

Cross-cultural Reading the Mind in the Eyes: An fMRI Investigation

Reginald B. Adams, Jr.¹, Nicholas O. Rule², Robert G. Franklin, Jr.¹,
Elsie Wang², Michael T. Stevenson¹, Sakiko Yoshikawa³,
Mitsue Nomura³, Wataru Sato³, Kestutis Kveraga⁴,
and Nalini Ambady²

Abstract

■ The ability to infer others' thoughts, intentions, and feelings is regarded as uniquely human. Over the last few decades, this remarkable ability has captivated the attention of philosophers, primatologists, clinical and developmental psychologists, anthropologists, social psychologists, and cognitive neuroscientists. Most would agree that the capacity to reason about others' mental states is innately prepared, essential for successful human social interaction. Whether this ability is culturally tuned, however, remains entirely uncharted on both the behavioral and neural levels. Here we provide the first behavioral and neural

evidence for an intracultural advantage (better performance for same- vs. other-culture) in mental state decoding in a sample of native Japanese and white American participants. We examined the neural correlates of this intracultural advantage using fMRI, revealing greater bilateral posterior superior temporal sulci recruitment during same- versus other-culture mental state decoding in both cultural groups. These findings offer preliminary support for cultural consistency in the neurological architecture subserving high-level mental state reasoning, as well as its differential recruitment based on cultural group membership. ■

INTRODUCTION

Mental state reasoning—also commonly referred to as mentalizing, mind reading, and theory of mind—refers to the ability to make accurate assessments of others' seemingly invisible internal mental states, beliefs, desires, and intentions (see also Allison, Puce, & McCarthy, 2000). The origin of this ability is often regarded as innately prepared (e.g., Brune & Brune-Cohrs, 2006; Baron-Cohen, 1995) due to selection pressures brought on by the computational demands associated with increasing social complexity (see Dunbar, 1998), and is considered an essential part of normal social functioning believed to distinguish humans from other species (see Saxe & Baron-Cohen, 2006).

Mental state reasoning has been argued to have at least two component processes: a social-perceptual process that enables mental state decoding from nonverbal cues, such as from the eyes, and a social-cognitive process that enables more abstract reasoning about another's mental state such as considering false beliefs that others may hold (Sabbagh, 2004; see also Tager-Flusberg, 2001). The work that has been done to examine the social-

perceptual process suggests that the eyes may hold special prominence in mental state reasoning. Indeed, popular folk wisdom asserts that "the eyes are the window to the soul," a presumption that remains nearly axiomatic in contemporary social exchange. This begs the question: Is there a language of the eyes and, if so, to what extent is this language translatable across cultures?

The first part of this question has received extensive theoretical and empirical attention over the past few decades in the study of social perception and theory of mind (see Allison et al., 2000). The answer appears to be that the eye region is richly informative and heavily relied upon in social communication (e.g., Rule, Ambady, Adams, & Macrae, 2008; Vinette, Gosselin, & Schyns, 2004). The eyes capture significantly more attention than do other areas of the face both in adults (Janik, Wellens, Goldberg, & Dell'Osso, 1978) and in infants (Farroni, Csibra, Simion, & Johnson, 2002), an attraction that is arguably inborn (Baron-Cohen, 1995; Argyle & Cook, 1976). Complex musculature changes such as the raising and lowering of eyelids and eyebrows enables perceivers to accurately decode emotions from just the eye region of the face (Baron-Cohen, Wheelwright, & Jolliffe, 1997; Nummenmaa, 1964). Additionally, participants perform equally well at decoding complex mental states when shown just the eye region as when shown the whole face (Baron-Cohen et al., 1997), suggesting that the eyes play

¹The Pennsylvania State University, University Park, PA, ²Tufts University, Medford, MA, ³Kyoto University, Kyoto, Japan, ⁴Harvard Medical School, Boston, MA

a dominant role in social communication. Based on this evidence, there does appear to be a “language of the eyes,” but whether this language is readily translatable across cultures has not been previously examined and is the primary focus of the current research. Specifically, we sought to examine whether mental state decoding from the eyes is culturally tuned, thereby giving rise to an intracultural advantage in mental state reasoning (i.e., better performance and corresponding neural sensitivity to same- vs. other-cultural group members).

Over the last few decades, predominant attention across most fields of study has focused on underlying processes enabling *accurate* mental state decoding. Notably, during this same period, social psychologists have focused largely on the attributional biases that might undermine this ability (see Mason & Macrae, 2008 for a review). Directly relevant to the current work is a bias people have for ascribing complex mental states to members of their own group versus members of other groups (Paladino et al., 2002). The question of whether mental state decoding varies as a function of cultural group membership—a social-perceptual process—remains entirely unexplored, however, on both the behavioral and neural levels. Recently, neural processes have been shown to vary when participants make mental state inferences of similar versus dissimilar others (e.g., Mitchell, Macrae, & Banaji, 2006), indicating that the neural operations underlying mental state reasoning can vary as a function of whose mental state is being inferred. These findings hold clear implications for the study of cross-cultural influences.

Culture implies profound differences in social experience including shared meaning systems, styles of relating, social practices and values, geographical location, religious values, language, diet, and ecology (Chiao & Ambady, 2007; see also Markus, Kitayama, & Heiman, 1996). The observation that social experiences during development impact the ability to reason about others’ minds (e.g., Peterson & Siegal, 1997; Jenkins & Astington, 1996; Perner, Ruffman, & Leekam, 1994) has led a number of theorists to consider potential *intercultural* influences on this ability as well (e.g., Flavell, 1999; Lillard, 1998). Cross-cultural studies on theory of mind examining this issue, however, remain limited and have yielded mixed results. Early studies provided support for universality in theory of mind. Avis and Harris (1991), for instance, found that the ability to understand false beliefs in others, a defining characteristic of theory of mind, arises at about the same time in both preliterate and literate cultures. In addition, Sugiyama, Tooby, and Cosmides (2002) found that individuals from a preliterate culture were similarly good at detecting cheating (a form of mental state reasoning) as those from literate cultures. More recently, Kobayashi, Glover, and Temple (2006) examined the influence of cultural and linguistic factors on theory of mind using a false belief task and found both culture/language-dependent and -independent neural re-

sponsivity. Thus, when investigating a hypothesized *intra-cultural* advantage in mental state reasoning as we do herein, we also must consider the potential for intercultural variation as well (i.e., differences that may occur as a function of culture of participant irrespective of the cultural identity of the person being read).

Reading the Mind in the Eyes

Because humans are preferentially attracted to the eyes and extract complex meaning from them, some theorists assign gaze perception a critical role in the development of the ability to reason about others’ intentions and feelings (Baron-Cohen, 1995). Given that the eyes are a salient cue in human social communication (Emery, 2000) and social categorization (Zebrowitz, 2006), they serve as an especially suitable stimulus for the present examination. Therefore, to achieve the aims of the current study, we utilized a well-validated test of mental state decoding, the “Reading the Mind in the Eyes” test, referred to henceforth as the RME (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001). The RME is a social-perceptual test of mental state reasoning that shows convergent validity with social-cognitive tests of theory of mind, and has been demonstrated in numerous studies to reliably differentiate nonclinical samples from clinical samples who exhibit certain psychopathologic disorders and brain damage associated with impaired social perception, such as autism spectrum disorders (e.g., Baron-Cohen et al., 1999) and amygdalotomy (Adolphs, Baron-Cohen, & Tranel, 2002).

