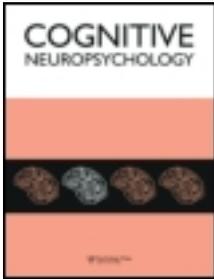


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Neural correlates of gesture processing across human development

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Co-speech gesture facilitates learning to a greater degree in children than in adults, suggesting that the mechanisms underlying the processing of co-speech gesture differ as a function of development. We suggest that this may be partially due to children's lack of experience producing gesture, leading to differences in the recruitment of sensorimotor networks when comparing adults to children. Here, we investigated the neural substrates of gesture processing in a cross-sectional sample of 5-, 7.5-, and 10-year-old children and adults and focused on relative recruitment of a sensorimotor system that included the precentral gyrus (PCG) and the posterior middle temporal gyrus (pMTG). Children and adults were presented with videos in which communication occurred through different combinations of speech and gesture during a functional magnetic resonance imaging (fMRI) session. Results demonstrated that the PCG and pMTG were recruited to different extents in the two populations. We interpret these novel findings as supporting the idea that gesture perception (pMTG) is affected by a history of gesture production (PCG), revealing the importance of considering gesture processing as a sensorimotor process.

Keywords: Gesture; Development; Neuroimaging; Multisensory integration; Perception–action.

As we actively engage with our environment, our actions determine what we perceive just as our perceptions drive our actions. Most often, the action–perception interactions that come to mind are those in which actions are directed at objects in the environment. Indeed, researchers have demonstrated that interacting with objects can change how objects are later perceived, substantiating the idea that active learning affects cognitive processing—our brains process objects differently after a history of active exploration (e.g., James,

2010; James & Atwood, 2009; James, Butler, & Mueller, 2008; James & Maouene, 2009; James & Swain, 2011; Longcamp, Anton, Roth, & Velay, 2003). A second domain, in which action–perception interactions may have explanatory power when considering cognitive and neural processing, is the domain of co-speech gesture.

Gestures are naturally produced actions (not explicitly taught) that accompany speech cross-culturally (e.g., Kendon, 2004). The meaning of a gesture is reliant on co-occurring speech,

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although the relation between speech and gesture varies. For instance, when gestures illustrate something concrete, they are known as iconic gestures, whereas when they illustrate an abstract concept, they are considered metaphoric (McNeill, 1992). When talking about an ant crawling along the ground, a person may move her index and middle fingers back and forth while moving her hand in one direction, thereby producing an iconic gesture representing the motion of the ant in a concrete way. This same gesture could be metaphoric in the verbal context of chills moving up someone's spine. Given the integral connection between gesture and speech, it is therefore not surprising that researchers, interested in the neural correlates of gesture, have primarily considered how gesture and language processing relate (e.g., Dick, Goldin-Meadow, Hasson, Skipper, & Small, 2009; Dick, Goldin-Meadow, Solodkin, & Small, 2012; Green et al., 2009; Holle & Gunter, 2007; Holle, Gunter, Rüschemeyer, Hennenlotter, & Iacoboni, 2008; Holle, Obleser, Rueschemeyer, & Gunter, 2010; Kircher et al., 2009; Skipper, Goldin-Meadow, Nusbaum, & Small, 2009; Straube, Green, Bromberger, & Kircher, 2011; Willems, Özyürek, & Hagoort, 2009).

In the present study, we investigate the neural correlates of gesture processing couched in a different framework. Clearly, gestures are related to language, but gestures can also be studied as a special class of actions; gesture (and nongesture actions) have been studied extensively with regard to both their production and their perception. In our action–perception framework, we consider production and perception of actions (and thus gestures) to be inextricably linked. Thus, in considering gestures as a specific class of actions, we hypothesize that the cognitive and neural systems underlying gesture perception will be influenced by the experience an individual has with gesture production.

There are three primary pieces of evidence for considering gesture perception as being affected by gesture production. First, there is a general and now well-known finding that how the brain processes perceptual information is affected by

whether or not we have a history of self-produced action associated with the percept. Several research groups have shown “reactivation” of motor systems during visual perception of objects *only* after active exploration of the objects has taken place (e.g., Butler, James, & James, 2011; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; James & Gauthier, 2006; James & Swain, 2011; Nyberg et al., 2001). Research groups have also shown that a history of producing a particular type of action affects how we perceive others producing that action—for example, reactivation of the motor cortex occurs when dancers perceive others dance (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005). These previous studies suggest that the recruitment of sensorimotor regions during gesture perception is related to one's experience self-generating gestures (e.g., Dick et al., 2009; Holle et al., 2008; Skipper, Goldin-Meadow, Nusbaum, & Small, 2007; Willems, Özyürek, & Hagoort, 2007).

Second, overlap of the neural substrates underlying gesture perception and the neural substrates underlying purposeful action has been reasonably well established in areas like the posterior middle temporal gyrus (pMTG; e.g., Green et al., 2009; Straube, Green, Qeis, Chatterjee, & Kircher, 2009; Villarreal et al., 2008; Willems et al., 2009). Evidence from the action literature suggests that the pMTG is a putative sensory region that has been implicated in the processing of sensory input that one associates with the movement of manipulable objects. For example, it is the pMTG that is more strongly recruited when individuals view objects that can be acted on as tools than when they view nontool objects (e.g., Beauchamp & Martin, 2007; Chao, Haxby, & Martin, 1999; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Martin, Wiggs, Ungerleider, & Haxby, 1996). Considered from a developmental perspective, as children age, their ability to complete a semantic-associations task improves, and this improvement is correlated with increased activation in the pMTG (Blumenfeld, Booth, & Burman, 2006). These findings may converge on the possibility that the pMTG is maximally recruited only when semantic

representations of object concepts and the words describing them are fully developed, and perhaps in particular after development of strong action-related object associations.

Work studying gesture specifically (as opposed to action more generally) supports our claim above that the pMTG is involved in perceiving meaningful actions, of which gestures are one type. For example, Villareal and colleagues (2008) found that the pMTG is sensitive to meaningful gesture (where “gesture” refers to the spontaneous gesticulations naturally produced with speech as described by McNeill, 1992); Kircher et al. (2009) found that the pMTG is sensitive to both gesture and speech, and they suggested that the pMTG is important for semantic processing; and Straube et al. (2009) showed that activity in the pMTG is correlated with the ability to recall meaningful gestures. But, Willems et al. (2009) found that the pMTG is *only* sensitive to gestures that have a codified meaning without speech, such as pantomimes. That is, they found that the pMTG is *not* sensitive to the meaning of co-speech gestures. However, all of these studies (even Willems et al.), found that the pMTG processed action and semantic meaning; the different conclusions of the studies were related to the exact involvement with meaningful actions. Thus, considering both the action–perception and gesture literatures, there is convergent evidence that the pMTG is recruited when semantic information about actions is accessed, which can occur when one perceives either actions or objects associated with actions.

The third piece of evidence comes from the observation that children produce significantly less gesture during speech than do adults. In a study of gesture use in narrative, Colletta, Pelleng, and Guidetti (2010) found that adults gesture significantly more than children. This finding was significant, even when controlling for narrative length. More specifically, adults gestured more than 10-year-olds, who gestured more than 6-year-olds. Given the well-known link between production and perception and the premise of the action–perception framework, this developmental difference in gesture production would

suggest that children perceive co-speech gestures differently than adults. Finding evidence for or against this conjecture has implications for our understanding of how children learn from co-speech gesture, which is used regularly in educational settings (e.g., Flevares & Perry, 2001).

