Attribution of Emotions to Body Postures: An Independent Component Analysis Study of Functional Connectivity in Autism

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Abstract: The ability to interpret others' body language is a vital skill that helps us infer their thoughts and emotions. However, individuals with autism spectrum disorder (ASD) have been found to have difficulty in understanding the meaning of people's body language, perhaps leading to an overarching deficit in processing emotions. The current fMRI study investigates the functional connectivity underlying emotion and action judgment in the context of processing body language in high-functioning adolescents and young adults with autism, using an independent components analysis (ICA) of the fMRI time series. While there were no reliable group differences in brain activity, the ICA revealed significant involvement of occipital and parietal regions in processing body actions; and inferior frontal gyrus, superior medial prefrontal cortex, and occipital cortex in body expressions of emotions. In a between-group analysis, participants with autism, relative to typical controls, demonstrated significantly reduced temporal coherence in left ventral premotor cortex and right superior parietal lobule while processing emotions. Participants with ASD, on the other hand, showed increased temporal coherence in left fusiform gyrus while inferring emotions from body postures. Finally, a positive predictive relationship was found between empathizing ability and the brain areas underlying emotion processing in ASD participants. These results underscore the differential role of frontal and parietal brain regions in processing emotional body language in autism. *Hum Brain Mapp* 35:5204–5218, 2014. © 2014 Wiley Periodicals, Inc.

Key words: autism; fMRI; independent component analysis; functional connectivity; emotion; body postures

INTRODUCTION

Although social and affective neuroscience research on autism has focused primarily on processing emotions and intentions from faces, of late there has been growing interest in the neural bases of body centered emotions. While there is extensive literature on face processing in autism spectrum disorders (ASD) [see Grelotti et al., 2002; Jemel et al., 2006 for reviews], processing body language has received relatively limited attention, despite its importance in social cognition. Bodies provide a wealth of social and emotional information not always conveyed by faces alone [de Gelder, 2009]. Body postures can convey the emotional

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states of others [Slaughter et al., 2004], help people infer others' feelings and intentions from a distance, formulate appropriate social responses [de Gelder, 2009], regulate one's own emotions [Bianchi-Berthouze et al., 2006], and help detect deception and threat [Grèzes et al., 2004; Sinke et al., 2010]. Understanding the neural underpinnings of emotional body language also provides a unique opportunity to study the *social brain* (brain areas that are primarily associated with social cognition) in individuals with ASD. Patients with ASD are particularly poor at recognizing emotions [Golan et al., 2006; Kuusikko et al., 2009; Law Smith et al., 2010], the neural bases of which are relatively underexplored. Thus, understanding the function and dysfunction of the social brain and its relevance to emotion processing is critical in explaining the social symptoms in individuals with ASD.

Bodily actions and expressions are processed at a few different levels in the brain. The extrastriate body area (EBA) [Downing et al., 2001, 2006; Pourtois et al., 2007] and the fusiform gyrus/fusiform body area [Peelen and Downing, 2005a,b; Schwarzklose et al., 2005] have been reported to be coding for the visual representation of the human body form. Processing movement-related aspects of body postures, which may involve motor simulation, recruits the superior temporal sulcus (STS), cingulate cortex, parietal cortex, inferior frontal gyrus (IFG), premotor, and primary motor cortex [Allison et al., 2000; de Gelder, 2006; de Gelder et al., 2004; Kana and Travers, 2012]. Finally, the social and emotional information to be gleaned from human body postures may be mediated by regions that are part of the mirror neuron system (MNS), such as the IFG, and superior/inferior parietal lobule [Gallese et al., 2004; Gazzola et al., 2006, 2007; Grafton and Hamilton, 2007; Hari et al., 1998], and core regions underlying theory-of-mind (ToM) processing, such as the cingulate cortex, STS/temporo-parietal junction (TPJ), and the medial prefrontal cortex (MPFC) [Fletcher et al., 1995; Gallagher et al., 2000; Ruby and Decety, 2003; Saxe and Kanwisher, 2003; Vogeley et al., 2001]. Emotion and intention conveyed by body language also activate the amygdala, orbitofrontal cortex (OFC), anterior cingulate cortex (ACC), posterior cingulate cortex (PCC), motor cortex, striatum, STS, and insula [de Gelder, 2004, 2006; Grèzes et al., 2004, 2007; Kana and Travers, 2012; Sinke et al., 2010; van de Riet et al., 2009].

fMRI studies in ASD have uncovered abnormalities in motor representation and the MNS [Bernier et al., 2007; Dapretto et al., 2005; Kana et al., 2011b; Martineau et al., 2008; Nishitani et al., 2004; Oberman et al., 2005; Williams et al., 2006], in ToM [Baron-Cohen et al., 1999; Kana et al., 2009, 2014; Pelphrey et al., 2005], and in understanding emotions [Ashwin et al., 2006; Critchley et al., 2000; Dalton et al., 2005; Kleinbans et al., 2010; Monk et al., 2010; Wang et al., 2004]. The marked deficits in social interaction seen in individuals with ASD pose challenge to the accurate assessment of emotional information [Ashwin et al., 2006; Baron-Cohen et al., 2000; Dapretto et al., 2005; Dawson

et al., 2004a,b; Hall et al., 2007; Pelphrey et al., 2007]. When viewing whole body movements in full-light and point-light displays, individuals with ASD are less accurate than typically developing (TD) peers in classifying emotions [Atkinson, 2009; Hubert et al., 2007]. Individuals with ASD have difficulty in matching postural cues representing emotions such as boredom [Doody and Bull, 2011] and show significantly poorer identification of bodily emotions such as fear [Doody and Bull, 2012]. In addition, previous studies found significantly longer reaction time for patients with ASD to make judgments of body language, compared to TD peers [Doody and Bull, 2011, 2012]. Moreover, it has been found that fearful body language failed to elicit activation in ASD in the ventral visual and IPL/IFG areas and did not elicit differential brain activity for emotional versus neutral body postures, compared to TD peers [Hadjikhani et al., 2009]. Bodies are usually processed holistically, demonstrated by an inversion effect similar to face processing, with the global whole taken into account when viewing [Reed et al., 2003, 2006]. The difficulty individuals with ASD have in global coherence [Bölte et al., 2007, 2008; Happé and Frith, 2006; Pellicano et al., 2005], and their difficulty with understanding the meaning of emotional faces (see [Grelotti et al., 2002] for a review) may suggest their challenge in understanding emotional body language.

Previous neuroimaging studies in ASD have pointed to disrupted cortical connectivity as a potential source for social cognitive dysfunction in the disorder (see [Maximo et al., 2014; Kana and Just, 2011; Kana et al., 2011a; Schipul et al., 2011] for reviews). For instance, a functional disconnection between the prefrontal cortex and the more posterior temporal/parietal brain areas may hinder the successful processing of complex inputs, such as others' actions and emotions. While there is evidence for differential patterns of activation in adults with ASD in response to fearful body language [Hadjikhani et al., 2009], functional connectivity underlying emotional body language processing in ASD is under-examined. The current study examined this in individuals with ASD using an independent component analysis (ICA). ICA is a functional connectivity technique that utilizes the fMRI time courses of participants to group the brain activity into regions or components that are spatiotemporally independent, in order to identify the neural networks with the same response pattern for a task [Calhoun et al., 2009]. ICA differs from traditional functional connectivity approaches in its focus on whole-brain connectivity, ranking neural components for a specific task rather than using predefined regions of interest (ROI). Whereas traditional techniques rely on previous theories of brain connectivity, or a priori definition of ROIs, ICA is not bound to previously set ROIs. As a result, the dynamics of connectivity can be uncovered without relying on a specific model [Calhoun et al., 2001b]. While task-based fMRI studies have used ICA analysis widely in typical individuals [McKeown et al., 1998; Calhoun et al., 2001, 2002, 2008], there are few,

TABLE I. Participant demographic information

Measure	Autism (N = 27)			Control (N = 23)			Group difference	
	Mean	Range	SD	Mean	Range	SD	<i>t</i> -value	<i>P</i>
Age (yrs)	21.04	13–40	1.40	21.38	13–36	1.44	0.21	0.83
Verbal IQ	108.7	79–135	3.09	109.2	82–129	2.65	0.1	0.92
Performance IQ	110.9	74–138	3.38	111.1	92–132	2.45	0.04	0.96
Full-scale IQ	111.1	75–140	3.19	113.1	94–134	2.25	0.49	0.62
RME	19	10–25	0.72	21	15–24	0.57	1.51	0.13
Empathy quotient	19	4–29	1.23	44	24–68	2.79	8.34	<0.001

if any, that used ICA in a task-related study in ASD. Thus, the current study is novel in examining functionally relevant neural networks underlying bodily emotion in individuals with ASD using ICA.