The RME task has previously been found to engage networks related to mind reading (see Appendix for a review) such as: (a) regions implicated in the theory of mind network, including medial prefrontal cortex (MPC), posterior STS (pSTS), and temporal poles (e.g., Gallagher & Frith, 2003); (b) the three-node pathway commonly referred to as the “social brain,” including the amygdala, orbito-frontal cortex (OFC), and the STS (e.g., Baron-Cohen, 1999); and (c) the putative mirror system, particularly the inferior frontal gyrus (IFG; e.g., Iacoboni, 2005). The pSTS and the IFG are two areas most consistently found using the RME. In the current examination, the pSTS stands out as a particularly prominent region of interest (ROI), as it is thought to be where social cues reach a final stage of visual integration (Haxby, Hoffman, & Gobbini, 2000; Perrett & Mistlin, 1990) and is recruited in the processing of facial expression and gaze direction, particularly when inferring social meaning from these cues (see Allison et al., 2000).

The Current Study

Early theorizing suggested that the ability to reason about others’ mental states evolved as a biological imperative for detecting deception in others, in order to reinforce group cooperation and assist coalition formation (Trivers,

1971). This implies that we might be particularly adept at reading the mental states of familiar others (i.e., those with whom we may perceive a heightened probability of strategic alliance), particularly given that our most serious lies tend to be exchanged among those with whom we are the closest (DePaulo, Ansfield, Kirkendol, & Boden, 2004). People tend to ascribe more complex mental states to members of their own versus other social groups (Paladino et al., 2002), and same-race faces are processed more holistically (Michel, Rossion, Han, Chung, & Caldara, 2006), more deeply (Levin, 1996), and are remembered better (Meissner & Brigham, 2001) than other-race faces. Subtle variation across cultures in how nonverbal messages are expressed (see Elfenbein & Ambady, 2003) and in how identical expressions may be construed (Baron-Cohen et al., 1996) offers convergent support for this prediction. Moreover, recent research has demonstrated cultural specificity in neural responses to even basic emotional expressions. Chiao et al. (in press), for instance, found greater activation in the bilateral amygdalae in response to same- compared to other-culture fear expressions, an effect that was consistent across both native Japanese and white American participants.

Given these findings, we predicted an intracultural advantage in the ability to infer mental states from the eyes. We utilized fMRI to examine whether brain regions previously associated with mental state reasoning—particularly those previously reported using the RME—are differentially recruited when reading the eyes of same-versus other-cultural group members. Eye gaze perception is thought to be critical in the development of theory of mind (Allison et al., 2000; Baron-Cohen et al., 1997), and both general gaze perception and theory of mind tasks yield converging activation in the pSTS (Allison et al., 2000), as does the RME (see Appendix). Thus, we were particularly interested in investigating potential culturally tuned responses within this region.

METHODS

Participants

Thirty-four participants were recruited from the Boston area, most from a local private university campus

(19 women). Six of these participants were subsequently excluded from the fMRI analyses. Four were excluded for excessive movement during the MRI scan, one for left-handedness, and one for being 2.58 standard deviations above the mean age of the participants to better balance age across our samples. The remaining sample included 14 right-handed native white American participants (9 women) and 14 right-handed native Japanese participants (9 women) between the ages of 18 and 27 years. The Japanese students were in the United States to attend a summer English language program and were either visiting the United States for the first time or had minimal previous experience in the United States, at most a previous 3-week home-stay program. All participants had normal or corrected-to-normal vision and had no known medical, neurological, or psychiatric history. Each participant gave written informed consent before participating in the experiment.

Stimuli

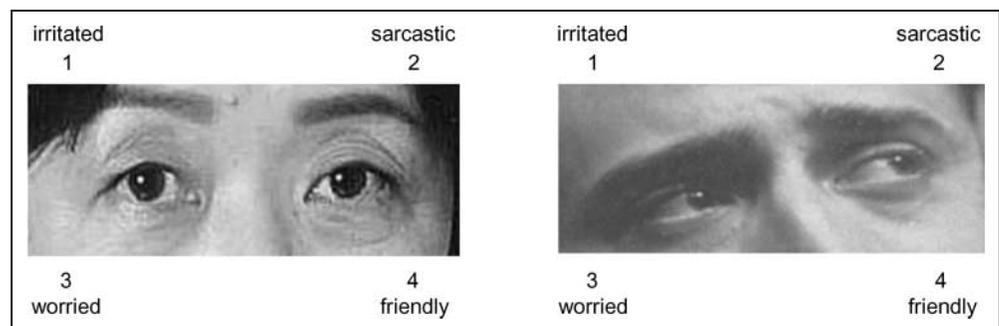
Caucasian Eyes Test

The original RME (Baron-Cohen et al., 2001) consists of 36 photographs depicting just the eye region of Caucasian individuals. A rectangular area of approximately 5 × 2 inches delineated the eye region, encompassing the entire width of the face from midway up the nose to right above the brow. All photographs were collected from magazines. Four mental state terms accompanied each stimulus (one target word and three foils) presented at each corner of the photograph (see Figure 1). Target words and foils were chosen by two of the original authors and pilot tested on groups of eight raters until each item met a criterion response of at least five raters choosing the target word. The resulting test was subjected to a nonclinical sample of 103 Cambridge University students, which yielded a 78% overall accuracy on the test (see Baron-Cohen et al., 2001 for additional details).

Asian Eyes Test

Cross-cultural comparisons necessitated generating an Asian version of the eyes test. To do this, we closely

Figure 1. Example stimuli for Asian and white American versions of the RME, where “worried” is the target response.



followed the procedures described above. Rather than generating new mental state words, however, we retained the words used in the original version of the test. These terms were translated into Japanese by a professor at Kyoto University, and Asian eye samples were collected from magazines, the World Wide Web, a database of amateur models, and commercial DVDs to generate a set of stimuli that matched each of the 36 sets of test words. To check for agreement with the original test, a Japanese student studying in the United States then translated the Japanese version back into English. This translation revealed exact agreement for all but six English terms. Importantly, in each case where an alternate English translation was offered, the alternate word was a close synonym of the original word (e.g., “daydreaming” vs. “fantasizing,” “scared” vs. “terrified,” etc.).

The Asian eyes test was piloted on two sets of nine students at Kyoto University until each test item reached criterion levels of consensus (i.e., at least five of nine judges picked the target word on each test item). One of these groups included four female and five male judges, the other group included five female and four male judges. Four iterations of these pilot tests were necessary (two per group) to yield a set of 36 items that reached criterion levels of accuracy. No obvious gender differences were apparent. Once the stimuli met criterion, a preliminary study revealed overall test performance exceeding 73% accuracy in a nonclinical sample of 61 Kyoto University undergraduate students, performance comparable to that previously reported for the Caucasian version of the eyes test.

As in previous brain imaging studies using the RME (Platek, Keenan, Gallup, & Mohamed, 2004; Russell et al., 2000; Baron-Cohen et al., 1999), a modified two-choice task was implemented in the fMRI portion of this study, including one target and one foil word presented in the bottom corners of the photograph. We chose foil words based on which of the original three foil words was chosen least often in our preliminary tests by both Japanese and white American participants who took both versions of the test. The resultant foil words were therefore identical across both the Asian and white American versions of the test used in this study.

