ABSTRACT

Title of Thesis: THE INTERPLAY BETWEEN SOCIAL MOTIVATION, SOCIAL EXPERIENCE, AND DEVELOPMENTAL NEURAL SPECIALIZATION FOR SOCIAL PERCEPTION

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From birth, infants preferentially attend to human motion, which allows them to learn to interpret other peoples' facial expressions and mental states. Evidence from adults shows that selectivity of the amygdala and the posterior superior temporal sulcus (pSTS) to biological motion correlates with social network size. Social motivation—one's desire to orient to the social world, to seek and find reward in social interaction, and to maintain social relationships—may also contribute to neural specialization for biological motion and to social network characteristics. The current study aimed to determine whether neural selectivity for biological motion relates to social network characteristics, and to gain preliminary evidence as to whether social motivation plays a role in this relation. Findings suggest that neural selectivity for biological motion in the pSTS is positively related to social network size in middle childhood and that this relation is moderated by social motivation.

THE INTERPLAY BETWEEN SOCIAL MOTIVATION, SOCIAL EXPERIENCE, AND DEVELOPMENTAL NEURAL SPECIALIZATION FOR SOCIAL PERCEPTION

by

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Table of Contents

Acknowledgements ii
Table of Contents iii
List of Figures iv
Introduction 1
Methods 5
Participants 5
Behavioral Measures 6
fMRI Portion 7
Data Analysis 8
Results 15
Behavioral Analyses 15
fMRI Analyses 16
Discussion 19
Appendices 28
Bibliography 37

List of Figures

Figure 1: Two possible models depicting relations between social network, social motivation, and neural selectivity to biological motion 26

Figure 2. The neural response to biological motion in independently defined pSTS and amygdala was significantly greater than the neural response to scrambled motion in these regions of interest.....26

Figure 3. Social network size was significantly correlated with neural selectivity for biological motion in left pSTS, controlling for age 27

Figure 4. Social motivation moderates the relation between neural selectivity to biological motion in left pSTS and social network size 27

The interplay between social motivation, social experience, and developmental neural specialization for social perception

Introduction

Humans are inherently social beings. From birth, infants preferentially attend to point-light displays of biological motion (e.g., humans performing actions) compared to scrambled, non-biological motion (Simion, Regolin, & Bulf, 2008). Researchers consider this preferential attention to the motion of other humans an evolutionarily conserved mechanism for social attention, allowing infants and young children to learn to interpret other peoples' facial expressions and mental states (Frith & Frith, 1999). Individuals diagnosed with autism spectrum disorder (ASD), a disorder characterized by impairments in social skills and communication, do not preferentially attend to biological motion (Klin, Lin, Gorrindo, Ramsay, & Jones, 2009). This reduced social attention, which begins as early as age two, may lead to cascading effects that impact social development, and eventually, the ability to form meaningful relationships.

Past research demonstrates a protracted period of development for biological motion processing. In early childhood, children become better at identifying biological motion masked within noise (Freire et al., 2006), and development continues up to 14 years of age (Hadad, Maurer, & Lewis 2011). Two regions of the brain that are preferentially active to biological motion beginning in childhood are the amygdala and the posterior superior temporal sulcus (pSTS). fMRI data suggest that between ages 7 and 10, the neural response to biological motion becomes more specialized, paralleling behavioral improvements in biological motion detection.

More specifically, the difference in blood oxygenation level dependent (BOLD) response in the pSTS between biological motion and non-biological motion becomes greater with age (Carter & Pelphrey, 2006). An open question remains as to what may be driving this increasing neural sensitivity to biological motion.

One factor that may contribute to increased neural and behavioral sensitivity to biological motion is a child's social experience. Increases in neural and behavioral specialization for biological motion occur during the same developmental period during which children begin to spend more time with same-aged peers and have more varied and complex social networks (Feiring & Lewis, 1991; Parker, Rubin, Erath, Wojslawowicz, & Buskirk, 2006). Evidence from the adult literature shows that selectivity of the amygdala and the pSTS to biological motion is related to social network size, or the number of people with whom an adult interacts consistently (Dziura & Thompson, 2014). Thus, it is possible that this relation between neural selectivity to biological motion and social network size is the developmental "end point" of a process that begins much earlier. Could the development of biological motion processing in early childhood be directly related to the size, diversity, or complexity of a child's friend group? No study to date has investigated the relation between brain systems involved in basic social perception and indices of children's everyday social landscape.

Past studies have made progress in trying to relate the neural response to biological motion to indices of social responsiveness, indexed by the Social Responsiveness Scale (SRS; Constantino, 2002). For example, children between the ages of 4 and 16 who were more socially responsive according to the SRS showed

increased neural response to *biological* > *scrambled* motion in several brain regions including bilateral inferior parietal lobule, right middle frontal gyrus, posterior cingulate cortex, and precuneus (Anderson et al., 2013). Although this study suggests that the brain response to biological motion is tied to children's social abilities, the SRS was developed for clinical contexts and gives limited insight into typically-developing children's daily social experiences with peers. A measure that taps into children's sociometrics may also be tied to the increase in performance on biological motion detection tasks and brain response to biological motion in middle childhood. Additionally, measures of social networks can tap into network size, diversity, and complexity, specificity not captured by the SRS, which measures a wide variety of social abilities including social awareness, social cognition, social communication, social motivation, and autistic mannerisms.

One component of social responsiveness captured by the SRS—social motivation—may also contribute to neural specialization for biological motion and to social network characteristics. Social motivation is one's desire to orient to the social world, to seek and find reward in social interaction, and to maintain social relationships (Chevallier et al., 2012). Social motivation is related to activation of the orbitofrontal-striatum-amygdala network (Schirmer et al., 2008) as well as the pSTS (Kohls et al., 2012). Interestingly, as stated above, selectivity of the amygdala as well as pSTS to biological motion is related to social network size in adults (Dziura & Thompson, 2014). The involvement of the amygdala and pSTS in both biological motion perception and social motivation, in addition to the relation of selectivity in

these regions to social network size in adults, suggests a possible interplay between neural selectivity to biological motion, social motivation, and social network size.