METHOD

Participants

Twenty-seven high-functioning adolescents and young adults with ASD (23 males/4 females; mean age: 21.04 years) and 23 age and IQ matched typically developing (TD) peers (20 males/3 female; mean age: 21.38 years) participated in this fMRI study (see Table I for demographic information). The IQ of participants was assessed using the Wechsler Abbreviated Scale of Intelligence (WASI) [Wechsler, 1999] handedness using the Edinburgh Handedness Inventory [Oldfield, 1971], theory-of-mind skills using the Reading the Mind in the Eyes (RME) test [Baron-Cohen et al., 2001], and empathizing ability using the Empathy Quotient (EQ) scale [Baron-Cohen and Wheelwright, 2004]. The study was approved by the Institutional Review Board of the University of Alabama at Birmingham, and all participants provided informed consent for their participation in the study. Participants with ASD had received a previous diagnosis of an ASD based on Autism Diagnostic Interview (ADI-R) symptoms, and Autism Diagnostic Observation Schedule (ADOS). TD participants were screened through a self-report history questionnaire to rule out neurological disorders, such as ASD, ADHD, or Tourette's Disorder, that could potentially confound the results.

Experimental Paradigm

The stimuli consisted of static stick figure characters depicting different body postures (adapted from [Kana and Travers, 2012]). The stick figure characters appeared to engage in either a physical action (e.g., jumping, throwing) or an emotion (upset, happy) (see Fig. 1 for examples). Stimuli were presented in a blocked design format, with two experimental conditions (physical action and emotion state), and a fixation baseline. This study consisted of six experimental blocks, with three blocks per condition (action and emotion). In addition, three 24-s long fixation baselines were presented at the beginning of the experiment, in the middle,

and at the end of the experiment. Six second breaks were presented between each block that did not end in fixation. Each experimental block lasted 18 s (three trials per block, lasting 6 s each), with the total experiment lasting for 198 s. During each trial, stick figure characters were presented one at a time on the screen and participants were asked to determine, from three answer choices, what the character was doing (in action condition) or feeling (in emotion condition). Participants made their responses on a fiber optic button response system. Prior to beginning the fMRI scan, participants practiced the task (utilizing similar, but novel, stimuli) on a laptop computer. In the MRI scanner, the experiment was presented using E-Prime 1.2 software (Psychology Software Tools, Pittsburgh, PA). An IFIS interface (Integrated Functional Imaging System, Invivo Corporation, Orlando, FL) was used to project the stimuli onto a screen for the participants to view in the scanner.

Neuroimaging Parameters

Functional and structural MRI data were collected at the UAB Civitan International Research Center on a Siemens 3.0

Figure 1.

Example stimuli presented during the fMRI task. Each static image depicts a stick figure character engaged in either (a) an action state (action condition), or (b) an emotion state (emotion condition).

Tesla Allegra head-only scanner (Siemens Medical Inc., Erlangen, Germany). For structural imaging, initial high resolution T1-weighted scans were acquired using a 160-slice 3D MPRAGE volume scan with TR = 200 ms, TE = 3.34 ms, flip angle = 7 degrees, FOV = 25.6 cm, 256×256 matrix size, and 1 mm slice thickness. For functional imaging, a single-shot gradient-recalled echo-planar pulse sequence was used for rapid image acquisition (TR = 1,000 ms, TE = 30 ms, flip angle = 60 degrees). Seventeen adjacent oblique-axial slices were acquired in an interleaved sequence with 5 mm slice thickness, 1 mm slice gap, a 24×24 cm field of view (FOV), and a 64×64 matrix, resulting in an in-plane resolution of $3.75 \times 3.75 \times 5$ mm³. Images were corrected for slice acquisition timing, motion-corrected, normalized to the Montreal Neurological Institute (MNI) template, resampled to $2 \times 2 \times 2$ mm³ voxels, and smoothed with an 8-mm Gaussian kernel to decrease spatial noise.

Distribution of Activation

The brain activation data were analyzed using Statistical Parametric Mapping (SPM8) software (Wellcome Department of Cognitive Neurology, London, UK). We performed statistical analysis on individual and group data using SPM8's implementation of the general linear model [Friston et al., 1994]. Within-group activation was analyzed for the ASD and TD groups of participants for all trials with separate regressors defined for action, emotion, and fixation baseline conditions, and participant ages as covariates. Within-group analyses used a cluster size of 80 mm³ determined by 10,000 Monte Carlo simulations at an uncorrected *P* value of 0.001, as simulations can implicate cluster size thresholds that produce the best balance between Type I and Type II error [Lieberman and Cunningham, 2009].

Addressing Head Motion Artifacts

Because head motion can impact functional connectivity analyses [Satterthwaite et al., 2012; Van Dijk et al., 2012], we had a conservative threshold of 0.5 mm for head motion in any direction. In addition, we computed the mean head motion for each subject in each direction (measured as translation and rotation in millimeters for each brain volume in the *x*, *y*, *z* planes for the duration of the run) and used these values to compare head motion for the ASD and TD groups. A two-way analysis of variance was conducted to test the effects of group (ASD and TD) and motion parameter (translation and rotation for *x*, *y*, and *z*). The interaction of group and motion type was not statistically significant, $F_{(5,235)} = 0.277$, $P = 0.925$.

Independent Component Analysis

The ICA was implemented via the Group ICA of FMRI Toolbox (GIFT v1.3i) in order to establish temporally coherent neural networks and determine their relationships to the task conditions [Calhoun et al., 2001a] (see Supporting

Information Fig. S1 for steps performed in the ICA and *t*-tests). GIFT was used to reduce all data through two stages of principal component analysis (PCA), then estimate the total number of whole-group components using the minimum descriptive length (MDL) criteria tool. Twenty-eight independent components were estimated at this stage. The reduced data were then used by the ICA algorithm to construct independent component time courses and spatial maps for each subject. Independent components for each subject and for the group (mean components) were then visualized within GIFT [Calhoun et al., 2001a, 2009]. Using the *temporal sorting tool* in GIFT, these components were ranked according to their relatedness to specific experimental conditions, as determined by their R^2 values. The ICASSO tool within GIFT was used to determine the stability of the components over 10 iterations of the ICA algorithm. Using these methods, eight components were identified as unstable (ICASSO), artifactual (visual inspection), and/or unrelated to any specific experimental condition (R^2 and visual inspection of component time course in relation to task design). These components were then eliminated from consideration for further analyses using the remove components utility, and the ICA was repeated minus their influence. This resulted in a final set of 20 components that correlated with the task. As many of these components had very low R^2 values, only the top two components for each group for each condition are reported and discussed in detail in the current study to represent the neural networks most strongly related to the experimental task.