Procedure

During scanning, participants viewed 72 photographs depicting 36 white American and 36 Asian eye stimuli, once with corresponding mental state labels and once with gender labels, for a total of 144 stimulus presentations. The photos within each run were presented in approximately 35-sec blocks in a periodic ABA design, where Task A utilized the two-choice RME (one target, one foil) and Task B utilized a gender discrimination (GD) task as a matched control for low-level visual and motor processing (see also Russell et al., 2000; Baron-Cohen et al., 1999).¹ Using a back-projection system, 500 × 200 pixel

gray-scale images were presented in the middle of the screen so the participants could view them from within the magnet. Functional data were acquired in two runs, one presenting just Asian and one just white American eye stimuli. In each block, stimuli were presented on the screen for 5 sec with randomized intertrial intervals ranging from 500 to 1000 msec. Participants indicated their choice of labels by pressing one of two buttons. Responses were collected for as long as the stimulus remained on the screen, and were coded as incorrect after that. The order in which participants performed the tasks and the order in which left and right button presses were assigned as correct responses for each trial were fully counterbalanced across participants. After scanning, participants completed the self-paced, four-choice version of Asian and Caucasian RME tasks. Stimuli were presented and behavioral responses were acquired on a Dell laptop computer using Direct RT in the fMRI phase, and on a Dell laptop computer using Cedrus Superlab Pro 2.0 in the self-paced, four-choice phase.

fMRI Data Analysis

Participants were scanned in a supine position with a 1.5-T Siemens Avanto whole-body scanner (Siemens.com) using a standard 12-channel birdcage head coil. The functional data were acquired with an echo-planar imaging sequence (TR = 2.5 sec, TE = 40 msec, 90° flip angle, FOV = 200, 64 × 64 matrix, voxel size = 3.125 × 3.125 × 5 mm³, 28 axial slices, 185 volumes, 2 runs). High-resolution T1-weighted (MP-RAGE, 128 slices) anatomical images were collected for each participant for coregistration with the participants' functional data and display of individual activations. Foam padding around the head was used to minimize head movement.

Data were preprocessed and analyzed following the classical analysis stream in SPM5 (www.fil.ion.ucl.ac.uk/spm/). Images were corrected for slice timing and realigned using a least squares approach and a six-parameter rigid-body spatial transformation. This was followed by coregistering the structural and the functional data in 3-D using rigid-body transformations. The anatomical images were then normalized to the Montreal Neurological Institute (MNI) space, which formed the basis of the spatial normalization of the functional images to this standardized space defined by the ICBM, NIH P-20 project that approximates that of Talairach and Tournoux (1988). To allow for intersubject averaging, the functional images were then smoothed with an 8-mm FWHM isotropic Gaussian smoothing kernel. Statistical analysis was performed using a mass-univariate GLM approach. First, effects related to the experimental tasks (RME/GD) and the ethnicity of eye stimuli (Asian/white American) were estimated using within-subject analyses. Stimulus conditions were modeled as delayed boxcar functions. Low-frequency signal components were eliminated with a standard SPM5 high-pass filter.

To make population inferences, the contrast images from each subject were then entered into a mixed effects model representing the summary measures of subject responses. Neural responses to mind reading were estimated by examining BOLD signal differences in the RME task while subtracting the GD task, which served as the baseline control (see also Russell et al., 2000). Thus, low-level visual processing associated with seeing the faces, and motor processing associated with responding to the faces, were controlled, isolating the neural responses uniquely associated with mental state reasoning. These secondary-level analyses utilized one-sample and paired-samples *t* tests. ROI analyses were conducted using the MarsBaR-dev ROI toolbox (<http://marsbar.sourceforge.net>) implemented within SPM5 to extract the estimated percent signal change within each condition. Based on our a priori hypotheses, we concentrated on the left and right pSTS defined on the basis of the SPM contrast comparing same- versus other-culture mental state decoding [i.e., (same-culture RME – GD) – (other-culture RME – GD)] at a set threshold of 0.01. For illustration purposes, all group contrast images were overlaid onto a representative T1 template anatomical image using MRIcron (www.sph.sc.edu/comd/rorden/mricron.html).

RESULTS

Behavioral

We tested both native Japanese and white American participants. Each group completed both the Asian and Caucasian versions of the RME test using a modified two-choice version of the test administered during fMRI scanning, and the traditional self-paced, four-choice

version when scanning was complete. Participants viewed pictures limited to the eye region of 72 individuals and were asked to choose one label (of the two or four depending on version) that they felt best described the mental state of the person depicted. From this we computed a 2 (participant culture: Japanese vs. U.S.) by 2 (stimulus eyes: Asian vs. white American) mixed-model ANOVA with repeated measures on the second factor for both the two-choice and four-choice versions of this task. Critically, performance on both revealed the predicted Culture of participant \times Race of stimulus interaction [four-choice, $F(1, 26) = 23.10, p < .0001, r = .69$ (see Figure 2); two-choice, $F(1, 26) = 15.76, p < .0006, r = .61$]. No main effects emerged, highlighting a clear pattern of intracultural advantage.

Functional Magnetic Resonance Imaging

To compare the activations associated with mental state reasoning in the current work with those found in previous studies using the RME, we first examined neural activations in response to mental state reasoning irrespective of culture (see Table 1). This analysis yielded activations in most of our ROIs, including bilateral portions of the pSTS extending into the temporo-parietal junction (TPJ; BA 22), bilateral temporal poles (BA 38), posterior and anterior rostral MPC (BAs 6, 9), and IFG (BAs 45, 47, 48) (height: $p < .05$, family-wise corrected, extent-threshold: 6 voxels). This offers convergence with previous studies using this test (see Appendix) and previous tests of theory of mind (see Gallagher & Frith, 2003).

Previous research has also reported both cultural consistency *and* pliancy in the neural networks associated with performance on a false belief theory of mind task

Figure 2. Proportion of correct responses on the Asian versus white American RME (four-choice version) as a function of Japanese versus U.S. participants (means and SEs).

