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Title: Alternative brain connectivity underscores age-related differences in the processing of interactive biological motion

Abbreviated title: Dev. connectivity of interactive bio. motion

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Abstract

Rapidly recognizing and understanding others' social interactions is an important ability that relies on deciphering multiple sources of information; for example, perceiving body information and inferring others' intentions. Despite recent advances in characterizing the brain basis of this ability in adults, its developmental underpinnings are virtually unknown. Here, we used fMRI to investigate which sources of social information support superior temporal sulcus (STS) responses to interactive biological motion (i.e. 2 interacting point-light human figures) at different developmental intervals in human participants (of either sex): Children show supportive functional connectivity with key nodes of the mentalizing network, while adults show stronger reliance on regions associated with body- and dynamic social interaction/biological motion processing. We suggest that adults employ efficient action-intention understanding via body and biological motion information, while children show a stronger reliance on hidden mental-state inferences as a potential means of learning to better understand others' interactive behavior.

Significance statement

Recognizing others' interactive behavior is a critical human skill that depends on different sources of social information (e.g. observable body-action information, inferring others' hidden mental-states etc.). Understanding the brain-basis of this ability, and characterizing how it emerges across development are important goals in social neuroscience. Here, we used fMRI to investigate which sources of social information support interactive biological motion processing in children (6-12 years) and adults. These results reveal a striking developmental difference in terms of how wider-brain connectivity shapes functional responses to interactive biological motion that suggests a reliance on distinct neuro-cognitive strategies in service of interaction understanding (i.e. children and adults show a greater reliance on explicit and implicit intentional inference, respectively).

Introduction

Rapidly understanding the contents of others' social interactions is an indispensable ability that is achieved via different levels of appraisal (e.g. extracting perceptual and action-related information from visible body-based cues, or making inferences about the hidden mental-states of interactors; Quadflieg & Koldewyn, 2017). Recent functional MRI (fMRI) work demonstrates that regions within posterior temporal cortex are important for the visual analysis of body-based interactions; for example, extrastriate body area (EBA) and fusiform body area (FBA; e.g. Downing et al., 2006) are sensitive to the spatial relations between human body dyads that convey or imply interactive behavior (Abassi & Papeo, 2020; Quadflieg et al., 2015; Walbrin & Koldewyn, 2019; Landsiedel et al., 2022).

Similarly, superior temporal sulcus (STS) - especially posterior STS (PSTS) - has a well-established role in processing human biological motion (e.g. Grossman et al., 2000) as well as understanding the intentions that underlie others' movements or actions (e.g. Brass et al., 2007; for an overview of the functional properties of STS see: Deen et al., 2015; Lahnakoski et al., 2012). Recent evidence shows that PSTS is engaged by dynamic interacting human stimuli above-and-beyond non-interactive stimuli (e.g. Centelles et al., 2011; Isik et al., 2017; Walbrin et al., 2018). Beyond visual analysis, medial prefrontal cortex (MPFC) responses are sometimes shown when probing mental-state inferences while viewing interacting individuals (Dolcos et al., 2012; Iacoboni et al., 2004), but are absent when such inferences are not elicited (Isik et al., 2017; Walbrin et al., 2018). Thus, social interaction understanding potentially draws upon diverse kinds of social information (that may, in part, be influenced by the cognitive processing goal(s) at hand, e.g. mentalizing, or not).

Currently, the few fMRI studies that have explored the developmental underpinnings of dyadic interaction processing broadly suggest gradual age-related changes. Sapey-Triomphe et al. (2017) showed age-related increases in fronto-parietal network regions, but common recruitment of PSTS across adults, adolescents, and children when discriminating interacting- from non-interacting point-light dyads. Using similar stimuli, Walbrin et al. (2020) showed poorer differentiation of interaction vs. non-interaction responses in a PSTS region-of-interest for children relative to adults, and more graded differences when considering sub-groups of children.

Indeed, gradual development is shown across social processes more generally. This is true for behavioral measures of interaction understanding (Goupil et al., 2022; Hamlin et al., 2007; Brey and Shutts, 2015; Balas et al., 2012; Centelles et al., 2013), and for mentalizing, body, face, and biological motion perception (Hadad et al., 2011; Simion et al., 2008; Wellman 2014; Weigelt et al., 2014). This is also shown with fMRI measures, for example, via weaker or less specific activation responses in children (for mentalizing, biological motion, body, & face stimuli: Lichtensteiger et al. 2008; Carter & Pelphrey, 2006; Deen et al., 2017; Ross et al., 2014; Scherf et al., 2007; Gweon et al., 2012) and via reduced functional segregation between social and non-social brain networks or connectivity strength differences within social brain networks (Richardson et al., 2018; O'Rawe et al., 2019; Wang et al. 2018; Morningstar et al., 2021).

In short, much remains to be learned about: a) the development of social interaction understanding, and; b) how constituent sources of social information meaningfully contribute to interaction understanding. Accordingly, we used a 'supportive connectivity' analysis to test which seed areas of the social brain (i.e. areas

that support body perception, social interaction recognition & mentalizing) demonstrate connectivity that is predictive of interactive dyadic biological motion responses in STS. This follows previous work that demonstrates how local-level brain activity is strongly related to connectivity with distal brain areas that share similar computational goals (e.g. between face network areas; Chen et al., 2017; Amaral et al., 2021; see also: Lee et al., 2019; Walbrin & Almeida, 2021). Thus, beyond simple activation differences, this approach affords an insight into the sources of social information that support interactive biological motion processing in STS, and whether the influence of these sources changes across development.