In summary, we know that a history of self-produced action alters one’s subsequent perception of that action and objects that are consistently targeted with the action. In addition to the motor system (e.g., primary motor, premotor, and supplementary motor cortices), the pMTG also shows changes in activation based on this history of action. Importantly for the present study, these same brain regions are recruited when adults perceive co-speech gesture. This overlap suggests that gesture may rely on the same neural systems as other actions and, like other actions, that processing may be shaped by one’s experience with producing gesture. Researchers have shown that the use of gesture in narrative changes across development—6-year-olds gesture less than adults (Colletta et al., 2010), and, in addition, younger children have less cumulative experience producing gestures than older children, who in turn have less experience than adults. We hypothesize that recruitment of the motor cortex and the pMTG with visual gesture processing will change across development as the history of gesture production increases. This hypothesis can be tested directly by examining the “gesture-processing brain network” at multiple developmental time-points.

In the present study, we used functional magnetic resonance imaging (fMRI) to ask how children (5–11-year-olds, at 1.5-year increments) and adults process iconic gesture in the context of speech and in isolation. It is a fact that younger children have less overall experience producing gestures than their older peers, who have less experience than adults. In addition, and as described above, adults produce more gestures than children; thus, adults’ recent experience with gesture production will also be greater than children’s. We therefore hypothesize that adults will show greater activation than children in motor areas that are recruited when one sees an

action that one has previously performed. We also hypothesize that processing of co-speech gesture will differ across age in the pMTG, as adults and older children have a different knowledge base of the meaning of actions than do younger children.

Method

Participants

Fifty-two individuals, 13 in each of four age groups, participated in the present study. Three age groups of children were recruited: 5.0- to 6.0-year-olds ($M = 5.5$, 7 males), 7.5- to 8.5-year-olds ($M = 7.7$, 7 males), and 10.0- to 11.0-year-olds ($M = 10.5$, 3 males), as well as a group of adults (21 to 27 years; $M = 24.8$, 5 males). All participants were right-handed, native English speakers, with no reported history of neurological or psychiatric disorders and normal or corrected-to-normal visual acuity. Informed consent was obtained from the 13 adult participants, and from the parent or guardian of 67 children. Assent was obtained from children over the age of seven. Data from 28 children were excluded from analysis, based on refusal to complete the experimental session, or excessive movement during the fMRI portion of the session.

Stimuli and apparatus

Thirty video clips were used in the present study, 10 clips within each of three conditions. These video clips came from a subset of 70 clips, created for a larger experiment; however, only three of the seven types of clips are relevant for the present study. In each 2.5-s clip, a female was shown (a) speaking a sentence with iconic content (S), (b) speaking a sentence with iconic content and performing a corresponding gesture (GS), or (c) performing a gesture in isolation, without speech (G; examples of the sentences and gestures are included in Appendix A). Sentences either described an event that had occurred (e.g., Bugs crawled up his arm), or described an object (e.g., She held a big purse). The same sentences were used across both conditions that included speech (S, GS). In the GS condition, iconic gestures were produced with

the sentences. The same gestures were produced in the absence of speech during the G condition. The remaining four conditions that were not analysed for the purposes of this study (they are analysed in the context of another study) included the same female (a) speaking a sentence with metaphoric content (b) speaking a sentence with metaphoric content and performing a corresponding gesture—gestures matched those used in the iconic content sentences, (c) speaking a sentence with iconic content and performing unrelated movement, (d) speaking a sentence with metaphoric content and performing unrelated movement. Video clips were presented via a Mitsubishi XL30 projector, which projects images onto a screen viewed through a mirror from the rear part of the bore of the scanner, with the auditory stream presented simultaneously through in-ear, universal fit earphones (Westone), or headphones. Both visual and audio stimuli were presented via Superlab 4.0.7b software on a Macintosh MacBook laptop.

Procedure

fMRI session (adults). Adult participants completed six functional imaging runs before completing a high-resolution structural scan. During functional runs, participants passively viewed short movies, blocked by condition. Movies were presented one after another, with no interstimulus intervals within blocks. The entire procedure lasted no more than one hour with individual runs lasting between 3.5 and 4 min. Blocks were 30 s with an interblock interval of 10 s. Adults saw four blocks of each condition, or 48 clips per condition. The order of the presentation of blocks was randomized across the runs, and no explicit response was required.

fMRI session (children). Unlike adults, children can be intimidated by the neuroimaging environment; thus, children were exposed to a simulated fMRI environment before undergoing neuroimaging. Children spent approximately 5 min in the simulator, during which time they listened to the sounds emitted by both echo-planar imaging (EPI) and structural scans and were shown how

the headphones and projector worked (for more on this methodology, see James, 2010; James & Maouene, 2009; James & Swain, 2011). Once children were comfortable in the simulator, they participated in the actual neuroimaging session that consisted of functional imaging runs and a high-resolution structural scan. Like adults, children passively watched videos from each of seven conditions, only three of which are included in this analysis, blocked by condition, and the presentation of blocks was randomized across participants. Unlike the adults, the children underwent the anatomical scan before the functional scans. Children saw 24 clips per condition (half of the presentations given to adults), such that the imaging session lasted no more than 30 min, with individual runs lasting between 2.5 and 3.5 min. Because adults were comfortable remaining in the scanner for longer than the children and were able to keep themselves still for longer, adults watched double the number of clips per condition than children (48), allowing for collection of double the data. Baseline maps for each condition, within each age group, are provided in Figure 1—these maps indicate that all groups could perceive the stimuli, both visually (all conditions) and auditorially (conditions S and GS).

More data were collected in adults than in children, creating a possible concern regarding comparisons across groups. One approach would have been to use only the first half of the adult data, which would make it equivalent to data for the children. However, we felt that the extra data in adults could be leveraged (especially with respect to defining reliable regions of interest) if we could demonstrate that the additional data in adults would not affect the reliability of comparisons across groups. To that end, a simulation was conducted to determine whether or not the difference in design could affect the results. Specifically, with half the presentations/data for children relative to adults, it is possible that the adults' design had sufficient statistical power to detect some effects of interest, whereas the children's design did not. Related to this issue is the concern that, even with the same amount of data, the children's data may have lower signal-to-noise ratio (SNR)

than the adults' data, due to movement artefacts or other factors. The shorter design and the possibility of lower SNR in children could contribute to observance of effects in adults that are not observed in children. To assess the suitability of the design for the measured SNR in children, we conducted a simulation (see Supplemental Materials) to estimate the SNR necessary to produce statistical power of 80% with the children's design and then compared that critical SNR value to the SNR in the pMTG and precen-tral gyrus (PCG) regions of interest (ROIs). For every child in the sample, the measured SNR in the pMTG was greater than the estimated criterion SNR value found with the simulation (see Supplemental Table 1). The SNR was more variable in the PCG ROI, and there were two children in the 7.5-year-old group who did not meet the SNR criterion.