Individual coherence maps of each subject were entered into one sample *t*-tests in SPM8 to create a sample-specific component map. These maps were used as a mask for group analyses within each component. The *z* values in these individual maps represent the fit of a specific voxel BOLD time-course to the group averaged component's time-course. Thus, group analyses test the connectivity strength (i.e. signal synchronization) of each voxel to the whole spatial component. To directly compare groups on connectivity strength of each voxel to the whole spatial component, two sample *t*-tests of the top ranked component for each condition (action and emotion) for the whole-group (all subjects combined) were conducted. In other words, for group comparison, all results were masked with the whole group's (ASD and control) average independent component to ensure that only effects restricted to the spatial extent of the component were included in the analyses.

RESULTS

Brain Activation

Separate whole brain within-group one-sample *t*-test analyses of the activation for the TD group and ASD group were conducted. For each condition (action > fixation and emotion > fixation) as well as the whole task activation (action and emotion conditions combined, action + emotion > fixation), both groups elicited a similar pattern of

Figure 2.

Within-group brain activation patterns (measured by general linear model) for autism (ASD) and typically developing (TD) participants for processing bodily actions and emotion states. Contrasts include (a) action > fixation, (b) emotion > fixation,

and (c) action + emotion > fixation ($P < 0.001$ uncorrected; cluster size = 80 mm³). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

brain activity. The main regions recruited by processing body language included bilateral inferior and middle occipital cortices, bilateral IFG, left SMA, bilateral EBA, and bilateral SPL and IPL ($P < 0.001$ uncorrected, cluster size = 80 mm³) (see Fig. 2). To assess group differences in brain activation, between-group two-sample *t*-test analyses of the activation were conducted for the ASD and TD groups. Across all contrasts, no significant differences between groups were found.

Within-Group ICA Components: ASD Group

In one-sample *t*-tests for the ASD group ($P < 0.05$, FWE corrected), the components most strongly correlated to processing actions (see Fig. 3 and Table II) were primarily composed of parietal and occipital areas. On further analysis of

the top two components, the first-ranked action component of the ASD group (also known as “ASD action 1”; $R^2 = 0.139$) was composed primarily of a cluster that included the left inferior and middle occipital gyri (LIOG and LMOG), as well as the right calcarine sulcus (RCALC) [$t_{(26)} = 19.34$, $P < 0.05$; $k = 8,534$] (“*k*” indicates cluster size). The second-ranked action component of the ASD group (ASD action 2; $R^2 = 0.138$) consisted of left postcentral and precentral gyri [$t_{(26)} = 17.87$, $P < 0.05$; $k = 5,600$]. The first-ranked emotion component for the ASD group (ASD emotion 1; $R^2 = 0.17$) was composed of the RIFG [$t_{(26)} = 14.94$, $P < 0.05$; $k = 3,713$], and the LIFG [$t_{(26)} = 12.03$, $P < 0.05$; $k = 3,085$]. The second-ranked emotion component of the ASD group (ASD emotion 2; $R^2 = 0.129$) was the same as that previously described for the action condition (ASD action 1) (see Fig. 3 and Table II). Thus, while the action condition elicited

Figure 3.

Top ranked components within each group for processing whole body actions in the autism (ASD) (top panel) and typically developing (TD) (bottom panel) participants. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

mostly visuospatial and motor components, emotion judgment additionally elicited frontal areas.

Within-Group Components: TD Group

Of the two TD group components that were most strongly associated with the action condition (see Fig. 4 and Table II), the first-ranked action component (TD action 1; $R^2 = 0.182$) was primarily an occipital component, consisting almost exclusively of bilateral calcarine areas [$t_{(22)} = 17.51$, $P < 0.05$; $k = 5,440$]. The second-ranked action component of the TD group (TD action 2; $R^2 = 0.142$) was composed of a cluster that included the bilateral precuneus, and right superior occipital areas [$t_{(22)} = 19.09$, $P < 0.05$; $k = 11,614$], along with a cluster in the left inferior temporal area [$t_{(22)} = 12.42$, $P < 0.05$; $k = 340$]. For the emotion condition, the top two components in the TD group (see Fig. 4 and Table II) included prefrontal, temporal, and midline cortical regions. The first-ranked emotion component of the TD group (TD emotion 1; $R^2 = 0.238$) included the left pars triangularis aspect of the IFG and left middle frontal gyrus (LMFG) [$t_{(22)} = 17.99$, $P <$

0.05 ; $k = 3,483$], along with left MPFC [$t_{(22)} = 13.54$, $P < 0.05$; $k = 466$], a cluster that included the left inferior parietal lobule (LIPL) [$t_{(22)} = 13.33$, $P < 0.05$; $k = 567$], and the RIFG [$t_{(22)} = 10.84$, $P < 0.05$; $k = 512$]. The second-ranked emotion component of the TD group (TD emotion 2; $R^2 = 0.132$) was the same as that described for the action condition (TD action 1).

Between-Group Comparison

To compare differences in functional connectivity between groups, we first identified the top components for action and emotion conditions for all subjects combined (ASD + TD). Using the masks of the top components from this analysis, the two groups were compared for statistically significant differences in their contributions to these components. The top component for the action condition (across all participants, ASD and TD) was dominated by a cluster that included calcarine, cuneus, and middle occipital areas ($R^2 = 0.145$) [$t_{(49)} = 27.88$, $P < 0.05$, $k = 8,205$]. The highest ranked component for emotion judgment ($R^2 = 0.236$) was

TABLE II. Top ranked components for processing action and emotion in the ASD and TD groups ($P < 0.05$ family-wise error corrected)

Group	Comp. rank	R^2	Hem	Region	x	y	z	t	k^a	
Action										
ASD	1	0.139	Left	Inferior occipital	-38	-90	-12	19.34	8,534	
			Left	Middle occipital	-24	-94	10			
			Right	Calcarine	8	-96	4			
	2	0.138	Left	Precentral	-38	-22	62	17.87	5,600	
			Left	Postcentral	-46	-26	54			
TD	1	0.182	Right	Calcarine	8	-82	4	17.51	5,440	
	2	0.142	Right	Precuneus	16	-76	46	19.09	11,614	
			Left	Cuneus	-6	-76	46			
Right			Superior occipital	32	-78	44				
			Left	Inferior temporal	-50	-66	-8	12.42	340	
Emotion										
ASD	1	0.17	Right	Inferior frontal	54	20	28	14.94	3,713	
			Left	Inferior frontal	-44	32	4	12.03	3,085	
			2	0.129	Left	Inferior occipital	-38	-90	-12	19.34
Left	Middle occipital	-24			-94	10				
Right	Calcarine	8			-96	4				
TD	1	0.238	Left	Pars triangularis	-48	24	22	17.99	3,483	
			Left	Middle prefrontal	-34	20	36			
			Left	Medial prefrontal	-2	44	36			
	2	0.182	Left	Inferior parietal	-38	-58	46	13.33	567	
			Right	Inferior frontal	58	28	24	10.84	512	

^a k values represent entire peak cluster size, with contained subregions listed as a part of the cluster.

HeM = hemisphere; Comp = component; k = cluster size.

composed of clusters including the pars triangularis aspect of the LIFG, and the left MPFC [$t_{(49)} = 21.87$, $P < 0.05$, $k = 6,021$]. For the action condition, we found significantly increased correlation in a cluster of the left precentral gyrus for the ASD group, relative to TD controls ($P < 0.005$, cluster size = 56 mm^3). The TD group, on the other hand, had significantly greater correlation in right superior temporal sulcus, and left Supporting Information motor area ($P < 0.005$, cluster size = 56 mm^3) (see Fig. 5). The threshold was determined using a significance threshold ($P = 0.005$ uncorrected) that Monte Carlo simulations indicated was significant at a $P < 0.05$ (corrected) level when restricted to clusters larger than 56 mm^3 .