Materials and methods

Participants

31 children (aged between 6–12 years) and 29 adults took part in an experiment that was previously published (Walbrin et al., 2020). All subjects' data were re-analysed for the current manuscript, except for 2 children and 1 adult who did not have connectivity data (i.e. did not complete the MRI task that connectivity was estimated from), resulting in final group sizes of 29 children (mean age = 9.10; SD = 1.86; 13 females) and 28 adults (mean age = 22.93; SD = 4.27; range = 18–35; 15 females). All subjects were neurotypical and right-handed. Children gave informed assent (consent was also given by a guardian of each child) and they received gift vouchers (or toys of equivalent value) as compensation for participation. Adult subjects gave consent and received monetary compensation for participation. Ethical procedures were approved by the Bangor University psychology ethics board.

MRI tasks

Inside the scanner, two video tasks were completed: 1) A biological motion task that was used to estimate STS activation responses. This consisted of 3 runs of videos from 3 conditions (see figure 1B): Interaction (INT; i.e. two profile-view human point-light figures interacting; for example, each figure gesturing towards the other), non-interaction (NON; i.e. two figures performing non-interactive actions separated by a vertical line; for example, one figure jumping, the other cycling), and scrambled interaction (SCR; i.e. average 'motion-matched' versions of the INT stimuli where the coordinates of each point-light dot were randomly shifted to disrupt the perception of coherent biological motion; block length = 16s, based on three videos of variable length that summed to 16s; 3 × 16s rest blocks, one presented at the beginning, middle, and end of each run; total run length = 144s). Each run consisted of two blocks per condition – one presented in either half of each run – in counterbalanced order with the other conditions. In order to minimize head motion in children, no button response task was used. Instead, all participants were instructed to simply maintain attention throughout each run. Although behavioral performance measures were not obtained here, children (aged 4 - 10) show good discrimination of similar interactive and non-interactive biological motion stimuli (Centelles et al., 2013). 2) A 'dynamic objects' task that was used here for the sole purpose of estimating 'background' functional connectivity (i.e. regressing away the task design (stimulus-locked activation) from the fMRI time-series). Thus, task-related activation for the conditions of this localizer task was not analyzed here (see Walbrin et al., 2020 for these results). Participants completed three runs of this task that contained counterbalanced blocks of videos that depicted either moving faces, moving bodies, or moving objects (block

length = 18 s (6 × 3 s videos); 4 blocks per condition; 5 × 16s rest blocks; total run length = 296 s). All 3 concatenated runs were used for connectivity estimation.

Head movement analysis

To minimize fatigue and head motion in children (e.g. Meissner et al., 2020), the scanning session was split into two halves (the biological motion task was always completed in the first half) with a short break where subjects came out of the scanner for approximately 5–10 minutes. For consistency adults also took this break. Group differences in average head motion were analysed by comparing head movement measures across subjects (e.g. Kang et al. 2003). Briefly explained, for each run (per subject), the mean absolute difference between head position at each TR and the average head position across the run was calculated. Two scores were created - one for translation movements (mean difference averaged across x, y, z), and another for rotation movements (mean difference averaged across roll, pitch, yaw). These values were then averaged across all runs, and entered into independent t-tests. Children showed greater head movement than adults for both translation ($t(55) = 5.19, p < .001$) and rotation measures ($t(55) = 4.94, p < .001$). However, the overall amount of head motion was small (average translation in mm = children mean: 0.15, SD: 0.09; adults mean: 0.06, SD: 0.03; average rotation in degrees = children mean: 0.0028, SD: 0.0022; adults mean: 0.0008 SD: 0.0003). These differences are in line with similar trends that are routinely reported in developmental MRI work (e.g. Kang et al., 2003; see Meissner et al., 2020 for a detailed analysis and overview). Importantly, the main results reported in this manuscript provide strong evidence against the presence of problematic head motion in children (i.e. children show seed-specific effects that

contradict the expectation of globally weaker effects arising from excessive head motion).

MRI parameters, pre-processing, & GLM estimation

Scanning was performed at Bangor University with a Philips 3T scanner. The same fMRI parameters were used for all data, as follows: T2*-weighted gradient-echo single-shot EPI pulse sequence (with SofTone noise reduction); TR = 2000 ms, TE = 30 ms, flip angle = 83°, FOV(mm) = 240 × 240 × 112, acquisition matrix = 80 × 78 (reconstruction matrix = 80); 32 contiguous axial slices in ascending order, acquired voxel size (mm) = 3 × 3 × 3.5 (reconstructed voxel size = 3mm³). Four dummy scans were discarded prior to image acquisition for each run. Structural images were obtained with the following parameters: T1-weighted image acquisition using a gradient echo, multi-shot turbo field echo pulse sequence, with a five echo average; TR = 12 ms, average TE = 3.4 ms, in 1.7 ms steps, total acquisition time = 136 s, FA = 8°, FOV = 240 × 240, acquisition matrix = 240 × 224 (reconstruction matrix = 240); 128 contiguous axial slices, acquired voxel size (mm) = 1.0 × 1.07 × 2.0 (reconstructed voxel size = 1mm³).

Pre-processing and general linear model (GLM) estimation were performed with SPM12 (fil.ion.ucl.ac.uk/spm/software/spm12) for both tasks. All SPM12 default pre-processing parameters were used, but to ensure good alignment of data across the two halves of the session, the following steps were performed: 1) Functional images were realigned for each sub-session separately; 2) T1 images, acquired in each sub-session, were then co-registered to their respective mean functional alignment image; 3) the second sub-session data (T1 and functional images) were then co-registered to data from the first sub-session, bringing all data into alignment.

Data were then normalized to MNI space (2mm³ voxels) but were not smoothed, to better preserve voxel-level activation and connectivity estimates.