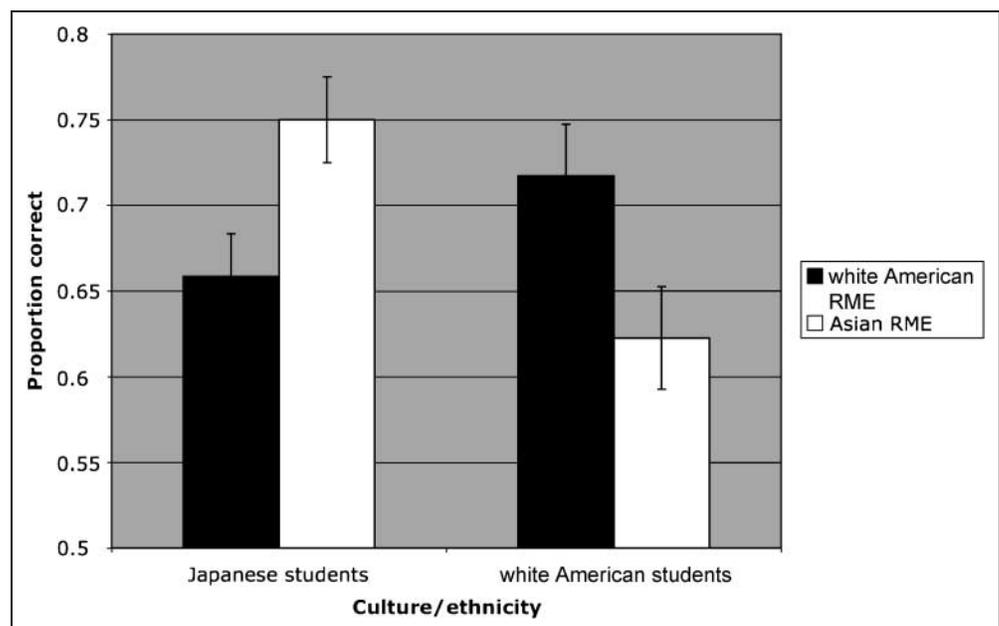


Table 1. Regions of Increased Activation Associated with Mental State Decoding (RME – GD), Irrespective of Culture of Participant or Race of Stimulus Eyes (Threshold: $p < .05$, Family-wise Corrected; Extent-threshold: 6 Voxels)

<i>Anatomical Location</i>	<i>BA</i>	<i>MNI Coordinates</i>			<i>t</i>
		<i>x</i>	<i>y</i>	<i>z</i>	
<i>Mental State Decoding</i>					
R. Cerebellum		10	-78	-30	7.92
L. Lingual gyrus	19	-8	-76	-6	6.53
R. Cerebellum		18	-74	-30	7.02
L. Superior temporal sulcus	21	-56	-52	6	9.33
L. Superior temporal sulcus	22	-48	-48	16	8.93
R. Superior temporal sulcus	22	52	-48	14	10.11
L. Fusiform gyrus	37	-44	-48	-14	7.49
R. Middle temporal gyrus/ superior temporal sulcus	21	46	-42	6	7.25
L. Superior temporal sulcus	21	-50	-42	8	9.41
L. Fusiform gyrus	20	-44	-28	-18	7.50
L. Middle frontal gyrus	6	-42	0	54	7.87
L. Middle frontal gyrus	6/8	-42	4	46	5.28
L. Temporal pole	38	-54	10	-22	8.10
L. Posterior rostral medial prefrontal cortex	6	-4	16	56	8.08
R. Temporal pole	38	44	16	-30	6.90
L. Dorsal anterior cingulate cortex	32	-12	18	48	9.43
L. Inferior frontal gyrus	45	-58	26	12	9.22
R. Inferior frontal gyrus	45	58	30	6	9.80
L. Inferior frontal gyrus	45	-54	32	-4	10.23
L. Inferior frontal gyrus	47	-46	36	-10	9.83
L. Anterior rostral medial prefrontal cortex	9	-10	58	38	6.09

Regions reported posterior to anterior.

when comparing Japanese and U.S. participants (i.e., Kobayashi, Glover, & Temple, 2007; Kobayashi et al., 2006). For example, Kobayashi et al. (2006) found that regions in the brain previously associated with theory of mind, such as MPC and the TPJ near the pSTS, were recruited in a culturally independent manner during performance on a false belief task. Other regions, such as the IFG, however, were engaged in a culturally specific manner. Therefore, as a point of comparison, we investigated convergence in our two cultural groups using similar conjunction analyses (Table 2), and divergence using two-sample t -test comparisons (see Table 3). Conjunction analyses revealed robust overlapping activa-

tion, particularly in the bilateral STS and the bilateral IFG among Japanese and white American participants. Direct contrasts between Japanese versus white American participants revealed limited activations, none involving the STS or the IFG.

In order to examine our primary hypothesis for cultural specificity in neural responses to mental state reasoning, we computed a contrast comparing same- versus

Table 2. Regions of Increased Activation Associated with Mental State Decoding (RME – Gender): Conjunction between Japanese and White American Participants (Height: $p < .001$, Uncorrected; Extent-threshold: 6 Voxels)

<i>Anatomical Location</i>	<i>BA</i>	<i>MNI Coordinates</i>			<i>t</i>
		<i>x</i>	<i>y</i>	<i>z</i>	
<i>Japanese and White American Conjunction</i>					
L. Inferior occipital gyrus	18	-28	-92	-8	3.47
L. Lingual gyrus	17	-14	-88	-6	3.57
L. Cuneus	17	-16	-80	6	3.67
R. Cerebellum		12	-78	-30	5.36
L. Lingual gyrus	18	-8	-76	-8	3.53
L. Superior temporal sulcus	22	-54	-52	6	6.43
R. Superior temporal sulcus	22	50	-48	16	6.25
L. Inferior parietal lobule	40	-60	-48	24	3.77
L. Superior temporal sulcus*	22	-50	-42	8	6.58
R. Superior temporal sulcus	22	46	-42	6	4.72
L. Temporal-occipital gyrus	35	-44	-36	-18	3.52
L. Superior temporal sulcus	22	-54	-34	4	6.39
L. Motor cortex		-42	-2	56	5.52
L. Precentral gyrus	6	-38	-2	38	3.58
L. Medial frontal gyrus	6	-42	4	42	4.31
R. Temporal pole	38	52	8	-24	4.38
L. Medial frontal gyrus	6	-4	12	62	5.05
R. Temporal pole	38	48	14	-28	4.5
L. Medial frontal gyrus	6	-4	16	52	5.83
R. Medial frontal gyrus	8	10	16	44	3.46
L. Anterior cingulate	32	-12	18	48	6.05
L. Inferior frontal gyrus	44/45	-56	24	10	6.41
L. Inferior frontal cortex*	47	-56	28	0	6.53
L. Inferior frontal gyrus	44/45	-54	32	10	6.45
R. Inferior frontal cortex*	45	58	32	8	6.55
L. Prefrontal cortex	9	-8	58	40	3.90

Regions reported posterior to anterior.

*Indicates regions surviving when correcting for multiple comparisons (threshold: $p < .05$, family-wise corrected; extent-threshold: 6 voxels).

Table 3. Regions of Increased Activation Associated with Japanese minus White American and White American minus Japanese Participants Mental State Decoding (RME – GD) (Height: $p < .001$, Uncorrected; Extent-threshold: 6 Voxels)

Anatomical Location	BA	MNI Coordinates			
		<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i>
<i>Japanese minus White American</i>					
L. Lingual gyrus	17	-4	-74	-6	4.53
M. Cerebellum		0	-66	-32	3.82
L. Cerebellum		-12	-66	-18	3.69
L. Cerebellum		-22	-42	-36	4.47
R. Temporal parietal junction	41	40	-42	30	4.61
<i>White American minus Japanese</i>					
No clusters reached significance					<i>ns</i>

Regions reported posterior to anterior.

other-culture mental state decoding [i.e., (same-culture RME – GD) – (other-culture RME – GD)]. Of the previously activated ROIs, only the bilateral pSTS (BA 22) survived this level of analysis (height: $p < .001$, uncorrected, extent threshold: 6 voxels). Also evident were two portions of right-lateralized postcentral gyrus activation (see Table 4), which was not an a priori ROI. The reverse contrast (i.e., other- minus same-culture mind reading) yielded no significant activations.