We also compared each group's contributions to the top ranked component for the emotion condition. In this case, the ASD group showed significant increase in temporal coherence, relative to TD, in the left fusiform gyrus, and left superior parietal lobule ($P < 0.005$, cluster size = 56 mm^3). On the other hand, the TD group showed significantly increased coherence, relative to ASD, in left ventral premotor cortex, left IFG, and right superior parietal lobule ($P < 0.005$, cluster size = 56 mm^3) (see Fig. 6).

Behavioral Performance

To assess possible group differences in performance accuracy and reaction time (RT) while making judgments about

body language, we conducted a 2 Group (ASD vs. TD) $\times$ 2 Condition (*action* vs. *emotion*) mixed ANOVA. Group was treated as a between-subject factor and action and emotion conditions were treated as within-subject variables, with the alpha level set at 0.05. There was no significant main effect of group in performance accuracy (ASD *action*: $M = 93\%$, $SD = 15\%$; *emotion*: $M = 77\%$, $SD = 23\%$; TD *action*: $M = 96\%$, $SD = 7\%$; *emotion*: $M = 84\%$, $SD = 15\%$) ($F_{(2,40)} = 1.451$, $P = 0.235$). A significant main effect of condition ($F_{(2,40)} = 27.86$, $P < 0.001$) was found, indicating both groups had significantly greater accuracy while judging actions compared to judging emotions. There was no significant interaction between group and condition for accuracy ($F_{(2,40)} = 0.529$, $P = 0.471$). For reaction time, there was no significant main effect of group (ASD *action*: $M = 2,367 \text{ ms}$, $SD = 494$; *emotion*: $M = 2,875 \text{ ms}$, $SD = 519$; TD *action*: $M = 2,202 \text{ ms}$, $SD = 413$; *emotion*: $M = 2,693 \text{ ms}$, $SD = 380$) ($F_{(2,42)} = 1.750$, $P = 0.193$). There was a significant main effect of condition ($F_{(2,42)} = 111.7$, $P < 0.001$) with both groups taking significantly longer time to process emotional body language compared to actions. No significant interaction between group and condition for reaction time ($F_{(2,42)} = 0.031$, $P = 0.861$) was found.

Brain-Behavior Correlations

We predicted that the participants' empathizing ability may be correlated with their emotion judgment and the

Figure 4.

Top ranked components within each group for processing whole body emotions in the autism (ASD) (top panel) and typically developing (TD) (bottom panel) participants. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

neural substrates underlying it. Parameter estimates (beta weights) for each subject were extracted from the component that was ranked first for the emotion condition in the whole-group ICA results. This component was primarily composed of the left IFG, the right IFG, LIPL, and the left MPFC. The EQ scores from participants and parameter estimates representing the cluster of the top emotion component (mask created representing the whole group of participants) were correlated. The ASD participants had a significant positive correlation between EQ scores and the top component for the emotion condition ($r = 0.50$, $P = 0.013$) (see Fig. 7), whereas TD participants did not have a significant relationship between EQ scores and their beta weights for the top emotion component ($r = 0.17$, $P = 0.437$).

DISCUSSION

The current study investigated the functional connectivity underlying emotion and action judgments in the context of processing body language in high-functioning

adolescents and young adults with ASD. While we found no significant group differences in brain activation, significant differences in functional connectivity between groups emerged in the ICA. Processing of bodily actions was strongly correlated with components comprised of occipital and parietal areas, while processing bodily emotions involved components that showed coherence among IFG, MPFC, and occipital areas. When comparing ASD participants to their TD peers in understanding emotional body language, reliably lower temporal coherence was found in ventral premotor cortex including the inferior frontal gyrus, and superior parietal areas. Finally, there was a positive predictive relationship between empathizing ability and processing emotion in ASD participants.

Processing Bodily Action and Emotion

Increased brain activity found in IFG, SPL, IPL, EBA, and middle and inferior occipital cortex during this task in both TD and ASD group suggests the role of this primarily

Figure 5.

Between-group comparison results for a comparison of functional connectivity between autism (ASD) and typically developing controls (TD) for processing whole body actions. (a): TD > ASD (left SMA, right STS); (b): ASD > TD (left precentral gyrus). The color bar represents *t*-values and the *x*, *y*, or *z* coordinate represents the slice. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Figure 6.

Between-group comparison results for a comparison of functional connectivity between autism (ASD) and typically developing controls (TD) for processing bodily emotions. Top panel: TD > ASD (right superior parietal lobule; left ventral premotor including IFG);

Bottom panel: ASD > TD (left fusiform gyrus; left paracentral lobule). The color bar represents *t*-values and the *x*, *y*, or *z* coordinate represents the slice. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Figure 7.

Predictive relationship using Pearson's correlation between the beta weights for the highest-ranked emotion component (a representation of strength of functional connectivity within the network) and empathizing quotient scores for each group of participants. A significant positive correlation in ASD group (left panel), and no significant correlation in TD participants (right panel).

frontal-parietal network in understanding the bodily actions of others. These results are in line with a previous study using the same stick figure character stimuli [Kana and Travers, 2012] as that in the current study. While a reliable group difference in brain activity was not found, significant differences in brain connectivity, measured by ICA, emerged in response to the experimental tasks. Thus, the ICA was more sensitive in detecting the neural responses, perhaps at a finer level, and uncovering significant group differences. It should be noted that while the relevant brain areas for action and emotion processing were active in the ASD group, the organization and synchrony of these regions were weaker relative to TD individuals.

The ICA in this study detected a strong role for visual and motor/sensorimotor regions in the processing of body postures depicting actions, in both ASD and TD participants. These areas included the calcarine sulcus, cuneus, middle and superior occipital cortex, and the IPL. On the other hand, processing emotional body postures elicited the strongest temporal coherence with prefrontal and motor regions, including IFG and MPFC, along with the cuneus, and middle occipital gyrus. The functional connectivity components identified through the ICA contained several brain areas consistent with previous fMRI findings of body language processing, including IPL, IFG and SMA [Kana and Travers, 2012]. The IPL in this network may be associated with processing the goals of actions [Buxbaum et al., 2005; Tunik et al., 2007]. The IFG component we found for emotion condition may code the social significance of actions (in this case emotion) [Oberman et al., 2007; Pobric and de C Hamilton, 2006; Urgesi et al., 2007], and the MPFC may be relevant for thinking about others' thoughts and feelings [Gallagher et al.,

2000]. Covarying activity in similar visual and motor regions for action and emotion trials indicates the importance of visuospatial and motor regions in understanding basic body language (actions at the most basic level). Additional recruitment of frontal areas to process emotion reflects the social elements in the stimuli, as participants were required to infer the characters' mental states.

Group Differences in Temporal Coherence

Between-group component contrasts for action understanding indicated significantly greater temporal coherence in the left precentral gyrus for ASD participants, relative to TD participants, and significantly reduced temporal coherence in right superior temporal cortex and left SMA. It is interesting to note that the group difference in connectivity was seen in two different aspects of the motor cortex, the precentral gyrus and the supplementary motor area (SMA). The role of motor cortex engagement during action observation has been found in studies using different neuroimaging modalities [Baldissera et al., 2001; Caetano et al., 2007; Cochin et al., 1998; Fadiga et al., 1995; Hari et al., 1998; Montagna et al., 2005; Nishitani and Hari, 2000; Raos et al., 2004, 2007]. SMA also seems to have a significant role in processing actions, especially in encoding movement sequences and in planning forthcoming movements in a motor sequence retrieved from memory [Schütz-Bosbach et al., 2007]. Thus, SMA seems to be a key area for organizing upcoming movements in a complex motor sequence [Gerloff et al., 1997] or in motor imagery [Abbruzzese et al., 1996]. STS activation has been found in studies of biological motion as well as

observation of actions [Iacoboni et al., 2001]. The posterior superior temporal sulcus (pSTS) is also involved in encoding intentionality of an agent's actions [Nummenmaa and Calder, 2009] and providing input to the mirroring circuits. Previous studies have indicated abnormalities in the function of the pSTS in ASD in action understanding and processing biological motion [Boddaert et al., 2003; Castelli et al., 2002; Gervais et al., 2004; Kaiser et al., 2010; Pelphrey et al., 2005].

