FAST-TRACK REPORT

Auditory verb perception recruits motor systems in the developing brain: an fMRI investigation

Karin Harman James and Josita Maouene

Department of Psychological and Brain Sciences, Indiana University, USA

Abstract

This study investigated neural activation patterns during verb processing in children, using fMRI (functional Magnetic Resonance Imaging). Preschool children (aged 4–6) passively listened to lists of verbs and adjectives while neural activation was measured. Findings indicated that verbs were processed differently than adjectives, as the verbs recruited motor systems in the frontal cortex during auditory perception, but the adjectives did not. Further evidence suggested that different types of verbs activated different regions in the motor cortex. The results demonstrate that the motor system is recruited during verb perception in the developing brain, reflecting the embodied nature of language learning and processing.

Introduction

Language is used to talk about objects, actions and events in the world. Thus, words may have broader associations to experienced objects, actions and events, associations that, although not isomorphic with linguistic meaning, may nonetheless play a role in language processing. Pertinent to this idea is recent evidence in adults showing that the processing of common verbs activates motor as well as linguistic representations in the brain. This paper provides the first evidence for the emergence of these functional connections in young children.

The link between verb processing and motor system activity in the adult brain is now well known (Pulvermüller, Harle & Hummel, 2001; Hauk, Johnsrude & Pulvermüller, 2004; Tettamanti, Buccino, Saccuman, Gallese, Danna & Scifo, 2005; Aziz-Zadeh, Wilson, Rizzolatti & Iacoboni, 2006; Bucccino, Riggio, Melli, Binkofski, Gallese & Rizzolatti, 2005; Boulenger, Roy, Paulignan, Deprez, Jeannerod & Nazir, 2006; Sato, Mengarelli, Riggio, Gallese & Buccino, 2008). In a series of studies, Pulvermüller and his colleagues have shown that reading verbs activates regions of the motor cortex that are used when actually performing the action associated with the verb (Pulvermüller *et al.*, 2001; Hauk *et al.*, 2004; Pulvermüller, Hauk, Nikulin & Ilmoniemi, 2005). These results have been demonstrated using both fMRI and ERPs (Pulvermüller, Lutzenberger & Preissl, 1999). In addition, there is evidence that it isn't just verbs that activate the motor system, but any word that is associated with an action – including nouns (Saccuman, Cappa, Bates, Arevalo, Della Rosa, Danna & Perani, 2006; Arevalo, Perani, Cappa, Butler, Bates & Dronkers, 2007; Arevalo, 2008). The essential factor seems to be whether or not the word is learned with the involvement of the action system. For example, nouns labeling 'manipulable' objects activate the motor system in a similar way to verbs (Saccuman *et al.*, 2006). Thus, the crucial factor seems to be the history of interactions with the object that the word represents. Although it is an open question as to whether, and how, motor system involvement may matter to language understanding, there are hints that it does in both studies of neuropsychological patients (Arevalo *et al.*, 2007; Arevalo, 2008) and in behavioral studies that show interference effects between comprehension and incongruent actions (Glenberg & Kashak, 2002; Richardson, Spivey, Barsalou & McRae, 2003; Zwaan & Taylor, 2006; Matlock, 2004). Such results suggest that the on-line processing of verb meanings may involve, or interact with, some of the same processes that generate bodily action (Barsalou, 1999, 2003, 2008).

Recent work has demonstrated that common and early-learned verbs often refer to highly specific actions by specific body parts (Maouene, Hidaka & Smith, 2008). Some (but not all) studies suggest that children learn and comprehend verbs best in the context of doing the actions themselves rather than observing actions (Huttenlocher, Smiley & Chaney, 1983; but see Childers & Tomasello, 2006). This might suggest that these functional links between motor and linguistic areas in verb comprehension should be early and strong. On the other hand, the patterns in adults need not indicate an essential

Address for correspondence: Karin Harman James, 1101 East 10th Street, Department of Psychological and Brain Sciences, Indiana University, Bloomington, IN 47405, USA; e-mail: khjames@indiana.edu

connection but merely the side effect of a long history of associations. That is, the functional connections observed in adults could be late emerging, the end product of a long history of language use, or the connection between verbs and motor systems could be foundational.