fMRI parameters. Imaging occurred in a 3-Tesla Siemens Magnetom Trio whole-body MRI system and a phased-array 12-channel head coil in the Imaging Research Facility located in the Indiana University Psychological and Brain Sciences department. The field of view was 220 mm with an in-plane resolution of 64×64 pixels and 33 slices per volume (3.4 mm thick, no gap). Images were acquired using an echo-planar technique (echo time, TE = 30 ms, time of repetition, TR = 2,000 ms; flip angle = 70°) for blood-oxygen-level-dependent (BOLD) imaging. High-resolution T1-weighted anatomical volumes were acquired using a Turbo-flash 3-D sequence: inversion time, TI = 900 ms, TE = 2.67 ms, TR = 1,500 ms, flip angle = 9° , with 120 sagittal slices of 1.5 mm thickness, a field of view of 192×192 mm, and an isometric voxel size of 1.5 mm^3 .

fMRI data analysis procedures. Analyses were conducted using the Brain Voyager QX analysis package, Version 2.2 (Brain Innovation, Maastricht, Netherlands). During preprocessing, images underwent 3D motion correction and linear trend removal, and a Gaussian spatial blurring (full width at half maximum, FWHM 6 mm) was

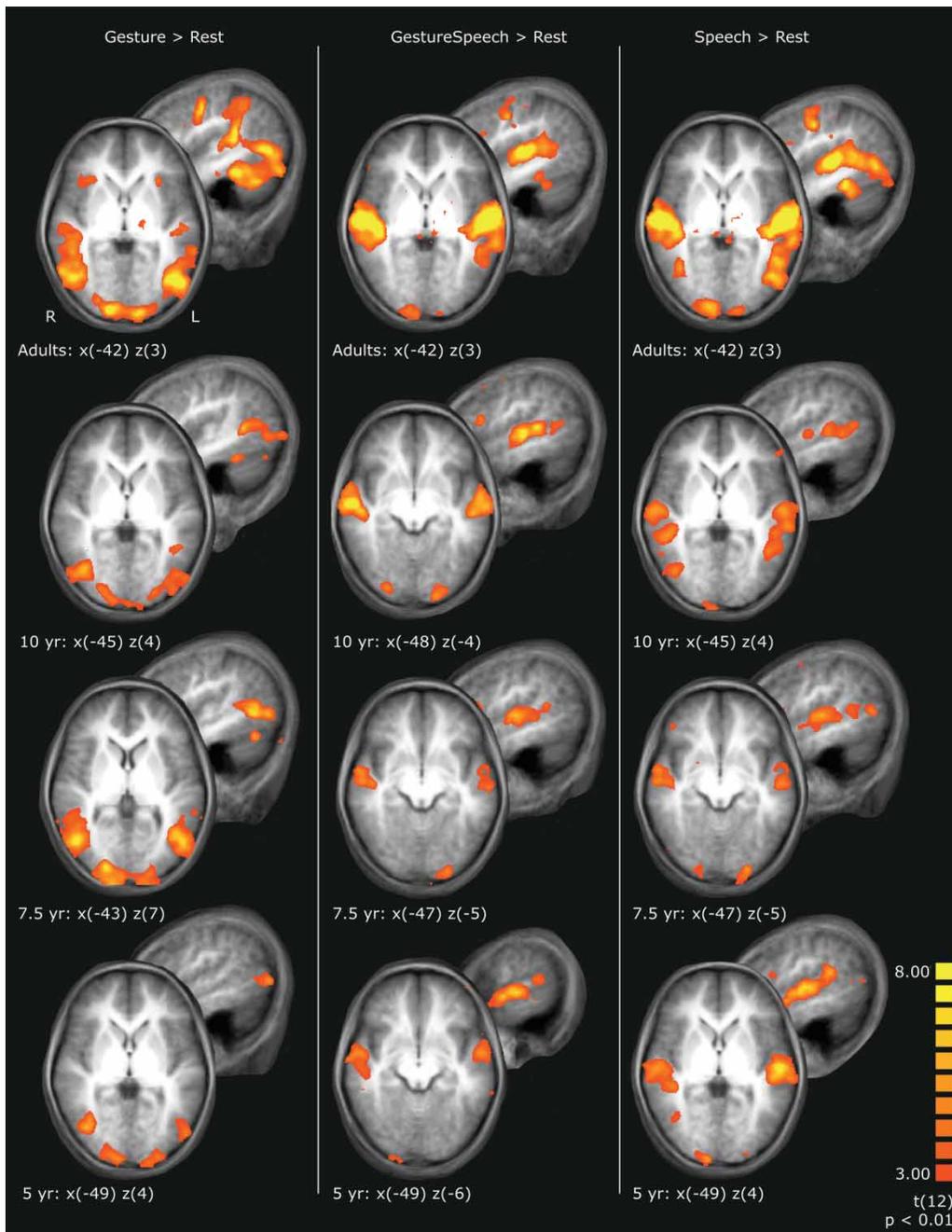


Figure 1. Baseline maps of activation to each conditions compared to fixation are presented at a threshold of $p < .01$. To view a colour version of this figure, please see the online issue of the Journal.

applied. Individual functional volumes were coregistered with anatomical volumes using an intensity-matching, rigid-body transformation algorithm. Individual anatomical volumes for children and adults were normalized to the Talairach reference frame using the eight-parameter affine transformation with parameters selected in relation to anatomical landmarks, identified manually (Talairach & Tournoux, 1988). Applying the same transformation to the coregistered functional volumes placed the functional data in a common brain space, allowing for comparisons across participants. Statistical analyses were performed with a random-effects generalized linear model (GLM) in which predictors were included for each of the task conditions and were generated from the timing of the experimental protocol for each condition, then convolved with a two-gamma hemodynamic response function. Parameters from the motion correction algorithm were included as predictors of no interest.

We were interested in determining the pattern of activation across conditions in the left PCG and left pMTG. Therefore, we performed a region of interest (ROI) analysis consisting of five stages.

Stage 1: We functionally localized the PCG and pMTG from a whole-brain statistical map generated in the adult group from the contrast $G, GS, S > \text{rest}$, weighted equally, and with an uncorrected statistical threshold of $p < .001$, $t(12) = 4.32$. Significant clusters were labelled PCG if they were found anatomically in the precentral gyrus. Significant clusters were labelled pMTG if they were found anatomically at the juncture of the posterior part of the middle temporal gyrus and the anterior section of the occipital lobe. The coordinates of the pMTG clusters were similar to coordinates of regions previously defined as the pMTG (e.g., Beauchamp & Martin, 2007; Blumenfeld et al., 2006; Chao et al., 1999; Doehrmann, Naumer, Volz, Kaiser, & Altmann, 2008; Green et al., 2009; Martin et al., 1995; Martin et al., 1996; Villareal et al., 2008; Willems et al., 2009).

Stage 2: Because of individual variability, we functionally localized PCG and pMTG in each and every individual (adults and children). Whole-brain statistical maps were calculated in

each individual using separate fixed-effects GLMs followed by a contrast of $G, GS, S > \text{rest}$, weighted equally, thresholded with an uncorrected statistical value of $t = 3$. Significant clusters of voxels in these individual maps were labelled PCG or pMTG if they overlapped with the PCG or pMTG regions, respectively, in the adult group map (from Stage 1). An uncorrected threshold was used to ensure that individual-specific clusters were identified in the *maximum* possible number of individuals; however, even with this relatively liberal threshold, we failed to find PCG clusters in a number of children, who were therefore excluded from the PCG ROI analysis. Maps depicting the locations of the localized ROIs in each and every individual are shown in Figure 2.