While inferring emotions from body postures, the ASD group showed significantly reduced temporal coherence in right superior parietal lobule and left ventral premotor cortex including the IFG, compared to TD peers. These regions are considered part of the frontal-parietal mirror neuron system critical for action representation [Buccino et al., 2001, 2004], and altered response in this network has been reported in ASD in previous studies [Cattaneo et al., 2007; Dapretto et al., 2005; Gallese, 2006; Kana et al., 2011b; Oberman and Ramachandran, 2007; Williams, 2008; Williams et al., 2001]. The reduced coherence in these structures in ASD while inferring emotions is noteworthy as the ventral premotor cortex and IFG have been found to be coding the goals [Johnson-Frey et al., 2003] and intentions [Iacoboni et al., 2005] of actions, and in emotion recognition [Carr et al., 2003; Dapretto et al., 2005; Gallese, 2001; Leslie et al., 2004]. Some of these structures have also been reported to have altered response in individuals with ASD during action and emotion processing [Dapretto et al., 2005; Oberman et al., 2005]. On the other hand, participants with ASD in the current study showed increased coherence in fusiform gyrus during emotion recognition. Fusiform gyrus, especially the fusiform body area, has been found previously to be involved in inferring emotions from body postures [Hadjikhani and de Gelder, 2003]. The peak MNI coordinate for this region, $x = -38$, $y = -60$, $z = -12$, in the current study has been found in previous studies of motion processing involving body parts [Sugiura et al., 2006]. It is possible that the participants with ASD in this study may be selectively encoding explicit low-level visual features of human bodies like body shape and posture [Downing and Peelen, 2011].

Despite finding similar behavioral and functional activation responses in participants with ASD and their TD peers, the ICA revealed significant differences in temporal coherence within neural networks for processing whole body actions and emotions. These findings mark a disruption in the synchronization of brain regions for processing body language in adolescents and adults with ASD. The reduced temporal coherence seen in ASD is consistent with weaker functional connectivity reported in ASD by previous studies of action understanding [Kana et al., 2014]. Significant reductions in temporal coherence between frontal, premotor, temporal, and parietal regions in ASD are in line with previous findings of altered frontal-posterior connectivity [Kana and Just, 2011; Kana et al., 2011a; Maximo et al., 2014; Schipul et al., 2011], and potentially affect the integration of neural information,

ultimately making complex cognitive and social tasks more difficult. Overall, the results of this study provide support for the disrupted connectivity theory of ASD (see [Maximo, Cadena, and Kana, 2014] for a review).

Behavioral Performance

An effect of experimental condition was found for both behavioral accuracy and reaction time, where both groups demonstrated better accuracy and reduced reaction time for the action trials compared to the emotion trials. These results are in line with the findings of a previous study on understanding physical actions and emotion states portrayed by stick figure characters [Kana and Travers, 2012]. Based on this effect, it is likely the emotional states were slightly more difficult for participants to decipher, compared to the action postures. Yet, no significant differences were found for accuracy or reaction time between groups for processing action and emotion characters. Thus, ASD participants performed equally well as their TD peers at identifying emotional states of stick figure characters, although the ICA revealed significant differences in processing at the neural level.

Relationship between Empathy and Body Language Processing

Empathizing ability in ASD participants was found to positively predict temporal coherence in LIFG and MPFC for emotional body language processing. This result is similar to those of previous studies, which found a significant correlation between empathy and left IFG activation for emotional animations in typical individuals [Hooker et al., 2010]. A previous study using ICA found a relationship between decreased temporal coherence in precuneus and MPFC/ACC at rest, and symptom severity in individuals with ASD [Assaf et al., 2010]. In the current study, greater empathy was positively correlated with greater temporal coherence for emotion processing in the ASD group, a trend not seen in the TD participants. The ASD participants with higher levels of empathy had higher functional connectivity within the neural network identified for processing emotional body language. In TD adults, emotion processing may be fairly automatic; whereas the ASD group may have to rely on active use of their social ability (such as empathizing) to read emotions. Previous neuroimaging studies have indicated that TD individuals recognize emotional body language automatically and on a non-conscious level, which results in measurable neurophysiological changes (such as increased skin conductance and heart rate changes) and emotional contagion (e.g., spontaneous imitation of facial expressions) (see [de Gelder, 2006; Tamietto and de Gelder, 2010] for reviews). This unconscious process potentially affects our social and emotional understanding of others, and thus our ability to appropriately respond to others in social situations. An

EMG study on automatic mimicry of facial expressions found that adolescents and adults with ASD did not automatically mimic facial expressions like their TD peers, although they could successfully mimic the facial expressions when asked to voluntarily do so [McIntosh et al., 2006]. If the automatic system for decoding emotions from others' bodies and faces is failing, individuals with ASD may require alternate cortical routes or additional cognitive effort to solve complex cognitive and social problems.

A disconnected neural system for processing emotional body language could be driving the impaired emotional understanding of those affected by ASD. The current study uncovered significant differences in functional connectivity of the neural networks underlying emotional body language understanding in participants with ASD, and a significant positive correlation between empathy and connectivity in this network. Yet, the cause of this functional disconnect in the ASD participants is unclear. A recent diffusion tensor imaging (DTI) study investigated the relationship between empathy and white matter integrity in the brain [Parkinson and Wheatley, 2012] finding a significant correlation between empathy and fractional anisotropy of several white matter tracts (including the superior longitudinal fasciculus, inferior longitudinal fasciculus, and inferior fronto-occipital fasciculus) in TD individuals. DTI studies have uncovered numerous abnormalities in the integrity of white matter tracts in ASD (see [Travers et al., 2012] for a review). It is possible that aberrations in white matter integrity are underlying the behavioral and functional connectivity abnormalities in emotional body language processing in ASD. Future studies should further investigate potential functional and structural connectivity abnormalities related to bodily emotion processing in ASD and their link to overall social functioning.

CONCLUSIONS

This is the first ICA study, to our knowledge, on body language processing in ASD, and the first to examine connectivity in emotional body language processing in ASD. This study found the synchronized functioning of parietal and occipital cortices in action understanding, and a network of IFG, MPFC, and occipital cortex underlying emotion processing. The reduced connectivity found among premotor and parietal areas in ASD participants for emotion processing may indicate altered motor simulation. Overall, these findings underscore the functional connectivity underlying social and emotion processing and the disruption of it in individuals with ASD.