Functional neuroimaging can be used to investigate the mechanisms that underlie verb processing and its potential relation to motor systems in children in a similar manner to the studies using adult participants. The potential benefits of fMRI for the investigation of normal development have been overshadowed to some extent by the difficulties inherent in the use of the technique with children. These include the effects of anxiety, claustrophobia, fatigue, and restlessness on children's compliance with the behavioral requirements of the imaging environment. In addition, children may have difficulty understanding the instructions and requirements of functional imaging tasks. Because fMRI is highly sensitive to artifacts produced by head motion, subject compliance is critical, as excessive motion compromises the quality of the images obtained. Despite these problems, a number of studies have focused on or included children but mostly older children (not 4-year-olds) and, as far as verbs are concerned, for verb generation tasks (e.g. Szaflarski, Schmithorst, Ataye, Byars, Ret, Plante & Holland, 2006; Holland, Plante, Weber Byars, Strawsburg, Schmithorst & Ball, 2001). Due to these and other studies we know that the developing brain is undergoing massive transformations. Structural as well as functional changes occur (Casey, Thomas & McCandliss, 2001; Holland *et al.*, 2001; Weber Byars, Holland, Richard, Strawsburg, Schmithorst, Dunn & Ball, 2002; Szaflarski *et al.*, 2006). But what we do not know is when and how the connections between verbs and the motor region develop.

The present study is a first step in investigating this developmental question by examining whether auditory verb perception is processed differently by the brain of 5-year-olds than neutral adjective perception and, in addition, whether verbs that refer to actions by particular body parts, leg verbs (kick, go, run, jump, hurry …) versus hand verbs (clap, give, open, carry, clean …) recruit regions in the motor cortex that overlap with the leg region and hand region that are activated in real time behaviors. These older preschool children, while not in the midst of the initial acquisition of these common verbs, are still in the process of working out aspects of verb meanings (Clark, 1973; Gentner, 1978; Gleitman, 1990; McGuire, Hirsh-Pasek & Golinkoff, 2006).

Method

Participants

Participants were 12 children between the ages of 4 years 2 months and 5 years 10 months. Six females and six males were included and all children had normal or corrected to normal vision and had normal hearing as reported by parents. Participants were not on any medication and had no history of neurological compromise; all were delivered at term without a record of birth trauma. Parents reported a right-hand dominance for all participants that was assessed by an Edinburgh handedness questionnaire.

Stimuli

Stimuli were word lists, pre-recorded by a male voice and presented over headphones. The stimuli were audible during scanning as assessed by pre-tests. Verbs were considered either 'hand' verbs or 'leg' verbs. Adjectives were non-active, descriptive words (see Appendix for words used). Verbs were considered either 'hand verbs' or 'leg verbs' based on ratings by adults (Maouene *et al.*, 2008). All words were equated for familiarity and frequency based on word norms (Fenson, Dale, Reznick & Bates, 1994) and were one or two syllables long.

Procedure

After screening and informed consent given by the parent, all participants were acclimated to the MRI environment by watching a cartoon in an MRI 'simulator'. The simulator is the same dimension as the actual MRI and the sound of the actual MRI environment is played in the simulator environment. This allows the children to become comfortable in the environmental set-up before entering the actual MRI environment. When the participant felt comfortable in this environment, and if the parent was comfortable with the participant continuing, they were introduced to the actual MRI environment.

Following instructions, a preliminary high-resolution anatomical scan was administered while the participant watched a cartoon. Following this scan, the functional scanning occurred. During functional scanning, participants heard lists of words presented through headphones. There was no specific visual stimulus at this time, only the projection screen which was left on to avoid the children feeling scared. The lists were presented in a blocked format, each block containing 16 verbs that were read at a rate of 1 second per word, resulting in 16-second blocks. Each block contained either 'leg' verbs, 'hand' verbs or adjectives. Blocks were counterbalanced and we included six blocks per run. There were 10-second inter-block intervals between each block, and each run began with a 20-second rest period and ended with a 10-second rest period. This resulted in runs that were just under 3 minutes long. There were 3–4 runs administered for each participant. Participants were required simply to passively listen to the stimuli. Neural activation, measured by the BOLD (Blood Oxygen Level Dependant) signal in the entire brain was then recorded during exposure to the stimuli. Imaging sessions took approximately 15 minutes in total.

