

Dorsal stream function in the young child: an fMRI investigation of visually guided action

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Funding information

National Science Foundation, Grant/Award Number: GRFP DGE-1419118; Lily Metacyte Initiative to the Indiana Research Facility; National Institute of Child Health and Human Development, Grant/Award Number: R01 HD057077

Abstract

Visually guided action is a ubiquitous component of human behavior, but the neural substrates that support the development of this behavior are unknown. Here we take an initial step in documenting visual-motor system development in the young (4- to 7-year-old) child. Through functional MRI and by using a new technique to measure the mechanisms underlying real-time visually guided action in the MRI environment, we demonstrate that children rely primarily on the IPS and cerebellum for this complex behavior. This pattern is consistent across three different visually guided actions, suggesting generalizability of these neural substrates across such tasks. However, minor differences in neural processing across tasks were also demonstrated. Overall, results are interpreted as demonstrating that the functions of the dorsal stream can be viewed as fairly mature in the young child. These results provide a benchmark for future studies that aim to understand the development of the neural circuitry for visually guided action.

RESEARCH HIGHLIGHTS

- This study is the first to document the neural correlates underlying real-time visually guided action in young children.
- A novel apparatus and scanning protocol is used to image brain function in the child while they perform visually guided actions.
- We find that children recruit similar neural substrates for visually guided actions as shown for adults in previous work, which we interpret as a fairly early maturity of the dorsal stream.
- We also find that children recruit the cerebellum while performing visually guided action, a region that is less documented in the adult literature.

1 | INTRODUCTION

A great deal of research has found that visual processing in the primate brain is divided between two pathways extending from the primary visual cortex: the ventral visual processing stream and the dorsal visual processing stream (Felleman & Van Essen, 1991; Goodale & Milner, 1992; Merigan & Maunsell, 1993; Ungerleider & Mishkin,

1982). The ventral stream extends to the inferior temporal cortex and processes visual information for object recognition and categorization (e.g., global shape information and surface properties) to ensure that an object can be recognized regardless of changes in size, location, and viewpoint (Cant & Goodale, 2007; Capitani, Laiacona, Mahon, & Caramazza, 2003; Gainotti, Silveri, Daniele, & Giustolisi, 1995; Grill-Spector, Kourtzi, & Kanwisher, 2001; Miceli et al., 2001; Rogers, Hocking, Mechelli, Patterson, & Price, 2005). In contrast, the dorsal stream extends to the posterior parietal cortex and processes visual information for visually guided action, including objects' metric properties (actual size and global shape) and object orientation (Jeannerod, Decety, & Michel, 1994; Perenin & Vighetto, 1988; Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006; for reviews see Goodale & Humphrey, 1998; Kravitz, Saleem, Baker, & Mishkin, 2011; Milner & Goodale, 1995). Both streams appear to have a certain amount of functional specialization within them that presumably emerges from interactions with the world coupled with developing visual-motor systems. Although little is known about the functioning of either of the visual streams early in childhood, we know far less about dorsal stream functioning than about the ventral stream. Mostly this is due to difficulties in developmental neuroimaging in general, compounded by difficulties imaging visually guided action. Because of these difficulties, it is

unclear *how* the dorsal stream becomes functionally specialized for visually guided tasks – are certain experiences required? If so, *when* would they be required and *how* are they acquired? To date, there is no information regarding how visually guided action is processed in the young child to begin to address these questions.

Behavioral research suggests that visually guided action develops rapidly through the first few years of life (e.g., Bertenthal, 2008; Von Hofsten, 2007). For instance, by 12 months, reaching for objects becomes quite accurate, and by 18 months, toddlers can easily adjust their hand position to insert objects into variously shaped openings (Street, James, Jones, & Smith, 2011). Nonetheless, different types of visually guided behaviors develop at different rates, suggesting that linking perceptions with actions, and actions with perceptions, have interconnected, cascading effects (for review see Spelke, Vishton, & Von Hofsten, 1995). For example, very early in development, linking object location with object color is quite immature. That is, 4-month-olds do not process both types of object features (location and color) together, even though they can process each individually (Mareschal & Johnson, 2003). Interestingly, between 24 and 30 months, toddlers show a marked transition from unsuccessful to successful integration of dorsal and ventral stream processing. At 24 months, toddlers can act on objects that they cannot visually match. Specifically, 24-month-old children can use visually guided action to place an object through a similarly shaped opening, but cannot point to a match between an object and an opening (Street et al., 2011; Von Hofsten, 2007). However, by 30 months of age, both tasks are performed without visible effort (Street et al., 2011).

Research with older children (4–12 years) that specifically examines aspects of reaching and reach-to-grasp actions suggests that adult-like coordination for reaching and grasping is not fully developed until 11 or 12 years of age (Kuhtz-Buschbeck, Stolze, Boczek-Funcke, et al., 1998; Kuhtz-Buschbeck, Boczek-Funcke, Illert, Joehnk, & Stolze, 1999; Kuhtz-Buschbeck, Stolze, Jöhnik, Boczek-Funcke, & Illert, 1998; Olivier, Hay, Bard, & Fleury, 2007; Schneiberg, Sveistrup, McFadyen, McKinley, & Levin, 2002). Importantly, Olivier et al. (2007) found that at 6 years of age, the motor programs underlying reach-to-grasp actions are variable and unstable, suggesting that even in early childhood, the neural correlates underlying visually guided actions are not mature or may be different from those relied on by adults.

Therefore, we know that some aspects of visually guided action are accurate by 12 to 24 months, and we know from both behavioral and neural studies that object recognition ability, particularly face recognition, has a protracted development (e.g., Carey, Diamond, & Woods, 1980; Chance, Turner, & Goldstein, 1982; Golarai et al., 2007; Golarai, Liberman, Yoon, & Grill-Spector, 2010; Grill-Spector, Golarai, & Gabrieli, 2008; Scherf, Behrmann, Humphreys, & Luna, 2007). But for visually guided action to be the truly flexible behavior that it is in the adult, the dorsal (vision for action) and ventral streams (vision for recognition) must work together and be interactive (Goodale & Westwood, 2004). Arguably to understand visually guided action and how it works, one needs to understand the mechanisms that support it in early childhood into adulthood. For instance, it is quite possible that infants and toddlers, who are still learning to perform visually

guided actions, and older children who show instability in their reach-to-grasp actions, rely on sub-cortical mechanisms involved in motor learning (e.g., the cerebellum). Although cerebellar activity is not commonly reported in studies with adults, who rely heavily on cortical structures to perform these functions (Culham et al., 2003; Culham, Cavina-Pratesi, & Singhal, 2006; Culham & Valyear, 2006), the cerebellum is involved in visuomotor skill learning (e.g., Albert, Robertson, & Miall, 2009; Doyon & Benali, 2005; Hikosaka et al., 1999; Thach, Keating, Thach, Goodkin, & Keating, 1992; Ungerleider, Doyon, & Karni, 2002), and therefore may be strongly involved in visually guided actions during early childhood while the motor programs are still very unstable.

Up until now, there have been no systematic studies of the *action* component of dorsal stream development using neuroimaging techniques in the young child. Therefore, while objects that afford actions (e.g., tools) are *visually* processed in a similar manner in children and adults (Dekker, Mareschal, Sereno, & Johnson, 2011; Kersey, Clark, Lussier, Mahon, & Cantlon, 2016), it is unknown how the brain responds *during* visually guided action. Here we address this gap in our understanding by investigating the mechanisms that underlie visually guided action and compare this to visual perception of the same stimuli in children.

2 | EXPERIMENT 1

A task that has been used extensively to study visually guided action is the ‘posting’ task – a simple way to probe whether an individual can place an object through an opening by adjusting the object appropriately such that it fits through the opening. Neuropsychological studies have revealed that patients with object agnosia from ventral stream damage can perform this task, but cannot perceptually recognize the object that they are posting or the opening (e.g., Goodale & Milner, 1992). In contrast, patients with dorsal stream damage cannot post objects that they can recognize (Perenin & Vighetto, 1988). Similar to the object agnostic, 24-month-old children can successfully post objects that they cannot perceptually match to openings (Street et al., 2011). In simple terms, this suggests a protracted ventral stream development and an early dorsal stream development. In Experiment 1, we investigated the neural substrates of the posting task in 4- to 7-year-old children and compared this to a visual task with the same objects and openings. If the dorsal stream matures earlier than the ventral stream, we would expect to see dorsal stream function during the posting task. It is possible, however, that the behavioral success in this task is supported by different or additional neural substrates in the young child. That is, even though the behavior looks similar to what we see in adults, the supporting mechanisms may be different.

To investigate this possibility, Experiment 1 compared the BOLD response during a visually guided posting task to baseline BOLD signal to identify regions involved in this task. We refer to these regions as those involved in visually guided action. We then performed a conjunction analysis comparing posting to its component tasks (motor-only task and visual-only task) to determine whether any of these

regions are *specific* to visually guided action. If a region is specific to visually guided action we would expect recruitment of the region for the posting task compared to both component tasks in the conjunction analysis. However, if the recruitment of a region is driven by one of the components of the task, we would expect no difference in recruitment of the visually guided action compared to its component tasks. This would then suggest that the neural correlates underlying visually guided action are recruited for their specific involvement in either a motor or a visual task rather than for a task that requires the *integration* of visual and motor information.

2.1 | Methods

2.1.1 | Participants

Eighteen right-handed children (ages 4.4 to 7.7 years, 9 females, mean age: 5.4 years) participated in this study. All were native English speakers with normal or corrected to normal visual acuity. Informed written consent was obtained from the parents who were compensated with a gift card, while the children were compensated with a small toy or book.

2.1.2 | Stimuli

Experiment 1 utilized an apparatus (described below) and a set of cardboard rectangles (4 cm × 7 cm). The apparatus was positioned at arm's length from the participant's head, which was propped up such that the apparatus was visible at all times during the experiment. Animal noises signaled the different tasks: a duck quack for the posting task, a dog bark for the motor-only task, and a cat meow for the visual-only task.

2.1.3 | Apparatus

An apparatus consisting of a flat panel, two arms on the side, and a rotatable box (Figure 1) was used in both Experiments 1 and 2. The rotatable box was modeled after the 'grasparatus' used in several adult studies (e.g., Culham, 2006; Culham et al., 2003; Króliczak, Cavina-Pratesi, Goodman, & Culham, 2007). Two sides of the box were Velcro panels, and the other two sides each contained a slot, one oriented vertically and one oriented horizontally. Experiment 1 used the panels with slots. The child was handed a stack of small cards (the cardboard rectangles described above in the stimulus section) that were to be inserted into the slots. Participants' arms were secured at the elbow with cushions to alleviate excessive arm movement during the posting task.

