NeuroImage 83 (2013) 751–760

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Sex differences in the development of brain mechanisms for processing biological motion

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ARTICLE INFO

Article history:
Accepted 15 July 2013
Available online 20 July 2013

Keywords:
Sex differences
Brain development
Biological motion
fMRI
Amygdala

ABSTRACT

Disorders related to social functioning including autism and schizophrenia differ drastically in incidence and severity between males and females. Little is known about the neural systems underlying these sex-linked differences in risk and resiliency. Using functional magnetic resonance imaging and a task involving the visual perception of point-light displays of coherent and scrambled biological motion, we discovered sex differences in the development of neural systems for basic social perception. In adults, we identified enhanced activity during coherent biological motion perception in females relative to males in a network of brain regions previously implicated in social perception including amygdala, medial temporal gyrus, and temporal pole. These sex differences were less pronounced in our sample of school-age youth. We hypothesize that the robust neural circuitry supporting social perception in females, which diverges from males beginning in childhood, may underlie sex differences in disorders related to social processing.

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Introduction

Disorders including autism and schizophrenia differ in incidence, symptomatology, and genetic mechanisms between males and females (Hartung and Widiger, 1998; Hines, 2004; Klein and Corwin, 2002; Levy et al., 2011; Sanders et al., 2011; Shors, 2002). In both of these disorders, males appear to be more vulnerable than females. In a groundbreaking review of sex differences in neuroscience, Cahill (2006) argued that we cannot begin to fully understand the etiology and treatment of these and other disorders until we take sex differences into account.

Behavioral sex differences in social perception and social cognition have been identified in neurotypical populations beginning in early infancy (Connellan et al., 2000), continuing throughout development (Hall, 1978; Happé, 1995; Lutchmaya and Baron-Cohen, 2002; Mestre et al., 2009; Olafsen et al., 2006; Willingham and Cole, 1997) and into adulthood (Bayliss et al., 2005; Montagne et al., 2005). The results of these studies consistently highlight behavioral advantages for females over males, with the magnitude of these advantages increasing in adolescence and young adulthood (Hall, 1978; McClure, 2000; McClure et al., 2004; Nelson et al., 2002). For example, females are more accurate than males at detecting biological motion as well as bodily emotions embedded in point-light displays (PLDs; Alaerts et al., 2011; Sokolov et al., 2011).

Researchers have begun to employ neuroimaging to elucidate the neural underpinnings of these behavioral sex differences, although the number of studies conducted in children is limited. One functional magnetic resonance imaging (fMRI) study investigating sex differences in brain mechanisms for processing emotional faces in adolescents and adults found that sex differences do not emerge until adulthood, when females begin showing greater activation relative to males in orbitofrontal cortex and amygdala while viewing unambiguous threat cues (McClure et al., 2004). In a social attribution magnetoencephalography (MEG) paradigm with adult participants, Pavlova et al. (2010) found sex differences in the left prefrontal cortex of adult participants. Specifically, females showed enhancement of gamma activity in this region earlier than males, which the authors interpreted as indicating more efficient social decision-making. Similarly, two event-related potential (ERP) studies found that relative to males, female adults exhibited longer latencies and higher amplitudes in the P450 ERP component in response to emotional faces (Orozco and Ehlers, 1998) and greater N200 activation in bilateral superior temporal gyri and cingulate cortex in response to pictures of social scenes with humans, indicating enhanced processing of social information (Proverbio et al., 2008). Sex differences have also been discovered in the neural processing of neutral faces, with females showing an overall more robust brain response to child versus adult faces (Platek et al., 2005) and females showing greater modulation of the N170 ERP component by task demands (e.g. identifying the gender of faces) relative to males (Sun et al., 2010). These findings indicate that females are more responsive than males to social and affective stimuli. Several other studies have shown sex differences in lateralization of amygdala activation during tasks that involve social and emotional processing, suggesting that males and females may encode salient stimuli in fundamentally different ways (Cahill et al., 2001; Killgore and Yurgelun-Todd, 2001; Williams et al., 2005).

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1053-8119/$ – see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neuroimage.2013.07.040

We sought to investigate sex differences in a relatively basic aspect of social perception as well as age-related changes in males and females from childhood to young adulthood. During an fMRI scan, participants passively viewed PLDs of coherent (hereafter referred to as biological) and scrambled biological motion in a block design procedure identical to that used in several of our previous studies (Kaiser and Pelphrey, 2012; Kaiser et al., 2010; Voos et al., 2013). While previous neuroimaging studies investigating sex differences have used complex tasks that assess the interaction of social, emotional, empathic, and attentional processes, the current design focused specifically on a critical building block of social cognition: the processing of human biological motion, with limited form information. On the basis of the existing behavioral and neuroimaging data, we hypothesized that adult females would show enhanced activity/functional connectivity in social perceptual brain circuitry compared to males. We also predicted that children would show similar, but less pronounced sex differences than adults.