No study to date has investigated this possible interplay. And, no study has examined any of these links in middle childhood, when social networks begin to expand and become more variable between children. One possibility is that the relation between social network characteristics and neural selectivity to biological motion is mediated by social motivation (Figure 1A). If the mediation model is supported, this would suggest that the relation between social network characteristics and neural selectivity to biological motion may be driven by social motivation. A second possibility is that the relation between social network characteristics and neural selectivity is moderated by social motivation (Figure 1B). If the moderation model is supported, this would suggest that the relation between social network characteristics and neural selectivity to biological motion differs as a function of social motivation. These mechanistic links are important in understanding how functional brain development interacts with social experiences; however, these questions cannot be answered by one study. A critical first step is testing the relation between each of these variables in middle childhood.

Specific Aims. Thus, the aims of the current study were to (1) replicate past work showing amygdala and posterior superior temporal sulcus (pSTS) selectivity to biological motion in middle childhood, (2) examine age related changes in the functional selectivity for biological motion between ages 7 and 13, given that this age range might be a key developmental period to examine social development, (3) determine whether neural selectivity for biological motion (controlling for age)

relates to social network characteristics, and (4) gain preliminary evidence as to whether social motivation mediates or moderates the relation between social network characteristics and neural selectivity to biological motion (Figures 1A and 1B).

Hypotheses. We hypothesized that we would replicate past work showing neural selectivity to biological motion in regions of the 'social brain' including the amygdala and pSTS. We also predicted that between ages 7 and 13, there would be an increase in neural selectivity to biological motion, particularly in the amygdala and pSTS, and that this greater selectivity would relate to greater size, diversity, and/or complexity of children's social networks, controlling for age. Finally, we explored whether social motivation would mediate or moderate the relation between the brain response to biological motion and social network characteristics (Figure 1).

Methods

Participants

Participants included 51 children between the ages of 7 and 13 without a family history of autism or schizophrenia. Informed consent to participate in the fMRI scan and behavioral portion was obtained from a parent or guardian. Due to motion artifacts (*N*=10) and failure to complete the scan (*N*=1), 11 children were excluded from further analyses; thus, the final sample comprised 40 children (*M* age: 10.37, *SD*: 1.89). One participant did not have a useable high-resolution anatomical image and was therefore not included in the surface-based analyses.

Behavioral Measures

Social Network Index. Parents ($N = 33$) completed a modified version of the Social Network Index (Cohen et al., 1997; see Appendix), a measure of a child's social network size (the number of people the child regularly sees or talks to), diversity (the number of social roles in which the child has regular contact with at least one person; e.g. sibling, friend, neighbor), and embeddedness (the number of social network domains in which the child is active; e.g. sports teams, clubs, religious groups). In order to assess parent-child reliability, children ($N = 19$) also completed a version of this questionnaire with help from a researcher.

Social Motivation Measures. We used a novel child observation measure in addition to a validated parent report questionnaire to measure participants' social motivation. Participants ($N = 25$) completed a novel interactive Social Probes task developed based on a study from the autism intervention literature (Doggett et al., 2013). In the context of a two-hour behavioral session consisting of several social cognitive tasks, experimenters delivered a series of leading statements (see Appendix for examples) that gave the participant a chance to ask a question, make a comment, or remain silent. The goal of this task was to see how motivated children were to spontaneously engage with another person, with limited prompting. Three dependent variables were calculated from the audio recordings based on past literature in the autism field (e.g. Doggett et al., 2013; Thiemann & Goldstein, 2001): number of on-topic questions, number of on-topic comments, and mean length of utterance. This task was completed both at the behavioral and scan sessions for a subset ($N = 17$) of participants to measure the test-retest reliability of the measure. Participants' parents

(N = 39) also completed the Social Responsiveness Scale (SRS; Constantino, 2002), a well-validated scale that measures social motivation as well as other constructs related to social responsiveness.

fMRI Portion

Stimuli. Visual displays of biological and scrambled motion were created using Matlab Psychophysics Toolbox Version 3 (PTB-3) and were based on coordinates from standard validated stimuli (Johansson, 1973; Vanrie & Verfaillie, 2004). The biological motion trials depicted point-light displays of an actor completing different actions such as chopping, painting, and rowing. Visual displays of scrambled motion were derived from the same coordinates as the biological motion videos. The biological and scrambled movies contained the same amount and type of motion; however, the biological motion videos resembled human actions whereas the scrambled videos did not.

Scan procedure. Before their scan, participants practiced staying still in our "mock" scanner while watching a movie to ensure they would be able to complete the scan. A version of the one-back task was presented to participants in the mock scanner to ensure they understand the instructions. During the actual scan, participants performed the biological motion task during EPI data acquisition (TR: 2000 ms, TE: 24 ms, flip angle: 90°, FOV: 1152 mm^2, image matrix: 64 mm^2, voxel size: 3mm^3) using a 12-channel head coil. High-resolution anatomical (T1-weighted) images were also acquired.

During the scan, children viewed point-light displays of biological and scrambled motion, and to maintain attention, they completed a one-back task,

pressing a button whenever two identical videos occur in a row. Stimuli were presented in two separate runs, each lasting approximately five minutes. Each run contained 12 blocks, alternating in a semi-random fashion between biological and scrambled motion stimuli. Each block contained seven 2s videos depicting either biological or scrambled motion. Six of these videos were unique, and one was a repeat for the purpose of the one-back task. In between each video (within blocks), there was a 500ms inter-stimulus interval (with a fixation cross), and between blocks, there was a 10s fixation.

Data Analysis

Behavioral Analyses: Measurement Reliability and Validity. Before conducting further analyses with the Social Network Index and Social Probes measures, we assessed reliability and validity. The Social Network Index has been previously validated with adults (and not children), so we sought to determine whether there would be high reliability between parent and child reports on this measure. Given that the Social Probes measure is completely novel, we sought to determine whether this measure had sound psychometric properties such as test-retest reliability, internal consistency, inter-rater reliability, and validity. We assessed parent-child agreement, test-retest reliability, and inter-rater reliability using the intraclass correlation coefficient (ICC), and we assessed internal consistency using Cronbach's alpha. Finally, we assessed validity using a Pearson's r correlation, measuring the relation between Social Probes measures and the previously validated social motivation subscale of the SRS (Constantino & Gruber, 2002). All analyses were conducted using R software (R Core Team, 2014).

