 60]

A priori regions (in bold) reported at $P < 0.05$ FDR, whole brain results reported at $P < 0.001$ uncorrected at the voxel level, cluster threshold >8.

derivative. Effects at each voxel were estimated and regionally specific effects were compared using linear contrasts in individual participants using a fixed effects analysis.

A group-level random effects analysis was then conducted, taking into account between-subject variability [Penny et al., 2004]. A priori regions of interest (ROIs) for the PMNS (left IFG and IPL) and the mentalizing systems (dmPFC, PCC, bilateral TPJ) were defined independently of the current dataset to avoid circularity [Kriegeskorte et al., 2009]. Functional definitions were taken from two relevant papers on the pMNS [Buccino et al., 2004b] and mentalizing system [den Ouden et al., 2005], with the criteria that each paper contained activity from all ROIs within the given system and were well-cited within the field. We used a small volume correction with a mask defining the six regions with 10-mm radius spheres with centers at the peak activations from these papers. Results were reported at the $P < 0.\ 05$ level, FDR-corrected for multiple comparisons over the six ROIs, and with a cluster threshold of eight contiguous voxels (≥ 8). Non-apriori regions of significant activation were reported at the whole-brain level using a threshold of $P < 0.001$ (uncorrected) and a cluster threshold of eight contiguous voxels (≥ 8).

ROI analyses were then performed by extracting beta-values from group-level results within each of the previously defined 10 mm ROIs. A 2 × 2 repeated measures ANOVA was performed on each ROI with the factors of

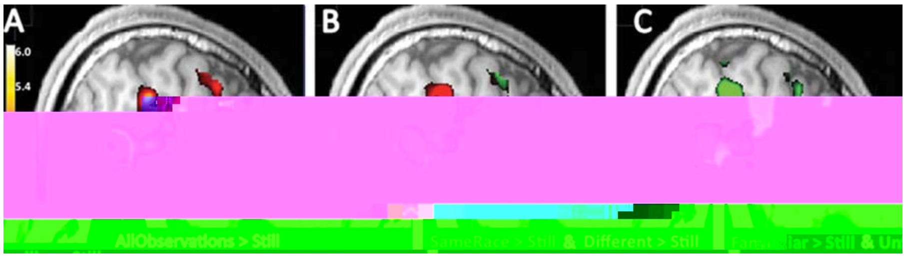

Figure 2.

Brain responses to observations of gestures versus still images (all images displayed at $P < 0.001$ uncorrected for visualization purposes; $x = -51$). **A**: Observation of all gestures across familiarity and races versus still images evoked greater activity in components of the pMNS [the left dorsal inferior frontal gyrus (IFG) and dorsal premotor cortex and inferior parietal lobule (IPL)], as well as the posterior superior temporal sulcus (pSTS) and posterior cingulate cortex (PCC; not shown). **B**: Observation of the same race versus still (red) evoked activity in the left IPL and pSTS, while observation of a different race versus still (green) evoked activity in the left dorsal premotor cortex and pSTS. **C**: Observation of familiar gestures versus still images (red) evoked greater activity in the left pSTS, while unfamiliar gestures versus still images (green) evoked activity in dorsal IFG, IPL, and pSTS.