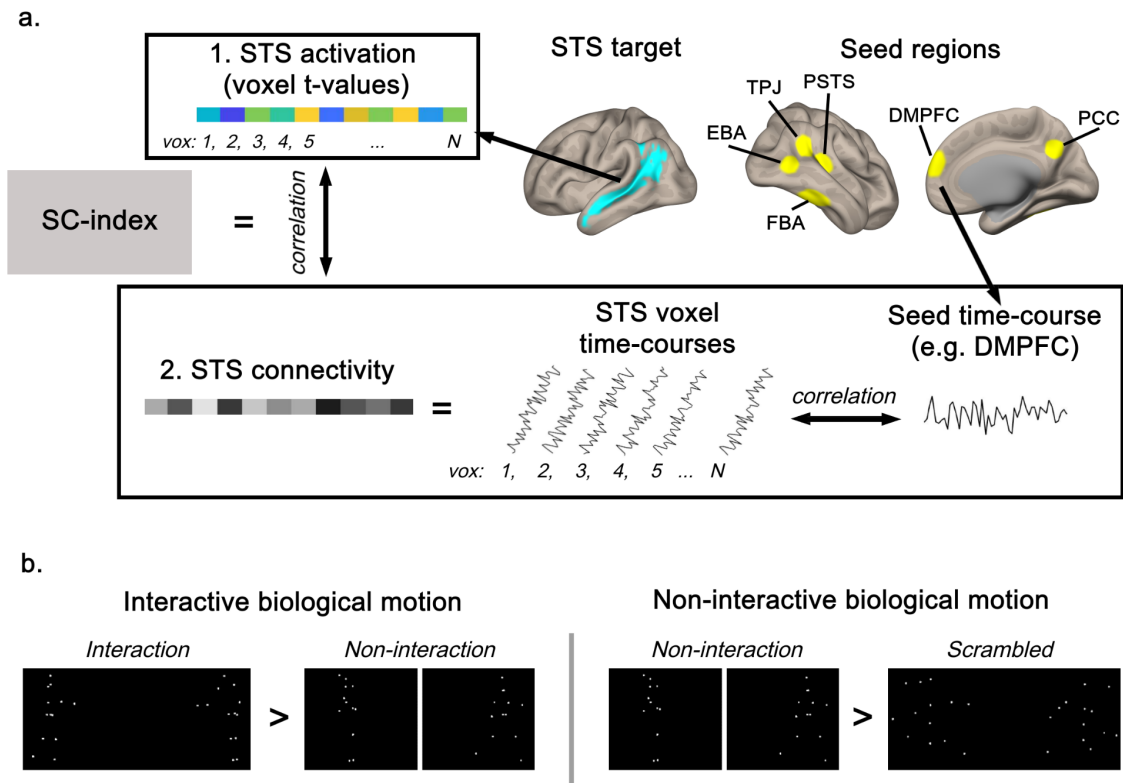


Figure 1. Overview of supportive connectivity estimation. a) The supportive connectivity index (SC-index) is calculated as the Pearson's correlation between: 1) STS activation (e.g. t-values for interactive biological motion (interaction > non-interaction contrast)) and 2) STS voxel-wise connectivity (Pearson's correlation coefficient) when seeding from a given seed region (e.g. DMPFC). b) Interactive- and non-interactive biological motion contrasts are shown with representative video frames from example stimuli.

Block durations and onsets for each experimental condition (per run) were modeled by convolving the corresponding box-car time-course with the SPM canonical hemodynamic response function (without time- or dispersion derivatives), with a high-pass filter of 128 s and autoregressive AR(1) model. Head motion parameters (3 translation & 3 rotation axes) were modeled as nuisance regressors. Background connectivity (e.g. Fair et al., 2007; Cole et al., 2014; Walbrin & Almeida, 2021) was

estimated from the dynamic objects task data, by regressing away task effects (i.e. convolving the canonical SPM12 haemodynamic response function with the block-events for each condition) along with other confound regressors (i.e. white matter and cerebrospinal fluid), and applying temporal band-pass filtering (0.01-0.1Hz) using the CONN Toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012).

Target & seed region definition

Previously, we showed that activation to interactive biological motion is strongest in PSTS, but similar activation is also present in more anterior portions of the sulcus too (in both children and adults). Therefore, we measured activation across the entire STS region. STS target region masks were generated for each hemisphere, for each subject individually, using the Freesurfer 'recon-all' function (based on the Destrieux atlas parcellation). These masks span the entire length of the STS (see figure 1A; including horizontal and ascending posterior branches). Masks were normalized and re-sliced to the same image resolution as the functional data.

For seed region masks, coordinates were identified by inspecting MNI-space meta-analysis brain maps generated for specific search terms from the Neurosynth database (neurosynth.org; see Yarkoni et al., 2011 for a detailed overview of this method). Briefly explained, a whole brain map is generated from the activation coordinates reported in previous fMRI studies that contain high-frequency usage of a given term (e.g. 'social interaction'). Although this approach adopts a lenient criterion for publication inclusion (e.g. does not distinguish papers that contain neurotypical vs. patient populations), each meta-analysis map was derived from >100 publications, and as such is large enough to capture average activation trends associated with each term (see Yarkoni et al., 2011 for validation of a similar approach). Moreover, we

manually inspected the location of seed regions to ensure that they were consistent with those reported in prior work (e.g. coordinates reported in a mentalizing meta-analysis; Schurz et al., 2014). We further note that the use of the same seed regions for both adults and children is justified, based on previous work showing strong spatial correspondence of category specific responses between adults and infants (Deen et al., 2017) and similar work demonstrating the appropriateness of comparing localized fMRI responses between adults and children in common stereotactic space (Kang et al., 2003). Further, the main results reported below provide strong evidence against the problematic localization of seed regions in children (i.e. across both main analyses, children show evidence of stronger positive supportive connectivity than adults in each of the seed areas).

