Developmental Science **WILEY**

Visual experiences during letter production contribute to the development of the neural systems supporting letter perception

Sophia Vinci-Booher | Karin H. James

Department of Psychological and Brain Sciences, Indiana University, Bloomington, IN, USA

Correspondence
Karin H. James, 1101 E. 10th St., Bloomington, IN 47405, USA.
Email: khjames@indiana.edu

Abstract

Letter production through handwriting creates visual experiences that may be important for the development of visual letter perception. We sought to better understand the neural responses to different visual percepts created during handwriting at different levels of experience. Three groups of participants, younger children, older children, and adults, ranging in age from 4.5 to 22 years old, were presented with dynamic and static presentations of their own handwritten letters, static presentations of an age-matched control's handwritten letters, and typeface letters during fMRI. First, data from each group were analyzed through a series of contrasts designed to highlight neural systems that were most sensitive to each visual experience in each age group. We found that younger children recruited ventral-temporal cortex during perception and this response was associated with the variability present in handwritten forms. Older children and adults also recruited ventral-temporal cortex; this response, however, was significant for typed letter forms but not variability. The adult response to typed letters was more distributed than in the children, including ventral-temporal, parietal, and frontal motor cortices. The adult response was also significant for one's own handwritten letters in left parietal cortex. Second, we compared responses among age groups. Compared to older children, younger children demonstrated a greater fusiform response associated with handwritten form variability. When compared to adults, younger children demonstrated a greater response to this variability in left parietal cortex. Our results suggest that the visual perception of the variability present in handwritten forms that occurs during handwriting may contribute to developmental changes in the neural systems that support letter perception.

KEYWORDS
development, fMRI, handwriting, letter perception, letter production, literacy

1 | INTRODUCTION

Experience producing letters through handwriting increases activation during letter perception relative to other letter learning experiences (e.g. typing; James & Atwood, 2009; James & Engelhardt, 2012; Kersey & James, 2013). It is not known, however, why handwriting has this effect on the neural response during visual processing. One possibility is that performing the motor movements of letter production may establish neural representations that influence

subsequent visual processing (James & Atwood, 2009; Kersey & James, 2013; Longcamp, Anton, Roth, & Velay, 2003). Another possibility, and the focus of this work, is that the visual experiences with letters created by those motor movements may establish neural representations that influence subsequent visual processing.

The visual experiences with letters created during handwriting can be broken down in at least three ways. First, as a letter is produced, children experience a letter unfolding in time, stroke-by-stroke (dynamic unfolding). Second, children experience the final product as a static handwritten letter that varies from one instance to the next, thereby exposing their visual system to category variability (variability of letter form). Third, the static handwritten letter was written by their own motor system and may, therefore, contain cues for motion that are specific to the person who produced it (ownership). The neural response to each of these visual inputs may be an important part of why it is that handwriting leads to increases in activation during letter perception relative to other letter learning activities. Typing, for instance, does not generate these three visual inputs and is not as effective at increasing activation during letter perception as handwriting (James & Atwood, 2009; James & Engelhardt, 2012; Kersey & James, 2013).

As a first step in understanding what causal relationship might exist between the visual experiences with letters that occur during handwriting and the development of neural representation for letters, we characterized the neural responses to the different visual experiences with letters that are created during handwriting in children and adults. Our rationale was that the degree to which cortical areas responded to each visual experience could be related to the sensitivity of those cortical regions to the particular visual experience being tested. We expected that sensitivity to each of the visual experiences might change as an individual gains experience with letters. There are currently no studies that have directly investigated the neural responses to the aforementioned visual experiences in children. We will, therefore, provide some background information on behavioral work in children that suggests that these visual experiences are important for the development of letter perception. We will also discuss neuroimaging work in adults that provides some indication that these visual experiences continue to be an important part of the neural representation for letters in adulthood.