Stage 3: Event-related averages were extracted from the two ROIs for each condition for each individual using event-related averaging. Twenty volumes were extracted for each ROI, beginning with the point of stimulus onset, to include the entire block (15 volumes) and the return to baseline during fixation periods (5 volumes).

Stage 4: For each ROI, a grand mean time course was calculated by averaging across conditions and participants. The grand mean time course represents the canonical response function for that ROI. The grand mean time course was used to find the *time* of peak magnitude. In this case, BOLD magnitude at volumes 7 and 8 post stimulus onset were almost identical in magnitude and were together considered the time (volume) of peak magnitude.

Stage 5: For each ROI, summary BOLD percentage signal change values were calculated for each condition and each participant. This was done by averaging time course values within a fixed time window (i.e., area under the curve). The time window was defined as the “peak” volume identified in Stage 4 plus one volume on either side of the “peak”. In this case, the fixed time window spanned volumes 6–9—that is, 4 volumes wide. Importantly, the same “peak”, and hence the same 4-volume time window, was used for all participants and conditions (i.e., was *fixed*). BOLD percentage signal change values

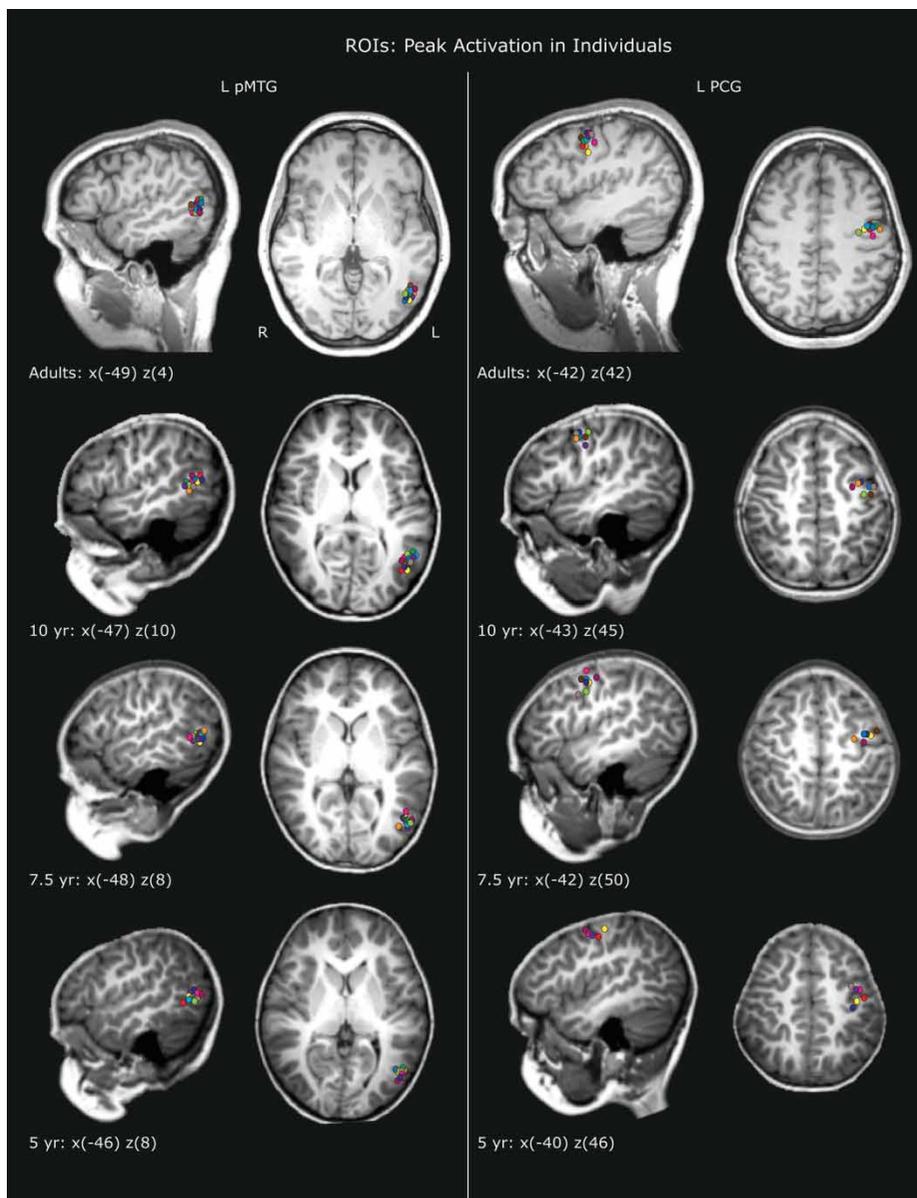


Figure 2. Regions of interest were identified in individuals by contrasting the three conditions of interest with fixation (G , GS , $S > \text{rest}$, weighted equally) in the group whole-brain statistical map at a threshold of $p < .001$. G = gesture alone; S = speech alone; GS = gesture and speech in combination; ROI = region of interest; pMTG = posterior middle temporal gyrus; PCG = precentral gyrus. The resulting regions were identified as voxels of interest (VOIs) and were used when extracting data from individuals. Range of peak activation for the pMTG ROI in each age group is: 5 yr: $x(-48 \text{ to } -40)$ $y(-75 \text{ to } -58)$ $z(-2 \text{ to } 13)$; 7.5 yr: $x(-51 \text{ to } -43)$ $y(-71 \text{ to } -76)$ $z(3 \text{ to } 10)$; 10 yr: $x(-54 \text{ to } -41)$ $y(-67 \text{ to } -51)$ $z(2 \text{ to } 15)$; adults: $x(-52 \text{ to } -43)$ $y(-70 \text{ to } -58)$ $z(-2 \text{ to } 10)$. Range of peak activation for the PCG ROI in each age group is: 5 yr: $x(-54 \text{ to } -31)$ $y(-15 \text{ to } -4)$ $z(32 \text{ to } 53)$; 7.5 yr: $x(-47 \text{ to } -30)$ $y(-14 \text{ to } 3)$ $z(39 \text{ to } 57)$; 10 yr: $x(-48 \text{ to } -32)$ $y(-14 \text{ to } 4)$ $z(34 \text{ to } 47)$; adults: $x(-47 \text{ to } -34)$ $y(-13 \text{ to } -1)$ $z(37 \text{ to } 58)$. To view a colour version of this figure, please see the online issue of the Journal.

were calculated using a “baseline” signal change value taken from the stimulus onset time point of the time course for each condition and each participant. Although the data used to select the two ROIs were the same as the data used for extraction of the BOLD time series, the selection contrast was orthogonal to the subsequent contrasts tested below; therefore the entire analysis was deemed *noncircular* based on the following equivalency: $C_S^T \cdot (X^T X)^{-1} \cdot C_T = 0$, where C_S and C_T are the selection and testing contrasts, and X is the design matrix (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009).