To examine the pSTS activation more closely for potential intercultural variation, mean signal intensities from the coordinates of the contrast described above were used to examine mental state decoding (i.e., RME – GD) by computing a 2 (participant culture: Japanese vs. U.S.) by 2 (stimulus eyes: same- versus other-race) ANOVA. This yielded only significant main effects for in-group versus out-group mental state decoding in both the left pSTS [$F(1, 26) = 13.44, p < .002, r = .58$] and the right pSTS [$F(1, 26) = 15.47, p < .001, r = .61$]. That culture did not interact with these effects (i.e., $F_s < 1, p_s > .39$) suggests consistency in the intracultural advantage effect across these two cultural groups. Direct *t*-test comparisons further substantiate this conclusion, revealing significantly greater activation for same- versus other-culture mental state decoding in both the left and the right STS, for both Japanese and white American participants (see Figure 3).

In our final analysis, we investigated the relationship between behavioral performance on the RME test and pSTS activation. The mean signal intensities extracted for same- and other-culture mental state reasoning as described above were next correlated with the intracultural advantage (same- minus other-culture performance) on the self-paced RME task. From this we found a significant negative correlation between intracultural

advantage in mental state decoding performance and pSTS activation during both other-culture mind reading and other-culture GD in both the left and right pSTS (r s larger than $-.33$, and p s $< .05$, one-tailed), indicating that as pSTS activation increased, intracultural advantage decreased. Correlations for pSTS activation during the same-culture mind reading and same-culture GD tasks, however, did not approach significance (all r s below $.1$, and p s $> .59$).

DISCUSSION

Our behavioral findings indicate that both Japanese and white American participants perform better on same-versus other-culture mental state decoding from the eyes. This performance pattern was mirrored by culturally tuned neural activation in the bilateral pSTS. In terms of areas implicated previously during mental state reasoning and eye gaze perception, the pSTS was predicted to be the most likely candidate involved in detecting and responding to cultural cues conveyed by the eyes. Consistent with this, significant culture-specific responses were apparent within both cultural groups in both the left and right pSTS, revealing more activation to same- versus other-culture mental state decoding.

Overall, the activations we found were highly consistent with those reported in previous neuroimaging studies, particularly those utilizing the RME (see Appendix for a review). We found robust and extensive activations in the bilateral pSTS and IFG, two regions consistently reported when using the RME task. Conjunction analyses between Japanese and white American participants yielded high correspondence in the bilateral pSTS and IFG. Direct contrasts comparing these cultural groups yielded no significant differences in pSTS or IFG

Table 4. Regions of Increased Activation Associated with Same- versus Other-culture Mental State Decoding (RME – GD) (Height: $p < .001$, Extent-threshold; Extent-threshold: 6 Voxels)

Anatomical Location	BA	MNI Coordinates			
		<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i>
<i>Same- minus Other-culture</i>					
R. Superior temporal sulcus	21	48	-44	12	4.00
R. Superior temporal sulcus	21	56	-40	10	3.60
L. Superior temporal sulcus	21	-56	-30	0	3.68
R. Postcentral gyrus	43	64	-14	38	3.50
R. Postcentral gyrus	43	66	-12	28	4.39
<i>Other- minus Same-culture-Contrast</i>					
No clusters reached significance					<i>ns</i>

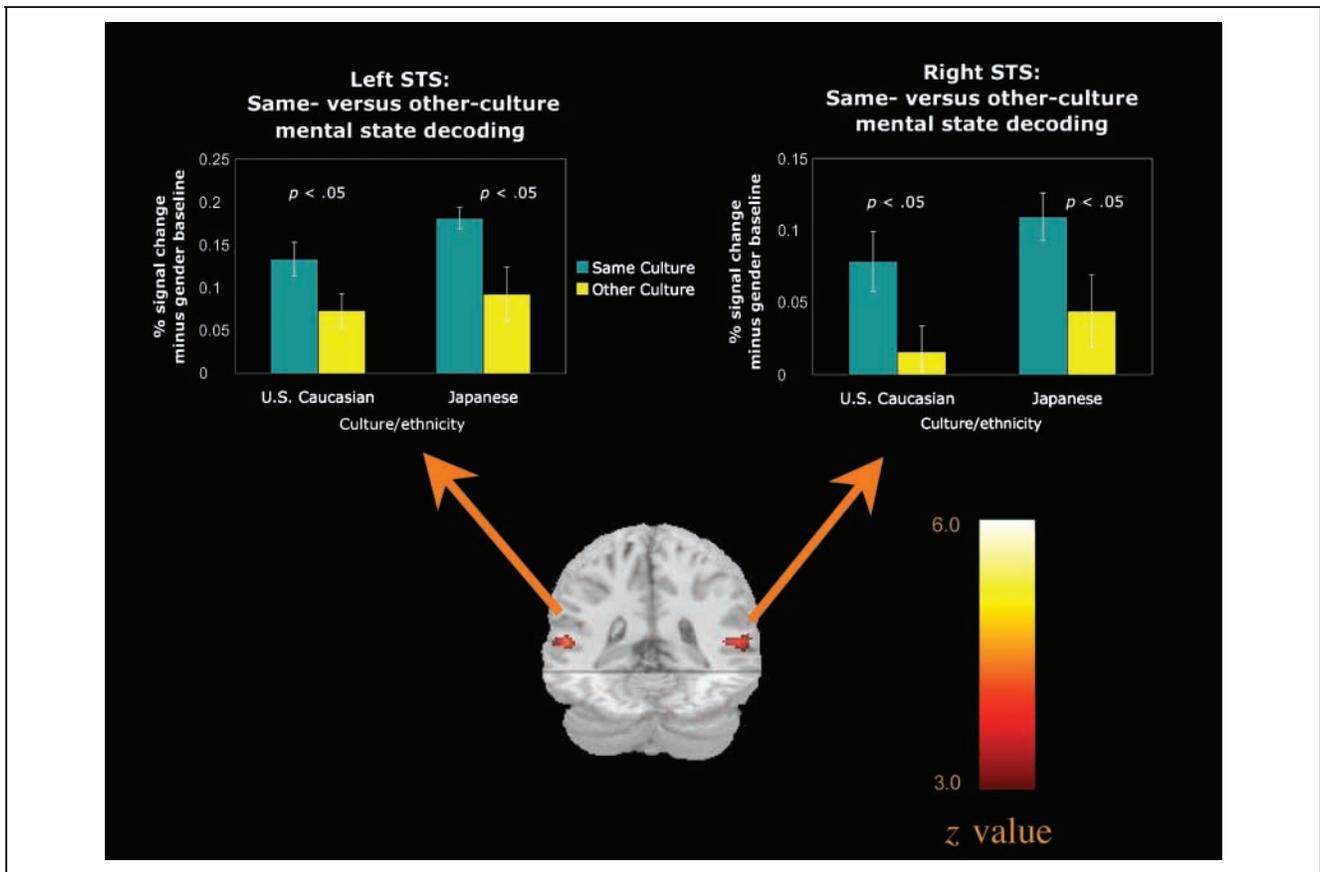


Figure 3. Graphs depict regions of left and right pSTS activation for same- versus other-culture mental state decoding (RME – GD). Mean signal intensities were extracted from the voxelwise contrast illustrated in the bottom half of the figure. Individual paired-sample *t* tests reveal significantly greater same- versus other-culture activation in both cultural groups for both the left and the right STS.

activation. These findings suggest a high-level of consistency in neural responses between Japanese and white American participants when decoding mental states from the eyes.