2.1.4 | Procedure

Pre-imaging sessions

Before the initial imaging session, children were taken to the MR simulator to acclimate them to the MRI environment and apparatus (see James, 2010; James & Engelhardt, 2012; Kersey & James, 2013).

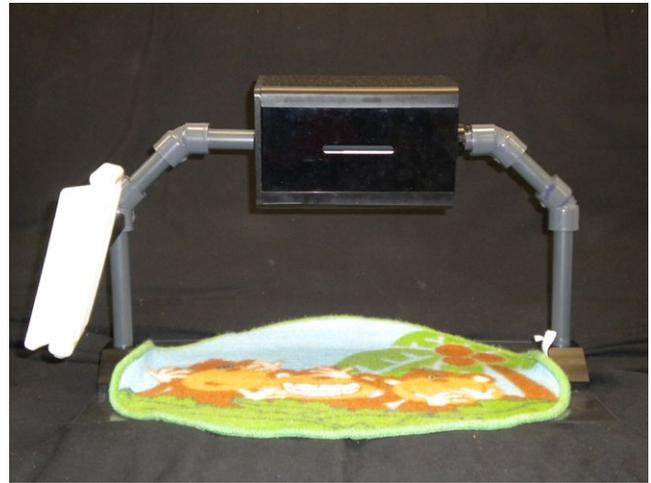


FIGURE 1 Apparatus used in both experiments. Shown here is one of two sides with slots. The slot on the other side is oriented vertically

If the child felt comfortable in the simulated environment, a training session occurred in the MR simulator. During training, the apparatus was introduced to the participant and placed such that the flat panel was under the child and the box was over the child's stomach within comfortable arm's reach. Experimenters propped the participant's head with a pillow so the child could see the box and placed a stack of rectangular cards in the child's left hand to be used in correspondence with three different sounds for our three tasks: the posting task and two control tasks (visual-only, and motor-only). Children were taught to perform each task during the corresponding sound cue. For the *posting* task, children used their right hand to pick up a card from their left hand and post it in the slot on the apparatus. Children were instructed to perform this action throughout the duration of the corresponding sound cue (approximately six posting actions per block). For the *visual-only* task, children looked at the slot on the box. Finally, for the *motor-only* task, children closed their eyes, picked up a card, and made reaching movements with their right arm towards the box as if they were to post the card, but to not actually insert the card into the slot. Children continuously made these movements using the same card over and over again as long as they heard the appropriate sound cue (approximately six movements per block). The task was practiced extensively until the child was proficient at performing the required task upon the auditory cue. Once the child was proficient, he or she was rewarded with two stickers and proceeded to the MR scanner.

Imaging sessions

The child was positioned in the actual MR scanner in the same manner as the simulator. First, a preliminary high-resolution anatomical scan was administered while the child listened to a child-friendly song. Next, the functional imaging occurred. Auditory stimuli were presented in 12-second blocks through headphones via SuperLab Pro 4 (Cedrus Corporation) on a Macintosh MacBook laptop. Seven task blocks were presented per run with 12 seconds of baseline (no audio cue) time between blocks. This resulted in two or three presentations

of each condition in a given run. Three runs were administered per session and were counterbalanced among participants. Children's accuracy in executing the tasks was monitored by a researcher who remained in the MRI room with the child throughout the imaging session. Neural activation was measured by the blood oxygen-level-dependent (BOLD) signal throughout the brain. Imaging sessions lasted approximately 30 min.

fMRI acquisition

Imaging was performed using a 3-T Siemens Magnetom Trio whole-body MRI system and a phased-array 32-channel head coil, located at the Indiana University Department of Psychological and Brain Sciences. The top part of the coil was removed so the participants could have their heads propped up slightly to see the box during the experimental tasks. Pre-testing with the top of the head coil removed revealed that all regions of interest were effectively imaged, given the smaller size of the participants' heads relative to adults. Signal drop out was evident only in the prefrontal cortex. Images were acquired using an echo-planar technique (TE = 20 ms, TR = 2000 ms, flip angle = 90°) for BOLD-based imaging. The field of view was

22 cm × 22 cm × 9.9 cm, with an in-plane resolution of 64 × 64 and 33 slices per volume that were 4 mm thick. The resulting voxel size was 3.0 mm × 3.0 × 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™ (Brain Innovation, Maastricht, The Netherlands). 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.

fMRI data analysis procedures

Whole-brain group contrasts were performed on the resulting data. The functional data were analyzed with a random effects general linear model (GLM) using Brain Voyager's™ multi-subject GLM procedure (Goebel, Esposito, & Formisano, 2006). 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

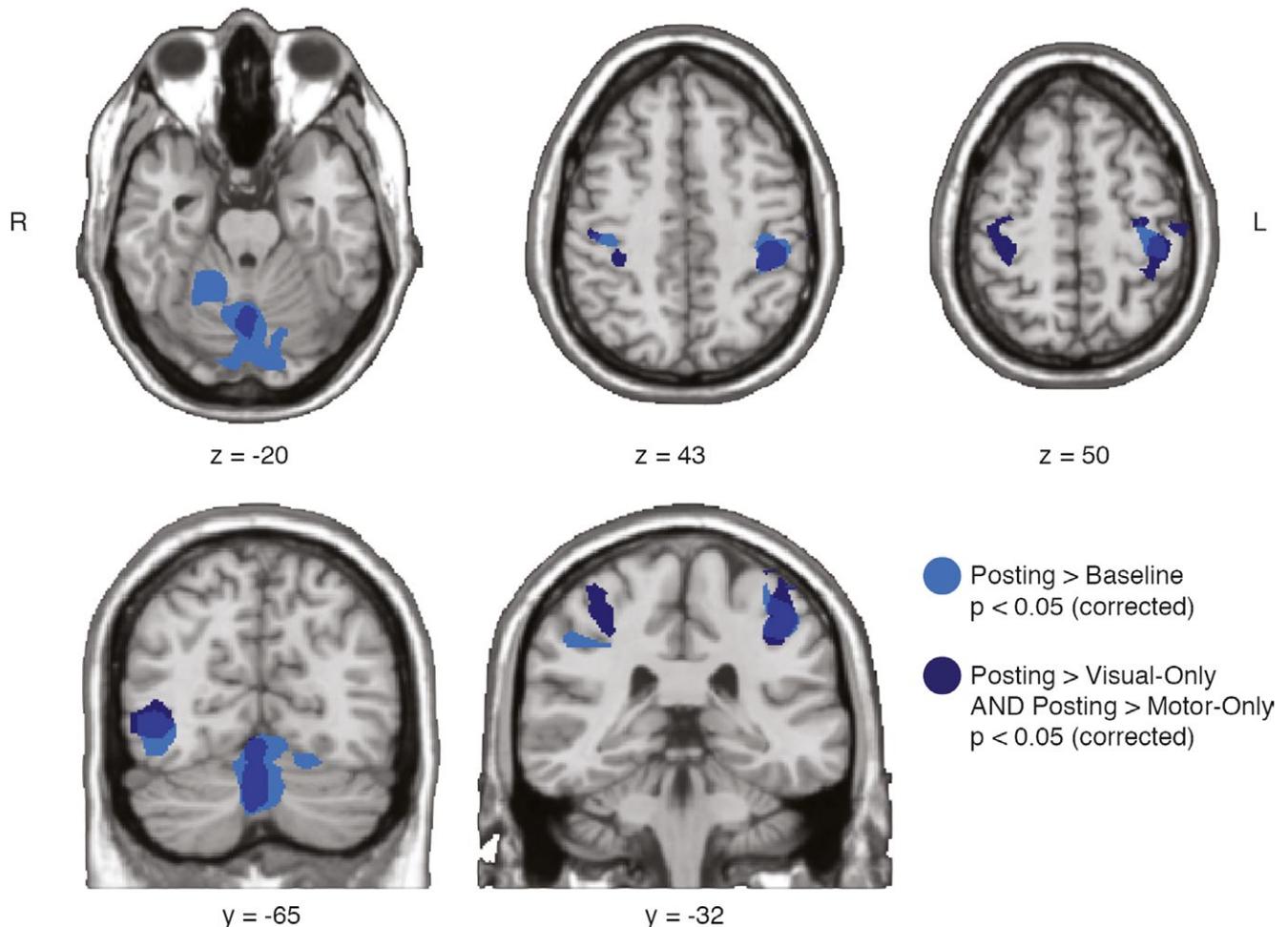


FIGURE 2 Whole-brain contrasts for Experiment 1. The light blue depicts the comparison of the posting task to baseline at $p < .05$ (corrected) and the dark blue depicts the conjunction of posting vs. visual-only and posting vs. motor-only ($p < .0025$, uncorrected at the conjunction level, $p < .05$ for each map when entered into conjunction; corrected to $p < .05$)

hemodynamic response during that run. Our analysis included four predictors: one for the posting task, one for the motor-only task, one for the visual-only task, and one for baseline, which served as an explicit predictor to model baseline BOLD signal. Any functional data that exceeded 5 mm of motion on any axis was excluded from the analysis. This resulted in the exclusion of data from nine participants consisting of six whole runs, 15 volumes of motor-only data, eight volumes of visual-only data, 11 volumes of posting data, and 43 volumes of baseline data. Volumes were removed from analyses by leaving that volume unmodeled in the single-study design matrices. Because the baseline was modeled as a separate predictor, excessive motion was not confounded with our baseline. Individual anatomical data were normalized to the stereotactic space of Talairach and Tournoux (1988) using an 8-parameter affine transformation, with parameters selected by visual inspection of anatomical landmarks.

Direct contrasts of BOLD activation were performed at the group level. Contrasts in the group statistical parametric maps (SPMs) were considered significant at a voxel-wise error rate of $p < .01$ with an applied cluster threshold (calculated using Monte Carlo simulation implemented in a BrainVoyager plugin) to achieve an overall family-wise error rate of $p < .05$. Conjunction analyses were considered significant at a voxel-wise error rate of $p < .0025$ (corresponding to the individual maps entered into the conjunction analysis at $p < .05$) with an applied cluster threshold to achieve an overall family-wise error rate of $p < .05$.