A special concern when imaging children is how to control for excessive head motion, as failure to acquire usable functional data from a child is most often due to motion (e.g., Poldrack, Paré-Blagoev, & Grant, 2002; Yerys et al., 2009; Yuan et al., 2009). We accounted for head motion in four ways: (a) Children with motion parameter estimates of movement that exceeded 6 mm in any axis were excluded from analysis, (b) during preprocessing, we used a motion correction (realignment) algorithm to estimate and correct for motion, (c) motion parameter estimates from the preprocessing stage were included in the GLM model as regressors of no interest (Evans, Todd, Taylor, & Strother, 2010; Poldrack et al., 2002). By including motion estimates in the GLM, the effects of head motion on ROI locations were reduced or eliminated. (d) From the motion estimates, severe motion “spikes” >5mm were identified, and those time-points were reassigned from the original experimental condition in the protocol to a “motion spike” condition. Motion spike time-points were added to the GLM model as dichotomous (and unconvolved) regressors of no interest. Using a combination of continuous time-series motion parameter predictors and dichotomous “motion spike” predictors accounts for more error variance than using continuous time-series motion parameters alone.

A second concern with paediatric imaging is whether or not children and adults can be compared in the same common space. Previous literature supports the comparison of children older

than 7 years of age to adults, within a common, Talairached space (Burgund et al., 2002; Kang, Burgun, Lugar, Petersen, & Schlaggar, 2003). Additionally, a recent analysis in our lab extends this finding to children as young as 5 years of age (Please see Appendix B for details and analysis).

Results

The present study was conducted to investigate activation patterns in the left PCG and pMTG, regions that have been implicated in processing percepts with which one has a history of self-produced action and/or that are part of the gesture-processing network. By considering activation to speech alone (S), gestures alone (G), and gestures and speech in combination (GS) we are able to explore how these facets of communication differentially influence the regions of interest. We consider activation patterns within each ROI separately.

ROI: Left PCG

In a number of children, a significant cluster was not found within the anatomical constraints specified for the PCG. A significant cluster was found for all adults, but was missing in four 5-year-olds, five 7.5-year-olds, and five 10-year-olds, when thresholding at $t = 3$ within each individual. This means that only 69% of our youngest group showed PCG activation, and 62% of our older groups of children. When *only* considering children with a significant PCG ROI, adults still showed greater activation in the left PCG than did children (see Table 1). A 3 (condition) \times 4 (group) factorial analysis of variance (ANOVA) revealed a main effect of group, $F(3, 34) = 7.04$, $p < .001$, but no main effect of condition, $F(2, 34) = 0.20$, *ns*, and no Group \times Condition interaction, $F(6, 34) = 2.06$, *ns*. To determine whether or not a systematic change in activation was occurring across age, we conducted a linear trend analysis post hoc, averaging across activation to the three conditions to get a dependent measure—as there was no main effect of condition or interaction—and using age group as a factor. Results revealed a significant linear increase in activation

Table 1. Mean percentage BOLD signal change in ROIs

ROI	Group	G	GS	S
L pMTG	5-year-olds	0.88 (0.53)	0.36 (0.60)	-0.18 (0.54)
	7.5-year-olds	1.38 (0.99)	0.71 (0.50)	0.20 (0.47)
	10-year-olds	0.83 (0.33)	0.57 (0.71)	0.39 (0.36)
	Adults	1.41 (0.28)	1.29 (0.46)	0.61 (0.41)
L PCG	5-year-olds	0.16 (0.42)	0.21 (0.21)	0.02 (0.31)
	7.5-year-olds	0.40 (0.30)	0.74 (0.84)	0.36 (0.60)
	10-year-olds	0.31 (0.49)	0.17 (0.50)	0.62 (0.49)
	Adults	0.86 (0.31)	0.77 (0.46)	0.68 (0.45)

Note: BOLD = blood-oxygen-level-dependent; ROI = region of interest; pMTG = posterior middle temporal gyrus; PCG = precentral gyrus; L = left; G = gesture alone; S = speech alone; GS = gesture and speech in combination. ROI: left pMTG.

across age, $F(3, 34) = 15.00$, $p < .001$. Although all three conditions must be considered together given the lack of a significant interaction, it is likely that the linear trend was driven by activation in the S condition: This is the only condition in which activation steadily increases across development. Thus, we interpret these results as showing a developmental progression: In general there is an increase in recruitment of the PCG across development, from low activation in 5-year-olds, to an intermediate level of activation in older children (7.5- and 10-year-olds), and finally to high activation in adults for processing input that is related to movement, both directly (through gesture, in the GS and G conditions) and indirectly (through speech, in the GS and S conditions). We suspect that this finding and our finding that many children do not show activation in this region are related to the differences in experience producing and processing similar stimuli between the children and adults and highlight the influence of experience on cognitive processes.

ROI: Left pMTG

A 3 (condition) \times 4 (group) ANOVA revealed main effects of condition, $F(2, 48) = 47.16$, $p < .001$, and group, $F(3, 48) = 8.23$, $p < .001$, as well as a significant Group \times Condition interaction, $F(6, 48) = 2.21$, $p < .05$. Paired-samples t tests reveal that the main effect of condition was driven by greater activation to G than to GS and S, $t(51) = 5.75$, $p < .001$; $t(51) = 8.86$,

$p < .001$, respectively, and greater activation to GS than to S, $t(51) = 4.06$, $p < .001$. This finding differs from previous results showing greater activation for bimodal communication (GS) than for unimodal communication (S, G) in this region for adults (e.g., Green et al., 2009; Straube et al., 2009; Willems et al., 2009) and may be driven by differences in experimental design. In short, we believe that activation was affected by whether participants were asked to explicitly focus on the message being communicated, as in the present study, or implicitly processed communicated messages while performing an unrelated task, as in previous work. Whereas participants in our study were required to interpret isolated gesture, participants in previous studies may not have processed isolated gesture as communicative, whereas the other conditions (S and GS) are *naturally* communicative and would have drawn attention, even while participants performed a separate task.

To determine whether a systematic change in activation was occurring across age, we conducted a linear trend analysis post hoc in each of the three conditions separately with age group as a factor and activation as a dependent measure. Results revealed a significant linear increase in activation across age for S alone, $F(3, 48) = 21.09$, $p < .001$, and GS, $F(3, 48) = 13.81$, $p < .001$, but not for G alone, $F(3, 48) = 2.01$, *ns*. Quadratic and cubic trends were not found to be significant.

The main effects, however, must be interpreted with caution, given the existence of a Group \times Condition interaction. To determine the patterns that were driving the interaction effect, repeated measures ANOVAs were conducted comparing conditions (S, GS, G) within each age group (see Figure 2). In the youngest two age groups, significant differences were found in left pMTG BOLD activation, warranting further post hoc comparisons among all three conditions [5-year-olds: $F(2, 12) = 38.84, p < .001$; 7.5-year-olds: $F(2, 12) = 11.86, p < .001$]. This analysis demonstrated that activation in the pMTG was significantly greater when children in the 5- and 7.5-year-old groups were presented with gesture in isolation than when gestures were presented in the context of speech [5-year-olds: $t(12) = 4.69, p < .001$; 7.5-year-olds: $t(12) = 2.37, p < .05$], and activation to the speech-gesture combination was greater than when speech was presented alone [5-year-olds: $t(12) = 4.42, p < .001$; 7.5-year-olds: $t(12) = 3.79, p < .001$]. Interestingly, in the 10-year-old group, the pattern of activation was similar to those of the younger groups, with greater activation occurring to G, followed by GS, and finally S; however, a repeated measures ANOVA only revealed a trend towards a significant difference among conditions, $F(2, 12) = 2.60, p = .10$. Finally, adults also showed a significant difference across conditions, $F(2, 12) = 21.17, p < .001$. Post hoc analyses revealed that activation was significantly greater to GS than to S, $t(12) = 6.14, p < .001$; however, unlike the findings in the youngest age groups, there was no significant difference between activation to GS and G, $t(12) = 0.88, ns$.