No studies, to date, have examined neural correlates associated with cross-cultural mental state decoding using a social-perceptual task such as the eyes test. The literature examining cross-cultural similarities and differences in the neural activity associated with mind reading has otherwise been limited to performance on false belief tasks (Kobayashi et al., 2006, 2007). One such study, examining Japanese versus U.S. adults, found high overlap in regions associated with the false belief task, including MPC and a TPJ activation close to the pSTS. However, other regions, such as the IFG, were recruited in a culturally dependent manner (Kobayashi et al., 2007). Thus, the neural underpinnings of mental state decoding—at least for theory of mind based on a false belief task—appear to reflect both culturally universal and pliant components. Our findings using the RME task offer support for cultural consistency in both the bilateral pSTS and IFG. Clearly, this question requires further examination across additional cultural groups using a broader range of mental state decoding tasks.

In addition, activation of the pSTS when viewing other-culture eyes was found to be negatively correlated with the intracultural advantage in the RME, whereas pSTS activation when viewing same-culture eyes was not correlated with the intracultural advantage in the RME. These findings are consistent with the conclusion that intracultural advantage in the RME is not so much influenced by enhanced pSTS engagement in response to same-culture eyes as it is by a failure to engage in response to other-culture eyes. Future research efforts are obviously necessary to examine and further clarify this relationship.

A number of previous lesion studies have implicated amygdala involvement in the RME task (see Appendix for review), although we did not find evidence for amygdala involvement here. It is notable that one of the reported lesion studies, which examined two patients with bilateral amygdala damage, found impaired responses in only one patient (Stone, Baron-Cohen, Calder, Keane, & Young, 2003). In addition, only one neuroimaging study has previously reported amygdala involvement when comparing a nonclinical versus autistic population (Baron-Cohen et al., 1999). The amygdala is not consistently discussed as a primary region involved in the theory of mind network (e.g., Gallagher & Frith, 2003). Yet, the

amygdala continues to be a region of great interest and importance in ongoing research examining high-level social cognition and emotion perception (Adolphs et al., 2002; Adolphs, Tranel, & Damasio, 2001).

Two areas considered part of the primary network involved in theory of mind, MPC and the temporal poles, were activated during mental state decoding in the current study. These are areas that, although not consistently reported during use of the RME task (see Appendix for review), are regularly found for other mental state reasoning tasks. MPC has rarely been found in tasks examining gaze perception (but see Calder et al., 2002). In the current study, we found involvement of both posterior and anterior rostral MPC and right temporal pole during mental state reasoning, but these were not implicated in culturally tuned responses. Combined with previous evidence for a primary role of the pSTS in both general gaze perception and theory of mind tasks, our findings help substantiate the critical role of pSTS in inferring social meaning, particularly from the eyes, and demonstrate sensitivity to cultural-relevant information conveyed by the eyes.

Although not an a priori ROI, we also found evidence for greater same- versus other-culture recruitment of the right postcentral gyrus. This is noteworthy given that recent work has revealed the right postcentral gyrus to be activated in response to self- versus other-perspective taking under emotional versus neutral conditions (Ruby & Decety, 2004; see also Saxe, Jamal, & Powell, 2006; Kircher et al., 2002). Our activations were considerably more ventrolateral to that reported by Ruby and Decety (2004), located instead in the eye and face areas of the somatosensory strip (Nguyen, Tran, Hoshiyama, Inui, & Kakigi, 2004; Penfield & Rasmussen, 1950). This suggests that participants may have used more self-oriented simulation when reading the minds of same- versus other-

cultural group members' eyes. This activation, however, was not an a priori ROI found in the previous tests using RME, and thus, requires further empirical corroboration before firm conclusions can be drawn.

Another important aspect of the current findings is that the intracultural advantage reported here reflects purely within-subject variability. Of the previous studies implicating pSTS involvement in mental state decoding, most have compared either different tasks or individual differences, particularly those between clinical and non-clinical populations. The current investigation, however, reveals variation occurring within individuals based on cultural group membership in otherwise identical tasks. These findings therefore offer a uniquely functional account of the neural operations associated with mental state decoding from nonverbal cues. Whether these effects are due to perceived ethnicity, culture-dependent variation in nonverbal expression, or both awaits future research efforts. Whether these effects might generalize to regional differences, racial group memberships within a culture, or even to smaller social cliques remains an intriguing question.

In summary, the current work reports evidence for a special role of the pSTS in inferring mental states from the eyes of others, one that is sensitive to nonverbal cues relevant to cultural group membership. On the one hand, we offer preliminary support for cultural consistency in the involvement of the pSTS in mental state reasoning. On the other hand, we demonstrate a clear intracultural advantage mirrored by culturally tuned bilateral pSTS responses to mental state decoding from the eyes. This intracultural advantage, marked by differential engagement of neural processes known to be related to mental state decoding, holds clear implications for furthering our understanding of the effects of culture on neural processing and behavior.

APPENDIX. Overview of Brain Imaging and Lesion Studies Implicating Specific Regions of Interest Using the RME Task

<i>Study Type</i>	<i>Article</i>	<i>Populations</i>	<i>Task</i>	<i>Outcome</i>	<i>Brain Areas</i>
Lesion	Adolphs et al., 2002	30 unilateral amygdala damage (16 left, 14 right), 2 bilateral amygdala damage, 47 brain-damaged controls, 19 normal	Modified RME-match 14 eyes stimulus to a list of mental states	Normal subjects performed better than patients. Amygdala patients were only worse than brain-damaged controls when the eyes stimuli were expressing <i>social</i> complex mental states	bilateral amygdala
Lesion	Farrant et al., 2005	14 frontal lobe epilepsy, 14 controls	RME (36 items)	Patients showed impairment	frontal lobe
Lesion	Shaw et al., 2005	54 temporal lobe damage (27 left, 27 right), 31 frontal lobe damage (16 right, 15 left), 91 controls	RME (36 items)	Temporal lobe (LT and RT) RF, showed impairment on task.	amygdala, VMPC

APPENDIX. (continued)

<i>Study Type</i>	<i>Article</i>	<i>Populations</i>	<i>Task</i>	<i>Outcome</i>	<i>Brain Areas</i>
Lesion	Stone et al., 2003	2 bilateral amygdala damage, 34 controls (10 British, 24 American)	RME (25 items, 2 choices)	One patient was impaired, the other was not.	bilateral amygdala
fMRI	Baron-Cohen et al., 2006	12 parents of children with Asperger Syndrome, 12 controls	RME (30 items, 2 choices)	No task accuracy differences.	controls vs. parents: more mid-temporal gyrus and inferior frontal gyrus males vs. females: more angular gyrus and dorsolateral prefrontal cortex; females vs. males: more bilateral inferior frontal gyrus
fMRI	Baron-Cohen et al., 1999	6 autism, 12 controls	RME (30 items, 2 choices)	Impairment	autistic vs. controls: greater bilateral STG; controls vs. autistic: greater left inferior frontal gyrus, right insula, and left amygdala
fNIRS	Platek et al., 2005	21 controls, correlate with Schizotypal Personality Questionnaire	RME (36 items)	Performance negatively correlated with SPQ—need to write for data	increased frontal lobe oxygenation positively correlated with SPQ
fMRI	Platek et al., 2004	5 nonclinical	modified RME (36 items, no words—asked to think about the mental state depicted in the photo)	No accuracies to report.	right hemisphere: middle frontal gyrus, superior frontal gyrus, medial superior frontal gyrus; left hemisphere: middle frontal gyrus, superior temporal gyrus/temporal pole
fMRI	Russell et al., 2000	5 schizophrenia, 7 controls	fMRI, RME (30 items, 2 choices)	Accuracy deficit	areas for controls: left IFG (into insula and medial frontal lobe), left middle, and left STG; less activation for schizophrenics: left IFG
ERP w/ LORETA-KEY source localization	Sabbagh, Moulson, & Harkness, 2004	18 nonclinical	ERP, modified RME (“does the word match the face?” 72 trials, one match, one mismatch per stim)		ERP: More N270–400 over right inferior frontal and right anterior temporal sites, more P300–500 over bilateral parietal sites LORETA-KEY source localization suggests right OFC and right anterior medial temporal cortex