Following the functional scans, participants were removed from the environment, debriefed, and rewarded for their time.

fMRI acquisition

Imaging was performed using a 3-T Siemens Magnetom Trio whole-body MRI system and a phased array eight channel head coil, located at the Indiana University Psychological and Brain Sciences Department. Whole-brain axial images were acquired using an echo-planar technique (TE = 30 ms, TR = 2000 ms, flip angle = 90°) for BOLD-based imaging. The field of view was $22 \times 22 \times 9.9$ cm, with an in-plane resolution of 64×64 pixels and 33 slices per volume that were 4 mm thick with a 0 mm gap between them. The resulting voxel size was 3.0 mm × 3.0 mm × 4.0 mm. Functional data underwent slice time correction, 3D motion correction, linear trend removal, and Gaussian spatial blurring (FWHM 6 mm) using the analysis tools in Brain Voyager™. Individual functional volumes were co-registered to anatomical volumes with an intensity-matching, rigid-body transformation algorithm. Voxel size of the functional volumes was standardized at 1 mm × 1 mm × 1 mm using trilinear interpolation. High-resolution T1-weighted anatomical volumes were acquired prior to functional imaging using a 3D Turbo-flash acquisition (resolution: 1.25 mm × 0.62 × 0.62, 128 volumes).

Data analysis procedures

Group contrasts

The functional data were analyzed with a random effects general linear model (GLM) using Brain Voyager's™ multi-subject GLM procedure. The GLM analysis allows for the correlation of predictor variables or functions with the recorded activation data (criterion variables) across scans. The predictor functions were based on the blocked stimulus presentation paradigm of the particular run being analyzed and represent an estimate of the predicted hemodynamic response during that run. Any functional data that exceeded 5 mm of motion on any axis were excluded from the analyses. This criterion resulted in excluding three blocks of data from one participant and two blocks of stimuli from another participant. Exclusion of these data does not significantly alter the power of the present analyses. Data were transformed into a common stereotactic space (e.g. Talairach & Tournoux, 1988) for group-based statistical analyses. Direct contrasts of BOLD activation were performed on the group between hand verbs and adjectives (Figure 1), leg verbs and adjectives (Figure 2) and between adjectives and rest (Figure 3).

Contrasts in the group statistical parametric maps (SPMs) were considered above threshold if they met the following criteria in our random effects analysis: (1)

Figure 1   *Statistical parametric map (SPM) of the contrast between 'hand' verb perception and adjective perception. All group maps (n = 12) of averaged data presented at a threshold of p < .001 (uncorrected). Hand verbs activate regions of the premotor cortex on the right precentral gyrus more than adjectives (Talairach coordinates: 23, −7, 58). This region is in Brodmann's area 6, corresponding to the supplementary motor area (SMA).*
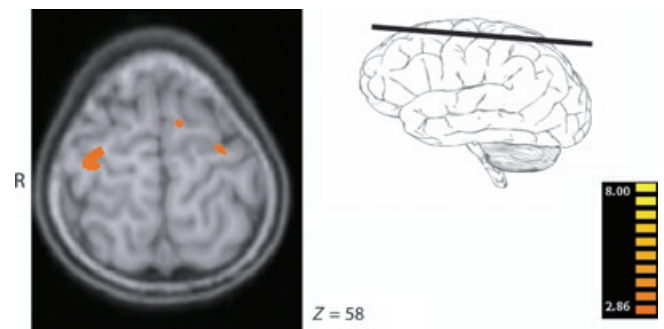
Figure 2   *SPM of the contrast between 'leg' verbs and adjectives: Bilateral premotor regions that overlap with the primary motor cortices (±31, −14, 59) (corresponding to Brodmann's area 4) are recruited more by leg verbs, as well as left middle frontal gyrus, the dorsal premotor cortex (−29, 4, 53) (area 6).*
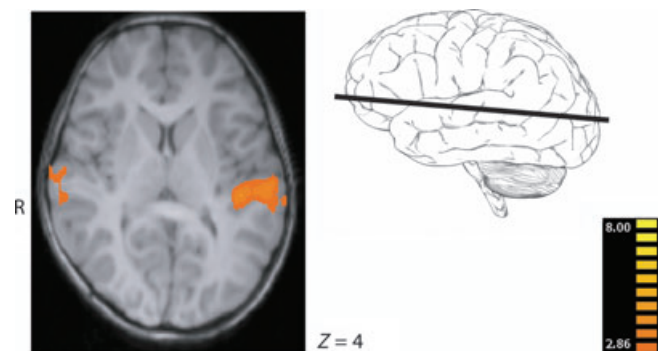
Figure 3   *SPM of the contrast between adjectives and rest. Adjective perception recruits bilateral regions of the superior temporal gyrus more than the rest condition (scanner noise). Peak Talairach coordinates: (±56, −15, 4).*

significant at $p < .001$, uncorrected, with a cluster threshold of 270 contiguous 1 mm isometric voxels; (2) peak statistical probability within a cluster at least

$p < .0001$, uncorrected. Resultant data were analyzed by performing contrasts among our conditions of interest: verbs and adjectives.