Behavioral Relations. We assessed the normality of the distribution for the three social network measures (size, diversity, and embeddedness) using Shapiro-Wilk tests. To assess age-related changes, we then conducted correlations between each social network measure and participant age. We also assessed the normality of the distribution for social motivation measures using Shapiro-Wilk tests. To assess age-related changes, we then conducted correlations between social motivation and participant age. Finally, to assess the relation between social network and social motivation, we conducted partial correlations (controlling for age) between the three social network measures and social motivation.

fMRI Analyses. We conducted both surface- and volume-based analyses in order to most accurately define our two regions of interest, the pSTS (surface) and the amygdala (volume).

Surface-based fMRI Analyses. Using Freesurfer's (version 5.1.0) automated pipeline (Fischl et al., 2012), we created cortical surface models from each participant's high-resolution anatomical image, which were subsequently inspected and corrected (if necessary) by trained research assistants. We then used the Analysis of Functional NeuroImages (AFNI; Cox, 1996) and surface mapping (SUMA) programs (Saad, Reynolds, Argall, Japee, & Cox, 2004; Saad & Reynolds, 2012) to perform surface-based fMRI analyses.

We used SUMA to create standard mesh surfaces (MNI N27) with 198,812 nodes per hemisphere from the surface models output in Freesurfer, and these surfaces were then aligned with the structural volume to create an aligned surface

volume. Subsequent preprocessing steps were accomplished using this surface volume to align the functional data to the surface.

We performed preprocessing steps for functional data in volume space. These steps include slice time correction within each volume, registration (using rigid transformation) of each functional volume to the first volume of the experiment, transformation of functional data from oblique to cardinal orientation, and co-registration with the structural volume. We then aligned the surface volume (described above) to the functional data and then projected the functional volume data (timeseries) to the surface. On the surface, data were intensity normalized and smoothed using a Gaussian smoothing kernel (FWHM: 5mm). We performed smoothing on the surface to avoid volumetric smoothing error (e.g. smoothing across two gyri that touch in volume—but not surface—space).

We ran Ordinary Least Squares regression analyses for each run separately. This regression included regressors for each of the two conditions (biological and scrambled) as well as nuisance regressors, which included baseline and linear, quadratic, and cubic trends as well as 12 motion regressors. The motion regressors were the frame deviation at each volume for the six directions of translational and rotational motion and their derivatives. Participants with greater than 4 mm maximum motion in any direction were excluded. We created regressors for each of the two conditions by convolving a gamma-variate basis function with the stimulus timing function with a duration of 19.25 seconds and an amplitude of 1. Contrasts were estimated for each condition of interest and a comparison of biological vs. scrambled.

Coefficients and t-statistics for each contrast were incorporated in the group-level analyses using mixed effect models (3dMEMA) (Chen, Saad, Britton, Pine, & Cox, 2013), modeling both within- and between-subject variance. Specifically, for each contrast, we calculated an effect of group across all participants for each node using mixed effect models. We corrected all group-level analyses for multiple comparisons using a cluster-correction of 1386 mm^2, which maintained an overall alpha of $p < 0.05$ with a voxel threshold of $p < 0.01$. The minimum cluster-volume needed was estimated using Monte Carlo simulations (1,000 iterations) on the surface volume.

Volume-based fMRI Analyses. We used the Analysis of Functional NeuroImages program (AFNI; Cox, 1996) to perform volume-based fMRI analyses. Preprocessing included slice time correction within each volume, registration (using rigid transformation) of each functional volume to the first volume of the experiment, transformation of functional data from oblique to cardinal orientation, and co-registration with the structural volume. We then spatially normalized participants' data to the MNI pediatric template for ages 7.5-13.5 (Fonov et al., 2011). Data were then intensity normalized and smoothed using a Gaussian smoothing kernel (FWHM: 5mm).

We ran Ordinary Least Squares regression analyses for the two runs concatenated. This regression included regressors for each of the two conditions (biological and scrambled) as well as nuisance regressors, which included baseline and linear, quadratic, and cubic trends as well as 12 motion regressors. The motion

regressors were the frame deviation at each volume for the six directions of translational and rotational motion and their derivatives. Participants with greater than 4 mm maximum motion in any direction were excluded. We created regressors for each of the two conditions by convolving a gamma-variate basis function with the stimulus timing function with a duration of 19.25 seconds and an amplitude of 1. Contrasts were estimated for each condition of interest and a comparison of biological vs. scrambled.

Coefficients and t-statistics for each contrast were incorporated in the group-level analyses using mixed effect models (3dMEMA) (Chen, Saad, Britton, Pine, & Cox, 2013), modeling both within- and between-subject variance. Specifically, for each contrast, we calculated an effect of group across all participants for each node using mixed effect models. We corrected all group-level analyses for multiple comparisons using a cluster-correction of 127 voxels, which maintained an overall alpha of $p < 0.05$ with a voxel threshold of $p < 0.01$. The minimum cluster size needed was estimated using Monte Carlo simulations (1,000 iterations).

Individually-defined Region of Interest (ROI) Analyses: pSTS. For each participant, pSTS ROIs were created using the contrast of biological > scrambled motion. Two trained research assistants identified clusters of activation on each participant's pSTS for each run and each hemisphere. Masks of these ROIs were then used to extract data from the opposite run (i.e., ROIs created for run 1 were extracted from run 2 and vice versa), ensuring that the creation and use of the ROIs were independent processes (Kriegeskorte et al., 2009). The ROIs included all significant voxels within a 9-node distance along the surface's mesh from the voxel of peak

activation. Using a paired t-test, we determined whether beta values for biological motion were significantly greater than beta values for scrambled motion within bilateral pSTS. We then conducted a Pearson's correlation between beta values for the contrast of biological > scrambled motion within each ROI and participant age (in months) to determine if the neural selectivity to biological motion in the pSTS changes with age.

Region of Interest (ROI) Analyses: amygdala. We used anatomical amygdala ROIs (Maldjian, Laurienti, Kraft, & Burdette, 2003) and thus the creation and use of amygdala ROIs was also independent. We extracted beta values for biological and scrambled motion from each participant using this anatomical amygdala ROI. Using a paired t-test, we determined whether beta values for biological motion were significantly greater than beta values for scrambled motion within bilateral amygdala ROIs. We then conducted a Pearson's correlation between beta values for the contrast of biological > scrambled motion within each ROI and participant age (in months) to determine if the neural selectivity to biological motion in the amygdala changes with age.