Acknowledgments

We thank Tomoko Kato, Ying Hao Lai, and Carl Becker for translation assistance; Annette Schmid for assistance in data analysis; and Katharine Donnelly Adams for comments on an early version of this manuscript. This research was supported in part by a Social Science Research Institute research grant,

The Pennsylvania State University to R. B. A., Jr., and a National Institute of Mental Health, National Institutes of Health research grant (1R01MH70833-01A1) to N. A.

Reprint requests should be sent to Reginald B. Adams, Jr., The Pennsylvania State University, 544 Moore Building, University Park, PA 16802, or via e-mail: radams@psu.edu.

Note

1. The GD baseline also controls for potential differences in activation due to physiognomic disparities among our Asian and white American eye stimuli. One prominent and easily measured example of this possible source of systematic variation is eyebrow height. To examine differences in this cue, an author on this article (M. T. S.) measured brow height, following the procedures outlined in Campbell, Wallace, & Benson (1996). This revealed that our Asian eye stimuli exhibit significantly higher brows (nearly twice as high) than the white American eye stimuli, $t(70) = 8.99, p < .001, r = .73$. Given that low versus high eyebrows on otherwise nonexpressive human faces yield both dominant versus submissive attributions, as well as anger versus fear attributions, respectively (Laser & Mathie, 1982; Keating, Mazur, & Segall, 1977), this finding demonstrates the importance of controlling for such physiognomic variability.

REFERENCES

- Adolphs, R., Baron-Cohen, S., & Tranel, D. (2002). Impaired recognition of social emotions following amygdala damage. *Journal of Cognitive Neuroscience, 14*, 1264–1274.
- Adolphs, R., Tranel, D., & Damasio, H. (2001). Emotion recognition from faces and prosody following temporal lobectomy. *Neuropsychology, 15*, 396–404.
- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences, 4*, 267–278.
- Argyle, M., & Cook, M. (1976). *Gaze and mutual gaze*. Cambridge, UK: Cambridge University Press.
- Avis, J., & Harris, P. L. (1991). Belief–desire reasoning among Baka children: Evidence for a universal conception of mind. *Child Development, 62*, 460–467.
- Baron-Cohen, S. (1995). *Mindblindness: An essay on autism and theory of mind*. Boston, MA: MIT Press/Bradford Books.
- Baron-Cohen, S., Ring, H., Wheelwright, S., Bullmore, E. T., Brammer, M. J., Simmons, A., et al. (1999). Social intelligence in the normal and autistic brain: An fMRI study. *European Journal of Neuroscience, 11*, 1891–1898.
- Baron-Cohen, S., Ring, H., Chitnis, X., Wheelwright, S., Gregory, L., Williams, S., et al. (2006). fMRI of parents of children with Asperger Syndrome: A pilot study. *Brain and Cognition, 61*, 122–130.
- Baron-Cohen, S., Riviere, A., Fukushima, M., French, D., Hadwin, J., Cross, P., et al. (1996). Reading the mind in the face: A cross-cultural and developmental study. *Visual Cognition, 3*, 39–59.
- Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The “reading the mind in the eyes” test revised version: A study with normal adults, and adults with asperger syndrome or high-functioning autism. *Journal of Child Psychology and Psychiatry, 42*, 241–251.
- Baron-Cohen, S., Wheelwright, S., & Jolliffe, T. (1997). Is there a “language of the eyes”? Evidence from normal adults, and adults with autism or asperger syndrome. *Visual Cognition, 4*, 311–331.
- Brune, M., & Brune-Cohrs, U. (2006). Theory of mind: Evolution, ontogeny, brain mechanisms and psychopathology. *Neuroscience and Biobehavioral Reviews, 30*, 437–455.
- Calder, A. J., Lawrence, A. D., Keane, J., Scott, S. K., Owen, A. M., Christoffels, I., et al. (2002). Reading the mind from eye gaze. *Neuropsychologia, 40*, 1129–1138.
- Campbell, R., Wallace, S., & Benson, P. J. (1996). Real men don't look down: Direction of gaze affects sex decisions on faces. *Perception, 3*, 391–412.
- Chiao, J. Y., & Ambady, N. (2007). Cultural neuroscience: Parsing universality and diversity across levels of analysis. In S. Kitayama & D. Cohen (Eds.), *Handbook of cultural psychology* (pp. 237–254). New York: Guilford Press.
- Chiao, J. Y., Iidaka, T., Gordon, H. L., Nogawa, J., Bar, M., Aminoff, E., et al. (in press). Cultural specificity in amygdala response to fear faces. *Journal of Cognitive Neuroscience*.
- DePaulo, B. M., Ansfield, M. E., Kirkendol, S. E., & Boden, J. M. (2004). Serious lies. *Basic and Applied Social Psychology, 26*, 147–167.
- Dunbar, R. (1998). The social brain hypothesis. *Evolutionary Anthropology, 6*, 178–190.
- Elfenbein, H. A., & Ambady, N. (2003). When familiarity breeds accuracy: Cultural exposure and facial emotion recognition. *Journal of Personality and Social Psychology, 85*, 276–290.
- Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience & Biobehavioral Reviews, 24*, 581–604.
- Farrant, A., Morris, R. G., Russell, T., Elwes, R., Akanuma, N., Alarcon, G., et al. (2005). Social cognition in frontal lobe epilepsy. *Epilepsy & Behavior, 7*, 506–516.
- Farroni, T., Csibra, G., Simion, F., & Johnson, M. H. (2002). Eye contact detection in humans from birth. *Proceedings of the National Academy of Sciences, U.S.A., 99*, 9602–9605.
- Flavell, J. H. (1999). Cognitive development: Children's knowledge about the mind. *Annual Review of Psychology, 50*, 21–45.
- Gallagher, H. L., & Frith, C. D. (2003). Functional imaging of “theory of mind.” *Trends in Cognitive Sciences, 7*, 77–83.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4*, 223–233.
- Iacoboni, M. (2005). Neural mechanisms of imitation. *Current Opinion in Neurobiology, 15*, 632–637.
- Janik, S. W., Wellens, A. R., Goldberg, M. L., & Dell'Osso, L. F. (1978). Eyes as the center of focus in the visual examination of human faces. *Perceptual and Motor Skills, 47*, 857–858.
- Jenkins, J. M., & Astington, J. W. (1996). Cognitive factors and family structure associated with theory of mind development in young children. *Developmental Psychology, 32*, 70–78.
- Keating, C. F., Mazur, A., & Segall, M. H. (1977). Facial gestures which influence the perception of status. *Social Psychology Quarterly, 40*, 374–378.
- Kircher, T. T., Brammer, M., Bullmore, E., Simmons, A., Bartels, M., & David, A. S. (2002). The neural correlates of intentional and incidental self processing. *Neuropsychologia, 40*, 683–692.
- Kobayashi, C., Glover, G. H., & Temple, E. (2006). Cultural and linguistic influence on neural bases of “theory of mind”: An fMRI study with Japanese bilinguals. *Brain and Language, 98*, 210–220.
- Kobayashi, C., Glover, G. H., & Temple, E. (2007). Cultural and linguistic effects on neural bases of “theory of mind” in American and Japanese children. *Brain Research, 1164*, 95–107.
- Laser, P. S., & Mathie, V. A. (1982). Face facts: An unbidden role for features in communication. *Journal of Nonverbal Behavior, 7*, 3–19.
- Levin, D. T. (1996). Classifying faces by race: The structure of face categories. *Journal of Experimental Psychology, 22*, 1364–1382.
- Lillard, A. S. (1998). Ethnopsychologies: Cultural variations in theories of mind. *Psychological Bulletin, 123*, 3–32.