Region-of-interest analyses

Although there are several reasons to perform regions-of-interest (ROI) analyses in fMRI, in the present study we chose to include this method for two main purposes: (A) to enhance our statistical power – whereas whole-brain group contrasts compare numerous voxels in the brain to one another, requiring a stringent correction for the comparisons, an ROI analysis increases power by comparing a smaller number of voxels, in more restricted brain regions (Poldrack, 2007); (B) for functional specification: In this case, ROIs can be used to assess the BOLD signal to conditions of interest in a region that is presumably functionally coherent. Often, ROIs are localized using functional data from the sample of interest. That is, one would include conditions that would localize ROIs, then pull data from these regions for the experimental conditions of interest (see Saxe, Brett & Kanwisher, 2006, for the usefulness of this approach). In the present case this was not optimal; we did not present separate conditions on which to perform a functional localizer outside of our experimental conditions because of the need to have short experimental sessions due to the age of the participants. If one used the experimental conditions to localize ROIs (thus not lengthening the experiment), one would be performing two statistics on the same data set – one GLM to localize the regions, and another to compare the conditions within the regions; this also is not optimal. Other ways to localize regions of interest include anatomical localization and localization using data from other experiments (Poldrack, 2007). Given that the adult data on verb processing up until now have been extremely consistent in the spatial domain, we used the latter method to localize our ROIs. To this end, we used the MNI coordinates reported by Hauk *et al*. (2004), converted them to Talairach coordinates using 'mni2tal' (matthew.brett) and localized these regions in each individual, and ensured that the coordinates corresponded to the anatomical locale reported by previous work. The data from the verb and adjective perception runs were then extracted from these regions and analyzed using a one-way ANOVA. The ROIs that we used were: the bilateral pre-central gyri (peak Talairach coordinates: [x] $\pm$ 31, [y] -34, [Z] 56); the bilateral middle frontal gyrus (premotor area) (±27, 10, 58); the medial dorsal frontal gyrus (supplementary motor area) (±9, -22, 60); and we also added the auditory cortex as an ROI (±56, -15, 4) hoping that it would provide an auditory baseline in which all conditions would be equally active. Around each of these peaks we acquired data from a 10 mm cube, using the peak as a centroid. It should be noted that because we are investigating very immature brains, localizing regions based on adult work is not ideal.

Although there are significant changes in subcortical and cortical grey and white matter throughout childhood, adult-like gyri and sulci are present at this age (Casey *et al*., 2001), the function of different brain regions may be substantially different. Given the paucity of fMRI research on children of this age, these developmental trends are virtually unknown. The present research maximized our signal to the auditory conditions of interest, instead of including functional localizers. Through this and other studies (e.g. James, 2009), we seek to further investigate localization of function of participants at this age, but the science itself is still in its very early stages.

Results

The results indicate that the regions of the cortex that process motor information were active while participants listened to verbs, but not while they listened to adjectives. This was shown by our first contrast, a comparison of BOLD activation during hand verb perception and adjective perception (Figure 1). This contrast revealed significantly more activation during hand verbs in the right premotor cortex (peak Talairach coordinates: 29, 4, 53). Upon contrasting leg verbs to adjectives, areas in the premotor cortex bilaterally were more active during verb perception (Figure 2); these activations were somewhat posterior to the hand verb activation and overlapped with the primary motor strip in some cases (±31, -14, 59). In addition, a region more anterior, in the medial frontal gyrus (dorsal premotor cortex) in the left hemisphere was more active during leg verb perception (-50, -36, 55) (Figure 2). There were no regions where adjectives activated the brain more than verbs. When we compared adjectives to the resting condition, however, the auditory cortex, bilaterally, was significantly activated (62, -7, 4 and -54, -14, 4) (Figure 3). Interestingly, when we compared all words to rest, in a conjunction analysis, the inferior frontal gyrus (ventral premotor cortex) was significantly active as was the auditory cortex (Figure 4) and the premotor cortices. Thus some overlapping activation to all words occurred in the inferior frontal gyrus in addition to the auditory cortex. Although not specifically designed to investigate activation in the inferior frontal gyrus, this interesting region deserves more investigation in the developing child. Future work will strive to localize this region and fully investigate its involvement in the development of language processing.