Brain-behavior Analyses: ROIs. We conducted separate partial correlation analyses (controlling for age) to determine if biological > scrambled beta values for the pSTS and amygdala were related to children's social network characteristics (size, diversity, and embeddedness; see Appendix for scoring rubric) or social motivation. These were corrected for multiple comparisons using Bonferroni correction.

Brain-behavior Analyses: Whole Brain. As an exploratory analysis, we assessed relations between social network and social motivation scores and participants' neural activation to biological > scrambled motion on the whole-brain level (both surface and volume). We included each social network measure (size, diversity, and embeddedness) and social motivation as whole-brain mean-centered regressors. These whole-brain correlations were corrected for multiple comparisons, maintaining an overall alpha of 0.05 with a voxel threshold of $p < 0.01$. The minimum cluster size needed was estimated using Monte Carlo simulations (1,000 iterations). For the surface analysis, the cluster correction was 1386 mm^2 and for the volume analysis, the cluster correction was 127 voxels.

The role of social motivation. If relations are seen between neural selectivity to biological motion, social network measures, and social motivation measures, then we will test for a mediating role of social motivation on the relation between social network characteristics and selectivity to biological motion. To test for a moderating role of social motivation on the relation between social network size and neural selectivity to biological motion, we conducted robust linear regressions, predicting social network size from social motivation and neural selectivity to biological motion in each region of interest, controlling for age.

Results

Behavioral Analyses

Measurement Reliability and Validity. For both the Social Network Index and Social Probes measures, we assessed reliability and validity to determine which measures to include in the brain-behavior analyses. We found that child-reported social network size, diversity, and embeddedness were not significantly correlated with parent-reported social network size, diversity, or embeddedness (ps > 0.05). This is finding is consistent with past evidence of limited parent-child agreement on questionnaires in middle childhood (Achenbach, Thomas, McConaughy, & Howell, 1987). Given that the Social Network Index was originally developed for use with adults, and children reported that some of the questions were confusing, we used the parent-report version for all analyses.

Importantly, we found that our newly developed social probes measure had high inter-rater reliability (ICC ranging from 0.90-0.99). There was also some evidence of construct validity, given that one social probes measure—number of on-topic comments—was significantly correlated with the motivation subscale of the SRS ($r(21) = -0.53$, $p < 0.01$). However, there was limited evidence of internal consistency (α ranging from 0.13 - 0.57) or test-retest reliability (ICC ranging from -0.12 – 0). Thus, for all analyses we chose to use the previously validated SRS motivation subscale as our measure of social motivation.

Social Network. Shapiro-Wilk tests for normality suggested that all three social network measures (size, diversity, and embeddedness) were not from a

normally distributed population (ps < 0.05). Thus, nonparametric correlation coefficients (Spearman's rho) are reported for all correlations. No measures of social network varied as a function of age, although both social network diversity ($r_s(27) = -0.31$, $p = 0.08$) and social network embeddedness ($r_s(27) = -0.35$, $p = 0.05$) showed moderate, though non-significant, relations with age.

Social Motivation: Motivation Subscale of SRS. The SRS motivation subscale was not significantly related to participant age (ps > 0.05). However, SRS motivation was correlated with social network size (but not diversity or embeddedness), controlling for age ($r_s(23) = -0.38$, $p < 0.05$), such that children with higher levels of social motivation had larger social networks. However, this relation was no longer significant after correcting for multiple comparisons (p > 0.02).

fMRI Analyses

Region of Interest (ROI) Analyses: pSTS. Seven participants only had one run of useable data due to maximum motion greater than 4mm within a functional run. Thus, given that both runs were required for the independent selection of ROIs, and an additional participant was excluded due to not having a useable high-resolution anatomical image, the following surface-based pSTS ROI analyses include 32 participants.

Consistent with past research (Grezes et al., 2001; Grossman et al., 2000; Pelphrey et al., 2005), the neural response to biological motion in independently defined pSTS was significantly greater than the neural response to scrambled motion

(left: $t(31) = 5.14$, $p < 0.001$; right: $t(31) = 3.37$, $p < 0.01$) (Figure 2). Neural selectivity to biological motion within pSTS did not vary as a function of age ($p > 0.05$).

Region of Interest (ROI) Analyses: amygdala. Volume-based amygdala ROI analyses included 40 participants. Consistent with past research (Bonda et al., 1996), the neural response to biological motion in independently defined amygdala was significantly greater than the neural response to scrambled motion (left: $t(39) = 2.37$, $p = 0.02$; right: $t(39) = 2.46$, $p = 0.02$)(Figure 2). Neural selectivity to biological motion within the amygdala did not vary as a function of age ($p > 0.05$).

Brain-behavior Analyses: ROIs. Social network size was significantly correlated with neural selectivity for biological motion in left pSTS, controlling for age ($r_s(23) = 0.51$, $p < 0.01$) (Figure 3). Social network size was not significantly related to neural response to biological > scrambled motion in right pSTS or amygdala. Neither social network diversity nor social network embeddedness was significantly related to neural selectivity for biological motion in pSTS or amygdala (ps > 0.05).

The motivation subscale of the SRS was not significantly correlated with neural selectivity for biological motion in either the pSTS or amygdala regions of interest, controlling for age (ps > 0.05); thus, a mediation model was not tested. However, a robust linear regression model predicting social network size from the neural response to biological > scrambled motion in the left pSTS ROI and social motivation, controlling for age, suggests a significant effect of left pSTS activation

(beta = 268.42, t(21) = 2.50) and a significant interaction between left pSTS activation and social motivation (beta = -30.51, t(21) = -2.19). This finding supports model B in Figure 1, wherein social motivation moderates the relation between pSTS activation to biological motion and social network size. We further probed the interaction using simple slopes and found that for participants high on social motivation, there was no relation between pSTS selectivity for biological motion and social network size. For participants low on social motivation, there was a significant positive relation between pSTS selectivity for biological motion and social network size (Figure 4).