2.2 | Results

First, to identify regions involved in visually guided action, we conducted a whole-brain analysis comparing the posting task to baseline (Figure 2, $p < .05$, corrected using a cluster threshold of 184 mm^3). This revealed bilateral recruitment of the intraparietal sulcus (IPS), a large cluster of activation in the cerebellum, and a region of the right posterior middle temporal gyrus (see Table 1 for all Talairach coordinates from the whole-brain analyses in Experiments 1 and 2), indicating that these regions were involved in executing the posting task. Next, to determine if these regions were unique to visually guided action, we performed a whole-brain conjunction analysis of the posting task > the visual-only task and the posting task > motor-only task ($p < .05$, corrected using a cluster threshold of 1022 mm^3). This revealed similar regions of the left IPS, cerebellum, and right posterior middle temporal gyrus. Notably, this region of the right IPS was more superior in the conjunction contrast than when posting was compared to baseline. The results of the conjunction contrast suggest that these regions of the bilateral IPS and the cerebellum were recruited specifically for the visually guided action and not simply the component processes of the task (motor and vision).

To ensure that differences between the posting and control conditions were not due to differences in head movement during the task, we calculated average displacement across the brain for each condition by squaring translation in the X, Y, and Z planes, adding the squared translations together, and then taking the square root (see Jao, James, & James, 2014; Satterthwaite et al., 2012; Van Dijk,

Sabuncu, & Buckner, 2012). A one-way repeated measures ANOVA (using the ez package for R: ezANOVA) revealed no significant effect of condition (four levels: posting task, motor-only task, visual-only task, and baseline) on displacement ($F(1.50, 25.56) = 1.67$, $p = .21$ using the Greenhouse-Geisser correction for violation of Mauchly's Test for Sphericity, $\chi^2(5) = 35.28$, $p < .01$; Figure 3).

2.3 | Discussion

Experiment 1 identified regions of the brain that were involved in a visually guided action (posting) during childhood by measuring changes in BOLD signal while children performed a visually guided posting task, a motor-only task, and a visual-only task. Bilateral recruitment of the IPS during the posting task suggests that by middle childhood, the IPS is recruited for visually guided actions. Although the recruitment of the IPS bilaterally may seem surprising given the unilateral nature of the task, Culham et al. (2006) propose two possible explanations for the recruitment of parietal regions ipsilateral to the acting hand during visually guided action. The first argues that the bilateral activation reflects cross-talk between hemispheres. In other words, the activation in the hemisphere ipsilateral to the acting hand is simply a result of signals sent across interhemispheric connections. The second suggests that activity in the ipsilateral hemisphere results from coding the possibility of using the other hand to complete the task. In this scenario, both hemispheres plan the actions required to complete the task, but only one hand is selected to carry out the action. Another possibility is that the right IPS was recruited due to the involvement of the left hand, which held the cards that were picked up by the right hand for posting. Because the results of the present study do not help to distinguish between these possibilities, the purpose of the right IPS in this task remains unclear but will be explored more in the general discussion.

This experiment also found recruitment of the cerebellum during the posting task. The middle cerebellum has been implicated in part

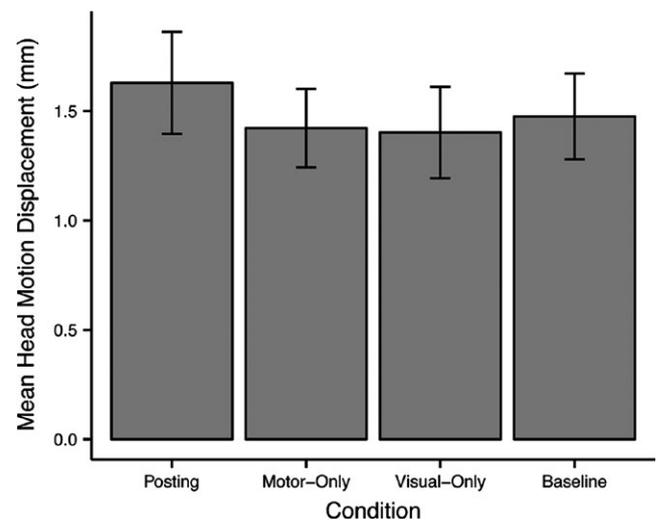


FIGURE 3 Average displacement for each condition in Experiment 1

TABLE 1 Peak Talairach coordinates, average t -value, average p -value, and cluster size (in mm^3) for regions recruited in the whole-brain contrasts of Experiment 1 and Experiment 2. The table lists the threshold for the uncorrected maps, but all reported clusters survive cluster correction to a family-wise error rate of $p < .05$

Region	Peak X	Peak Y	Peak Z	Avg T	Avg p	Size (mm^3)
Experiment 1: Posting > Baseline (uncorrected $p = .01$)						
Left IPS	-45	-28	43	3.07	0.007	2729
Left Superior Parietal Cortex	-36	-46	58	3.10	0.007	550
Right IPS	45	-34	34	3.07	0.007	1729
Right Posterior Middle Temporal Gyrus	39	-64	-8	3.44	0.004	2859
Cerebellum	-9	-8	-20	3.42	0.004	13428
Experiment 1: Posting > Motor-Only and Posting > Visual-Only (uncorrected $p = .05$ per map)						
Left IPS	-48	-22	55	2.34	0.030	5327
Right IPS	36	-13	55	2.25	0.039	2001
Right Posterior Middle Temporal Gyrus	42	-61	1	2.64	0.022	2175
Middle Cerebellum	3	-64	-29	2.54	0.026	2595
Experiment 2: Reach-to-Grasp > Baseline and Reach-to-Touch > Baseline (uncorrected $p = .01$ per map)						
Left IPS	-42	-22	55	3.54	0.004	7554
Left Transverse Temporal Gyrus	-51	-25	10	3.12	0.008	512
Right Transverse Temporal Gyrus	57	-13	10	3.29	0.006	944
Left Posterior Middle Temporal Gyrus	-39	-70	-5	3.15	0.007	681
Right Posterior Middle Temporal Gyrus	42	-67	-8	3.21	0.007	605
Left Occipital Cortex	-24	-95	10	3.53	0.004	1254
Right Occipital Cortex	21	-95	16	3.54	0.004	908
Cerebellum	3	-70	-35	3.52	0.004	8780
Experiment 2: Reach-to-Grasp > Motor-Only and Reach-to-Grasp > Visual-Only (uncorrected $p = .05$ per map)						
Left IPS	-45	-31	43	2.57	0.026	3855
Bilateral Occipital Cortex	9	-82	7	2.85	0.019	64885
Experiment 2: Reach-to-Grasp > Reach-to-Touch (uncorrected $p = .05$)						
LIPS	-45	-31	52	2.46	0.030	1400
Left Posterior Parietal Cortex	-24	-64	37	2.51	0.028	4223
RIPS	36	-37	43	2.49	0.029	4581
Bilateral Occipital Cortex & Cerebellum	-9	-88	-2	2.57	0.027	41701
Experiment 2: Reach-to-Grasp > Reach-to-Touch (uncorrected $p = .01$)						
Left Posterior Parietal Cortex	-24	-64	37	3.17	0.007	244
Left Occipital Cortex	-9	-88	-2	3.47	0.005	6394
Right Occipital Cortex	9	-85	10	3.31	0.006	1691
Right Cerebellum	18	-46	-17	3.22	0.007	422

of the 'control' network for visually guided action in adults (Glover, Wall, & Smith, 2012). It is thought to process proprioceptive feedback during visually guided actions and compare the movement of the body

to the motor plan for an action (Glover, 2004; Glover et al., 2012; Ramnani, 2006). The results of the present experiment support this hypothesis in that this area was recruited more strongly for posting

compared to baseline and compared to the control conditions. One important difference is that the recruitment of the cerebellum for posting compared to baseline was more extensive than when posting is compared to the conjunction of the visual-only and motor-only tasks. This suggests that one of the control conditions recruited the cerebellum in a similar way to the posting task, but to a lesser extent. To determine which of the control conditions was driving this result, we conducted a post-hoc paired samples *t*-test comparing the motor-only condition and the visual-only condition in the cerebellar region recruited for Posting > Baseline, but not for the conjunction of Posting > Motor-Only and Posting > Visual-Only. A voxel-by-voxel analysis revealed that the motor-only task recruited the cerebellum more than the visual-only task ($t(548) = 13.56$, $p < .00001$, mean motor-only - baseline beta value = 0.18 mean visual-only - baseline beta value = -0.14). This is likely because the motor-only task, like the posting task, requires proprioceptive feedback. Recruitment of the cerebellum for both motor tasks is also in line with studies that report the involvement of the cerebellum during motor learning tasks (Albert et al., 2009; Doyon & Benali, 2005; Hikosaka et al., 1999; Thach et al., 1992; Ungerleider et al., 2002).

Overall, the results of Experiment 1 suggest that by the time children reach 5 years of age, they rely on bilateral IPS and the middle cerebellum for a simple visually guided action. Experiment 2 will determine whether or not children recruit these same regions for other types of visually guided actions.

3 | EXPERIMENT 2

To determine whether the pattern of activity seen for the posting task is generalizable to other visually guided actions, Experiment 2 investigated the development of the reaching and grasping systems in the young child. In adult participants reaching for an object and grasping an object recruit interconnected, but disparate, regions of the dorsal visual processing stream in the posterior parietal cortex (PPC) (Cavina-Pratesi et al., 2010; Culham et al., 2006; Króliczak et al., 2007). It is an open question as to whether children recruit similar, dissociable sub-systems in the PPC to execute a reach vs. a grasp. We address this question by comparing reach-to-touch and reach-to-grasp actions in a new group of children (4- to 6-year-olds). We use the regions identified for visually guided action in Experiment 1 to perform region-of-interest analyses to determine if the same neural correlates that subserve the posting task are also involved in visually guided reach-to-grasp actions, visually guided reach-to-touch actions, or reach-to-grasp actions performed without visual guidance. If the regions that are recruited for the posting task are important for many types of visually guided actions in the developing brain, then we should see significant recruitment of these regions for both reaching and grasping actions. Following the ROI analysis, we then performed whole-brain comparisons to determine whether young children recruit any additional regions of the brain for visually guided reaching and grasping. As in Experiment 1, we defined any region that is recruited more for a visually guided action than baseline as being involved in visually guided action and any region

that is involved more for a visually guided action than the control tasks (motor-only and visual-only) as being *specific* to visually guided action.