Although these data suggest that the motor cortex is being activated during verb perception, they do not conclusively suggest that these were actually motor regions associated with the effector in question. This later interpretation would have required localizing specific motor regions in individual participants, which was beyond the patience of the child participants. The 4–5-year-olds that we test here will stay still for on average 15 minutes – making experimental design a challenge.
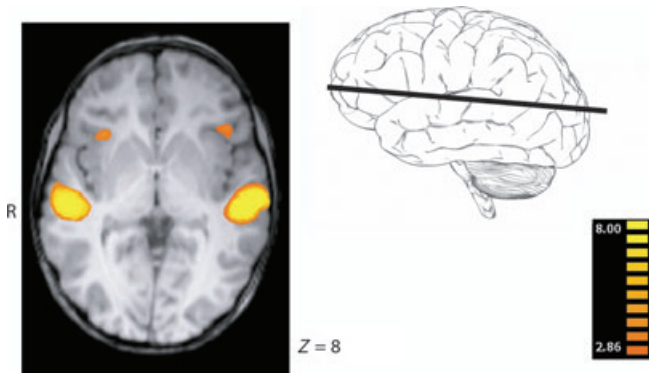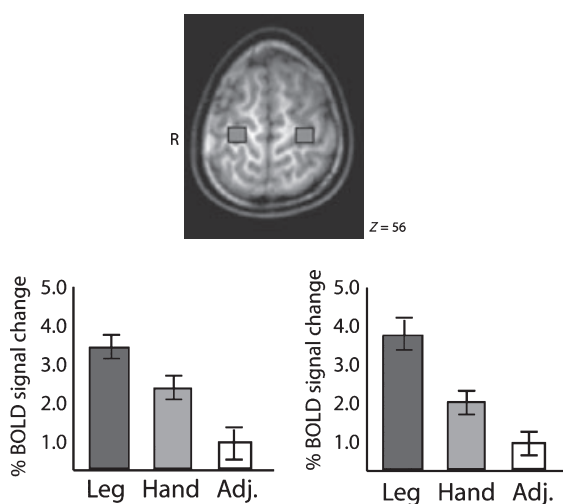
Figure 4 *SPM of the conjunction contrast between all word types vs. rest. The words activated auditory cortex, but also the frontal operculum (area 44). Peak Talairach coordinates: (±46, 22, 8).*

Generally we have to sacrifice some experimental power in order to acquire useable data. Thus, to increase statistical power, and also to relate these findings to previous work, we used the regions-of-interest that were localized by Hauk *et al.* in the 2004 study to assess whether or not we would see differential activation to verbs and adjectives in these effector-specific motor regions in adults. A 2 (hemisphere) × 3 (word type) repeated measures ANOVA was run on the data from these ROIs and subsequent simple effects *t*-tests were performed when a significant main effect or interaction resulted.

Bilateral pre-central gyri (primary motor cortex) (Figure 5)

The ANOVA that was performed on the data from this region revealed an effect of word type ($F(1, 10) = 7.6$, $p < .05$, MSe = .02) with leg verbs activating the region more than hand verbs ($t(10) = 4.40$, $p < .01$), which, in

turn, activated more than adjectives ($t(10) = 6.01$, $p < .01$). There was no effect of hemisphere ($F(1, 10) = 2.3$, *ns*) nor an interaction ($F(2, 20) = 2.91$, *ns*).

Bilateral middle frontal gyri (dorsal premotor cortex) (Figure 6)

Although the ANOVA here revealed a significant effect of word type ($F(1, 10) = 7.0$, $p < .005$, MSe = .07), it was due to a difference between leg verbs and adjectives ($t(10) = 4.48$, $p < .01$) and hand verbs and adjectives ($t(10) = 6.01$, $p < .004$). There was no difference between hand and leg verbs ($t(10) = .03$, *ns*).