1.1 | Dynamic unfolding

Children are typically taught to produce letters with particular stroke orders—top to bottom and left to right (i.e. for an 'R' they are first asked to produce the vertical line, then the curve, and then the diagonal line), leading to the perception of a letter that unfolds over time, stroke by stroke, and in the same stroke order each time. Experience producing letters in standard stroke orders gives children knowledge concerning how the form is typically produced. These stroke orders may become integrated into the representation of a letter and, in turn, influence letter perceptual processing. Such a suggestion is in

Research Highlights

- Adult-like letter processing emerges earlier in ventral-temporal cortex than in parietal and frontal motor regions.
- The perception of handwritten forms that occurs during letter production may contribute to the development of ventral-temporal letter processing.
- The motor experience of letter production may contribute to the development of parietal-frontal letter processing.
- The development of ventral-temporal and parietal-frontal systems for letter perception may be supported by different components of letter production.

line with several works that demonstrated that knowledge of how an object typically moves is influential in perceptual judgments (Babcock & Freyd, 1988; Freyd, 1983a, 1983b, 1985; Freyd & Finke, 1984; Orliaguet, Kandel, & Boe, 1997). Stroke orders are, essentially, knowledge concerning how a letter typically moves. While we know of no work that has looked for stroke-order effects during symbol perception in young children, there are two recent works focusing on these effects in adults.

Two recent studies have demonstrated stroke-order effects during symbol recognition—better recognition for symbols unfolding stroke-by-stroke than letters presented in static, typed form. Recognition benefits from stroke-by-stroke unfolding are, importantly, strongest for stroke orders with which the observer has experience. In healthy adults trained on novel symbols, recognition for the trained symbols was faster and more accurate when symbols were presented unfolding in learned compared to unlearned stroke orders (Vinci-Booher, Sehgal, & James, 2018). An adult with an acquired, selective impairment in letter identification demonstrated higher recognition rates for letters that were presented dynamically unfolding compared to letters presented in static, typed form (Schubert, Reilhac, & McCloskey, 2018). The patient's improvements were greater for letters presented in a standard stroke order relative to a non-standard order (Schubert et al., 2018). Both studies suggest that dynamic information about the typical 'movement' of a letter is a part of letter representation and that it influences letter perceptual processing in adults.

The case study provides additional information regarding the neural correlates of stroke-order effects on visual recognition. The patient had suffered a lesion to left ventral-temporal cortex, an area that has traditionally been associated with letter and word perception (Cohen et al., 2000; Dehaene, Le Clec'H, Poline, Le Bihan, & Cohen, 2002; James, James, Jobard, Wong, & Gauthier, 2005). The neural correlates of stroke-order effects are, therefore, not likely to rely upon letter- and word-selective regions in ventral-temporal cortex. Indeed, the authors of the case study suggest that the observed stroke-order effects may have been accomplished by the influence

of motor plans in premotor cortex and, perhaps, mediated through visual motion processing regions in parietal cortex (Schubert et al., 2018). The patient's motor and parietal cortices were intact, and the patient demonstrated no impairment in letter production. We would, therefore, expect that motor and/or visual-motion-related regions in parietal cortex might underlie these stroke-order effects.

1.2 | Variability of letterform

Children will experience both visual and motor variability during production. There is evidence to suggest that experiencing visual variability may be more important for letter recognition than experiencing the motor variability, however. Li and James (2016) directly addressed the contribution of motor and visual experiences with symbols to the development of symbol categorization abilities. Five-year-old children learned novel Greek symbols through training activities that differed in terms of the motor and visual experiences with the symbols. Children who were exposed to visually variable exemplars of each Greek symbol category during training (e.g. visual study of a handwritten symbol produced by themselves or by another child or typed symbols presented in different fonts) were better able to categorize the symbols than children who were not exposed to visual variability. There were, importantly, no differences between motor and non-motor conditions or between handwritten and variable typed fonts, indicating that the gains in categorization after handwriting maybe driven by visual experience with variability of the symbols' forms.

We are aware of no neuroimaging work that has directly addressed how exposure to visual variability may lead to changes in brain function during perception. We are aware of one study, however, that suggests that a sensitivity to variability might precede the establishment of category representations (Emberson, Cannon, Palmeri, Richards, & Aslin, 2017). Emberson et al. (2017) used fNIRS to assess the presence of repetition suppression effects in infants. Although their focus was not on variability, specifically, they report that neural activity in occipital cortex was above baseline when infants were visually presented with different category exemplars, but not when they were repetitively presented with the same exemplar. The same infants did not demonstrate neural adaptation in occipital cortex, suggesting that the infants did not yet have adult-like neural representation for the categories tested (i.e. faces and fruits). This study suggests that sensitivity to visual variability in occipital cortex may occur before the establishment of adult-like category representation.