3.1 | Methods

3.1.1 | Participants

Sixteen right-handed children (4.7 to 6.7 years, 10 female, mean age = 6.02 years) participated in this study. All were native English speakers and had normal or corrected to normal visual acuity. Parents gave their informed written consent and were compensated with a gift card, while the children were compensated with a small toy or book.

3.1.2 | Stimuli

The stimuli were four small objects that were attached to the apparatus used in Experiment 1 using Velcro. The objects were a toy peanut (6 cm × 2 cm), a plastic marshmallow (3 cm diameter), and two novel, 3D shapes (measuring 5 cm × 5 cm and 7 cm × 5 cm) (see Figure 4). Objects were presented in isolation, and the type of object was counterbalanced among runs. Animal noises signaled each type of trial: a duck quack for the reach-to-grasp task, a cow moo for the reach-to-touch task, a dog bark for the motor-only task, and a cat meow for the visual-only task.

3.1.3 | Apparatus

Experiment 2 used the Velcro sides of the apparatus from Experiment 1 (Figure 5).

3.1.4 | Procedure

Pre-imaging sessions

The same procedures as in Experiment 1 were followed to ensure that the children were comfortable in the MR simulator and could lie still in the scanner without moving their head or body. The training session used the Velcro panels of the same apparatus from Experiment



FIGURE 4 Stimuli used in Experiment 2



FIGURE 5 Demonstration of a child reaching and grasping with the apparatus

1. One of four objects was placed in the center of the panel for training. Children were given the following instructions for the four tasks. For the *reach-to-grasp* task children used their right hand to reach for and grasp, but not remove, the object on the panel. During the *reach-to-touch* task, children formed their right hand into a fist and then reached out to tap the object on the panel with their knuckles. For the *motor-only* task, children reached out and grasped the object with their right hand (as in the reach-to-grasp condition), but did so with their eyes closed. For the *visual-only* task, children looked at the panel without moving. Children were instructed to continuously perform each task for the duration of the corresponding animal noise. This resulted in a variable number of actions (approximately 10 reach-to-touch or reach-to-grasp actions per block) performed across the experiment and across children. After the children were proficient at the tasks, they were rewarded with two stickers before proceeding to the MR scanner.

Imaging sessions

Imaging procedures were the same as in Experiment 1. In Experiment 2, the four audio sounds (see stimuli) that signaled the different tasks were presented throughout eight blocks (two blocks of each task condition). Each block consisted of one sound repeated for 12 seconds. Twelve seconds of baseline (no audio cues) separated the condition blocks. Three runs were presented in a random order for each participant. The object on the Velcro panel was switched after each run so that each child was exposed to all four objects throughout the practice and imaging sessions. A second researcher remained in the MRI room to monitor children's accuracy in executing the tasks.

fMRI acquisition

fMRI acquisition was the same as Experiment 1.

fMRI data analysis procedures

Data analysis followed the same procedures as in Experiment 1. Consequently any functional data that exceeded 5 mm of motion on any axis were excluded from the analysis. This resulted in the exclusion of data from five children consisting of five complete runs, two

volumes of reach-to-touch data, four volumes of visual-only data, five volumes of reach-to-grasp data, and nine volumes of baseline data. In addition, one participant was excluded entirely due to excessive motion, resulting in a sample size of 15 participants.

First, we conducted region of interest (ROI) analyses using MATLAB and R-Studio. Our regions of interest were independently defined using the whole-brain results of the conjunction analysis from Experiment 1. Next, we performed whole-brain analyses of direct contrasts of BOLD activation on group statistical parametric maps (SPMs). Following Experiment 1, for single-contrast maps a voxel-wise error rate of $p < .01$ with an applied cluster to achieve an overall family-wise error rate of $p < .05$ was used to denote significance. Conjunction contrasts are reported significant at a more stringent conjunction threshold of either $p < .0025$ or $p < .001$ (corresponding to thresholds of $p < .05$ or $p < .01$ per map entered into the conjunction analysis) corrected to a family-wise error rate of $p < .05$.

3.2 | Results

3.2.1 | Region of interest analyses

To determine whether the same neural substrates that subserved posting were also involved in reaching and grasping, we identified four regions of interest from Experiment 1, defined independently of the current data, that were selective for posting in young children: the left and right IPS, the middle cerebellum, and the right posterior middle temporal gyrus. We then extracted beta values from these regions and subtracted the baseline betas from each task condition (reach-to-grasp, reach-to-touch, visual-only, and motor-only) before conducting our analyses. We first performed one-sample t -tests to determine if the brain activation in response to visually guided actions (reach-to-grasp and reach-to-touch) was significantly above 0. Brain activation in response to the reach-to-grasp task was significant in all ROIs except for the right IPS (Left IPS: mean = 0.34, $t(14) = 4.38$, $p = .0006$; Right IPS: mean = 0.13, $t(14) = 1.41$, $p = .18$; Middle Cerebellum: mean = 0.39, $t(14) = 4.24$, $p = .0008$; Right Posterior Middle Temporal Gyrus: mean = 0.37, $t(14) = 3.12$, $p = .0075$). The same result was found for the reach-to-touch task (Left IPS: mean = 0.25, $t(14) = 4.59$, $p = .0004$; Right IPS: mean = -0.02, $t(14) = -0.45$, $p = .66$; Middle Cerebellum: mean = 0.35, $t(14) = 4.05$, $p = .0012$; Right Posterior Middle Temporal Gyrus: mean = 0.17, $t(14) = 2.49$, $p = .0257$). This suggests that the same regions of the left IPS, right posterior middle temporal gyrus, and cerebellum that were recruited specifically for visually guided action in Experiment 1 are also involved in executing other visually guided actions, namely reach-to-grasp and reach-to-touch.

Next, to determine if these regions were specific to another visually guided action, we conducted one-way repeated measures ANOVAs using the ez package for R (ezANOVA) (Figure 6). These ANOVAs were significant in the left IPS ($F(3, 42) = 9.03$, $p = .0001$), the middle cerebellum ($F(3, 42) = 6.92$, $p = .0007$), and the right posterior middle temporal gyrus ($F(3, 42) = 6.64$, $p = .0009$), but not in the right IPS ($F(3,$

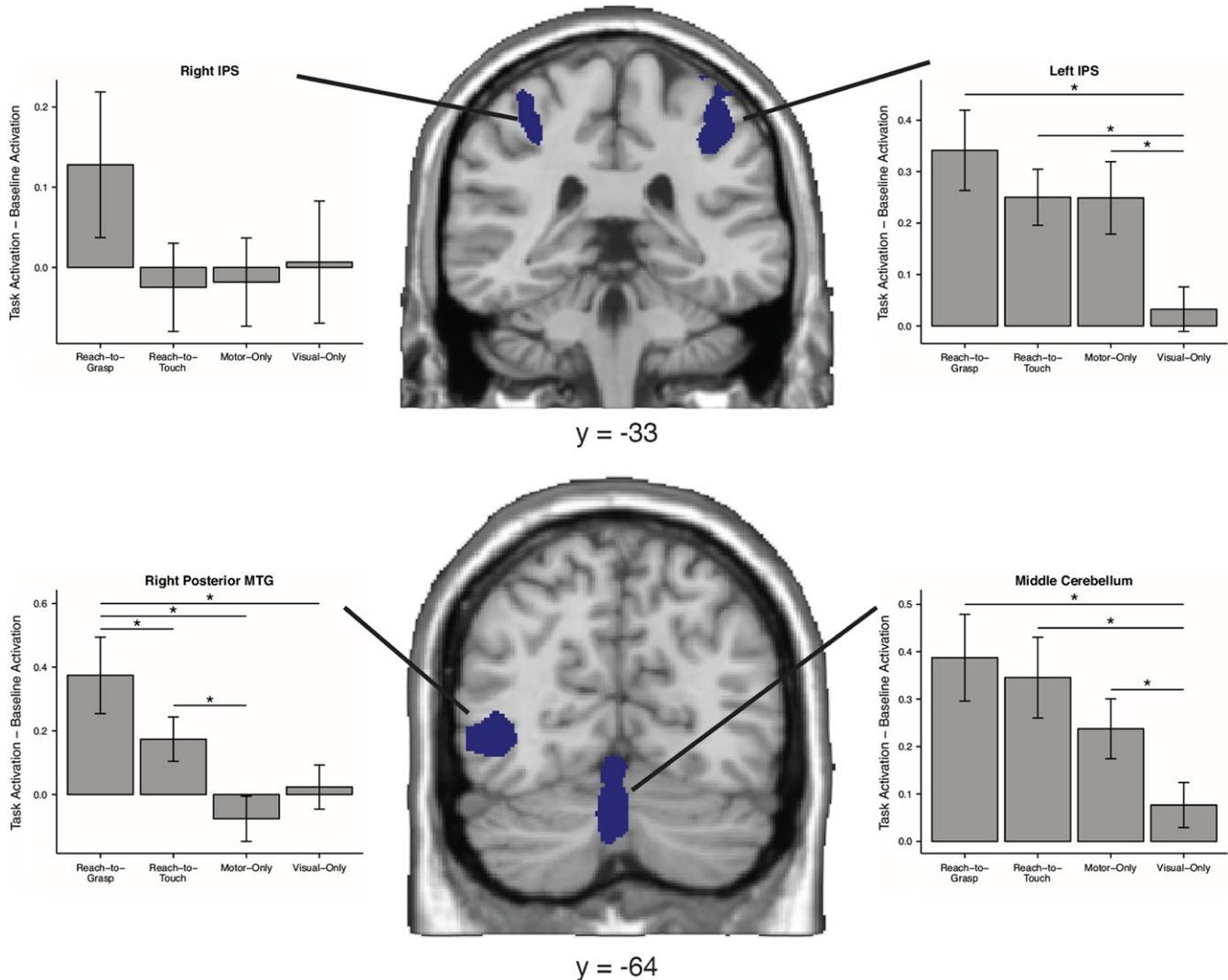


FIGURE 6 Region-of-Interest analysis. Regions were defined from the conjunction analysis of Experiment 1 (Posting vs. Visual-Only and Posting vs. Motor-Only), and analyses were conducted on data from Experiment 2. Asterisks (*) denote a significant difference between conditions ($p < .05$). Error bars denote standard error

42) = 1.73, $p = .17$), suggesting that all conditions recruited the right IPS to a similar degree. Post-hoc paired t -tests between conditions in the other three ROIs revealed that in the left IPS, all motor actions resulted in greater activation than the visual-only condition (Reach-to-Grasp vs. Visual-Only: $t(14) = 4.33$, $p = .001$; Reach-to-Touch vs. Visual-Only: $t(14) = 4.00$, $p = .001$; Motor-Only vs. Visual-Only: $t(14) = 2.71$, $p = .017$). No other comparisons were significant (all $ps > .1$, all $ts < 1.75$), but there were trends toward greater activation of the reach-to-grasp condition compared to the reach-to-touch ($t(14) = 1.74$, $p = .10$) and the motor-only conditions ($t(14) = 1.75$, $p = .10$).