Materials and methods

Participants

The current study included male and female child, adolescent, and adult participants. Individuals were not recruited for the current study if they had experienced brain injury, brain disease, brain malformation, seizures, epilepsy, hearing or vision loss, motor impairment, or severe allergies. Individuals were also excluded from the current study if they had a diagnosis of an intellectual disability or a learning disability. Finally, if there were any concerns about possible signs of autism spectrum disorder (ASD) or developmental problems, or if the individual had a sibling with an ASD diagnosis, he or she was not recruited for the current study. Following these recruitment criteria, participants included in the following data analyses were 48 healthy adults (24 females) and 38 healthy children and adolescents (19 females). Some of these participants (17 children) were included in a previously published study of biological motion perception (Kaiser et al., 2010). However, this study did not examine sex-related differences in neural activation. Ages ranged from 20 to 35 years in the adult sample (males: $M = 24.75$, $SD = 3.18$; females: $M = 24.65$, $SD = 3.36$) and from 4 to 16 years in the child/adolescent sample (males: $M = 11.73$, $SD = 2.78$; females: $M = 11.56$, $SD = 2.96$). Males and females in both groups were matched on age, and independent sample *t*-tests confirmed that ages did not differ significantly between males and females in either group ($ps > 0.05$). An additional 12 adults and 15 children (all males) completed the experiment but were not included in analyses, given that participants were matched pairwise according to age. Informed written consent was obtained from each participant (or guardian) according to a protocol approved by the Yale University Human Investigations Committee. Each participant received $50 dollars for participating in the study.

Experimental design

The experimental design was identical to that used in Kaiser et al. (2010). Participants viewed 24-second silent video clips containing PLDs of biological or scrambled motion presented at a video frame rate of 30 frames per second. The biological motion stimuli were created using motion capture technology and included an adult male performing continuous, social-interactive streams of body movement including waving, pat-a-cake, and peek-a-boo (Klin et al., 2009). To control for the amount and type of motion in each condition, the scrambled videos were created by combining 16 randomly selected points from the biological motion videos (Klin et al., 2009). Thus, although both types of videos had the same local motion information, biological motion videos resembled a moving person, whereas scrambled motion videos did not.

Stimuli were presented using E-Prime 2.0 software (Psychological Software Tools, Pittsburgh, PA). Twelve biological and scrambled motion clips (6 of each condition) were displayed in an alternating block design, with 20-second fixation periods before and after stimulus presentation. Participants were instructed to simply attend to the videos throughout the experiment. The procedure lasted for 5.47 min (328 s).

Imaging protocol

Images were collected on a Siemens 3T Tim Trio scanner located in the Yale University Magnetic Resonance Research Center. High-resolution T1-weighted anatomical images were acquired using an MPRAGE sequence (TR: 1900 ms, TE: 2.96 ms, FOV: 256 mm, image matrix: 256 mm^2, voxel size: $1 \times 1 \times 1$ mm, 160 slices). Whole-brain functional images were acquired using a single-shot, gradient-recalled echo planar pulse sequence (TR: 2000 ms, TE: 25 ms, flip angle: 60°, FOV: 220 mm, image matrix: 64 mm^2, voxel size: $3.4 \times 3.4 \times 4.0$ mm, 34 slices) sensitive to blood-oxygenation-level-dependent (BOLD) contrast. Runs consisted of the acquisition of 164 successive brain volumes.

fMRI analyses

Data were processed and analyzed using BrainVoyager QX version 2.0.8 (Brain Innovation, Maastricht, The Netherlands). The 10 volumes before onset of the first stimulus (corresponding to the 20 second fixation) were discarded prior to preprocessing to allow for T1 equilibrium. Preprocessing of the functional data included slice time correction (cubic spline interpolation), spatial smoothing (FWHM 4-mm Gaussian kernel), three-dimensional rigid-body motion correction (trilinear sinc interpolation), linear trend removal, and temporal high-pass filtering (General Linear Model (GLM) with Fourier basis set, using 2 cycles per time course). Functional data sets were coregistered to within-session T1-weighted anatomical images, which were then normalized to Talairach space (Talairach and Tournoux, 1988). Functional MRI slices were oriented to the anterior–posterior commissure. Estimated motion plots of the functional data were examined for each participant. General linear model (GLM)-based analyses were conducted for each participant to assess task-related BOLD responses. Regressors were defined as boxcar functions with values of 1 during each condition and 0 otherwise, convolved with a double-gamma hemodynamic response function (HRF). To help account for head motion, functions of motion in all six parameters (3 translations, 3 rotations) were included as predictors of no interest in single-participant GLM analyses, along with task predictors for each of the 2 experimental conditions (biological, scrambled). To further account for head motion, we removed volume acquisitions where movement between two consecutive volumes exceeded 1 mm, or integrated movement across four volumes exceeded 2 mm. Children had an average maximum movement from initial head position of 1.10 mm or degrees, and adults had an average maximum motion from initial head position of 0.68 mm or degrees. An independent samples *t*-test corrected for unequal variance indicated that children and adolescents exhibited significantly more motion in the scanner than adults ($t = 2.01$, $p = 0.049$). Importantly, an independent samples *t*-test confirmed that both in the child/adolescent group and the adult group, males and females had equivalent values of maximum motion ($ps > 0.20$).

Group-level analyses were performed by combining data from all participants in a random-effects GLM. Group-level GLM analyses were conducted separately for adults ($n = 48$) and children/adolescents ($n = 38$). All group-level analyses were restricted to voxels within the Montreal Neurological Institute (MNI) template brain normalized to Talairach space, and assessed at $p < 0.01$ and corrected for multiple comparisons with a cluster threshold estimated through the BrainVoyager QX Cluster-level Statistical Threshold Estimator plug-in (Forman et al., 1995; Xiong et al., 1995). Using 1000 iterations of a

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