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REFERENCES

- Abbruzzese G, Trompetto C, Schieppati M (1996): The excitability of the human motor cortex increases during execution and mental imagination of sequential but not repetitive finger movements. *Exp Brain Res* 111:465–472.
- Allison T, Puce A, McCarthy G (2000): Social perception from visual cues: role of the STS region. *Trends Cogn Sci* 4: 267–278.
- Ashwin E, Chapman E, Colle L, Baron-Cohen S (2006): Impaired recognition of negative basic emotions in autism: A test of the amygdala theory. *Soc Neurosci* 1:349–363.
- Assaf M, Jagannathan K, Calhoun VD, Miller L, Stevens MC, Sahl R, O'Boyle JG, Schultz RT, Pearson GD (2010): Abnormal functional connectivity of default mode sub-networks in autism spectrum disorder patients. *Neuroimage* 53:247–256.
- Atkinson AP (2009): Impaired recognition of emotions from body movements is associated with elevated motion coherence thresholds in autism spectrum disorders. *Neuropsychologia* 47:3023–3029.
- Baldissera F, Cavallari P, Craighero L, Fadiga L (2001): Modulation of spinal excitability during observation of hand actions in humans. *Eur J Neurosci* 13:190–194.
- Baron-Cohen S, Wheelwright S (2004): The empathy quotient: an investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. *J Autism Dev Disord* 34:163–175.
- Baron-Cohen S, Ring HA, Wheelwright S, Bullmore ET, Brammer MJ, Simmons A, Williams SC (1999): Social intelligence in the normal and autistic brain: an fMRI study. *Eur J Neurosci* 11: 1891–1898.
- Baron-Cohen S, Ring HA, Bullmore ET, Wheelwright S, Ashwin C, Williams S (2000): The amygdala theory of autism. *Neurosci Biobehav Rev* 24:355–364.
- 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. *J Child Psychol Psychiatry* 42:241–251.
- Bernier R, Dawson G, Webb S, Murias M (2007): EEG mu rhythm and imitation impairments in individuals with autism spectrum disorder. *Brain Cogn* 64:228–237.
- Bianchi-Berthouze N, Cairns P, Cox A, Jennett C, Kim WW (2006): On Posture as a Modality for Expressing and Recognizing Emotions. In: *Emotion and HCI Workshop, BCS HCI, London, September 2006*.
- Boddaert N, Belin P, Chabane N, Poline J-B, Barth-Aÿsmy C, Mouren-Simeoni M-C, Brunelle F, Samson Y (2003): Perception of complex sounds: Abnormal pattern of cortical activation in autism. *Am J Psychiatry* 160:2057–2060.
- Bölte S, Holtmann M, Poustka F, Scheurich A, Schmidt L (2007): Gestalt perception and local-global processing in high-functioning autism. *J Autism Dev Disord* 37:1493–1504.
- Bölte S, Hubl D, Dierks T, Holtmann M, Poustka F (2008): An fMRI-study of locally oriented perception in autism: altered early visual processing of the block design test. *J Neural Transm* 115:545–552.
- Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, Freund HJ (2001): Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *Eur J Neurosci* 13:400–404.
- Buccino G, Binkofski F, Riggio L (2004): The mirror neuron system and action recognition. *Brain Lang* 89:370–376.

- Buxbaum LJ, Kyle KM, Menon R (2005): On beyond mirror neurons: Internal representations subserving imitation and recognition of skilled object-related actions in humans. *Cogn Brain Res* 25:226–239.
- Caetano G, Jousmäki V, Hari R (2007): Actor's and observer's primary motor cortices stabilize similarly after seen or heard motor actions. *Proc Natl Acad Sci USA* 10:9058–9062.
- Calhoun V, Adali T, Pearlson G, Pekar J (2001a): A method for making group inferences from functional MRI data using independent component analysis. *Hum Brain Mapp* 14:140–151.
- Calhoun V, Adali T, Pearlson G, Pekar J (2001b): Spatial and temporal independent component analysis of functional MRI data containing a pair of task-related waveforms. *Hum Brain Mapp* 13:43–53.
- Calhoun VD, Liu J, Adali T (2009): A review of group ICA for fMRI data and ICA for joint inference of imaging, genetic, and ERP data. *Neuroimage* 45:S163–S172.
- Carr L, Iacoboni M, Dubeau M-C, Mazziotta JC, Lenzi GL (2003): Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proc Natl Acad Sci USA* 100:5497–5502.
- Castelli F, Frith C, Happé F, Frith U (2002): Autism, Asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. *Brain* 125:1839–1849.
- Cattaneo L, Fabbri-Destro M, Boria S, Pieraccini C, Monti A, Cossu G, Rizzolatti G (2007): Impairment of actions chains in autism and its possible role in intention understanding. *Proc Natl Acad Sci USA* 104:17825–17830.
- Cochin S, Barthelemy C, Lejeune B, Roux S, Martineau J (1998): Perception of motion and qEEG activity in human adults. *Electroencephalogr Clin Neurophysiol* 107:287–295.
- Critchley HD, Daly EM, Bullmore ET, Williams SC, Van Amelsvoort T, Robertson DM, Rowe A, Phillips M, McAlonan G, Howlin P (2000): The functional neuroanatomy of social behaviour changes in cerebral blood flow when people with autistic disorder process facial expressions. *Brain* 123:2203–2212.
- Dalton KM, Nacewicz BM, Johnstone T, Schaefer HS, Gernsbacher MA, Goldsmith H, Alexander AL, Davidson RJ (2005): Gaze fixation and the neural circuitry of face processing in autism. *Nat Neurosci* 8:519–526.
- Dapretto M, Davies MS, Pfeifer JH, Scott AA, Sigman M, Bookheimer SY, Iacoboni M (2005): Understanding emotions in others: Mirror neuron dysfunction in children with autism spectrum disorders. *Nat Neurosci* 9:28–30.
- Dawson G, Toth K, Abbott R, Osterling J, Munson J, Estes A, Liaw J (2004a): Early social attention impairments in autism: Social orienting, joint attention, and attention to distress. *Dev Psychol* 40:271.
- Dawson G, Webb SJ, Carver L, Panagiotides H, McPartland J (2004b): Young children with autism show atypical brain responses to fearful versus neutral facial expressions of emotion. *Dev Sci* 7:340–359.
- de Gelder B (2006): Towards the neurobiology of emotional body language. *Nat Rev Neurosci* 7:242–249.
- de Gelder B (2009): Why bodies? Twelve reasons for including bodily expressions in affective neuroscience. *Philos Trans R Soc Lond B Biol Sci* 364:3475–3484.
- de Gelder B, Snyder J, Greve D, Gerard G, Hadjikhani N (2004): Fear fosters flight: a mechanism for fear contagion when perceiving emotion expressed by a whole body. *Proc Natl Acad Sci USA* 101:16701–16706.
- Doody JP, Bull P (2011): Asperger's syndrome and the decoding of boredom, interest, and disagreement from body posture. *J Nonverb Behav* 35:87–100.
- Doody JP, Bull P (2012): Evidence for impaired verbal identification but intact nonverbal recognition of fearful body postures in Asperger's syndrome. *J Autism Dev Disord* 43:1652–1661.
- Downing PE, Peelen, M.V (2011). The role of occipitotemporal body-selective regions in person perception. *Cognit Neurosci* 2:186–226.
- Downing PE, Jiang Y, Shuman M, Kanwisher N (2001): A cortical area selective for visual processing of the human body. *Science* 293:2470–2473.
- Downing PE, Chan A-Y, Peelen M, Dodds C, Kanwisher N (2006): Domain specificity in visual cortex. *Cereb Cortex* 16:1453–1461.
- Fadiga L, Fogassi L, Pavesi G, Rizzolatti G (1995): Motor facilitation during action observation: a magnetic stimulation study. *J Neurophysiol* 73:2608–2611.
- Fletcher P, Frith C, Baker S, Shallice T, Frackowiak R, Dolan R (1995): The mind's eye—Precuneus activation in memory-related imagery. *Neuroimage* 2:195–200.
- Friston KJ, Holmes AP, Worsley KJ, Poline JP, Frith CD, Frackowiak RS (1994): Statistical parametric maps in functional imaging: A general linear approach. *Hum Brain Mapp* 2:189–210.
- Gallagher H, Happe F, Brunswick N, Fletcher P, Frith U, Frith C (2000): Reading the mind in cartoons and stories: An fMRI study of 'theory of mind' in verbal and nonverbal tasks. *Neuropsychologia* 38:11–21.
- Gallese V (2001): The 'shared manifold' hypothesis. From mirror neurons to empathy. *J Conscious Stud* 8:5–7.
- Gallese V (2006): Intentional attunement: A neurophysiological perspective on social cognition and its disruption in autism. *Brain Res* 1079:15–24.
- Gallese V, Keysers C, Rizzolatti G (2004): A unifying view of the basis of social cognition. *Trends Cogn Sci* 8:396–403.
- Gazzola V, Aziz-Zadeh L, Keysers C (2006): Empathy and the somatotopic auditory mirror system in humans. *Curr Biol* 16:1824–1829.
- Gazzola V, Rizzolatti G, Wicker B, Keysers C (2007): The anthropomorphic brain: The mirror neuron system responds to human and robotic actions. *Neuroimage* 35:1674–1684.
- Gerloff C, Corwell B, Chen R, Hallett M, Cohen LG (1997): Stimulation over the human supplementary motor area interferes with the organization of future elements in complex motor sequences. *Brain* 120:1587–1602.
- Gervais H, Belin P, Boddaert N, Leboyer M, Coez A, Sfaello I, Barthélemy C, Brunelle F, Samson Y, Zilbovicius M (2004): Abnormal cortical voice processing in autism. *Nat Neurosci* 7:801–802.
- Golan O, Baron-Cohen S, Hill JJ, Golan Y (2006): The "reading the mind in films" task: Complex emotion recognition in adults with and without autism spectrum conditions. *Soc Neurosci* 1:111–123.
- Grafton ST, Hamilton AF (2007): Evidence for a distributed hierarchy of action representation in the brain. *Hum Move Sci* 26:590–616.
- Grelotti DJ, Gauthier I, Schultz RT (2002): Social interest and the development of cortical face specialization: what autism teaches us about face processing. *Dev Psychobiol* 40:213–225.
- Grèzes J, Frith C, Passingham RE (2004): Brain mechanisms for inferring deceit in the actions of others. *J Neurosci* 24:5500–5505.