The locations of the six seed regions were identified (for each hemisphere) by selecting the voxel with the strongest magnitude for each seed area, that was associated with one of the following three search terms: 1) 'Body': EBA [MNI coordinates (x, y, z): Right: 49, -72, 3 ; Left: -46, -74, 4] and FBA [Right: 44, -46, -20; Left: -44, -46, -20]; 2) 'Mentalizing': TPJ (temporo-parietal junction) [Right: 49, -58, 21; Left: -50, -58, 21], DMPFC (dorsomedial prefrontal cortex) [Right: 7, 55, 22; Left: -7, 55, 22], and PCC (posterior cingulate cortex) [Right: 7, -57, 35; Left: -7, -52, 38]. 3) 'Social interaction': PSTS [Right: 48, -42, 8; Left: -55, -52, 12]. Importantly, we note that although we used the search term 'social interaction' to identify the PSTS seed, we do not claim that this region is solely engaged by social interactions/interactive dyadic biological motion (e.g. PSTS is also responsive to single-human biological motion (Allison et al., 2000; Grossman et al., 2000; Carter & Pelphrey, 2006) as well as the intentionality of others' actions (e.g. Brass et al., 2007; Saxe et al., 2004;

Pelphrey et al., 2004)). The resulting seed regions (see figure 1A) consisted of 6mm-radius spheres centred at peak coordinates (or slightly adjusted when the coordinate was close to the edge of the brain to avoid capturing non-brain voxels within the sphere) and white matter voxels were removed (for each subject individually). Adjacent seed regions did not overlap. Importantly, because of the presence of seed regions within/bordering STS (i.e. PSTS and TPJ) we adopted a contralateral seeding approach for all seed regions. For example, for right STS target, we only used seed regions in the left hemisphere, and vice versa. This ensured that we never circularly extracted connectivity from voxels that overlapped both target and seed regions.

Supportive connectivity estimation

In each STS target region, we estimated the relationship between local activation and distal connectivity with the same approach as Chen et al. (2017) and Amaral et al. (2021), described as follows. First, we focused on STS activation to *interactive biological motion*, by extracting STS voxel t-values for the INT > NON contrast (figure 1B). Specifically, this contrast was intended to capture interactive biological motion information (e.g. contingent movements/actions, person-directed movements) above-and-beyond (non-interactive) biological motion. In a follow-up analysis we examined STS activation to *non-interactive biological motion*, by extracting STS voxel t-values for the NON > SCR contrast (figure 1B); this captures human biological information without the presence of interactive motion information.

An index of supportive connectivity (SC-index) was calculated for each seed region as follows (figure 1A). 1) For each measure of activation (e.g. interactive biological motion), we obtained an activation vector (t-values) of all STS voxels (for each hemisphere separately). 2) For a given seed region, a connectivity vector was

generated by correlating (Pearson's r) the connectivity time-course of each STS voxel with the mean time-course of the seed region. 3) The activation and connectivity vectors were then correlated (Pearson's r) to yield an SC-index. Seed hemisphere was always contralateral to the STS target hemisphere. Subjects' SC-indices were Fisher-transformed before being entered into group-level tests.

Searchlight-seeding analysis

To test whether other brain areas - beyond the a-priori seed regions featured in the main analyses - yield a significant SC-index, we ran a whole brain analysis, as follows. A searchlight consisting of approximately 100 contiguous voxels was iteratively centered on each gray matter voxel of the brain (white matter was masked out beforehand); the mean voxel time-course was extracted and then correlated with voxel-wise time-courses of STS to generate a connectivity vector that was then correlated with voxel-wise STS activation (as in the main analysis), and then the Fisher-transformed SC-index was assigned to the central voxel of the corresponding searchlight. As such, the resulting maps show which brain areas 'seed' a significant SC-index. For each analysis, this was performed twice - once with the right, and once with the left STS serving as target regions (target STS voxels were masked out from the searchlight space in the target hemisphere, but not in the other hemisphere).

Subject's searchlight maps were smoothed (6mm FWHM kernel) prior to group-level inference. To test which regions showed an SC-index different from zero, in either group, one-sample t-tests were run with threshold-free cluster enhancement (TFCE) based on 10,000 Monte-Carlo simulations, for adults and children, and for each (target STS) hemisphere, separately. The resulting maps were thresholded at $Z > 1.65$ (no significantly negative effects were observed) and projected to a surface rendered brain

(with the CONN toolbox) for visualization. To directly test for differences in SC-index between age-groups, independent t-tests were performed (TFCE, 10,000 Monte-Carlo simulations, maps thresholded at $Z > 1.65$ & $Z < -1.65$). Resulting inference maps for both adults and children were projected to the brain surface for visualization. For consistency with the contralateral target-seeding approach in the main analyses, contralateral searchlight coverage is shown here on a single map (i.e. left hemisphere shows searchlight seeding to right STS, and right hemisphere shows seeding to left STS).