Whole-Brain Analyses. Whole brain analyses included 39 and 40 participants for surface and volume analyses respectively. As predicted, and consistent with past research (Bonda et al., 1996; Grezes et al., 2001; Grossman et al., 2000; Pelphrey et al., 2005), there was significant bilateral pSTS and amygdala activation, in addition to activation in other areas of the 'social brain' including orbitofrontal cortex, fusiform gyrus, and inferior frontal gyrus (surface: $p < 0.01$, $\alpha = 0.05$, k = 1386 mm^2 ; volume: $p < 0.01$, $\alpha = 0.05$, k = 127 voxels). Two small clusters of activation in bilateral pSTS were significantly positively related to age; however, these did not survive cluster correction. Notably, there was significant activation within the anatomical amygdala ROI used for brain-behavior correlations.

Brain-behavior Analyses: Whole-brain. On the whole-brain level, a cluster of activation on the right pSTS was significantly correlated to social network size; however, this did not survive cluster correction (cluster size = 268). Neither social

network diversity nor embeddedness showed any significant correlations with neural selectivity to biological motion at the whole-brain level. There was no significant relation between the motivation subscale of the SRS and whole-brain activation to biological > scrambled motion.

Discussion

Findings suggest that in middle childhood, the size of a child's social network is directly related to neural selectivity in a core region of the social brain, the pSTS. Importantly, this relation between a child's real world social landscape and neural systems involved in basic social perception is moderated by his or her level of social motivation—the desire to orient to the social world, to seek and find reward in social interaction, and to maintain social relationships. We replicated past findings of neural selectivity in bilateral pSTS and amygdala, as well as other regions of social brain; however, we did not find strong evidence for a relation between neural selectivity to biological motion and age, in contrast to a past study (Carter and Pelphrey, 2006).

The finding of a relation between social network size and neural selectivity in the pSTS is consistent with a recent study in adults with a similar design (Dziura and Thompson, 2014) as well as past work in humans and primates linking social network size to cortical thickness of the STS (Kanai, Bahrami, Roylance, & Rees, 2012; Sallet et al., 2011). One possible explanation for these previous findings is that the relation between social networks and selectivity to biological motion is driven by a feedback loop: social perception (e.g., interpreting eye gaze) is foundational for the social skills

that build a larger social network and these resultant social experiences further tune the brain's social perceptual system. By adulthood, however, individuals have great control over the size of their social network, which means that previous adult data cannot speak to a direct link between social experience and social perception; instead, the motivation to enter into social interactions may account for the relation. The current findings, in contrast, evidence a relation between social network size and neural selectivity to biological motion in middle childhood, a developmentally earlier period in which children have less control over their social networks. Thus, these findings provide evidence for an early emerging relation between social interaction and the neural bases of social perception and suggest that simply interacting with more social partners may explain this relation.

To further disambiguate the number of interactions with other people from the motivation to enter into such interactions, we investigated the relation between social network size, social motivation, and pSTS selectivity for biological motion. As hypothesized, social motivation played a role in the relation between social network size and neural selectivity to biological motion. We did not assess the mediation model (model A, Figure 1), because a precondition of this model was not met—social motivation was not related to neural selectivity for biological motion. However, we found that social motivation *moderated* the relation between social network size and neural selectivity to biological motion in the left pSTS, consistent with model B (Figure 1). In other words, there was no relation between social network size and pSTS selectivity to for children with high levels of social motivation, whereas for

children with low social motivation, there was a significant positive relation between social network size and pSTS selectivity to biological motion.

One possible explanation for this finding is that children with high levels of social motivation tend to enter into more complex or affectively-charged interactions within their social circles, making social network size a less accurate metric for assessing variability in these children's social experiences. In contrast, for a group of children low on social motivation, social network size may be a more accurate reflection of individual differences in social experience. Thus, the link between social experience and social perception may be present in both groups, but social experience is not well captured by this study's metrics for those children with high social motivation. Future studies should add additional measures of social experience such as friendship quality and behavioral assays of interpersonal effectiveness in order to test this hypothesis.

Interestingly, given the present study's finding of a relation between social motivation and social network size, it is reasonable to assume that many children with low social motivation but large social networks did not seek out such friendships (e.g., perhaps parents enrolled them in many clubs). The fact that the relation between network size and neural selectivity is strong for this group is indicative that mere exposure to a wide group of peers may be sufficient to influence the social perceptual system in middle childhood, at least for children who have not sought out much social interaction. That is, developmentally, children with low social motivation may have been less attuned to social perceptual experiences early in development, and thus they

require more exposure to other people later in development to develop adult-like neural selectivity to biological motion. Children with high social motivation may have been more attuned to social perceptual experiences beginning in infancy and thus do not require the extra perceptual experience that comes along with having a large social network. These differential patterns of emerging neural specialization may explain why there are conflicting findings of increasing neural selectivity to biological motion with age; neural selectivity may increase as a function of perceptual experience, which occurs at various time points for different children.

Unlike Dziura and Thompson's (2014) study with adults, children's social network embeddedness and diversity were *not* related to neural selectivity to biological motion. There are several possible explanations for the lack of correlation between social network diversity and embeddedness and neural selectivity for biological motion in children. One is that in middle childhood, social network size may uniquely be influenced by (or influence) the response of the pSTS to biological motion. Another possibility is that these two social network metrics have different meanings for children compared to adults. For example, the embeddedness and/or diversity of an adult's social network may depend more on the adult's level of social motivation or personality traits like extraversion, whereas the embeddedness and/or diversity of a child's social network may depend more on the parents' motivation to involve their child in a variety of activities. Thus, children have less control over their social networks. Future research will be needed to determine both the directionality of the relation between social network size and pSTS selectivity to biological motion

and to determine correlates of social network measures (e.g. extraversion) in adults versus children and their parents.

Consistent with Dziura and Thompson (2014), selectivity to biological motion in the amygdala was not as strongly related to social network size, diversity, or embeddedness. Although past research has found a positive relation between social network size and amygdala volume in human adults (Bickart, Wright, Dautoff, Dickerson, & Barrett, 2011), it is possible that the lack of correlation in children and a weaker correlation (compared to pSTS) in adults (Dziura and Thompson, 2014) between social network size and amygdala selectivity to biological motion lies in the amygdala's functional role in biological motion processing. While the amygdala, like the pSTS, is selective to biological motion, its role in biological motion processing may differ. Past research has implicated the amygdala in processes such as attention modulation and detection of salience (Adolphs and Spezio, 2006; Gamer and Buchel, 2009; Kennedy and Adolphs, 2010; Whalen, 2007). Once visual cues are detected by the amygdala, projections to cortical regions such as the pSTS shape perception (Armony and LeDoux, 1999; Armony et al., 1997; Whalen et al., 1998). Thus, it appears that perception—but not detection—of biological motion relates to social network size.