As the interesting change across development appears to be the relative change in activation to G and GS, an additional analysis was conducted to further investigate this finding (see Figure 3). The difference between activation to G and GS (G - GS) was calculated, and a correlational analysis was conducted between age and difference score. A two-tailed Pearson R correlation revealed a significant negative correlation between age and difference score, $r = -.27, p < .05$. This indicates that with an increase in age, the gap between the

amount of activation to G and GS decreases. These results may suggest a change across development in the ability to draw on gesture as a part of semantic representations of concepts, a finding that we consider in the discussion.

Discussion

We approached the question of the relationship between gesture perception and gesture production from a neurophysiological viewpoint: If gesture perception is affected by experience producing gesture, then we would see developmental changes in neural processing in brain regions that subserved both perception and production. This hypothesis was confirmed by our findings. The frontal motor system was recruited consistently in adults when they perceived co-speech gesture, but was not recruited consistently in young children. This suggests that for the frontal motor system to be recruited during perception of gesture, an individual must have accumulated substantial experience producing and perceiving gesture. In contrast to the results in motor cortex, the pMTG was consistently recruited in all age groups, even the youngest children, during perception of co-speech gesture. Interestingly, there were also age differences in the pattern of activation across conditions in pMTG. Specifically, activation with co-speech gesture (GS) showed an age-dependent increase, but, the difference in activation between co-speech gesture (GS) and gesture in isolation (G) decreased with age. This result suggests that experience producing gesture shapes the response of brain regions involved in processing the perception of co-speech gesture. Although this type of finding is well established in the action understanding literature, it is novel to co-speech gesture. Our results highlight the utility of exploring gesture processing in an action-perception framework.

Differences in PCG activation across development

To claim that gesture perception has any relationship to gesture production, one must show that, in the mature system, gesture perception recruits

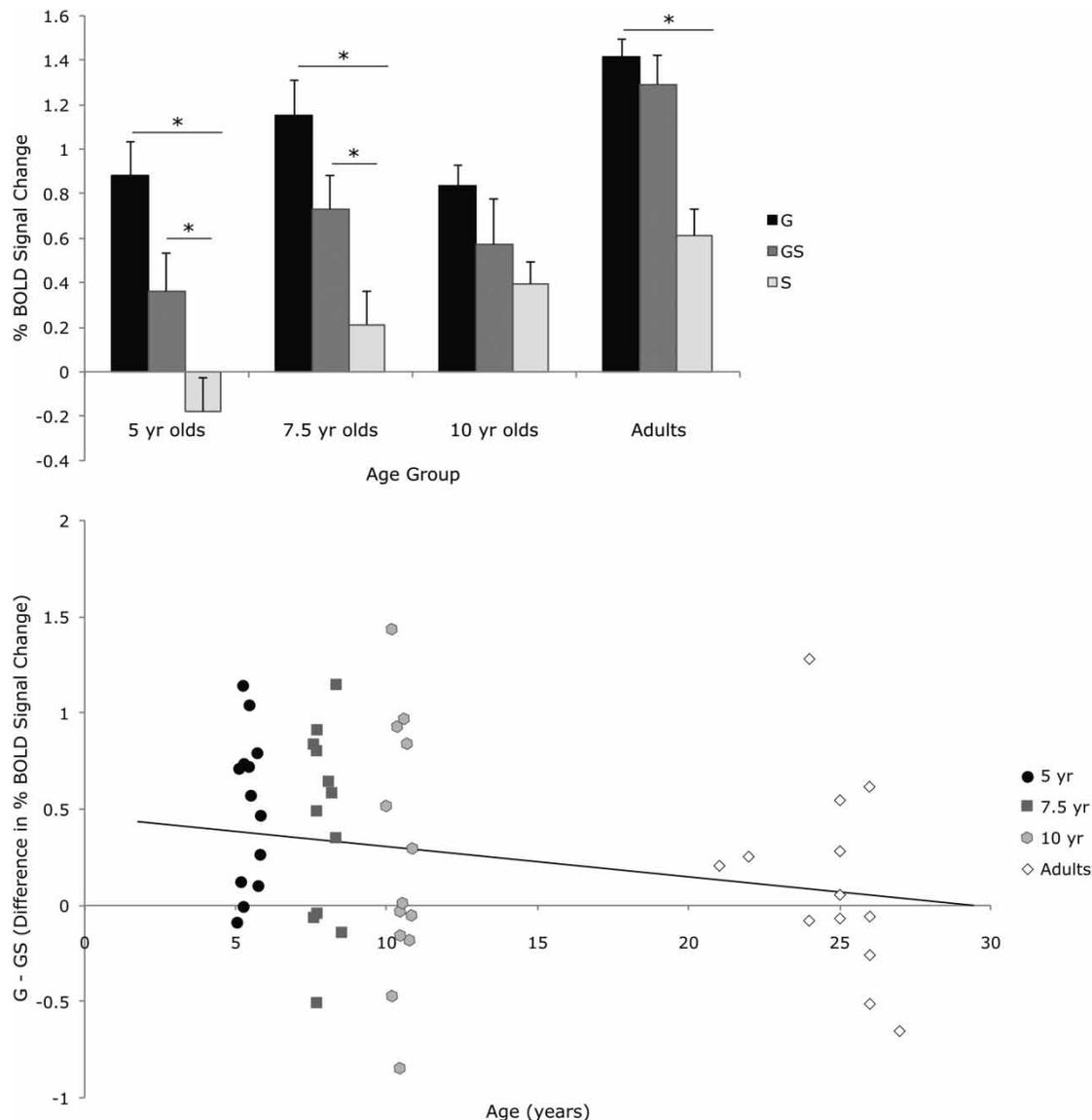


Figure 3. (a) Mean percentage BOLD (blood-oxygen-level-dependent) signal change in the left pMTG ROI (posterior middle temporal gyrus region of interest) for each condition in each age group. (b) Mean difference between activation (BOLD signal change) to G (gesture alone) and GS (gesture and speech in combination) in left pMTG for each age group. Trend line signifies the significant correlation, $r = -.27$, $p < .05$ of G - GS and age.

appropriate nodes of the motor network. We confirmed this by showing that adults recruited the PCG during gesture *perception*, thus, perceiving another performing an action recruits the motor system. However, our hypothesis was not just

about motor system recruitment during perception; rather, it relates to the effect of production *experience* on motor system recruitment during perception, a question that cannot be answered by looking at adults alone. Because children

produce gesture less than adults (Colletta et al., 2010), and gain more cumulative experience producing gesture gradually over development, we would expect—in a perception–action framework—less activation of the motor system in children than in adults during perception. This hypothesis was partially confirmed by showing that many children did not recruit the PCG at all during gesture perception. Furthermore, we found an age-related modulation in activation in the PCG across development, even after excluding the children who did not show significant activation in PCG. We conclude that less cumulative experience producing gesture results in less reliable motor system recruitment during gesture perception.