Experimental design & statistical analyses

For the main analysis, we considered the supportive connectivity of seed regions for interactive biological motion information. A 3-way mixed ANOVA was used to assess statistical differences in SC-index across 3 factors: 1) Age-group (adults, children); 2) Seed region (PSTS, FBA, EBA, TPJ, DMPFC, PCC; repeated measures factor); and 3) target region hemisphere (right STS, left STS; repeated measures factor). A 3-way ANOVA was also used for the follow-up analysis where we tested supportive connectivity for non-interactive biological motion. For conciseness, we only report significant ANOVA effects for interactions and follow-up t-contrasts. In addition to direct comparisons of SC-indices between groups, we also performed one-sample t-tests against 0 (two-tailed) to test indirect group differences (e.g. one group may show above zero SC-indices for a particular seed, but the other group might not). A Bonferroni-corrected threshold was calculated for each set of follow-up tests ($p=.008$ for both independent and one-sample tests). All reported tests survive correction unless explicitly stated. We further note the reporting of several uncorrected results

here that we consider important to distinguish from marginal results (i.e. results with uncorrected p-values closer to .01 than .05).

Results

Interactive biological motion: A-priori seed analyses

We tested which of the six a-priori seed regions share connectivity with STS that is, in turn, correlated with STS activation to interactive biological motion. A 3-way mixed ANOVA (age-group x seed region x target region hemisphere) revealed an interaction between age group and seed region ($F(5,275) = 6.09$, $p = .001$, $\eta^2 = .100$; 3-way interaction was not significant: $F(5,275) = 0.11$, $p = .990$, $\eta^2 = .002$). Follow-up tests revealed two key results (figure 2A): First, adults showed a higher SC-index than children in PSTS ($t(326.94) = 2.88$, $p = .004$). A similar effect was shown for FBA but at an uncorrected level only ($t(326.94) = 2.36$, $p = .019$). Similar trends for EBA were not significant ($t(326.94) = 0.89$, $p = .373$). Second, for the remaining 3 seed regions, children showed trends towards higher SC-indices than adults. This trend was significant in TPJ ($t(326.94) = -2.85$, $p = .005$). Similar marginal trends for DMPFC and PCC were not significant (DMPFC: $t(326.94) = -1.69$, $p = .092$; PCC: $t(326.94) = -1.87$, $p = .062$). Additionally, an interaction between seed and target region hemisphere ($F(5,5) = 3.00$, $p = .012$, $\eta^2 = .052$) indicated higher SC-indices for left than right seed regions in PSTS ($t(329.89) = 2.95$, $p = .003$) and EBA ($t(329.89) = 2.76$, $p = .006$; other seed $ps > .091$). The age-group x target region hemisphere interaction was not significant ($F(1,55) = 0.00$, $p = .993$, $\eta^2 = .000$).

In addition to the direct group comparisons above, we tested whether either group showed SC-indices that are significantly different from zero for each of the six

seed regions. One-sample t-tests (two-tailed) were performed. As age-group did not interact with hemisphere, we collapsed across hemispheres for each seed region. For adults, above-zero SC-indices were shown for PSTS ($t(27) = 4.03$, $p < .001$) and FBA ($t(27) = 4.55$, $p < .001$), complementing the previous independent t-test results for these regions. All other seed regions were not significant ($ps > .286$). For children, above-zero SC-indices were shown for DMPFC ($t(28) = 3.32$, $p < .001$) and TPJ at an uncorrected level ($t(28) = 2.69$, $p = .012$). All other seeds were not significant ($ps > .061$). Together, these analyses suggest distinct roles of supportive connectivity of interactive biological motion for each age group: For adults, evidence is shown for PSTS and FBA, and in children for TPJ and DMPFC.

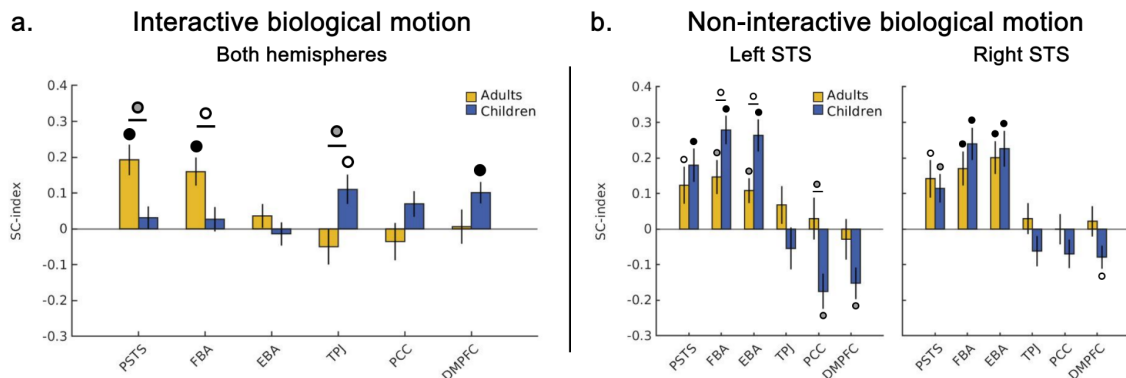


Figure 2. Bar charts showing group mean supportive connectivity (SC-index) from each seed region to STS (seeds are contralateral to STS hemisphere), for each age group respectively, for: a) Interactive biological motion (plotted across both STS hemispheres combined; no age group \times hemisphere interaction) and; b) Non-interactive biological motion (plotted separately for each STS hemisphere following a significant age group \times hemisphere interaction). Error bars are SEM. Filled black-, filled gray-, and unfilled circles denote p -values of $< .001$, $< .01$, & $< .05$, respectively.