Finally, the current study cannot disambiguate whether neural differences in social perceptual processing are developmentally prior to differences in social network size. That is, the interaction between social networks and social perception may unfold over development, such that increased experience with or attention to

nonverbal cues like gestures and posture throughout early development may tune the neural networks involved in basic social perception, helping children become more adept at interpreting social cues and thus form larger social networks. Conversely, larger social networks might expose children to more varied social experiences, which in turn contribute to the development of neural networks for social perception.

Although the current study is cross-sectional in nature, past research does provide a hint that social perception may lay a foundation for later skills. For example, children with autism spectrum disorder (ASD) do not preferentially attend to visual displays of biological motion as early as age two (Klin et al., 2009), and it has been hypothesized that this is the cause of a blunted neural response to biological motion (Freitag et al., 2008) and lower ability to detect biological motion masked within noise (Blake et al., 2003) later in development. A study related to the development of the fusiform gyrus (Golarai et al., 2007) supports the idea that perceptual experience of particular stimuli in early development subsequently affects the functionality of brain regions related to those stimuli. Longitudinal studies will be needed to determine the directionality of the relation between social network size, social motivation, and neural selectivity to biological motion in the pSTS, which could have broad implications for the treatment of disorders related to deficits in social motivation, such as autism spectrum disorder (ASD). In particular, past studies have shown that increased ability to detect biological motion within noise correlates with higher levels of mental state inference ability in middle childhood (Rice, Anderson, Velnoskey, Thompson, & Redcay, 2015). If future research shows that increasing social network size predicts higher levels of neural selectivity to biological

motion, this could be one way to ameliorate social cognitive deficits characteristic of ASD.

Figures

Figure 1. Two possible models depicting relations between social network, social motivation, and neural selectivity to biological motion.

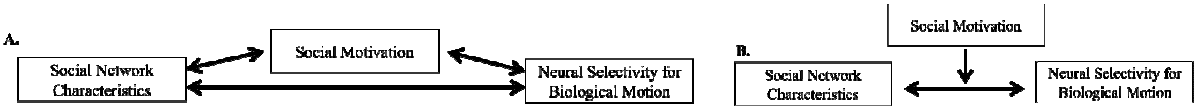


Figure 2. The neural response to biological motion in independently defined pSTS and amygdala was significantly greater than the neural response to scrambled motion in these regions of interest. The functionally defined pSTS ROI from an individual participant is displayed on the left, and the structurally defined amygdala ROIs are displayed on the right.

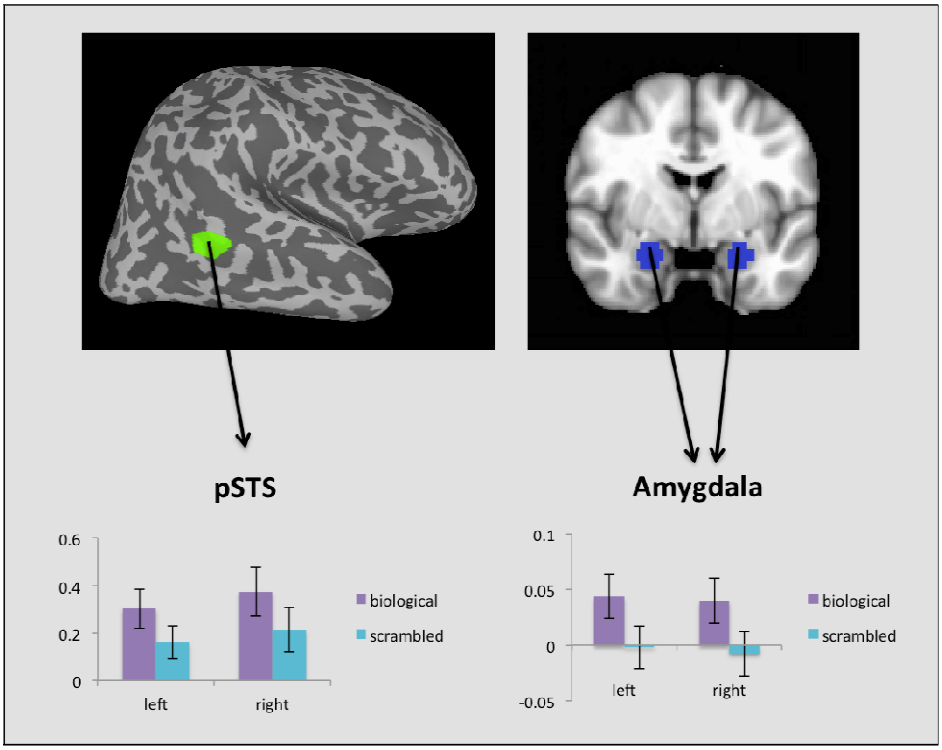


Figure 3. Social network size was significantly correlated with neural selectivity for biological motion in left pSTS, controlling for age. An individual's left pSTS ROI is displayed as an example.