- Grezes J, Pichon S, De Gelder B (2007): Perceiving fear in dynamic body expressions. *Neuroimage* 35:959–967.
- Hadjikhani N, de Gelder B (2003): Seeing fearful body expressions activates the fusiform cortex and amygdala. *Curr Biol* 13:2201–2205.
- Hadjikhani N, Joseph RM, Manoach DS, Naik P, Snyder J, Dominick K, Hoge R, Van den Stock J, Flusberg HT, de Gelder B (2009): Body expressions of emotion do not trigger fear contagion in autism spectrum disorder. *Soc Cogn Affect Neurosci* 4:70–78.
- Hall GB, West CD, Szatmari P (2007): Backward masking: Evidence of reduced subcortical amygdala engagement in autism. *Brain Cogn* 65:100–106.
- Happé F, Frith U (2006): The weak coherence account: Detail-focused cognitive style in autism spectrum disorders. *J Autism Dev Disord* 36:5–25.
- Hari R, Forss N, Avikainen S, Kirveskari E, Salenius S, Rizzolatti G (1998): Activation of human primary motor cortex during action observation: A neuromagnetic study. *Proc Natl Acad Sci USA* 95:15061–15065.
- Hooker CI, Verosky SC, Germine LT, Knight RT, D'Esposito M (2010): Neural activity during social signal perception correlates with self-reported empathy. *Brain Res* 1308:100–113.
- Hubert B, Wicker B, Moore DG, Monfardini E, Duverger H, Da Fonseca D, Deruelle C (2007): Brief report: Recognition of emotional and non-emotional biological motion in individuals with autistic spectrum disorders. *J Autism Dev Disord* 37:1386–1392.
- Iacoboni M, Koski LM, Brass M, Bekkering H, Woods RP, Dubeau M-C, Mazziotta JC, Rizzolatti G (2001): Reafferent copies of imitated actions in the right superior temporal cortex. *Proc Natl Acad Sci USA* 98:13995–13999.
- Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G (2005): Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol* 3:e79.
- Jemel B, Mottron L, Dawson M (2006): Impaired face processing in autism: Fact or artifact? *J Autism Dev Disord* 36:91–106.
- Johnson-Frey SH, Maloof FR, Newman-Norlund R, Farrer C, Inati S, Grafton ST (2003): Actions or hand-object interactions? Human inferior frontal cortex and action observation. *Neuron* 39:1053–1058.
- Kaiser MD, Hudac CM, Shultz S, Lee SM, Cheung C, Berken AM, Deen B, Pitskel NB, Sugrue DR, Voos AC (2010): Neural signatures of autism. *Proc Natl Acad Sci USA* 107:21223–21228.
- Kana RK, Just M (2011): Autism as a disorder of functional brain connectivity. In: Amaral DG, Geschwind D, Dawson G, editors. *Handbook of Autism Spectrum Disorders*. New York: Oxford University Press, pp. 981–989.
- Kana RK, Travers BG (2012): Neural substrates of interpreting actions and emotions from body postures. *Soc Cogn Affect Neurosci* 7:446–456.
- Kana RK, Keller TA, Cherkassky VL, Minshew NJ, Just MA (2009): Atypical frontal-posterior synchronization of theory of mind regions in autism during mental state attribution. *Soc Neurosci Engl* 4:135–152.
- Kana RK, Libero LE, Moore MS (2011a): Disrupted cortical connectivity theory as an explanatory model for autism spectrum disorders. *Phys Life Rev* 8:410–437.
- Kana RK, Wadsworth HM, Travers BG (2011b): A systems level analysis of the mirror neuron hypothesis and imitation impairments in autism spectrum disorders. *Neurosci Biobehav Rev* 35:894–902.
- Kana RK, Libero LE, Hu CP, Deshpande HD, Colburn JS (2012): Functional brain networks and white matter underlying theory-of-mind in autism. *Soc Cogn Affect Neurosci* 9:98–105.
- Kana RK, Libero LE, Hu CP, Deshpande HD, Colburn JS (2014): Functional brain networks and white matter underlying theory-of-mind in autism. *Soc Cogn Affect Neurosci* 9:98–105.
- Kleinmans NM, Richards T, Weaver K, Johnson LC, Greenson J, Dawson G, Aylward E (2010): Association between amygdala response to emotional faces and social anxiety in autism spectrum disorders. *Neuropsychologia* 48:3665–3670.
- Kuusikko S, Haapsamo H, Jansson-Verkasalo E, Hurtig T, Mattila M-L, Ebeling H, Jussila K, Bölte S, Moilanen I (2009): Emotion recognition in children and adolescents with autism spectrum disorders. *J Autism Dev Disord* 39:938–945.
- Law Smith MJ, Montagne B, Perrett DI, Gill M, Gallagher L (2010): Detecting subtle facial emotion recognition deficits in high-functioning autism using dynamic stimuli of varying intensities. *Neuropsychologia* 48:2777–2781.
- Leslie KR, Johnson-Frey SH, Grafton ST (2004): Functional imaging of face and hand imitation: towards a motor theory of empathy. *Neuroimage* 21:601–607.
- Lieberman MD, Cunningham WA (2009): Type I and Type II error concerns in fMRI research: re-balancing the scale. *Soc Cogn Affect Neurosci* 4:423–428.
- Martineau J, Cochin S, Magne R, Barthelemy C (2008): Impaired cortical activation in autistic children: is the mirror neuron system involved? *Int J Psychophysiol* 68:35–40.
- Maximo JO, Cadena EJ, Kana RK (2014): The implications of brain connectivity in the neuropsychology of autism. *Neuropsychol Rev* 24:16–31.
- McIntosh DN, Reichmann-Decker A, Winkielman P, Wilbarger JL (2006): When the social mirror breaks: deficits in automatic, but not voluntary, mimicry of emotional facial expressions in autism. *Dev Sci* 9:295–302.
- Monk CS, Weng S-J, Wiggins JL, Kurapati N, Louro HM, Carrasco M, Maslowsky J, Risi S, Lord C (2010): Neural circuitry of emotional face processing in autism spectrum disorders. *J Psychiatry Neurosci* 35:105.
- Montagna M, Cerri G, Borroni P, Baldissera F (2005): Excitability changes in human corticospinal projections to muscles moving hand and fingers while viewing a reaching and grasping action. *Eur J Neurosci* 22:1513–1520.
- Nishitani N, Hari R (2000): Temporal dynamics of cortical representation for action. *Proc Natl Acad Sci USA* 97:913–918.
- Nishitani N, Avikainen S, Hari R (2004): Abnormal imitation-related cortical activation sequences in Asperger's syndrome. *Ann Neurol* 55:558–562.
- Nummenmaa L, Calder AJ (2009): Neural mechanisms of social attention. *Trends Cogn Sci* 13:135–143.
- Oberman LM, Ramachandran VS (2007): The simulating social mind: the role of the mirror neuron system and simulation in the social and communicative deficits of autism spectrum disorders. *Psychol Bull* 133:310.
- Oberman LM, Hubbard EM, McCleery JP, Altschuler EL, Ramachandran VS, Pineda JA (2005): EEG evidence for mirror neuron dysfunction in autism spectrum disorders. *Cogn Brain Res* 24:190–198.
- Oberman LM, Pineda JA, Ramachandran VS (2007): The human mirror neuron system: A link between action observation and social skills. *Soc Cogn Affect Neurosci* 2:62–66.
- Oldfield RC (1971): The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* 9:97–113.