One possible limitation of this finding, however, is that the proportion of children that recruited the PCG did not change with age—reactivation was observed in just over half of the children in each age range studied. One would expect that if experience changes motor system recruitment during perception, that the consistency of that recruitment should increase with increasing age. Our results showed a strong difference in consistency of recruitment between adults and children, but not between different ages of children. However, there was an overall age-related modulation in PCG activation, even with adults excluded from the analysis. This suggests that PCG reactivation—in the children who show above-threshold activation—does become more reliable with age. Still, there are several possible explanations for why there were no strong age differences in the consistency of PCG recruitment during perception. It is possible that perception and production systems are not linked until children have gained a certain amount of experience producing gestures. Some children may produce gesture at a higher rate than others and reach this threshold more quickly, whereas others may not reach this threshold until adolescence. If this is the case, the children who showed PCG activation happen to be children who have more experience producing gesture. Alternatively, children may be recruiting different parts of the motor cortex than adults, and this is why we did

not see strong age differences in recruitment of the PCG. To address the possibility that other regions in the motor cortex may be active in children (aside from the PCG) we investigated the motor cortex activation in individuals using the same contrast as the one that localized the PCG (“G, GS, S > rest” conditions, weighted). There were no additional regions in the children in the motor cortex that were active as a result of this contrast, suggesting that the PCG is the region recruited during gesture observation after considerable experience producing gesture.

Differences in pMTG activation across development

To interpret our findings on gesture perception with respect to activation in the pMTG, it is relevant to summarize the general activation profile of pMTG in adults and the behavioural profile of our different age groups. The pMTG has been shown to respond when co-speech gesture is being processed (e.g., Green et al., 2009), the meaning of an utterance is ambiguous (Rodd, Davis, & Johnsrude, 2005), or in cases when perceived stimuli are related to prior action knowledge (e.g., Beauchamp & Martin, 2007; Chao et al., 1999; Martin et al., 1995; Martin et al., 1996). To understand why activation is elicited in the present study, we can consider additional behavioural results that suggest that our age groups were able to understand the meaning of sentences presented in isolation (see Appendix C). Activation of the pMTG in the present study is thus more likely attributable to action knowledge, rather than ambiguity of speech. Towards an involvement in action knowledge processing, previous literature has posited that the pMTG is a sensory region that is involved in processing semantic representations—information about stimuli in our environment that we acquire through learning (e.g., Beauchamp & Martin, 2007; Binder, Desai, Graves, & Conant, 2009; Martin & Chao, 2001). According to the sensorimotor model of semantic representations (Martin, 1998; Martin, Ungerleider, & Haxby, 2000), the pMTG responds to information that is related to the motion or movement components of environmental stimuli, which, in combination, construct part of semantic

knowledge. For example, the pMTG is recruited when individuals see tools in use (James, VanDerKlok, Stevenson, & James, 2011) or the motion of tools without an actual tool present (Beauchamp & Martin, 2007), as well as upon hearing tool sounds or seeing a picture of a tool (e.g., Doehrmann et al., 2008; James et al., 2011; Lewis, Brefczynski, Phinney, Janik, & DeYoe, 2005). All of this information is thought to combine to form part of the concept of the tool—the putative semantic representation.

Similar to tools, gestures may also provide information that is processed as part of semantic representations of objects or concepts. For example, the gesture for “big” (stretching the two hands apart) may be associated with the word “big” in certain contexts, along with elephants, New York City, and so on. Perhaps gestures are processed as motions that could either add to the semantic representation of the content of the speech they are accompanying, or be a way to access knowledge about a concept represented by the motion.

Considering this literature, it is interesting that we see differences in how the pMTG processes gesture in children and adults. First, we see an increase in activation to speech alone across development. As our sentences were iconic in nature and were somewhat based in action, the sentences alone could lead to limited reactivation of the motion aspects of a semantic representation, and this may increase in age as individuals gain ability to store and access these representations in the pMTG. Indeed, this region is sensitive not only to the motion of tools, but to the sound of tools in use (Doehrmann et al., 2008); thus sensory input that is merely *representative* of motion may elicit some reactivation in the pMTG. Second, and more importantly, we find that overall, groups showed greater activation to G than to GS, but that GS activation *increased* with age, such that there was no significant difference between activation to G and GS in adults. It is not surprising that the pMTG would show the strongest activation to gesture alone. This form of communication is not only motoric, perhaps activating previous action-based knowledge, but is also

ambiguous—the meaning of the gesture is unclear without the speech context, and, thus, we may expect pMTG involvement (Rodd et al., 2005). The interesting difference in how children and adults process gestural communication comes in the difference in activation shown by the youngest age groups between the G and GS conditions ($G > GS$), which decreases across development and is absent in adults. The stark difference in pMTG activation patterns between young children and adults suggests that speech–gesture representations become more robust through development, and the action–perception framework would suggest that this is due to increased experience producing gesture. In adults, speech–gesture representations have reached a level of robustness that appears equal to gesture-only representations.

Our finding that GS activation *increased* with age, but also that the difference between G and GS *decreased* suggests that children *acquire* the ability to integrate the meaning of gesture and speech through development, and that this development is not complete at the age of eleven. These findings corroborate behavioural evidence that children are less proficient than adults at integrating co-speech gesture into their understanding of a message, even though they are able to extract meaning from an individual’s gesture if prompted (Kelly & Church, 1998). Interestingly, recent neuroimaging data indicate that although integration of speech and gesture may be difficult, older children are able to expend effort to integrate these streams if they interpret the gesture as being important to message understanding (Dick et al., 2012). Eight- to 11-year olds show greater activation in a more anterior portion of the pMTG when processing co-speech gesture, than when processing speech accompanied by self-adaptors (Dick et al., 2012). What we may see, developmentally, is effort to process gesture along with speech in childhood changing into the ability to integrate gesture information into semantic representations in adulthood.

One developmental change that might contribute to the ability to integrate gesture information into semantic representation is the *use* of gesture

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by an individual. Children do not have the same experience producing gesture that adults do and therefore have less experience *using* these movements to represent ideas (Colletta et al., 2010). Because of this, it may be more difficult for children to draw on gestures as meaningful representations of concepts and integrate these meanings with speech. With increased experience with gesture, children may integrate gesture into their semantic representations of words and concepts, allowing for easier integration when gesture and speech are later perceived.

In conclusion, within our framework, adults have the greatest PCG activation because they have more cumulative experience producing gestures than children and produce gesture at a greater rate during speech (Colletta et al., 2010). They also show equal activation to gesture in the context of speech and gesture by itself in the pMTG because of their production experience: Producing gesture gives rise to stronger semantic representation of gesture, so much so that the representation elicited by the gesture in the context of speech is as strong as the multiple possible representations that may be elicited when an isolated, ambiguous gesture is perceived.

The present study suggests that an individual's experience producing gesture shapes the response of brain regions involved in processing the perception of co-speech gesture. We demonstrate differences in how children and adults process gesture within two regions that are involved in perception and production of action (the PCG and pMTG). Whereas the influence of producing and perceiving action on subsequent perception has been established in the action-understanding literature, it is novel in the literature on co-speech gesture. Our results highlight the utility of exploring gesture processing in an action-perception framework.