Interactive biological motion: Exploratory searchlight seeding analyses

Next, we ran searchlight analyses to test whether brain areas beyond the a-priori seed areas showed a significant SC-index. One-sample t-test maps are shown in figure 3A (left panel); these maps show which areas yield a significantly 'above-zero' SC-index, for each age group separately (no significant negative effects were observed for either group). Two main observations are noted here. First, the two groups showed distinct searchlight coverage, with very minimal overlap. Most notably, bilateral PSTS was shown for adults, while children showed unique coverage more posteriorly, in bilateral posterior temporo-occipital cortex, along with extensive coverage along the middle-to-anterior STS (left hemisphere). Second, coverage is more diffuse for adults, predominantly left hemisphere effects in middle fusiform gyrus, middle cingulate cortex, dorsal precentral gyrus, superior parietal cortex, and anterior STS/superior temporal gyrus (small right hemisphere clusters were shown for anterior STS, insula, & posterior cingulate). Children also showed unique coverage in medial prefrontal cortex (dorsal and ventral aspects) that was mostly confined to the left hemisphere. Direct comparisons between groups (independent t-test; figure 3A, right panel), show small clusters in right PSTS and anterior superior temporal gyrus/insula, along with left insula and middle-cingulate cortex, indicating a significantly higher SC-index for adults than children in these areas. Together, these results show an age-related difference in terms of how activation to interactive biological motion in STS is related to functional connectivity to the wider brain.

Follow-up analyses: Non-interactive biological motion

We next tested SC-indices for seed regions when considering STS activation to non-interactive biological motion. The primary aim of these analyses was to test whether the results in the preceding analyses are specific to interactive biological motion. A 3-way mixed ANOVA (age-group x seed region x target region hemisphere) revealed a significant 3-way interaction ($F(5,275) = 2.44$, $p = .035$, $\eta^2 = .042$). We focused on follow-up comparisons between the two age-groups (i.e. comparing SC-index between adults and children, per each seed region, per hemisphere; see figure 2B). Unlike for interactive biological motion, few differences were shown when directly comparing the two groups, and these results were specific to right hemisphere seed regions. Children showed a significantly lower (more negative) SC-index than adults for PCC ($t(500.77) = 3.08$, $p = .002$). Children showed an uncorrected trend towards a higher SC-index than adults in EBA ($t(500.77) = -2.33$, $p = .020$) and a marginal trend in FBA ($t(500.77) = -1.98$, $p = .048$). No differences were shown for the remaining right hemisphere, or any left hemisphere, seed regions (right hemisphere seed $ps > .171$; left hemisphere seed $ps > .064$).

Next, one-sample t-tests (two-tailed) were conducted. Adults showed above-zero indices in FBA (right: $t(27) = 3.07$, $p = .005$; left: $t(27) = 3.55$, $p = .001$) and EBA (right: $t(27) = 3.12$, $p = .004$; left: $t(27) = 4.39$, $p = .002$). Similar trends were shown at an uncorrected level only in PSTS (right: $t(27) = 2.35$, $p = .026$; left: $t(27) = 2.69$, $p = .012$). Adults did not show differences in any other area (all other seed $ps > .506$). For children, above-zero SC-indices were shown for FBA (right: $t(28) = 6.94$, $p < .001$; left: $t(28) = 5.25$, $p < .001$), EBA (right: $t(28) = 5.84$, $p < .001$; left: $t(28) = 4.46$, $p < .001$), and PSTS (right: $t(28) = 3.79$, $p < .001$; left: $t(28) = 2.84$, $p = .008$). Children also showed

significantly negative SC-indices for bilateral DMPFC (right: $t(28) = -3.41$, $p=.002$; left: $t(28) = -2.42$, $p=.022$), and right PCC ($t(28) = -3.53$, $p=.002$). All other seeds were not significant (all other seed p s $>.160$). Importantly, these analyses show that the group differences demonstrated for interactive biological motion are not shown for non-interactive biological motion.