Although Emberson et al. (2017) were unable to measure activation in ventral-temporal cortex, it is likely that similar developmental processes occur in ventral-temporal cortex as in occipital cortex. Ventral-temporal cortex is a region that is broadly associated with categorization processes for letters (Dufor & Rapp, 2013; James et al., 2005; Rothlein & Rapp, 2014) and objects (for review, see Grill-Spector & Weiner, 2014), and it has also been shown to be more responsive to handwritten than typed letters in adults (Gauthier et al.,

2000; Vinci-Booher, Cheng, & James, 2019). Category-selective regions in ventral-temporal cortex exhibit reliable repetition suppression effects in adults (Grill-Spector, Henson, & Martin, 2006). There are many ideas about how these category-selective responses develop (Dehaene & Cohen, 2007; Gauthier, 2000; Ishai, Ungerleider, Martin, Schouten, & , 1999; Kanwisher, 2000; Saygin et al., 2016). We offer the idea, here, that experience with category variability might contribute in some way to this developmental trajectory, at least for symbols. We would expect that sensitivity to visual variability in ventral-temporal cortex may also occur before the establishment of category representation.

1.3 | Ownership

Letters produced by one's self are likely processed differently than letters produced by another, provided the owner has had enough experience with their own handwriting. Adults can readily distinguish their own handwritten letter trajectories from those of another (Knoblich & Prinz, 2001; Knoblich, Seigerschmidt, Flach, & Prinz, 2002) as can 10-year-old children (Mattaloni, 2013). Eight-year-old children, however, do not demonstrate this ownership effect, suggesting that a certain level of experience with one's own handwritten forms is important for sensitivity to one's own letters compared to another's letters.

Ownership effects may be most strongly related to the motor experiences with letters that are created during handwriting and not the visual experience alone. Adults make accurate ownership judgments for symbols that were learned by producing them without visual feedback (i.e. with their hand, pen, and paper occluded), suggesting that the motor experience alone is sufficient for an ownership effect (Knoblich & Prinz, 2001). Neuroimaging work also supports the notion that motor experience underlies ownership effects for symbol recognition. Fronto-parietal systems, often associated with motor execution and guidance, were more active when adults viewed their own handwritten symbol unfold as if it were being written compared to viewing another's symbol unfold (Mattaloni, 2013). Differences in neural processing between handwritten letters produced by one's self and letters produced by another were also apparent when the handwritten letters were presented in static, non-dynamic form (Sawada, Doi, & Masataka, 2016). Based on these results, we would expect to see differences in the neural response when viewing one's own versus another's handwritten forms in fronto-parietal motor systems. We would expect, further, that this response would be most apparent in adults who have a long history of experience with their own handwriting.

1.4 | Present study

The purpose of this study was to better understand the differences in the neural systems that respond to the visual experiences created during letter production among children in the very early

stages of learning about letters, children in later stages, and in literate adults. We focused specifically on the visual experiences encountered during letter production discussed above—dynamic unfolding, variability, and ownership—and how responses to those aspects of letter production might differ at different levels of experience.

We presented all participants with different presentations of letters designed to characterize the different visual experiences that result from letter production. We also presented participants with stereotypical typed letters to identify the neural system that supports typical letter perception, as in prior work (James, 2010; James & Atwood, 2009; James & Engelhardt, 2012; James & Gauthier, 2006; Kersey & James, 2013; Longcamp et al., 2003). Our analyses identified differences within and between groups in the neural response to the different visual experiences that result from letter production. Our rationale was that between-group differences in activation associated with each visual experience would be related to between-group differences in the sensitivity of cortical regions to the particular visual experience being tested.

Our predictions were focused, first, on the developmental trajectory of sensitivity to these visual experiences and, second, on the brain region that demonstrated sensitivity. We expected that sensitivity to dynamic unfolding and to ownership would be more evident in the adults than in either child group because adults have a long history of experience with symbols' typical movement trajectory and, more specifically, with one's own movement cues in those trajectories. We expected that sensitivity to variability, on the other hand, would be more evident in the youngest children than either the older children or adults because the youngest children would still be learning letter categories. Regarding the brain regions most involved in processing these visual experiences, we expected that dynamic unfolding would activate motor and/or visual motion processing systems, as suggested by Schubert et al. (2018), that variability of letterform would activate occipital and ventral-temporal cortices, as suggested by Emberson et al. (2017) and prior work in category-selective repetition suppression in adults (Grill-Spector et al., 2006), and that ownership would activate fronto-parietal cortices, as suggested by Mattaloni (2013).