Supplementary material

Supplementary Material is available via the "Supplementary" tab on the article's online page (<http://dx.doi.org/10.1080/02643294.2013.794777>).

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APPENDIX A

Examples of sentences and gestures used in stimuli

Sentences are presented on the left. Gestures were produced on the italicized word. Gestures are described on the right.

Bugs <i>ran</i> up his arm	Right hand moved across body from right to left; alternately moving the index and middle finger back and forth.
The bubblegum <i>popped</i> onto her head	Hands are raised in front of face in fists and moved quickly away from face as fingers are spread apart.
The teacher <i>spoke</i> to her	Fingertips of right hand are placed together towards mouth and spread apart as they are rotated away from mouth and outward.
The model <i>grabbed</i> his arm	Right hand is moved away from body; fingers are closed into a fist in a grabbing motion.
The string was <i>wrapped</i> around her finger	Index finger of left hand is extended in front of body, right index finger is rotated in a circular moment around left index finger.
She has a <i>big</i> purse	Palms are cupped and turned inwards towards each other, raised briefly and then lowered.
He sits at a <i>low</i> desk	Right hand is extended in front of lower stomach; hand is flat and fingers are together.
She held a <i>short</i> stick	Hands are extended in front of body, close together; hands are flat, fingers together. Hands are raised briefly, then lowered.
The teacher stood on a <i>high</i> stool	Right hand is extended in front of chest; hand is flat and fingers are together.
She held a <i>long</i> rope	Palms are flat and turned inwards towards each other, far apart. Hands are raised briefly and then lowered.

Table A1. Mean difference between original system coordinate and transformed coordinate

Talairach transformation points	5 year-olds	7.5-year-olds	10-year-olds	Adults
PC	1.23 (1.01)	2.54 (1.45)	3.62 (1.45)	4.08 (0.95)
AP	2.54 (2.54)	2.38 (1.44)	3.00 (2.27)	1.92 (1.26)
PP	2.92 (2.02)	3.61 (3.07)	4.38 (2.66)	3.69 (2.18)
SP	2.46 (1.94)	2.31 (1.75)	2.77 (2.01)	1.92 (1.04)
IP	2.54 (1.90)	3.23 (1.92)	2.38 (1.98)	1.85 (1.07)
RP	2.00 (1.73)	1.69 (1.84)	2.77 (1.36)	1.69 (1.44)
LP	2.15 (2.34)	1.92 (1.32)	2.23 (1.17)	1.85 (1.57)

APPENDIX B

Applicability of common stereotactic space for young children and adults

A concern in paediatric neuroimaging has been whether we can normalize individual data from children within the same common space as adults and make comparisons (e.g., Burgund et al., 2002; Gaillard, Grandin, & Xu, 2001; Kang et al., 2003). Two studies have directly assessed whether typically developing children and adult brains can be analysed within a common stereotactic space, despite the reduced size of the child brain compared to the adult, and the

dynamic structural changes that are occurring across development (Burgund et al., 2002; Kang et al., 2003). Both studies determined that with spatial smoothing, the effects of differences in alignment are negligible; however, the youngest age of the children considered was 7 years. In the present study, we transform children as young as 5 years into the same common space as adults. In order to justify this comparison, we have conducted an analysis comparing the location of the 8 points used in the Talairach transformation before and after the transformation into common space.

For each individual, the BrainVoyager QX system coordinates were acquired for the 8 points used during the affine transformation (AC, PC, AP, PP, SP, IP, RP, LP) that were

selected manually by an experimenter after the ACPC plane had been defined (Subj_3Danat_ISO_ACPC.tal). The system coordinates for each point of interest gave the location of the point in space, which could be compared to a standard set of coordinates to which all brains were transformed. In BrainVoyager, the AC point is held constant during the transformation; thus, we only considered the changes between the original coordinates and standard coordinates for the other 7 points. The absolute value of the difference score was taken for the original and transformed coordinates within the meaningful plane for each point (i.e., for the SP and IP, only a change in the z plane should be meaningful). Table A1 provides these data.

A one-way analysis of variance (ANOVA) was conducted for each point of interest, to determine whether groups differ significantly on the amount of transformation required: AP: $F(3, 48) = 0.67$, *ns*, PP: $F(3, 48) = 0.73$, *ns*, SP: $F(3, 48) = 0.54$, *ns*, IP: $F(3, 48) = 1.37$, *ns*, RP: $F(3, 48) = 1.30$, *ns*, LP: $F(3, 48) = 0.16$, *ns*, PC: $F(3, 48) = 13.60$, $p < .001$. The only significantly different transformation was the PC transformation. A post hoc analysis revealed that the 5-year-olds underwent significantly *less* of a transformation than any of the other age groups. Seven-and-a-half year-olds underwent significantly less of a transformation than adults, and adults underwent a greater transformation than the two youngest age groups but showed the same amount of transformation as 10-year-olds. Our results suggest that it is permissible to compare adults and children within a Talaraich space, as the only significant difference in transformation actually involved the adult brain becoming *more* warped than the child brain, to fit into stereotactic space.

APPENDIX C

Analysis of Sentence Understanding

Previous literature suggests that the pMTG shows greater activation when an individual cannot rely on speech content alone to understand the meaning of a sentence. Although the sentences used in the present study were designed to be unambiguous, it is nevertheless necessary to determine whether children

and adults were equally able to comprehend them. A second set of children from each of our age groups was asked to listen to sentences (i.e., those used during the scan) and explain their meaning. We chose to use an independent set of children to prevent any effects of the behavioural session on the fMRI session and vice versa.

Participants. A total of 42 children were recruited to participate in this study. Children were separated into three age groups, 5.0–6.0 ($n = 16$, $M = 5.5$), 7.5–8.5 ($n = 15$, $M = 7.8$), and 10.0–11.0 ($n = 12$, $M = 10.4$) years. All participants were right-handed, native English speakers with no reported history of neurological or psychiatric disorders, and normal or corrected-to-normal visual acuity. Informed consent was obtained from each child's parent or guardian. Assent was obtained from children over the age of 7.

Procedure. Participants received a comprehension test for sentences presented in the present study. A researcher read each sentence to the child, making sure not to gesture, and asked the child to explain the meaning of the sentence. All responses were video-recorded and coded for comprehension. A second research assistant coded 20% of the data, to check for reliability. The coders agreed on 80% of the responses (193 out of 240 responses), suggesting a high degree of reliability.

Results. Considering the codes for full understanding and no understanding of sentence meaning, the proportion of sentences understood was .78, .90, and .92 (5; 7.5; 10). Paired-sample t tests were conducted to determine whether there were significant differences between the proportion of sentences understood and those that were not understood, as chance of understanding is difficult to define in this case. For each age group, children showed significant comprehension: 5-year-olds: $t(15) = 3.51$, $p < .01$; 7.5-year-olds: $t(14) = 5.85$, $p < .001$; 10-year-olds: $t(11) = 6.96$, $p < .001$. Additionally, a one-way ANOVA revealed no significant difference between the groups on proportion of comprehended sentences, $F(2, 41) = 2.58$, *ns*.