- Parkinson C, Wheatley T (2012): Relating anatomical and social connectivity: White matter microstructure predicts emotional empathy. *Cereb Cortex* 24:614–625.
- Peelen MV, Downing PE (2005a): Selectivity for the human body in the fusiform gyrus. *J Neurophysiol* 93:603–608.
- Peelen MV, Downing PE (2005b): Within-subject reproducibility of category-specific visual activation with functional MRI. *Hum Brain Mapp* 25:402–408.
- Pellicano E, Gibson L, Maybery M, Durkin K, Badcock DR (2005): Abnormal global processing along the dorsal visual pathway in autism: A possible mechanism for weak visuospatial coherence? *Neuropsychologia* 43:1044–1053.
- Pelphrey KA, Morris JP, McCarthy G (2005): Neural basis of eye gaze processing deficits in autism. *Brain* 128:1038–1048.
- Pelphrey KA, Morris JP, McCarthy G, LaBar KS (2007): Perception of dynamic changes in facial affect and identity in autism. *Soc Cogn Affect Neurosci* 2:140–149.
- Pobric G, de C Hamilton AF (2006): Action understanding requires the left inferior frontal cortex. *Curr Biol* 16:524–529.
- Pourtois G, Peelen MV, Spinelli L, Seeck M, Vuilleumier P (2007): Direct intracranial recording of body-selective responses in human extrastriate visual cortex. *Neuropsychologia* 45:2621–2625.
- Raos V, Evangeliou MN, Savaki HE (2004): Observation of action: grasping with the mind's hand. *Neuroimage* 23:193–201.
- Raos V, Evangeliou MN, Savaki HE (2007): Mental simulation of action in the service of action perception. *J Neurosci* 27:12675–12683.
- Reed CL, Stone VE, Bozova S, Tanaka J (2003): The body-inversion effect. *Psychol Sci* 14:302–308.
- Reed CL, Stone VE, Grubb JD, McGoldrick JE (2006): Turning configural processing upside down: part and whole body postures. *J Exp Psychol* 32:73.
- Ruby P, Decety J (2003): What you believe versus what you think they believe: a neuroimaging study of conceptual perspective-taking. *Eur J Neurosci* 17:2475–2480.
- Satterthwaite TD, Wolf DH, Loughhead J, Ruparel K, Elliott MA, Hakonarson H, Gur RC, Gur RE (2012): Impact of in-scanner head motion on multiple measures of functional connectivity: relevance for studies of neurodevelopment in youth. *Neuroimage* 60:623–632.
- Saxe R, Kanwisher N (2003): People thinking about thinking people: the role of the temporo-parietal junction in “theory of mind”. *Neuroimage* 19:1835–1842.
- Schipul SE, Keller TA, Just MA (2011): Inter-regional brain communication and its disturbance in autism. *Front Syst Neurosci* 5:7.
- Schütz-Bosbach S, Haggard P, Fadiga L, Craighero L (2007): Motor cognition: TMS studies of action generation. In *Oxford Handbook of Transcranial Stimulation*. Oxford: Oxford University Press. pp. 463–478.
- Schwarzlose RF, Baker CI, Kanwisher N (2005): Separate face and body selectivity on the fusiform gyrus. *J Neurosci* 25:11055–11059.
- Sinke C, Sorger B, Goebel R, de Gelder B (2010): Tease or threat? Judging social interactions from bodily expressions. *Neuroimage* 49:1717–1727.
- Slaughter V, Stone VE, Reed C (2004): Perception of faces and bodies similar or different? *Curr Direct Psychol Sci* 13:219–223.
- Sugiura M, Sassa Y, Jeong H, Miura N, Akitsuki Y, Horie K, Sato S, Kawashima R (2006): Multiple brain networks for visual self-recognition with different sensitivity for motion and body part. *Neuroimage* 32:1905–1917.
- Tamietto M, de Gelder B (2010): Neural bases of the non-conscious perception of emotional signals. *Nat Rev Neurosci* 11:697–709.
- Travers BG, Adluru N, Ennis C, Tromp do PM, Destiche D, Doran S, Bigler ED, Lange N, Lainhart JE, Alexander AL (2012): Diffusion tensor imaging in autism spectrum disorder: a review. *Autism Res* 5:289–313.
- Tunik E, Rice NJ, Hamilton A, Grafton ST (2007): Beyond grasping: representation of action in human anterior intraparietal sulcus. *Neuroimage* 36:T77–T86.
- Urgesi C, Calvo-Merino B, Haggard P, Aglioti SM (2007): Transcranial magnetic stimulation reveals two cortical pathways for visual body processing. *J Neurosci* 27:8023–8030.
- van de Riet WA, Grèzes J, de Gelder B (2009): Specific and common brain regions involved in the perception of faces and bodies and the representation of their emotional expressions. *Soc Neurosci* 4:101–120.
- Van Dijk KR, Sabuncu MR, Buckner RL (2012): The influence of head motion on intrinsic functional connectivity MRI. *Neuroimage* 59:431–438.
- Vogeley K, Bussfeld P, Newen A, Herrmann S, Happe F, Falkai P, Maier W, Shah N, Fink G, Zilles K (2001): Mind reading: Neural mechanisms of theory of mind and self-perspective. *Neuroimage* 14:170–181.
- Wang AT, Dapretto M, Hariri AR, Sigman M, Bookheimer SY (2004): Neural correlates of facial affect processing in children and adolescents with autism spectrum disorder. *J Am Acad Child Adolesc Psychiatry* 43:481–490.
- Wechsler D (1999): Wechsler Abbreviated Scale of Intelligence. San Antonio, TX: Psychological Corporation.
- Williams JH (2008): Self-other relations in social development and autism: Multiple roles for mirror neurons and other brain bases. *Autism Res* 1:73–90.
- Williams JH, Whiten A, Suddendorf T, Perrett DI (2001): Imitation, mirror neurons and autism. *Neurosci Biobehav Rev* 25:287–295.
- Williams JH, Waiter GD, Gilchrist A, Perrett DI, Murray AD, Whiten A (2006): Neural mechanisms of imitation and ‘mirror neuron’ functioning in autistic spectrum disorder. *Neuropsychologia* 44:610–621.