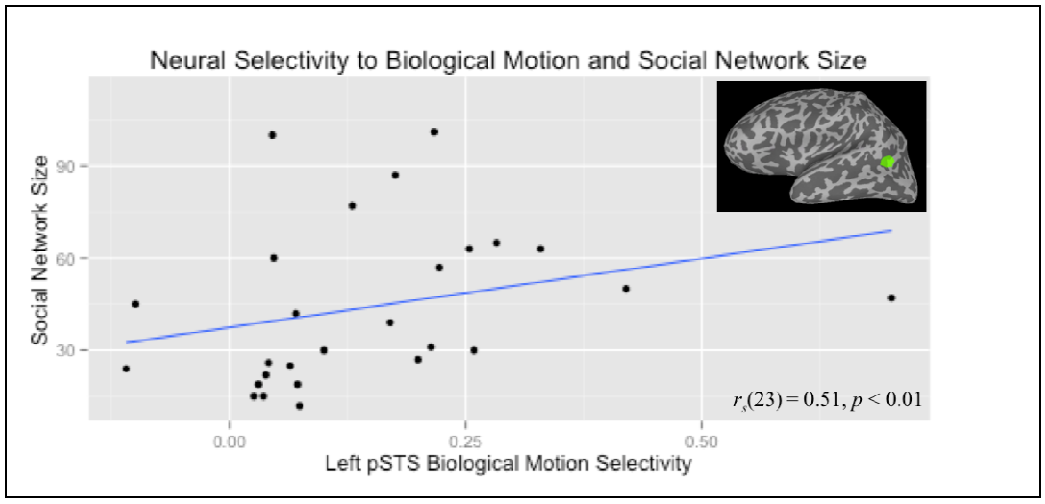
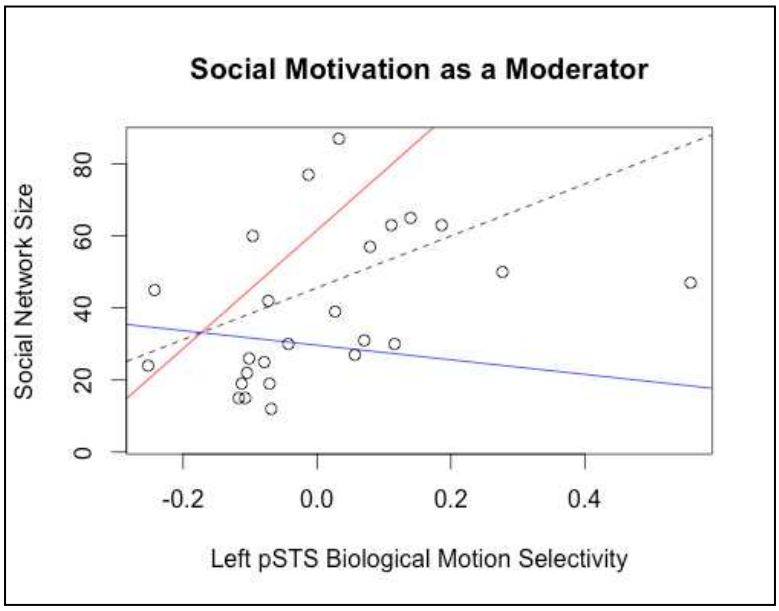


Figure 4. Social motivation moderates the relation between neural selectivity to biological motion in left pSTS and social network size. Simple slopes for low and high levels of social motivation (± 1 SD from the mean) are displayed on the graph in red and blue respectively.



Appendices

Social Network Index

Instructions: This questionnaire is concerned with how many people your child sees or talks to on a regular basis including family, friends, workmates, neighbors, etc. Please read and answer each question carefully. Answer follow-up questions where appropriate.

1. How many siblings does your child have? (If you don't have any siblings, check '0' and skip to Q2.)
____0 ____1 ____2 ____3 ____4 ____5 ____6 ____7 or more

1a. How many of your child's siblings does your child live with?
____0 ____1 ____2 ____3 ____4 ____5 ____6 ____7 or more

1b. Please list the names of everyone in 1a:

_____

2. Are both of your child's parents living? (If neither is living, check '0' and skip to question 3.)
____ (0) neither ____ (1) one parent only ____ (2) both

2a. Does your child live with both of his/her parents or speak with them once every 2 weeks?
____ (0) neither ____ (1) one parent only ____ (2) both

3. How many other relatives (other than parents and siblings) does your child feel close to? (If '0', check that space and skip to Q4.)
____0 ____1 ____2 ____3 ____4 ____5 ____6 ____7 or more

3a. How many of these relatives does your child see or talk to on the phone at least once every 2 weeks?
____0 ____1 ____2 ____3 ____4 ____5 ____6 ____7 or more

3b. Please list the names of everyone in 3a:

_____
____

_____
____

4. Is there someone that your child considers his or her best friend?
____ (1) currently has a best friend
____ (2) does not currently have a best friend
____ (3) never has had a best friend

4a. Please list this person's name (choose **one** if your child has multiple), if applicable:

_____

5. How many close friends does your child have other than the person in Q4? (meaning people that he/she feels at ease with, can talk to about private matters, and can call on for help)
____0 ____1 ____2 ____3 ____4 ____5 ____6 ____7 or more

5a. How many of these friends does your child see or talk to at least once every 2 weeks?
____0 ____1 ____2 ____3 ____4 ____5 ____6 ____7 or more

5b. Please list the names of everyone in 5a:

_____
_____

_____
_____

6. Does your child belong to a church, temple, or other religious group? (If not, check 'no' and skip to Q7.)

_____ no _____ yes

6a. How many members of your church or religious group does your child talk to at least once every 2 weeks? (This includes at group meetings and services.)

____0 ____1 ____2 ____3 ____4 ____5 ____6 ____7 or more

6b. Please list the names of everyone in 6a:

_____

_____

7. Does your child attend school with others on a regular basis? (If not, check 'no' and skip to Q8) _____ no _____ yes

7a. How many fellow students does your child talk to at least once every 2 weeks?

____0 ____1 ____2 ____3 ____4 ____5 ____6 ____7 or more

7b. Approximately how large is your child's class _____

7c. Please list the names of everyone in 7a (if less than 7):

_____

8. How many of your neighbors does your child visit or talk to at least once every 2 weeks?

_____0 ____1 ____2 ____3 ____4 ____5 ____6 ____7 or more

8a. Please list the names of everyone in Q8 (if less than 7):

_____

9. Is your child currently involved in regular volunteer work? (If not, check 'no' and skip to Q10).

_____ no _____ yes

9a. How many people involved in this volunteer work does your child talk to at least once every 2 weeks?

____0 ____1 ____2 ____3 ____4 ____5 ____6 ____7 or more

9b. Please list the names of everyone in 9a (if less than 7):

_____

_____

10. Does your child belong to any groups outside of school that meet at least once every 2 weeks? Examples include social clubs, recreational groups, sports teams, student government, professional organizations, Girl or Boy Scouts, groups concerned with community service, etc. (If your child doesn't belong to any such groups, check 'no' and skip the section below.)

_____ no _____ yes

Consider those groups in which your child talks to a fellow group member at least once every 2 weeks. Please provide the following information for each such group: the name or type of group and the total number of members in that group *that your child talks to at least once every 2 weeks*.