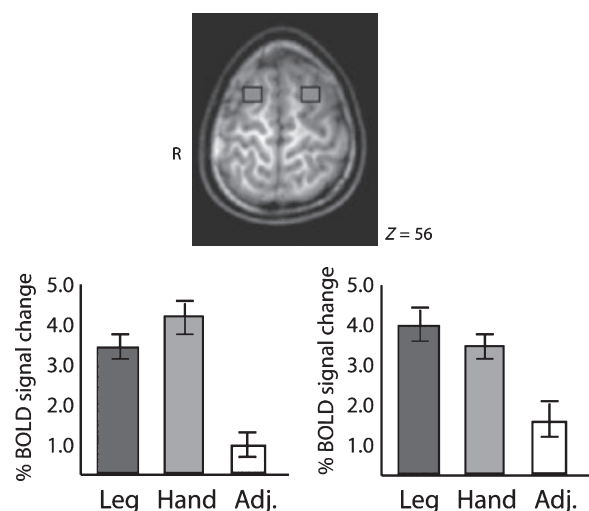Bilateral medial frontal gyri (supplementary motor area) (Figure 7)

Analyses here also revealed a main effect of word type ($F(1, 10) = 6.60$, $p < .01$, MSe = .18), but again, leg and hand verbs did not differ ($t(10) = 1.3$, *ns*); only leg verbs and adjectives ($t(10) = 5.48$, $p < .005$), and hand verbs and adjectives ($t(10) = 5.71$, $p < .001$). There were no other significant effects.

Bilateral superior temporal gyri (auditory cortex) (Figure 8)

In the auditory cortex, the ANOVA revealed no significant effects. All stimuli elicited the same neural response in these regions.

Discussion

The results show that even in an immature language system, auditory verb perception elicits activation in

Figure 5 *Region-of-interest (ROI) analyses: Bilateral precentral gyrus (grayed squares). Graphs below are the peak activations from this region for all participants averaged together. Error bars are the standard error of the group mean. Peak Talairach coordinates: (±31, −20, 56).*

Figure 6 *ROI analysis of bilateral middle frontal gyrus (grayed squares), part of the dorsal prefrontal cortex. Graphs below are the peak activations from this region for all participants averaged together. Error bars are the standard error of the group mean. Peak Talairach coordinates: (±27, 10, 58).*
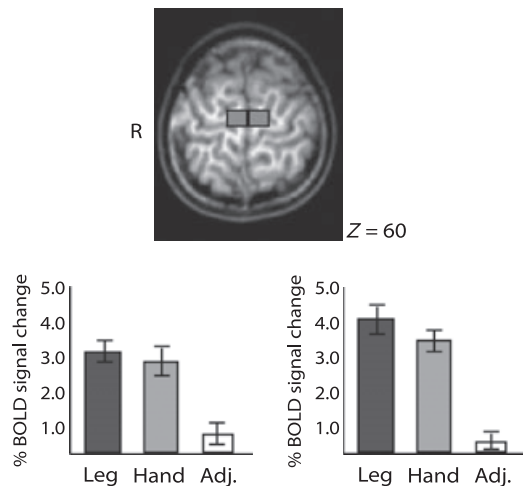
Figure 7   *ROI analysis of bilateral medial dorsal frontal gyrus, the supplementary motor area (grayed squares). Graphs below are the peak activations from this region for all participants averaged together. Error bars are the standard error of the group mean. Peak Talairach coordinates: (±9, −22, 60).*
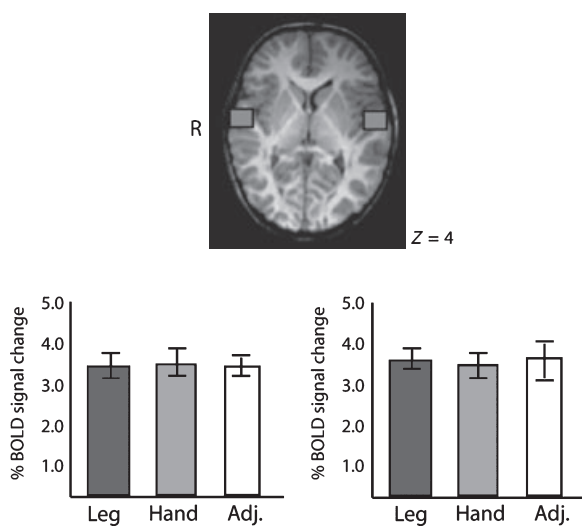
Figure 8   *ROI analysis of bilateral superior temporal gyrus, auditory cortex (grayed squares). Graphs below are the peak activations from this region for all participants averaged together. Error bars are the standard error of the group mean. Peak Talairach coordinates: (±56, −15, 4).*