Post-hoc t -tests in the middle cerebellum yielded a similar pattern. Visually guided and motor actions recruited the middle cerebellum significantly more than the visual-only condition (Reach-to-Grasp vs. Visual-Only: $t(14) = 4.05$, $p = .001$; Reach-to-Touch vs. Visual-Only: $t(14) = 3.96$, $p = .001$; Motor-Only vs. Visual-Only: $t(14) = 2.18$, $p = .046$). Comparisons between visually guided actions and the motor-only condition were not significant, nor were the visually

guided actions different from each other (all $ps > .1$, all $ts < 1.71$). Like the left IPS, the middle cerebellum was strongly recruited for tasks that involve arm movement.

Finally, post-hoc t -tests in the right posterior middle temporal gyrus revealed that the reach-to-grasp condition recruited this region significantly more than the control conditions (Reach-to-Grasp vs. Visual-Only: $t(14) = 2.86$, $p = .013$; Reach-to-Grasp vs. Motor-Only: $t(14) = 3.37$, $p = .005$) and marginally more than the reach-to-touch condition ($t(14) = 2.06$, $p = .059$), suggesting a degree of specialization for reach-to-grasp actions in the right cerebellum. The reach-to-touch condition recruited this region more than the motor-only condition ($t(14) = 2.85$, $p = .013$), but no other comparisons approached significance (all $ps > .13$, all $ts < 1.61$).

In sum, the ROI analyses suggest that similar regions of the child brain are recruited across various visually guided actions, with the exception of the right IPS, which was indifferent to the conditions of Experiment 2. The right posterior middle temporal gyrus was the only

region that displayed a preference for visually guided action, specifically, for the reach-to-grasp task. Unlike Experiment 1, the middle cerebellum and left IPS were not specific for visually guided actions, but were generally sensitive to tasks involving movement.

3.2.2 | Whole-brain analyses

Next, we performed complementary whole-brain analyses. If the regions identified in Experiment 1 for visually guided posting are important for several types of visually guided actions in the developing brain, the whole-brain comparisons for Experiment 2 should mirror those from Experiment 1. Whole-brain analysis also allow us to determine whether any additional regions of the developing brain were recruited for visually guided reaching and grasping. Finally, we take a whole-brain approach to directly compare the two visually guided actions from Experiment 2 (reach-to-grasp vs. reach-to-touch).

First, we compared visually guided actions to baseline activation by performing a conjunction analysis of Reach-to-Grasp > Baseline *and*

Reach-to-Touch > Baseline ($p < .0001$ uncorrected, corrected to $p < .05$ using a cluster threshold of 198 mm^3). This resulted in recruitment of the left IPS, bilateral posterior middle temporal gyrus, and a large portion of the middle cerebellum (Figure 7: red; see Table 1 for a complete list of regions). Importantly, the left IPS, right posterior middle temporal gyrus, and middle cerebellum overlap with the regions seen for the equivalent contrast in Experiment 1 (Posting > Baseline, Figure 7: Experiment 1 in blue, overlap in purple), suggesting that similar neural mechanisms are recruited across different visually guided actions in children.

Next, we conducted a conjunction analysis of Reach-to-Grasp > Visual-Only *and* Reach-to-Grasp > Motor-Only to determine if there were any regions specific to the reach-to-grasp visually guided action ($p < .0025$ uncorrected, corrected to $p < .05$ using a cluster threshold of 1040 mm^3 ; Figure 8). This revealed large regions of the bilateral occipital cortex, and a region of the left IPS. However, this region of the left IPS is mostly inferior to the region of the left IPS from the conjunction of Reach-to-Grasp > Baseline *and* Reach-to-Touch > Baseline. This suggests that the regions that show specificity for reach-to-grasp actions are not necessarily the same as those that

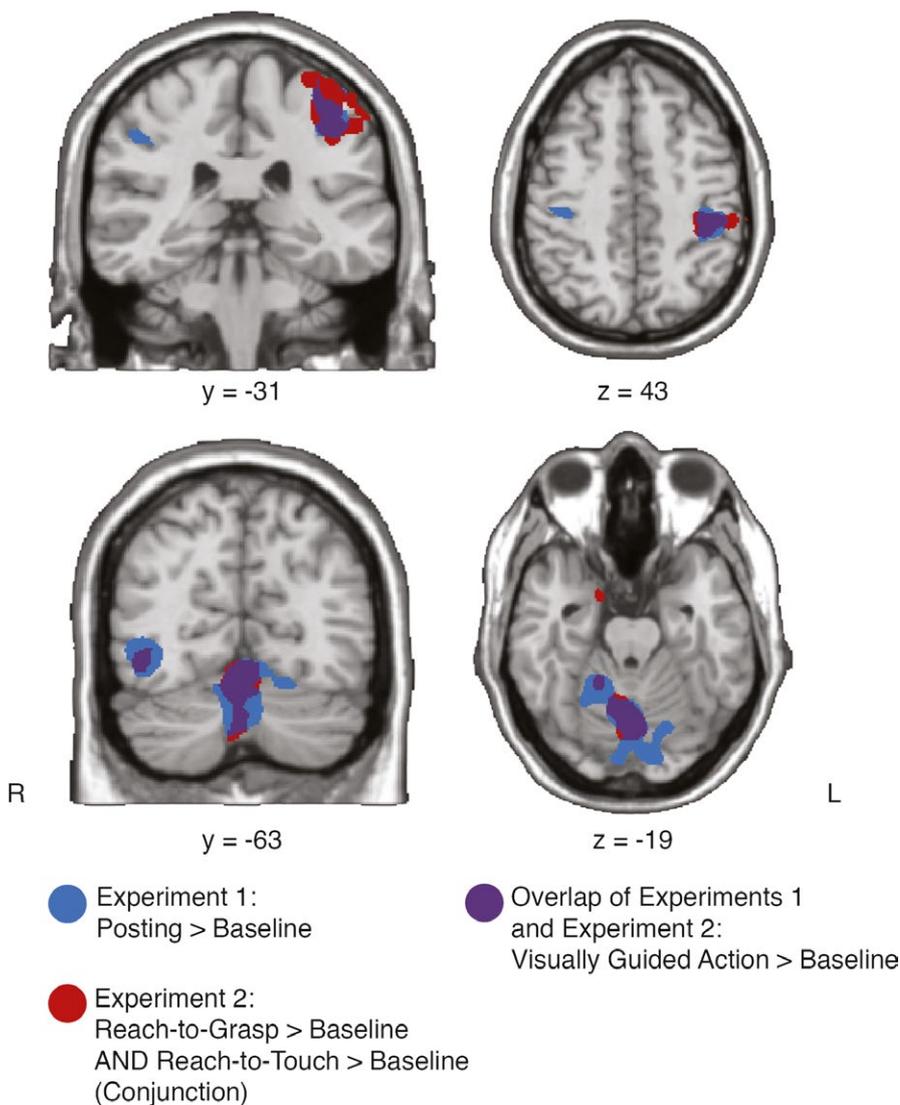


FIGURE 7 Whole-brain comparison of the Posting Task vs. Baseline in blue (Experiment 1, $p < .05$, corrected) and the conjunction of the Reach-to-Grasp Task vs. Baseline and the Reach-to-Touch Task vs. Baseline in red (Experiment 2, $p < .0001$, uncorrected at the conjunction level, $p < .01$ for each map when entered into conjunction; corrected to $p < .05$). The overlap is denoted in purple