List **Name of group** and **Approximate number of group members** child talks to at least once every 2 weeks

---

1.

2.

3.

4.

5.

6.

Social Network Index Scoring

MEASURES
Number of high-contact roles (network diversity)
Number of people in social network
Number of embedded networks

Number of High-Contact Roles (Network Diversity)
Definition: This is the number of social roles in which the respondent has regular contact (i.e., at least once every 2 weeks) with at least one person. **The maximum number of high-contact roles is 10**. They are: sibling, child, relative, partner, close friend, church member, student, employee, neighbor, volunteer, and group member. [It would also be possible to count each group a person belongs to (question 11) as a separate social role, however we have not done this in our previous work.]
Computation: For each of the 11 possible high-contact roles, assign a 0 if the respondent does not have the role and a 1 if he/she does. The total number of high-

contact roles is computed by summing the 0s and 1s. The table below shows which scale items are used in the computation and how each is scored.

Role Item # Scores 1 if response is …
sibling 1a not 0
parents 2a not 0
close relative 3a not 0
best friend 4 1
close friend 5a not 0
church/temple member 6a not 0
student 7a not 0
neighbor 9 not 0
volunteer 10a not 0
group member 11 not 0 for # of group members talked to every 2 weeks

Number of People in Social Network
Definition: This is the total number of people with whom the respondent has regular contact (i.e., at least once every 2 weeks).
Computation: For each of the 12 possible roles, determine the number of people with whom the respondent has regular contact. The total number of people in the social network is computed by summing across the 12 roles. The table below shows which scale items are used in the computation and how each is scored.

Role Item # Scoring
sibling 1b use the number indicated
parent 2a 1=1; 2=2
close relative 3a use the number indicated
best friend 1=1; 2,3=0
close friend 5a use the number indicated
church/temple member 6a use the number indicated
student 7a use the number indicated
neighbor 9 use the number indicated
volunteer 10a use the number indicated
group member 11 sum of number of group members talked to at least once every 2 wks

Number of Embedded Networks
Definition: This measure is meant to reflect the number of different network domains in which a respondent is active. **The maximum possible is 7**. They are: family, friends, church/temple, school, work, neighbors, volunteering, and groups. To receive a point for a domain, a respondent must have at least 4 high-contact people within that domain. The 5 family roles are collapsed into one network for this

measure.
Computation: If the subject meets the criteria for an embedded network, assign a score of 1 for that network, otherwise assign a 0. The total number of embedded networks is computed by summing the 0s and 1s. The table below shows the criteria used for each embedded network.

Embedded Network Scores 1 if S has at least 4 high-contact…
family members 1a, 2a, 3a
friends 4, 5a
church/ temple church/temple members 6a
school students/teachers 7a
neighbors 9
volunteering fellow volunteers 10a
groups group members 11

Reference: Cohen S, Doyle WJ, Skoner DP, Rabin BS, Gwaltney JM (1997). Social ties and susceptibility to the common cold. JAMA, 277, 1940-4. Link to full-text (pdf)

Social Probes Task

The goal of this task is to see if participants will ask the experimenter questions about him/herself and show interest in another person's experiences (i.e. social motivation).

Experimenter:
Present the social probe (e.g. "I went on an awesome vacation last week!"). * Note: try to present in a naturalistic way at the beginning of the session. For example, you can say, "Before we start, I wanted to give us a chance to get to know each other a little better."

List of social probes:
I went on an awesome vacation last week!
I had something weird for breakfast this morning!
I have a really cute pet at home!
I saw a funny movie last night!

Participant:
1. Responds with question: (e.g. "Where did you go?", "What did you eat?", "What kind of pet?", "What movie?")

2. Responds with comment: (e.g. “I went on a vacation too”, “I had cereal”, “I have a pet too”, “I saw a movie too”)
3. No response / minimal response: (e.g. “Oh”, “Cool”)

Experimenter:

1. Answer with comment: (e.g. “I went to the beach!”, “I had a chicken burrito,” “I have a puppy named Piper,” “I saw Toy Story”)
2. Answer with another probe: (e.g. “My vacation was so much fun!”, “I am so full from my weird breakfast!”, “My pet is the cutest pet in the world!”, “The movie made me laugh really hard!”)
3. Answer with another probe: (e.g. “My vacation was so much fun!”, “I am so full from my weird breakfast!”, “My pet is the cutest pet in the world!”, “The movie made me laugh really hard!”)

Participant:

1. Responds with another comment or question: (e.g. “Was it hot there?”, “A burrito? That’s not a breakfast food!”, “Aww what kind of puppy?”, “I love Toy Story!”)
2. Responds with another comment about themselves (e.g. “So was mine!”, “Me too,” “So is mine!”, “My movie was funny too”)
3. No response / minimal response: (e.g. “Oh”, “Cool”)

Experimenter:

1. Give another one-sentence comment in response to the participant (remember, the goal is to get them to talk, so keep it brief).
2. Move on to next task.
3. Move on to next task.

Participant:

1. Responds with another comment or question: (e.g. “Was it hot there?”, “A burrito? That’s not a breakfast food!”, “Aww what kind of puppy?”, “I love Toy Story!”)
2. Responds with another comment about themselves (e.g. “So was mine!”, “Me too,” “So is mine!”, “My movie was funny too”)
3. No response / minimal response: (e.g. “Oh”, “Cool”)

Experimenter:

1. Continue conversation naturalistically for as many turns as possible, with a one-sentence comments in response to the participant (remember, the goal is to get them to talk, so keep it brief).
2. Move on to next task.
3. Move on to next task.

Social Probes Task Scoring

List of social probes:
I went on an awesome vacation last week!
I saw a funny movie last night!
I had something weird for breakfast this morning!
I have a really cute pet at home!

The spreadsheet for scoring can be found in DSCN/Experiments/LL Behavioral Battery/Data Entry

For **each social probe**, calculate the following variables for each child:

1. Number of questions: each time a child asks the experimenter a question during an interaction following a social probe. The spreadsheet will add these for the 4 social probes to calculate total number of questions.
2. Number of comments: each time a child makes a comment (i.e. a statement that is not a question) during an interaction following a social probe. The spreadsheet will add these for the 4 social probes to calculate total number of comments.
3. Mean length of utterance: number of words a child says in response to each social probe.

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