the motor regions involved in performing actions, during the processing of verbs that refer to those actions. The frontal motor system in the human adult comprises primarily five neuroanatomical locations, defined both by their cellular structure and organization, and by their functions (Geyer & Zilles, 2005). The primary motor cortex (Brodmann's area 4) is located on the precentral gyrus and comprises somatotopically organized regions that are recruited in an effector-specific manner for action execution (Penfield & Boldrey, 1937). The supplementary motor areas (SMA and pre-SMA), located anteriorly to the primary motor cortex on the dorsal-

medial surface of the brain, are also engaged during motor execution, and may also have a somatotopic organization, but are usually thought to be involved in well-learned motor sequences (SMA) and in learning new, unfamiliar sequences (pre-SMA) (Sergent, Zuck, Terriah & MacDonald, 1992). The dorsal premotor region (Brodmann's area 6) has been shown to be involved with the preparation and execution of motor acts and motor learning (e.g. Grafton, Fagg & Arbib, 1998), whereas the ventral premotor cortex (Brodmann's areas 44 and 45) is involved with hand movements, the imagery of hand movements (Decety, Perani, Jeannerod, Bettinardi, Tadary, Woods, Mazziotta & Fazio, 1994), and has also been shown to be involved with action observation (e.g. Grafton, Arbib, Fadiga & Rizzolatti, 1996). Traditionally, language function was thought to be subserved by brain regions in the superior temporal gyrus and inferior frontal gyrus (usually part of ventral premotor cortex) (Geschwind, 1967; Perani, Dehaene, Grass, Cohen, Capp, Dupoux, Fazio & Mehler, 1996; Binder, Frost, Hammeke, Bellgowen, Springer, Kaufman & Possing, 2000); however, growing evidence suggests a larger network of connectivity that involves more of the motor system as well. The present work makes the following new contributions: First, the findings document that regions of the premotor and primary motor cortices are recruited when children process verbs. Second, the results also suggest that the activation may be effector specific: that is, verbs associated with hand movements activated different regions of the frontal cortex than verbs associated with leg movements. However, there are also motor regions that are active during the processing of both leg and hand verbs, suggesting possible broader activation patterns, or effector overlap. Third, this is the first demonstration of *auditory* verb perception (rather than visual presentation) activating the motor cortex in children or typical adults. Finally, the results constitute a first indication that the connection between verbs and motor regions is early and provide new directions for pursuing the fundamental question of how children learn concrete verbs. We consider these contributions more fully below.

Verbs recruit premotor and primary motor cortices

Although the link between verb processing and motor system activity in the adult brain is now well known (Pulvermüller *et al.*, 2001; Hauk *et al.*, 2004; Tettamanti *et al.*, 2005; Aziz-Zadeh *et al.*, 2006; Bucccino *et al.*, 2005; Boulenger *et al.*, 2006; Sato *et al.*, 2008), this is the first time that verb processing in the developing brain has been investigated. Activation during verb perception was found in three motor system regions: the primary motor cortex, the supplementary motor cortex and the dorsal premotor cortex. Interestingly, we also found some verb-specific activation in the ventral premotor cortex (inferior frontal gyrus). Unlike other work (e.g.

Table 1   *Talairach coordinates, cluster size, peak t-value at a group random effects threshold of* p < .001, *uncorrected*

Contrast	Region	Talairach coordinates	Cluster size	Peak *t*
Hand>adjectives	R. Supplementary motor cortex	23, −7, 58	340	7.1
Leg>adjectives	L. Premotor cortex	(−31,−14, 59)	300	6.7
	R. Premotor cortex	(31,−14, 59)	574	7.2
	L. Dorsal premotor cortex	(−29, 4, 53)	270	6.8
Adjectives>rest	L. Auditory cortex	(−56, −15, 4)	604	5.9
	R. Auditory cortex	(56, −15, 4)	270	5.0
Words>rest	L. Frontal operculum	(−46, 22, 8)	275	5.1
	R. Frontal operculum	(−46, 22, 8)	275	4.9

Seitz & Roland, 1992), this latter finding was not hand-verb specific. The set of verbs examined are all 'early-learned' in the sense of being normatively acquired before the age of 3 years (Fenson *et al.*, 1994) and they are all quite concrete. Thus the link between these verbs and the motor regions involved in performing the labeled actions may be specific to these verbs. However, results from Maouene *et al.* (2008) suggest that even abstract verbs like *have, make, get, take* have strong associations with one body part (such as hand or leg) and thus it will be of value to examine these more abstract (but also early learned) verbs. Other early learned verbs, in particular psychological verbs such as *wish, think, pretend, hate* do not, by adult judgment, have strong body part associations and would make an interesting contrast comparison. Examining verbs beyond the obvious cases in both children and adults is important to understanding the role of the observed functional connections between language processing and their developmental origins.