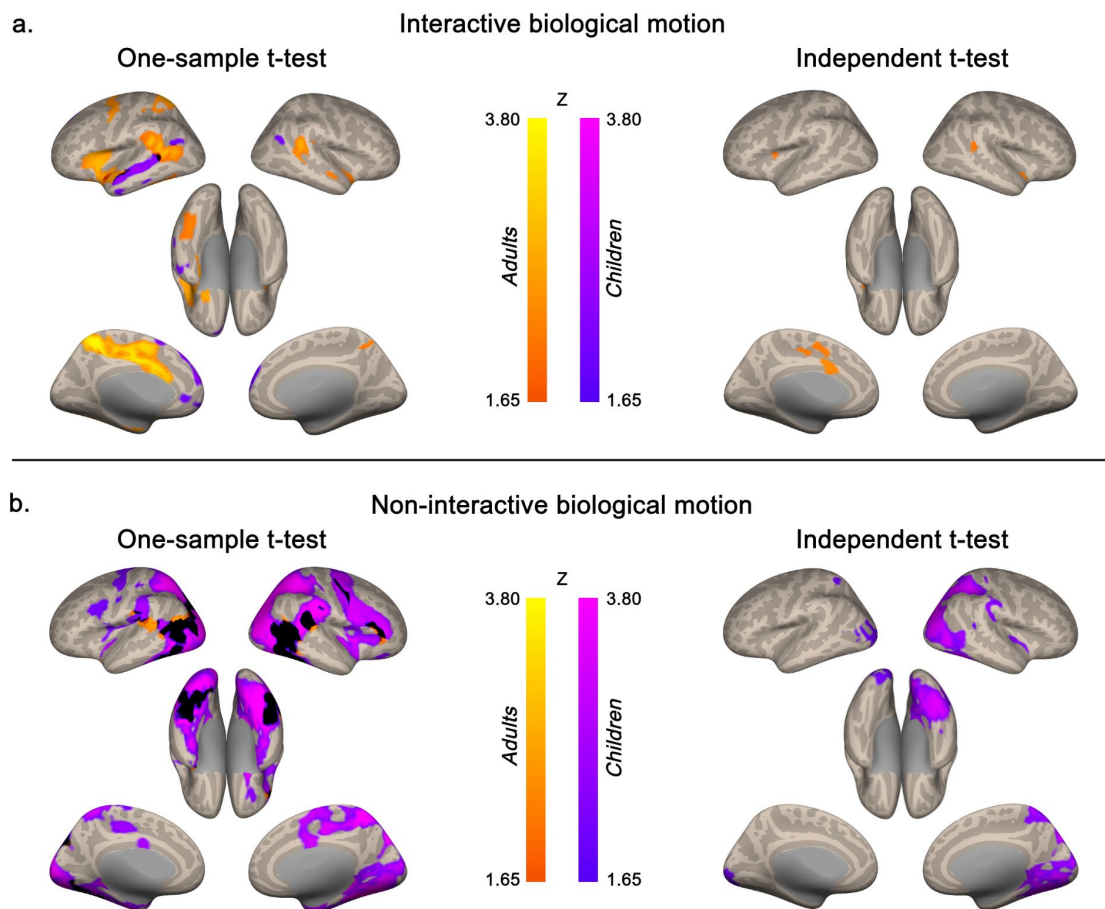


Figure 3. Surface maps showing group-level searchlight seeding analysis results. a) Results for interactive biological motion for one-sample t-tests for each group (left) and independent t-tests directly comparing the two groups (right). b) Results for non-interactive biological motion for one-sample t-tests (left) and independent t-tests (right). Orange scale shows significant coverage for adults (coverage significantly different from zero for one-sample t-tests, or significantly greater than children for independent t-tests); purple scale shows significant coverage for children; black coverage shows overlap between groups for the one-sample t-tests).

Finally, complementary searchlight analyses were conducted. Two main observations are noted from the one-sample t-test maps (figure 3B, left panel; no

significant, negative SC-index coverage was observed). First, overlap is shown in bilateral lateral occipito-temporal cortex and fusiform gyrus (consistent with EBA and FBA regions), along with right lateralized supramarginal gyrus, precentral gyrus and inferior frontal gyrus). Second, adults showed unique coverage in left superior temporal gyrus only, while children showed extensive unique coverage across many brain areas including PSTS, dorsal precentral gyrus, superior parietal cortex, ventral temporal cortex, lateral occipital cortex, middle cingulate cortex, and lateral prefrontal cortex. When directly comparing between groups (i.e. independent t-test map; figure 3B, right panel), children showed a stronger SC-index than adults in many areas (and adults did not show significantly higher SC-index in any area); this coverage was stronger in right hemisphere regions (i.e. posterior- and inferior parietal cortex, posterior cingulate cortex, lateral-, ventral- and medial posterior temporal cortex), with effects also in left superior parietal cortex and occipito-temporal cortex). These results suggest that non-interactive biological motion processing in STS is supported by connectivity to EBA, FBA, and PSTS in adults. In children, similar coverage is shown for EBA, FBA, and PSTS, but also much broader coverage in the wider brain, indicating that immature biological motion responses are, in part, characterized by widespread connectivity to the rest of the brain.

Discussion

Here, we show that different connectivity supports social interaction processing in adults and children. Specifically, supportive connectivity to contralateral PSTS (which favors biological motion (e.g. Gobbini et al. 2007; Grossman et al., 2000), action-intention understanding (e.g. Brass et al., 2007; Saxe et al., 2004), and dynamic interactive information (e.g. Isik et al., 2017; Walbrin et al., 2018) and body-preferring

FBA, is shown in adults. By contrast, connectivity to DMPFC and TPJ - two areas that form central nodes of the mentalizing network (e.g. Schurz et al., 2014; Richardson et al., 2018) - is shown in children. Importantly, these connectivity differences are specific to interactive biological motion.

We suggest that these age-differences in supportive connectivity reveal different cognitive strategies that support understanding interactive biological motion. That is, that children may engage in more effortful, covert inferential processing than adults, who rely on more overt inferences (i.e. children tend more towards making hidden mental state inferences, while adults understand the immediate intentions of interactions via observable actions). Indeed, previous meta-analysis results (Schurz et al., 2014) show that TPJ and MPFC are core mentalizing network areas that are routinely engaged by tasks that probe covert inferences (e.g. correctly inferring the beliefs of a character in a story, correctly associating a personality trait with the behavior of an individual, and inferring the strategy of another player in a game (e.g. rock, paper, scissors)). Similarly, previous studies that use visual interaction stimuli *and* prompt participants to make covert inferential judgements show MPFC activation (Dolcos et al., 2012; Iacoboni et al., 2004) while such activation is typically missing from studies that do not prompt these kinds of judgements (Georgescu et al., 2014; Isik et al., 2017; Walbrin et al., 2018; Walbrin et al., 2019).

Previous work shows that, relative to adults, children and adolescents demonstrate increased MPFC activation (Blakemore et al., 2007; Pfeifer et al. 2007; Kobayashi et al., 2007; Sebastian et al. 2012) and connectivity between MPFC and other social brain areas while performing tasks that probe covert judgements about other people (Burnett & Blakemore, 2009; Somerville et al., 2013). The role of MPFC

in these studies has been interpreted as reflecting an increase in cognitive effort required for making mental-state inferences (Blakemore, 2012), as well a general functional mechanism in service of higher-level skill acquisition (e.g. increased recruitment of MPFC while learning to master complex cognitive abilities; Johnson, 2011). In the context of the current findings, increased reliance on covert inferential processing may be a necessary mechanism that supports a gradual shift towards a more automatic (and less cognitively effortful) form of interaction understanding in adults.