Conjunction of: Reach-to-Grasp > Visual-Only AND Reach-to-Grasp > Motor-Only

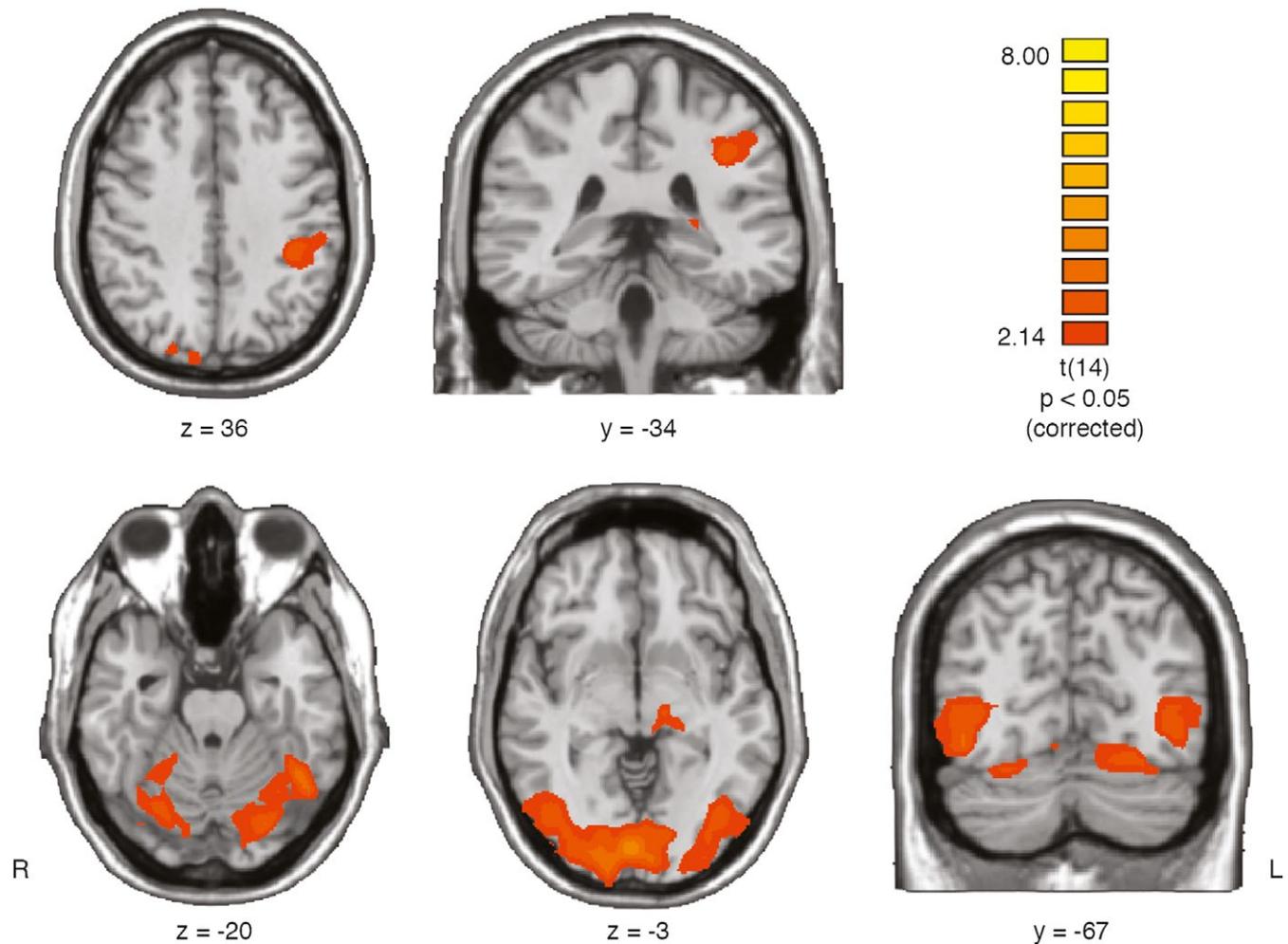


FIGURE 8 Whole-brain comparison of the conjunction of the reach-to-grasp task compared to the visual-only task and the reach-to-grasp task compared to the motor-only task at a threshold of ($p < .0025$, uncorrected at the conjunction level, $p < .05$ for each map when entered into conjunction; corrected to $p < .05$)

show consistent recruitment while executing visually guided actions. The equivalent conjunction was not conducted for the reach-to-touch condition because the reach-to-touch condition employed a different motor movement from the motor-only condition, which was modeled after the reach-to-grasp action.

Finally, to identify any regions throughout the brain that responded more strongly for either the reach-to-grasp or reach-to-touch tasks, a whole brain contrast between these two conditions was performed. This revealed regions of the bilateral occipital cortex, right cerebellum, and left posterior parietal cortex that responded more strongly for the reach-to-grasp condition ($p < .01$ uncorrected, corrected to $p < .05$ using a cluster threshold of 197 mm^3). Examining the map at a more liberal threshold ($p < .05$ uncorrected, corrected to $p < .05$ using a cluster threshold of 39 mm^3) revealed regions of the bilateral IPS (Figure 9) that responded more strongly for the reach-to-grasp condition. This suggests a trend towards greater recruitment of the IPS for the more complex visually guided actions (reach-to-grasp). No regions

responded more strongly during the reach-to-touch condition than the reach-to-grasp condition.

In sum, these whole-brain results indicate that for reach-to-grasp and reach-to-touch visually guided actions, children relied on the left IPS, right posterior middle temporal gyrus, and the cerebellum. However, the left IPS, as defined in Experiment 1, was not recruited specifically for visually guided actions. Based on the ROI analysis, which found greater recruitment of a largely overlapping region of the left IPS during the motor-only task compared to the visual-only task, we suggest that the left IPS was recruited more generally for motor actions in Experiment 2.

3.2.3 | Analysis of head movement

As in Experiment 1, a one-way repeated measures ANOVA revealed no significant effect of condition (five levels: reach-to-touch, reach-to-grasp, motor-only, visual-only, and baseline) on displacement ($F(1.82, 25.49) = 1.10$, $p = .34$ using Greenhouse-Geisser correction

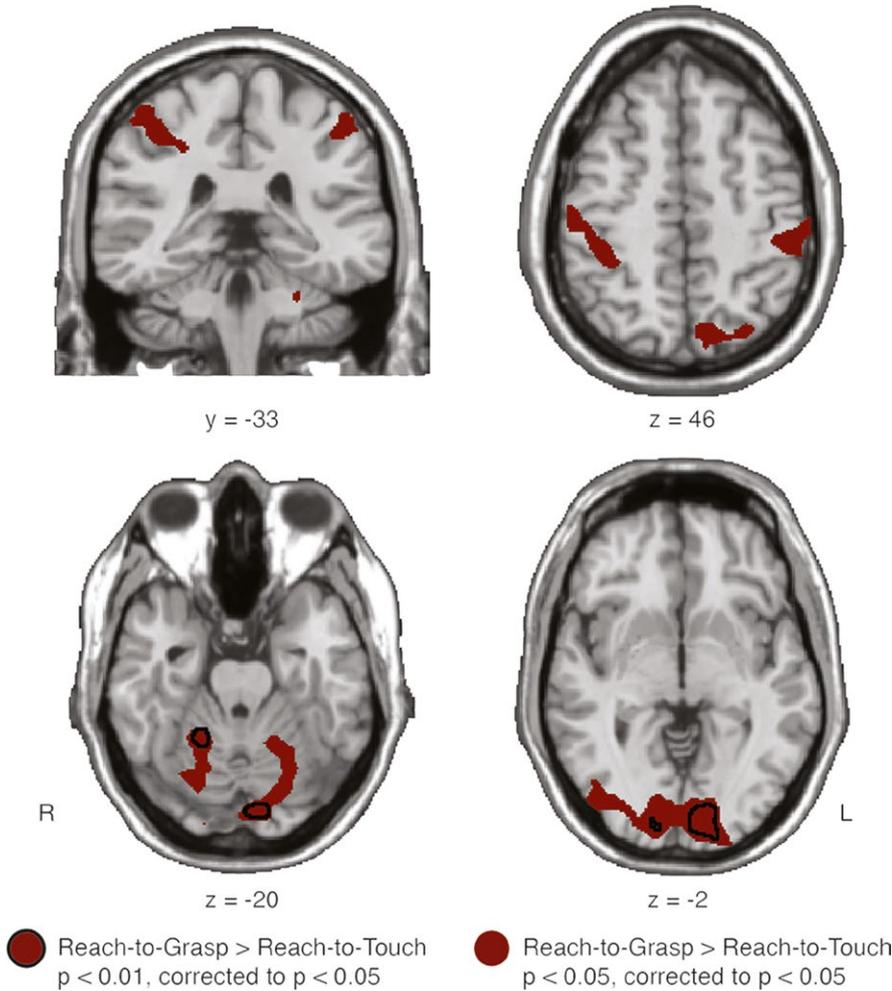


FIGURE 9 Whole-brain contrast comparing Reach-to-Grasp and Reach-to-Touch in Experiment 2. The dark red regions that are not outlined represent areas that were recruited more for the reach-to-grasp than the reach-to-touch task at a threshold of $p < .05$ (corrected from an uncorrected map set at $p < .05$). The dark red areas that are outlined represent the regions that survive at a more stringent threshold ($p < .05$ corrected from an uncorrected map set at $p < .01$)

for violation of Mauchley's Test for Sphericity, $\chi^2(9) = 41.14$, $p < .01$; Figure 10), suggesting that differences between conditions are not due to differences in head motion between conditions.

Taken together, the results of the whole-brain and ROI analyses suggest that the visually guided reaching and grasping rely on the left IPS, right posterior middle temporal gyrus, and the cerebellum during early childhood. Very few differences emerged between the reach-to-grasp and reach-to-touch actions, suggesting that the child brain processes these actions similarly in most regions involved in visually guided action. Finally, we found that the left IPS and middle cerebellum were not specific for visually guided action, but instead were involved in processing conditions that required motor movement.

3.3 | Discussion

Here, we explored the neural correlates underlying reach-to-touch and reach-to-grasp actions in young children. In a whole-brain analysis, we find that children recruit the left IPS for reach-to-grasp and reach-to-touch visually guided actions. This region of the left IPS that was recruited for both the reach-to-touch and reach-to-grasp tasks is similar to the left IPS as seen in Experiment 1, but unlike Experiment 1, this region does not show specificity for visually guided actions (instead a more inferior region shows specificity

for reach-to-grasp actions compared to the component tasks). This suggests that this region may also be involved in processing the visual- and/or motor-only components of reaching and grasping tasks. Specifically, the ROI analysis revealed that comparing the motor-only task with the visual-only task in an overlapping region of the

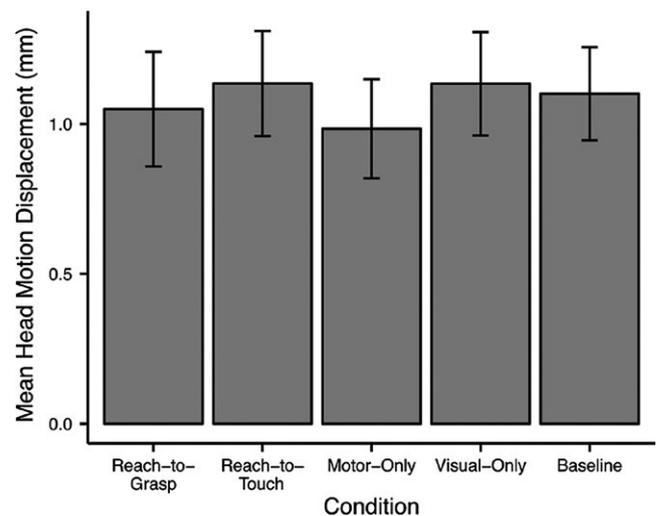


FIGURE 10 Average displacement for each condition in Experiment 2



left IPS approached significance. However, because the region is not exactly the same, it could be that the visual-only condition, during which children viewed the graspable objects, also recruits this area. This would be in line with studies in children that found IPS activation while viewing graspable objects such as tools (Dekker et al., 2011; Kersey et al., 2016).

We also find that visually guided reaching and grasping recruited the cerebellum. The recruitment of the middle cerebellum seen in the whole-brain results for Experiment 2 is consistent with the region seen in Experiment 1. This further supports the idea that the cerebellum is involved during visually guided actions. However, in the ROI analysis the motor-only task was associated with marginally more activation than the visual-only task, suggesting that the middle cerebellum may be a region recruited generally for motor movements.