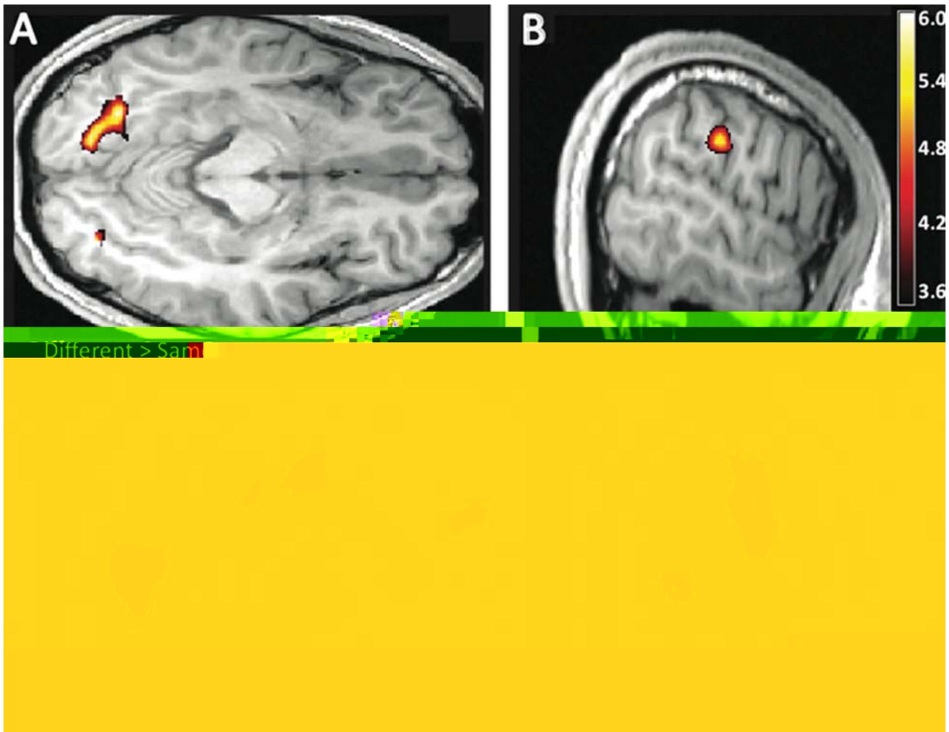

Figure 3.

Race-driven and experience-driven brain responses (all images displayed at $P < 0.001$ uncorrected for visualization purposes). **A**: Observations of another race versus one's own race (DifferentRace > SameRace) evoked greater activity in the occipital cortex bilaterally in the fusiform gyrus and middle temporal gyrus (area V5/MT; not shown; $z = -11$). **B**: Observations of one's own race versus another race (SameRace > DifferentRace) evoked greater activity in the left IPL and right posterior insula (not shown; $x = -59$). **C**: Observations of familiar gestures versus unfamiliar gestures (Familiar > Unfamiliar) evoked greater activity in the dorsal medial prefrontal cortex (dMPFC), the posterior cingulate (PCC), the cuneus, and the bilateral temporoparietal junctions (not shown), regions associated with mentalizing and reasoning processes ($x = -4$). **D**: Observations of unfamiliar gestures versus familiar gestures (Unfamiliar > Familiar) evoked greater activity in the left IPL and postcentral gyrus and the bilateral middle temporal gyri (area V5/MT) in the putative extrastriate body area (EBA; $x = -53$).

familiarity and race using the R statistical package [Ihaka and Gentleman, 1996], and results were subjected to a Bonferroni correction for multiple comparisons.

RESULTS

Behavioral Results

Participants rated gestures from the category "familiar gestures" as significantly more familiar than gestures from the category "unfamiliar gestures" (familiar: 9.40 ± 1.27; unfamiliar: 3.17 ± 1.96; $P < 0.001$). Participants also accurately identified all familiar gestures and were unable to accurately identify any of the unfamiliar gestures. Participants also rated half of the gestures as neutral (51.7%), followed by positive (28.3%), and negative (20.0%). Furthermore, there was no significant difference in subjects' responses to the question "How much do you like [actor's name]?" as subjects reported liking Caucasian and Chinese actors equally (Caucasian: 6.78 ± 2.05; Chinese: 6.17 ± 1.54; $P > 0.3$). All of the participants reported having had limited interactions with Caucasian individuals, primarily through the media only. In addition, participants' scores on the MEIM were correlated with the fMRI data, as described below (see Fig. S2).

fMRI Results

All gestures versus control still images

Observation of all gestures versus control still images activated a priori pMNS regions of interest in the left dorsal inferior frontal gyrus (IFG) and the left inferior parietal lobe (IPL). At the whole brain level, the right posterior cingulate cortex, left middle temporal gyrus (MT/V5), right fusiform gyrus, bilateral superior parietal lobules, left precentral gryus, and left posterior superior temporal gyrus (pSTG), including Wernicke's area, were active (see Fig. 2 for fMRI results, Table I for all peak activations, and Fig. S3 for bar diagrams of beta values from ROIs).

Same and different race observations

Observation of gestures performed by the same race (Chinese) and different race (Caucasian) actors were separately contrasted to the control condition (still images). The same race (Chinese) actors compared to stills displayed activity in a priori pMNS regions of interest (the left IFG and the left IPL) along with a large region of activity in the left postcentral gyrus and bilaterally in the pSTS, SPL and the V5/MT region. In contrast, the different race (Caucasian) versus stills resulted in no significant activity in a priori regions. Whole-brain analyses at the $P < 0.001$ uncorrected level revealed activity in the dorsal precentral gyrus (BA 6) bilaterally, the left pSTS, and the middle occipital gyrus bilaterally.