Accordingly, mature interaction responses are supported by connectivity to (contralateral) PSTS (as well as FBA). While PSTS has long been associated with human biological motion perception (Allison et al., 2000; Gobbini et al. 2007; Grossman et al., 2000; Carter & Pelphrey, 2006), it is also associated - and potentially, at least partially, confounded - with processing the immediate, overt intentions that underlie others movements and actions (Brass et al., 2007; Saxe et al., 2004; Pelphrey et al., 2004; Gao et al., 2012; Lee et al., 2014; Deen & Saxe, 2012; Vander Wyk et al., 2009). For example, Saxe et al. (2004) demonstrate PSTS involvement when subjects viewed stimuli depicting a walking human figure momentarily pausing behind a bookshelf (vs. no momentary pausing); the immediate intention (i.e. the person is browsing) is grasped with relatively minimal abstraction compared to higher-level covert judgements (e.g. the person likes to read, they are curious), that are supported by areas of the mentalizing network. It is perhaps inevitable then that PSTS is strongly engaged by dynamic social interactions - which involve perceiving and processing both action and intention information - in adults (Centelles et al., 2011; Isik et al., 2017; Masson & Isik, 2021; Walbrin et al., 2018; Walbrin & Koldewyn, 2019; Walbrin et al.,

2020; Bellot et al., 2021; Georgescu et al., 2014; Landsiedel et al., 2022; Wordecha et al., 2018).

In short, adults may rely on the PSTS to grasp the immediate, overt intentional contents of interactions - a complex ability that likely undergoes refinement across development. By contrast, in lieu of this ability, children may rely more on an effortful, covert strategy that depends on areas of the mentalizing network. Although the present data cannot reveal the exact nature of the kinds of inferences that children make, we consider two possibilities. First, children may build a hierarchical 'piece-by-piece' understanding of interactions that requires multiple inferences (e.g. "the two people are moving quickly" > "they seem angry" > "they are arguing"). Second, children may engage more in cognitive and affective mental state attributions (e.g. "they are angry at each other", "they don't like each other"). By contrast, adults may understand the gist of an interaction without covert mental-state inferences (e.g. the kinematics of the 2 people imply an argument; as experience suggests that anger is typical for most arguments, inferring that the interactors are angry is redundant, and not necessary for a basic understanding of the scenario). However, these possibilities are not exhaustive and future studies may better specify the kinds of spontaneous attributions that children make in these scenarios.

We also consider that neural maturation is an important factor when considering the current results. For example, gray matter volume changes occur relatively slowly in STS compared to most other brain areas (Gogtay et al., 2004). Other similar morphological changes of STS, such as reduction in cortical thickness (Mills et al., 2014) and changes in sulcal depth (Bonte et al., 2013), have also been shown. These

structural changes across development undoubtedly contribute to the present age-related effects (e.g. by refining the functional organization of STS).

We also note both differences and commonalities across groups in the involvement of body-perception areas. FBA demonstrates supportive connectivity of interactive biological motion in adults but not children. This aligns with previous findings that FBA (as well as EBA) shows sensitivity to dyadic body cues such as facing direction (Abassi & Papeo, 2020) and apparent congruency of interactants (Quadflieg et al., 2015) that are likely important computations for differentiating interactive- from non-interactive biological motion. Both children and adults also showed FBA involvement for non-interactive biological motion, suggesting that the computations in this area are also relevant for biological motion per se (i.e. differentiating non-interactive biological motion from scrambled motion).

By comparison, supportive connectivity effects for EBA were not shown (for either age group) for interactive biological motion, but instead these effects were shown for non-interactive biological motion, suggesting a more general involvement of this area in supporting body- and biological motion processing per se. This lack of involvement, at first glance, appears at odds with previous work that links EBA with the processing of dyadic stimuli (Abassi & Papeo, 2020; Landsiedel et al., 2022; Walbrin & Koldewyn, 2019; Quadflieg et al., 2015). This discrepancy might, in part relate to stimulus differences - the stimuli used across these studies contained strong body-form information that is known to drive EBA responses (e.g. Downing et al., 2006) but is comparatively weaker (though still present in point-light stimuli e.g. Vangeneugden et al., 2014), and therefore may not contribute sufficiently to STS responses that differentiate interactive and non-interactive biological motion in these

data. Interestingly, a recent study showed that the degree of feedforward connectivity from EBA to PSTS is dependent on the kind of movement portrayed by point light dyads (i.e. moving towards vs. moving away; Bellot et al., 2021). However, methodological differences in the present study make a direct comparison difficult (i.e. directed dynamic causal modeling with mean ROI time-courses vs. bi-directional background connectivity with voxel-wise STS time-courses). Parsimoniously we suggest that, given different response preferences between ventral body areas - that is, stronger preference for body-part- and whole-body stimuli in EBA and FBA, respectively (Taylor et al., 2007) - stronger supportive connectivity of FBA than EBA likely reflects the higher relevance of elaborated whole-body information that is more useful for whole-body interactive biological motion discrimination.

Finally, we note several limitations and aspects of the current experiment that merit further research. First, we are agnostic as to the causal nature of the present connectivity effects. Future research may use brain stimulation approaches to directly target and perturb the contribution of individual seed areas. Second, we used sparse, visually-controlled point-light stimuli that do not contain information that would otherwise be important in most interactive contexts (e.g. spoken language), and as such, future research may focus on other interactive information not present in the current stimuli. Third, we demonstrate compelling effects when considering a broad age-range of children, but future work is needed to provide a more fine-grained developmental understanding across childhood, as well as to explore continued change across adolescence.

In summary, we show age-related differences in how the functional connectivity of social brain areas supports interactive biological motion processing in STS. These

results are an important first step towards understanding how distinct sources of social information may contribute to social interaction understanding in the brain across development.

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