Here we find minimal differences in the recruitment of regions for the reach-to-touch vs. the reach-to-grasp tasks. In fact, in a whole-brain comparison of the two tasks, the only regions that survived at the more stringent threshold were the bilateral occipital cortex, the right cerebellum, and the left posterior parietal cortex, which responded more strongly for the reach-to-grasp task. Similarities between the reach-to-touch and reach-to-grasp tasks were also seen in the ROI analysis, which found a significant difference between the two tasks only in the right posterior middle temporal gyrus. Great recruitment of regions for grasping compared to reaching is consistent with adult studies (Cavina-Pratesi et al., 2010; Culham et al., 2006; Króliczak et al., 2007), which argue that separation between reaching and grasping reflects differences in the task demands. Adding a grip or grasping component further complicates visually guided actions because the features and goals of an action (as well as object properties) must be understood for successful execution of the task. For example, in the reach-to-grasp task the size, shape, and orientation of the object must be processed so that the participant knows how to scale and shape his hand. However, in the reach-to-touch task, it is only necessary to understand where the object is located in space. These added demands may be responsible for the additional recruitment of bilateral occipital cortex and right cerebellum.

Overall, these results suggest that as early as 5 years old, children rely on regions of the IPS and cerebellum for reaching and grasping tasks.

4 | GENERAL DISCUSSION

These experiments used a novel procedure for investigating the neural substrates underlying visually guided action in the young child. Results suggest that by approximately 6 years of age children rely on neural circuitry in the IPS and cerebellum for visually guided actions. The general discussion will interpret the results from Experiments 1 and 2 in relation to each other and in relation to the adult literature for visually guided actions.

First, we find that similar regions of the IPS are recruited for all three visually guided actions across the two experiments. This region is largely consistent with coordinates from adult studies of visually

guided actions (Supplementary Table 1), but is slightly more anterior and borders on primary sensorimotor cortex (Figure 7). This suggests that at a general level similar systems that subserve visually guided actions in adults may also be involved in visually guided actions in childhood. However, we find that the left IPS showed more specificity for visually guided action in Experiment 1 than Experiment 2. In Experiment 1, the IPS was recruited for the posting task both in comparison to baseline and to the control tasks (visual-only and motor-only), but in Experiment 2 there were no differences between the visually guided actions and the motor-only task in that specific region of the left IPS. Therefore, we suggest that the left IPS is an important region for executing visually guided tasks, but is not specifically involved in visually guided action in young children. It is also possible that there is not an effect of visually guided action relative to control conditions because the motor-control condition is better matched to the visually guided action in Experiment 1 than in Experiment 2.

Another difference between the visually guided tasks in Experiments 1 and 2 is that only the posting task significantly recruited the right IPS. In contrast, in Experiment 2 there was no significant recruitment of the right IPS for visually guided actions. However, two of our analyses suggested a trend toward recruitment of the right IPS for the reach-to-grasp task. Specifically, the whole-brain comparison of the reach-to-grasp task to the reach-to-touch task found stronger recruitment of the right IPS for the reach-to-grasp task at a more liberal threshold. In addition, although the ROI analysis did not reveal a main effect of condition in the right IPS, a post-hoc *t*-test between the reach-to-grasp and reach-to-touch tasks suggests that the right IPS may be important for reach-to-grasp actions, but not general reaching ($t(14) = 1.93, p = .07$; mean of reach-to-grasp - baseline = 0.13, reach-to-grasp - baseline = -0.02). These preliminary findings in Experiment 2, taken with the recruitment of the right IPS for the posting task, suggest that the right hemisphere could be important for processing grasping and gripping components in early childhood. Interestingly, the adult literature is mixed as to whether or not visually guided actions invoke bilateral (Binkofski et al., 1998; Culham et al., 2003; Grefkes & Fink, 2005) or unilateral (Desmurget et al., 2001; Frey, Vinton, Norlund, & Grafton, 2005) recruitment of the IPS (see Castiello & Begliomini, 2008; Grafton, 2010, for reviews). Although some studies do find bilateral activity when comparing grasping actions to pointing and reaching actions (Binkofski et al., 1998; Culham et al., 2003), which would be in line with the results presented here, the relevant data are sparse. Thus, it is possible that the bilateral recruitment seen here may reflect a pattern of activation that is important for processing visually guided grasping actions in the developing brain, but is not commonly seen in adults. It is also worth noting that the recruitment of the right IPS in Experiment 1 could be due to the involvement of the left hand for holding the cards that were used for posting.

In addition to dorsal stream regions in the IPS, both Experiments 1 and 2 found that children recruit the cerebellum for visually guided tasks. Specifically, a region of the middle cerebellum was recruited for all three visually guided actions and a region in the right cerebellum recruited for the reach-to-grasp and posting tasks (Figures 7 and 9). This region of the middle cerebellum has also been reported

in adult grasping studies (Cavina-Pratesi et al., 2010; Glover et al., 2012; Króliczak et al., 2007) and is thought to process proprioceptive feedback during visually guided actions and compare the movement of the body to the motor plan for an action (Glover, 2004; Glover et al., 2012; Ramnani, 2006). This is further supported by studies that have found recruitment of the cerebellum during the observation of reach errors (Diedrichsen, Hashambhoy, Rane, & Shadmehr, 2005; Malfait et al., 2010), which requires comparison of the movement of a body part with an expected motor plan. The present study further supports this hypothesis because these areas are only recruited for motor actions. However, very few studies report recruitment of the cerebellum during visually guided actions. Although this may be because most studies tend to exclude the cerebellum from analysis (Culham, 2006), an exciting possibility is that the cerebellum could play an important role in the execution of visually guided action during development when motor programs are not yet stable (Olivier et al., 2007).

The present results also suggest that visually guided actions may require more cerebellar processing in the developing brain than the same motor actions performed in the absence of vision. For example, Experiment 2 found stronger recruitment of the right cerebellum for the reach-to-grasp task than the motor-only task (Figure 8), and Experiment 1 found stronger recruitment of the cerebellum compared to both the visual-only and motor-only conditions. However, comparing the reach-to-touch task to the motor-only task in Experiment 2 did not reveal stronger recruitment of the middle cerebellum for reach-to-touch compared to the motor-only condition, but the middle cerebellum was recruited more strongly for the motor-only task than the visual-only task. This could suggest two possibilities. First, it could indicate that the middle cerebellum responds equally to motor actions, regardless of the presence of visual feedback, but it could also suggest that the reach-to-grasp actions from the reach-to-grasp and motor-only conditions require more cerebellar processing than those same actions performed without grasping. Therefore, it possible that some of the added demands of the reach-to-grasp tasks are processed in the cerebellum.

In adults, it is commonly reported that reaching and grasping recruit different regions of the dorsal visual processing stream in the PPC (Cavina-Pratesi et al., 2010; Culham et al., 2006; Króliczak et al., 2007). Across the two experiments the most notable difference that we find is that tasks that involve grasping (i.e., posting and reach-to-grasp) uniquely recruit the right IPS and a small region of the right cerebellum, which is a different pattern from that observed in adults. This suggests that the segregation of neural correlates in the left IPS for reaching and grasping may not develop until later in childhood, perhaps when reaching and grasping motor programs become more stable (Olivier et al., 2007). However, it is also possible that the lack of different neural correlates for reaching and grasping in the left IPS is due to differences in tasks rather than differences in neural circuitry. For instance, to date there have not been any fMRI studies of the neural correlates that subserve posting in the adult. In addition, although we have modeled our tasks and apparatus after adult fMRI studies (e.g., Culham, 2006; Culham et al., 2003; Króliczak et al., 2007), one

key difference is that with adults the reaching and grasping actions were performed in the dark after a brief illumination of the target. Therefore, it is unclear whether children truly rely on different neural circuitry than adults for the reach-to-grasp and reach-to-touch tasks reported here. Future work should more directly address differences between children and adults by having all participants perform the same task under the same conditions.

This work provides the first look into the neural correlates that underlie children's processing of visually guided actions. We find that as early as 4 or 5 years old, children rely on dorsal stream regions similar to those used by adults for visually guided actions. This is the first neural evidence of dorsal stream functioning during visually guided action tasks in children and suggests an early maturation of the dorsal stream. In addition, we find that the cerebellum may play an important role for visually guided action in the developing brain. This role should be more fully explored in future work to better understand how these regions work together for the successful completion of visually guided actions.

ACKNOWLEDGEMENTS

The authors would like to thank the Indiana Research Facility for financing the MRI scans as well as the MRI technicians: Thea Atwood, Colleen McCracken, Ben Pruce, and Rebecca Ward. We would also like to thank members of the Cognition and Action Neuroimaging Lab, especially Paroma Bose, Laura Engelhardt, Angie Huh, Harinder Kaur, Shelley Swain, and Emily Thomas.

REFERENCES

- Albert, N.B., Robertson, E.M., & Miall, R.C. (2009). The resting human brain and motor learning. *Current Biology*, *19*, 1023–1027.
- Bertenthal, B.I. (2008). Perception and action. In M.M. Haith & J.B. Benson (Eds.), *Encyclopedia of infant and early childhood development* (pp. 1–42). Oxford: Elsevier.
- Binkofski, F., Dohle, C., Posse, S., Stephan, K.M., Hefter, H., Seitz, R.J., & Freund, H.J. (1998). Human anterior intraparietal area subserves prehension: A combined lesion and functional MRI activation study. *Neurology*, *50*, 1253–1259.
- Cant, J.S., & Goodale, M.A. (2007). Attention to form or surface properties modulates different regions of human occipitotemporal cortex. *Cerebral Cortex*, *17*, 713–731.
- Capitani, E., Laiacona, M., Mahon, B., & Caramazza, A. (2003). What are the facts of semantic category-specific deficits? A critical review of the clinical evidence. *Cognitive Neuropsychology*, *20*, 213–261.
- Carey, S., Diamond, R., & Woods, B. (1980). Development of face recognition: A maturational component? *Developmental Psychology*, *16*, 257–269.
- Castiello, U., & Begliomini, C. (2008). The cortical control of visually guided grasping. *The Neuroscientist*, *14*, 157–170.
- Cavina-Pratesi, C., Monaco, S., Fattori, P., Galletti, C., McAdam, T.D., Quinlan, D.J., ... & Culham, J.C. (2010). Functional magnetic resonance imaging reveals the neural substrates of arm transport and grip formation in reach-to-grasp actions in humans. *Journal of Neuroscience*, *30*, 10306–10323.
- Chance, J.E., Turner, A.L., & Goldstein, A.G. (1982). Development of differential recognition for own- and other-race faces. *Journal of Psychology*, *112*, 29–37.