The direct comparison of same race versus different race observations did not reveal any significant activation in a priori regions of interests. However, at the whole-brain level, the same versus different race contrast demonstrated activity in the left anterior IPL (supramarginal gyrus) and the right posterior insula. Different race versus same race showed increased activity only in the bilateral fusiform gyri and left middle occipital gyrus extending into the middle temporal gyrus (V5/MT; see Fig. 3).

In addition, scores on the MEIM were correlated with fMRI activity during observations of one's own race versus a different race (Fig. S2). Higher MEIM scores were positively correlated with activity in the dmPFC when observing one's own race versus a different race, and with activity in the left dorsal premotor cortex when observing a different versus same race.

Familiar and unfamiliar gestures

Familiar gestures compared to still images did not demonstrate significant activity in a priori regions of interest, but did reveal activity in the left dorsal IFG, left pSTS and bilateral visual cortices (V5/MT, middle occipital gyri) at the whole brain level. Unfamiliar gestures, compared to still images, activated a priori regions of interest in the left dorsal IFG and left IPL. They also activated the left pSTS, bilateral SPL, and bilateral lateral middle temporal gyrus (V5/MT) into the putative extrastriate body area (EBA), as well as in the fusiform gyri, at the whole brain level.

Familiar versus unfamiliar gestures revealed activity in a priori regions of interest, the posterior cingulate cortex (PCC), the dorsal portion of the medial prefrontal cortex (dmPFC) and the bilateral TPJ. Whole-brain analysis further demonstrated activation in the bilateral occipital gyri within the primary visual cortex (BA 17/18). In contrast, unfamiliar versus familiar gestures generated activity in an a priori region of interest in the left IPL, along with additional activity at the whole brain level along a large vertical region of the left postcentral gyrus, from the dorsal aspect of the postcentral gyrus to the ventral portion of the supramarginal gyrus. Additional activity also appeared in the bilateral SPL and bilateral V5/MT in the putative EBA and fusiform gyri (see Fig. 3).

Region of interest analyses

Beta values from our regions of interest in the pMNS (L IFG, L IPL) and mentalizing systems (mPFC, PCC, L TPJ, R TPJ), as previously defined, were then extracted and analyzed in 2 × 2 repeated measures ANOVAs with factors of race and familiarity, corrected for multiple comparisons, to examine whether there was a main effect or interaction effect between race and familiarity in these regions (see Fig. S3). We found a main effect of familiarity, with beta values significantly greater for unfamiliar than familiar conditions in the IPL ($F = 18.45$, $P < 0.00012$), whereas there was a main effect of familiarity, with beta values significantly greater for familiar than unfamiliar conditions in three of the four mentalizing ROIs, with the last one nearing significance (mPFC: $F = 15.35$, $P < 0.00058$; L TPJ: $F = 9.89$, $P < 0.010$; R TPJ: $F = 12.79$, $P < 0.0022$; PCC: $F = 5.67$, $P < 0.11$). In addition, the IPL demonstrated a significant effect of race with beta values for observations of the same-race actor greater than those of the different-race actor ($F = 7.0$, $P < 0.05$). Although none of the ROIs demonstrated a significant interaction effect between race and familiarity with the gesture, two fMRI contrasts exploring interactions between race and familiarity (Same Race + Familiar > Different Race + Unfamiliar; Different Race + Unfamiliar > Same Race + Familiar) found significant results in regions of the pMNS and mentalizing systems (see Fig. S4).

In addition, post hoc analyses demonstrated a significant overlap between BOLD signal from action execution and action observation conditions, suggesting validation of the presence of pMNS activity as found by using independently defined ROIs in the small volume correction (see Fig. S5).