Activation is effector specific and also overlapping

Adult findings on verb processing (e.g. Hauk *et al.*, 2004) indicate effector specificity. The present developmental results are broadly consistent with this specificity; however, they do not conform to the adult motor homunculus as originally specified by Penfield and Boldrey (1937) in that 'leg' verbs did not activate regions on the medial surface of the cortex. There are several possible interpretations of this finding. Although unlikely given the adult ratings of these verbs (see Maouene *et al.*, 2008), it could be that the stimuli that we used were not as effector specific as the verbs used in adult studies. Potentially more interesting, it could be that the brain of the child is just not organized in the same way as the adult brain in terms of localization of motor function. Critically, there has been no mapping of the motor cortex in young children. Third, it is possible that with more experience in *learning verbs*, the activation for specific verbs becomes more specialized. That is, the functional connectivity between linguistic and motor regions evident in adults *may still be forming* and thus lead to broader and less well-formed activation patterns in motor areas. Future work will address this issue by varying exposure and experience to verbs and measuring connectivity among brain regions.

Another possibility is that the overlapping activations observed for the hand and leg verbs accurately reflect the actions, but are not necessarily effector specific. Maouene *et al.* (2008) used a word association task to elicit the body parts that adults associated with a large set of verbs. Many verbs were strongly associated with a specific body part or region. But there were systematic second- and third-order associations as well; for example, across the set of 100 verbs, some verbs strongly associated with hands were also associated (though less strongly) with legs. Since many actual movements, such as kicking, involve whole-body coordination, the children's overlapping activation patterns could just reflect this. All these possibilities underscore the value of studying these questions developmentally: All in all, there is simply a great deal that is not known about these developing systems.

Auditory verb perception activates motor cortex

Finally, we note the result that children *listening* to words can (for certain kinds of words) yield motor and premotor activation. To our knowledge, this study is the first demonstration of aurally presented verbs activating the motor cortex in any population. Together with the previous adult studies on verb comprehension, the evidence now indicates that motor cortex activation is linked to both visual and auditory representations of the verbs. As such, the findings contribute to the shift from thinking of the cortical systems for language and action control as independent modules (Fodor, 1975: Shallice, 1988) to instead being a distributed interactive system (Hebb, 1949; Palm, 1982; Braitenberg & Schüz, 1998; Mesulam, 1998; Fuster, 2003).

There are significant challenges involved in imaging children this young, including experimental design, participant recruitment, participant testing, data analysis, motion correction algorithms, comparison of the young brain to older children and adult brains. The rewards, however, are substantial, as we can now measure functional development using sophisticated neuroimaging methods starting at the preschool ages. We are currently taking the current work to different levels, including work on verb learning, asking the question of

the type of experience that a child needs in order for motor systems to become active during verb perception. In addition, current work focuses on whether active interaction with novel objects will lead to motor system recruitment during visual perception of objects. Through the present work and future investigations we hope to better understand the role of active experience in perceptual development, and how motor systems interact with sensory systems during development.

Conclusion

This is the first imaging study in children showing that the recruitment of the motor cortex by an aurally presented verb is developmentally early. In addition this is one of a few studies (e.g. James, 2009) that successfully measures functional activation in typically developing 4–6-year-old children, and thus demonstrates that we can take BOLD measures from children this young. The findings indicate that the link between verbs and the sensory-motor ramifications of their meaning are there early in development, as well as in adults. As well as informing us about functional connections in the brain, the present results may be pointing to the need for a fundamental rethinking about verbs, their meaning, and their acquisition. Traditional research on verb meaning and early verb learning has concentrated on the abstract and relational structure of verbs and their role in sentential syntax (e.g. Fisher, 1994; Gleitman, 1990; Naigles, 1990). The present results make clear that the physical nature of the action – and the body that performs it – also matters.

Appendix

'Leg verbs': Chase, hurry, skate, kneel, tiptoe, dance, go, jump, run, stand, walk, skip, hop.

'Hand verbs': Clap, hit, hold, wave, tear, push, throw, wipe, write, catch, hug, knock, touch.

Adjectives: cold, dark, full, good, hot, small, soft, loud, furry, big, warm, heavy, tiny.

Acknowledgements

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