- Culham, J.C. (2006). Functional neuroimaging : Experimental design and analysis. In R. Cabeza & A. Kingstone (Eds.), *Handbook of functional neuroimaging of cognition* (2nd edn., pp. 53–82). Cambridge, MA: MIT Press.
- Culham, J.C., Cavina-Pratesi, C., & Singhal, A. (2006). The role of parietal cortex in visuomotor control: What have we learned from neuroimaging? *Neuropsychologia*, *44*, 2668–2684.
- Culham, J.C., Danckert, S.L., DeSouza, J.F.X., Gati, J.S., Menon, R.S., & Goodale, M.A. (2003). Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Experimental Brain Research*, *153*, 180–189.
- Culham, J.C., & Valyear, K.F. (2006). Human parietal cortex in action. *Current Opinion in Neurobiology*, *16*, 205–212.
- Dekker, T., Mareschal, D., Sereno, M.I., & Johnson, M.H. (2011). Dorsal and ventral stream activation and object recognition performance in school-age children. *NeuroImage*, *57*, 659–670.
- Desmurget, M., Gréa, H., Grethe, J.S., Prablanc, C., Alexander, G.E., & Grafton, S.T. (2001). Functional anatomy of nonvisual feedback loops during reaching: A positron emission tomography study. *Journal of Neuroscience*, *21*, 2919–2928.
- Diedrichsen, J., Hashambhoy, Y., Rane, T., & Shadmehr, R. (2005). Neural correlates of reach errors. *Journal of Neuroscience*, *25*, 9919–9931.
- Doyon, J., & Benali, H. (2005). Reorganization and plasticity in the adult brain during learning of motor skills. *Current Opinion in Neurobiology*, *15*, 161–167.
- Felleman, D., & Van Essen, D. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, *1*, 1–47.
- Frey, S.H., Vinton, D., Norlund, R., & Grafton, S.T. (2005). Cortical topography of human anterior intraparietal cortex active during visually guided grasping. *Cognitive Brain Research*, *23*, 397–405.
- Gainotti, G., Silveri, M.C., Daniele, A., & Giustolisi, L. (1995). Neuroanatomical correlates of category-specific semantic disorders: A critical survey. *Memory*, *3*, 247–264.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioral and Brain Sciences*, *27*, 3–24–78.
- Glover, S., Wall, M.B., & Smith, A.T. (2012). Distinct cortical networks support the planning and online control of reaching-to-grasp in humans. *European Journal of Neuroscience*, *35*, 909–915.
- Goebel, R., Esposito, F., & Formisano, E. (2006). Analysis of functional image analysis contest (FIAC) data with brainvoyager QX: From single-subject to cortically aligned group general linear model analysis and self-organizing group independent component analysis. *Human Brain Mapping*, *27*, 392–401.
- Golarai, G., Ghahremani, D.G., Whitfield-Gabrieli, S., Reiss, A., Eberhardt, J.L., Gabrieli, J.D.E., & Grill-Spector, K. (2007). Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nature Neuroscience*, *10*, 512–522.
- Golarai, G., Liberman, A., Yoon, J.M.D., & Grill-Spector, K. (2010). Differential development of the ventral visual cortex extends through adolescence. *Frontiers in Human Neuroscience*, *3*, 80.
- Goodale, M.A., & Humphrey, G.K. (1998). The objects of action and perception. *Cognition*, *67*, 181–207.
- Goodale, M.A., & Milner, A.D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*, 20–25.
- Goodale, M.A., & Westwood, D.A. (2004). An evolving view of duplex vision: Separate but interacting cortical pathways for perception and action. *Current Opinion in Neurobiology*, *14*, 203–211.
- Grafton, S.T. (2010). The cognitive neuroscience of prehension: Recent developments. *Experimental Brain Research*, *204*, 475–491.
- Grefkes, C., & Fink, G.R. (2005). The functional organization of the intraparietal sulcus in humans and monkeys. *Journal of Anatomy*, *207*, 3–17.
- Grill-Spector, K., Golarai, G., & Gabrieli, J. (2008). Developmental neuroimaging of the human ventral visual cortex. *Trends in Cognitive Sciences*, *12*, 152–162.
- Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research*, *41*, 1409–1422.
- Hikosaka, O., Sakai, K., Lu, X., Nakahara, H., Rand, M.K., Nakamura, K., ... & Doya, K. (1999). Parallel neural networks for learning sequential procedures. *Trends in Neurosciences*, *22*, 464–471.
- James, K.H. (2010). Sensori-motor experience leads to changes in visual processing in the developing brain. *Developmental Science*, *13*, 279–288.
- James, K.H., & Engelhardt, L. (2012). The effects of handwriting experience on functional brain development in pre-literate children. *Trends in Neuroscience and Education*, *1*, 32–42.
- Jao, R.J., James, T.W., & James, K.H. (2014). Multisensory convergence of visual and haptic object preference across development. *Neuropsychologia*, *56*, 381–392.
- Jeannerod, M., Decety, J., & Michel, F. (1994). Impairment of grasping movements following a bilateral posterior parietal lesion. *Neuropsychologia*, *32*, 369–380.
- Kersey, A.J., Clark, T.S., Lussier, C.A., Mahon, B.Z., & Cantlon, J.F. (2016). Development of tool representations in the dorsal and ventral visual object processing pathways. *Cerebral Cortex*, *26*, 3135–3145.
- Kersey, A.J., & James, K.H. (2013). Brain activation patterns resulting from learning letter forms through active self-production and passive observation in young children. *Frontiers in Psychology*, *4*, 567.
- Kravitz, D.J., Saleem, K.S., Baker, C.I., & Mishkin, M. (2011). A new neural framework for visuospatial processing. *Nature Reviews Neuroscience*, *12*, 217–230.
- Króliczak, G., Cavina-Pratesi, C., Goodman, D.A., & Culham, J.C. (2007). What does the brain do when you fake it? An fMRI study of pantomimed and real grasping. *Journal of Neurophysiology*, *97*, 2410–2422.
- Kuhtz-Buschbeck, J.P., Boczek-Funcke, A., Illert, M., Jöhnk, K., & Stolze, H. (1999). Prehension movements and motor development in children. *Experimental Brain Research*, *128*, 65–68.
- Kuhtz-Buschbeck, J.P., Stolze, H., Boczek-Funcke, A., Jöhnk, K., Heinrichs, H., & Illert, M. (1998a). Kinematic analysis of prehension movements in children. *Behavioural Brain Research*, *93*, 131–141.
- Kuhtz-Buschbeck, J.P., Stolze, H., Jöhnk, K., Boczek-Funcke, A., & Illert, M. (1998b). Development of prehension movements in children: A kinematic study. *Experimental Brain Research*, *122*, 424–432.
- Malfait, N., Valyear, K.F., Culham, J.C., Anton, J.-L., Brown, L.E., & Gribble, P.L. (2010). fMRI activation during observation of others' reach errors. *Journal of Cognitive Neuroscience*, *22*, 1493–1503.
- Mareschal, D., & Johnson, M.H. (2003). The 'what' and 'where' of object representations in infancy. *Cognition*, *88*, 259–276.
- Merigan, W., & Maunsell, J. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369–402.
- Miceli, G., Fouch, E., Capasso, R., Shelton, J.R., Tomaiuolo, F., & Caramazza, A. (2001). The dissociation of color from form and function knowledge. *Nature Neuroscience*, *4*, 662–667.
- Milner, A.D., & Goodale, M.A. (1995). *The visual brain in action*. New York: Oxford University Press.
- Olivier, I., Hay, L., Bard, C., & Fleury, M. (2007). Age-related differences in the reaching and grasping coordination in children: Unimanual and bimanual tasks. *Experimental Brain Research*, *179*, 17–27.
- Perenin, M.T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain*, *111*, 643–674.
- Pisella, L., Binkofski, F., Lasek, K., Toni, I., & Rossetti, Y. (2006). No double-dissociation between optic ataxia and visual agnosia: Multiple sub-streams for multiple visuo-manual integrations. *Neuropsychologia*, *44*, 2734–2748.
- Rammani, N. (2006). The primate cortico-cerebellar system: anatomy and function. *Nature Reviews Neuroscience*, *7*, 511–522.

- Rogers, T.T., Hocking, J., Mechelli, A., Patterson, K., & Price, C. (2005). Fusiform activation to animals is driven by the process, not the stimulus. *Journal of Cognitive Neuroscience*, *17*, 434–445.
- Satterthwaite, T.D., Wolf, D.H., Loughhead, J., Ruparel, K., Elliott, M.A., Hakonarson, H., ... & Gur, R.E. (2012). Impact of in-scanner head motion on multiple measures of functional connectivity: Relevance for studies of neurodevelopment in youth. *NeuroImage*, *60*, 623–632.
- Scherf, K.S., Behrmann, M., Humphreys, K., & Luna, B. (2007). Visual category-selectivity for faces, places and objects emerges along different developmental trajectories. *Developmental Science*, *10*, F15–F30.
- Schneiberg, S., Sveistrup, H., McFadyen, B., McKinley, P., & Levin, M.F. (2002). The development of coordination for reach-to-grasp movements in children. *Experimental Brain Research*, *146*, 142–154.
- Spelke, E.S., Vishton, P., & Von Hofsten, C. (1995). Object perception, object-directed action, and physical knowledge in infancy. In M.S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 165–179). Cambridge, MA: MIT Press.
- Street, S.Y., James, K.H., Jones, S.S., & Smith, L.B. (2011). Vision for action in toddlers: The posting task. *Child Development*, *82*, 2083–2094.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.
- Thach, T., Keating, G., Thach, W.T., Goodkin, H.P., & Keating, J.G. (1992). The cerebellum and the adaptive coordination of movement. *Annual Review of Neuroscience*, *15*, 403–442.
- Ungerleider, L.G., Doyon, J., & Karni, A. (2002). Imaging brain plasticity during motor skill learning. *Neurobiology of Learning and Memory*, *78*, 553–564.
- Ungerleider, L.G., & Mishkin, M. (1982). Two cortical visual systems. In D.J. Ingle, M.A. Goodale & R.J.W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.
- Van Dijk, K.R.A., Sabuncu, M.R., & Buckner, R.L. (2012). The influence of head motion on intrinsic functional connectivity MRI. *NeuroImage*, *59*, 431–438.
- Von Hofsten, C. (2007). Action in development. *Developmental Science*, *10*, 54–60.

SUPPORTING INFORMATION

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How to cite this article: James KH, Kersey AJ. Dorsal stream function in the young child: an fMRI investigation of visually guided action. *Dev Sci*. 2017;00:e12546. <https://doi.org/10.1111/desc.12546>