- Markus, H., Kitayama, S., & Heiman, R. (1996). Culture and “basic” psychological principles. In E. T. Higgins & A. W. Kruglanski (Eds.), *Social psychology: Handbook of basic principles* (pp. 857–913). New York: Guilford.
- Mason, M. F., & Macrae, C. N. (2008). Perspective-taking from a social neuroscience standpoint. *Group Processes and Intergroup Relations, 11*, 215–232.
- Meissner, C. A., & Brigham, J. C. (2001). Thirty years of investigating the own-race bias in memory for faces. *Psychology, Public Policy, and Law, 7*, 3–35.
- Michel, C., Rossion, B., Han, J., Chung, C., & Caldara, R. (2006). Holistic processing is finely tuned for faces of one’s own race. *Psychological Science, 17*, 608–615.
- Mitchell, J. P., Macrae, C. N., & Banaji, M. R. (2006). Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. *Neuron, 50*, 655–663.
- Nguyen, B. T., Tran, T. D., Hoshiyama, M., Inui, K., & Kakigi, R. (2004). Face representation in the human primary somatosensory cortex. *Neuroscience Research, 50*, 227–232.
- Nummenmaa, T. (1964). The language of the face. *Jyväskylä Studies in Education, Psychology and Social Research, 9*.
- Paladino, P. M., Leyens, J. P., Rodriguez, R. T., Rodriguez, A. P., Gaunt, R., & Demoulin, S. (2002). Differential association of uniquely and nonuniquely human emotions to the ingroup and the outgroups. *Group Processes and Intergroup Relations, 5*, 105–117.
- Penfield, W., & Rasmussen, T. (1950). *The cerebral cortex of man: A clinical study of localization of function*. New York: Macmillan.
- Perner, J., Ruffman, T., & Leekam, S. R. (1994). Theory of mind is contagious: You catch it from your sibs. *Child Development, 65*, 1228–1238.
- Perrett, D. I., & Mistlin, A. J. (1990). Perception of facial characteristics by monkeys. In M. Berkeley & W. Stebbins (Eds.), *Comparative perception*. New York: Wiley.
- Peterson, C. C., & Siegal, M. (1997). Psychological, physical, and biological thinking in normal, autistic, and deaf children. In H. M. Wellman & K. Inagaki (Eds.), *The emergence of core domains of thought: Children’s reasoning about physical, psychological, and biological phenomena (New directions for child development, No. 75)* (pp. 55–70). San Francisco: Jossey-Bass.
- Platek, S. M., Fonteyn, L. C. M., Myers, T. E., Izzetoglu, M., Ayaz, H., Li, C., et al. (2005). Functional near infrared spectroscopy reveals differences in self–other processing as a function of schizotypal personality traits. *Schizophrenia Research, 73*, 125–127.
- Platek, S. M., Keenan, J. P., Gallup, G. G., Jr., & Mohamed, F. B. (2004). Where am I? The neurological correlates of self and other. *Cognitive Brain Research, 19*, 114–122.
- Ruby, P., & Decety, J. (2004). How would you feel versus how do you think she would feel? A neuroimaging study of perspective-taking with social emotions. *Journal of Cognitive Neuroscience, 16*, 988–999.
- Rule, N. O., Ambady, N., Adams, R. B., Jr., & Macrae, C. N. (2008). Facets of the face: Accuracy and awareness in the perception and categorization of male sexual orientation. *Journal of Personality and Social Psychology, 95*, 1019–1028.
- Russell, T. A., Rubia, K., Bullmore, E. T., Soni, W., Suckling, J., Brammer, M. J., et al. (2000). Exploring the social brain in schizophrenia: Left prefrontal underactivation during mental state attribution. *American Journal of Psychiatry, 157*, 2040–2042.
- Sabbagh, M. A. (2004). Understanding orbitofrontal contributions to theory-of-mind reasoning: Implications for autism. *Brain and Cognition, 55*, 209–219.
- Sabbagh, M. A., Moulson, M. C., & Harkness, K. L. (2004). Neural correlates of mental state decoding in human adults: An event-related potential study. *Journal of Cognitive Neuroscience, 16*, 415–426.
- Saxe, R., & Baron-Cohen, S. (2006). Editorial: The neuroscience of theory of mind. *Social Neuroscience, 1*, 1–9.
- Saxe, R., Jamal, N., & Powell, L. (2006). My body or yours? The effect of visual perspective on cortical body representations. *Cerebral Cortex, 16*, 178–182.
- Shaw, P., Bramham, J., Lawrence, E. J., Morris, R., Baron-Cohen, S., & David, A. S. (2005). Differential effects of lesions of the amygdala and prefrontal cortex and recognizing facial expressions of complex emotions. *Journal of Cognitive Neuroscience, 17*, 1410–1419.
- Stone, V. E., Baron-Cohen, S., Calder, A., Keane, J., & Young, A. (2003). Acquired theory of mind impairments in individuals with bilateral amygdala lesions. *Neuropsychologia, 41*, 209–220.
- Sugiyama, L. S., Tooby, J., & Cosmides, L. (2002). Cross-cultural evidence of cognitive adaptations for social exchange among the Shiwiar of Ecuadorian Amazonia. *Proceedings of the National Academy of Sciences, U.S.A., 99*, 11537–11542.
- Tager-Flusberg, H. (2001). A reexamination of the theory of mind hypothesis of autism. In J. A. Burack, T. Charman, N. Yimiyi, & P. R. Zelazo (Eds.), *The development of autism: Perspectives from development and theory* (pp. 173–193). Mahwah, NJ: Erlbaum.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology, 35–57*.
- Vinette, C., Gosselin, F., & Schyns, P. G. (2004). Spatio-temporal dynamics of face recognition in a flash: It’s in the eyes. *Cognitive Science, 28*, 289–301.
- Zebrowitz, L. A. (2006). Finally, faces find favor. *Social Cognition, 24*, 657–701.