DISCUSSION

Abstract Gestures

Observations of all gestures compared to still images generated activity within both the left dorsal IFG and the left IPL, which comprise the human pMNS, as well as the right PCC, which is thought to be a component of the mentalizing system [Van Overwalle and Baetens, 2009], in line with our initial hypotheses. Previous studies have focused on the task-dependent activity of either pMNS or mentalizing regions during gesture observation, with results reported in one system or the other [Gallagher and Frith, 2004; Skipper et al., 2009; Straube et al., 2009; Villarreal et al., 2008]. The current findings, however, support recent literature demonstrating activity of both systems during the general process of understanding the intentions behind an observed gesture [Schippers et al., 2009]. Furthermore, these data support previous findings indicating that regions of the human pMNS are involved in the processing of manual gestures and abstract communication [Corina and Knapp, 2006; Gentilucci and Dalla Volta, 2008; Willems et al., 2007]. The activation of the PCC, a region commonly associated with the mentalizing system as well as with episodic and autobiographical memory retrieval [Maddock et al., 2001], may be involved in interpreting the actor's intentions and/or comparing the observed stimulus to prior memories in order to understand the gesture's meaning. Altogether, our findings suggest that observing symbolic gestures requires the interplay between regions from both pMNS and mentalizing regions.

Processing Perceptual Familiarity in Individuals of the Same Versus a Different Race

Observations of the same race compared to still images demonstrated significant activity in pMNS regions of interest (IFG, IPL). Observations of a different race compared to still images generated no significant activity in any a priori regions of interest. However, there was activity in regions associated with the pMNS at the whole brain level [e.g., the dorsal premotor cortex and pSTS; Van Overwalle and Baetens, 2009], suggesting a less robust signal for observing a different race compared to one's own race, possibly in different regions of the pMNS from observations of one's own race. In addition, in accordance with our hypothesis, observations of same-race actors directly contrasted with different-race actors demonstrated greater activity in the posterior component of the pMNS (the anterior IPL), further contributing to the suggestion that actions of more perceptually familiar and/or physically similar individuals are more readily mapped onto sensorimotor representations of the self. Additional activity was found in the insula and may indicate enhanced emotional processing for individuals of the same race. These results are consistent with prior research suggesting that greater shared physical properties are associated with increased activity in the pMNS [Buccino et al., 2004a; Molnar-Szakacs et al., 2007]. Furthermore, prior research has found that racial group membership increases emotional responses to members of one's own group [Xu et al., 2009].

In contrast, observations of different-race actors versus same-race actors generated greater visual activity within the fusiform gyrus bilaterally, which is thought to support processing of face stimuli [Kanwisher et al., 1997], as well as in the middle occipital gyrus extending into area V5/MT which is the putative extrastriate body area (EBA) and thought to support processing of body movements [Downing et al., 2001; Astafiev et al., 2004]. These findings are also in accordance with prior research demonstrating that physically different others generate greater activity in visual regions [Buccino et al., 2004a].

Interestingly, one's self-reports of ethnic identification as being Chinese correlated with higher mentalizing activity for one's own race versus a different race and higher motor-related activity for a different race versus one's own race. These results suggest that the more one identifies with one's ethnic group, the more one utilizes mentalizing regions to process one's own race versus another race, a finding that is in accordance with previous research [e.g., Adams et al., 2009]. In contrast, the more one identifies with one's own ethnic group, the more motor-related activity they have when observing different-race individuals. This result seems to conflict with our previous suggestion that we map those who are more perceptually familiar onto our own sensorimotor representations than those who are perceptually less familiar. Thus, it is likely that there are other variables at play when we begin to incorporate ethnic identification into the analysis.

All together, these results suggest that humans are more apt to process the actions of those more perceptually familiar by engaging their own sensory-motor representations and emotional responses more strongly, as seen here when Chinese participants viewed their own race. Thus, it appears that activity in pMNS and mentalizing regions may be modulated by social factors such as perceptual familiarity and, in this case, race. This effect may be strengthened by one's daily life practice, particularly if one has limited experience or perceptual familiarity with another racial group, as found in our pool of participants.

By contrast, when observing actors that are perceptually less familiar from ourselves (e.g., actors of difference race), we may engage in increased visual processing, particularly of individuals' faces and body movements, as these often may provide additional information that might assist us in understanding the "other." Notably, these results are seen despite the fact that, in the current study, participants were asked to attend to the hand gesture rather than to the face of the actor, thus decreasing the amount of direct attention to race, while in many prior studies on race, parsimulate the observed action using the IPL and other sensorimotor regions to try to use our pre-existing motor representations to generate a basic understanding of the observed action.

Interestingly, the IPL, which is a multi-modal region commonly associated with grasp affordances, motor attention, body awareness, and action planning [Oztop and Arbib, 2002; Fogassi et al., 2005], showed increased activa-

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