2 | MATERIALS & METHODS

2.1 | Participants

Children (4.5–8.5 years, n = 41) were recruited through an in-house database of parents in the local community and through word-of-mouth. Parents provided written informed consent and were compensated with a gift card. Children who were 7 years or older provided written informed assent. All children were compensated with a small toy or gift card. Adult participants (21–25 years, n = 15) were recruited through an in-house database and through word-of-mouth. Adult participants provided written informed consent and were compensated with a gift card. All participants were screened

FIGURE 1 Experimental setup. Adults and children used the same apparatus and special care was taken to ensure the comfort of the participants. The MRItab, arm pillow, and Wheaton® elastic shoulder immobilizer were adjusted for each participant. Subject-specific adjustments ensured that the participants were in a comfortable writing position and could see the screen of the MRItab

for neurological trauma, developmental disorders, and MRI contraindications. All participants were right-handed with English as their native language.

Four children were excluded due to difficulty following instructions and/or technical problems with the functioning of the tablet (e.g. cable attachment was damaged). Data from one child were lost in a technical error from the MRI facility. Four adults and nine children were excluded due to an unacceptable amount of motion during the MRI scanning procedure (see Neuroimaging Preprocessing). We, therefore, obtained useable fMRI data from 11 adults and 27 children. The 14 youngest children (M = 5.5 years, SD = 0.5 years) were assigned to the younger age group and the 13 oldest children (M = 7.6 years, SD = 0.5 years) were assigned to the older age group.

2.2 | Design

Participants were presented with letters in four different formats during fMRI scanning in a blocked design: Watch Typed Letter, Watch Handwritten Other, Watch Handwritten Own, and Watch Dynamic Own (see Figure 2). During the Watch Typed Letter condition, participants passively viewed letters presented on the tablet, one letter at a time. During the Watch Handwritten Other condition, participants passively viewed letters handwritten by an age-matched control on the tablet, one letter at a time. During the Watch Handwritten Own condition, participants passively viewed letters handwritten by themselves within the same experimental session. During the Watch Dynamic Own condition, participants passively
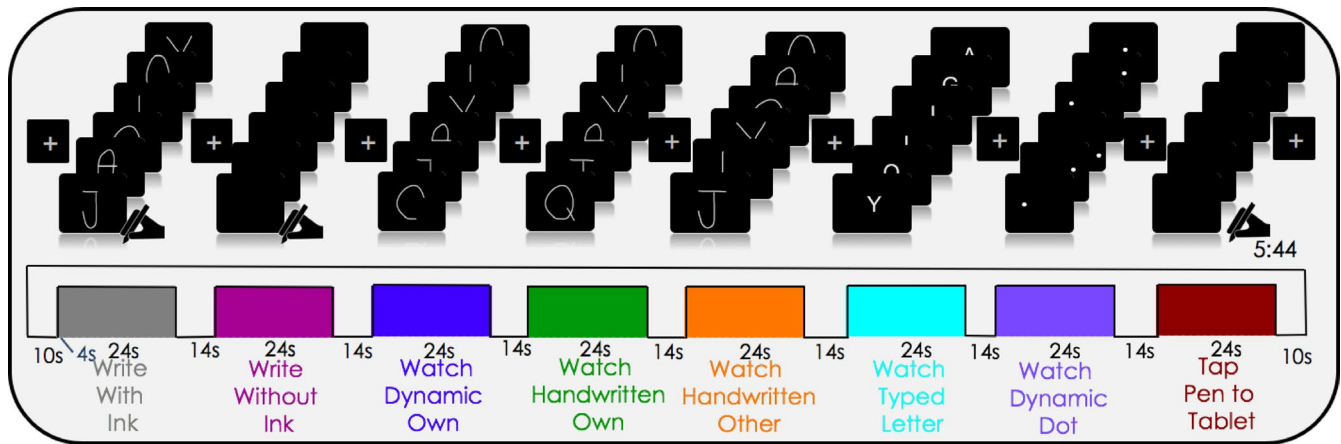
FIGURE 2 Stimulation protocol during fMRI scanning. The figure presents a depiction of the blocks within each run and the trials within each block. Block orders were pseudo-randomized and counter-balanced across runs. The six letters used for each condition within a run were the same set of six letters. Letter orders within a block were randomized. Block instructions and letter names were pre-recorded. Block instructions were played at the beginning of each block to alert participants to the task. Letter names were played at the beginning of each trial to alert the participant to the letter that they should write or to the letter that would be displayed

viewed letters handwritten by themselves within the same experimental session unfolding just as it had done when they had produced it. There were an additional four blocks in each run that contained trials for conditions that focused on the motor aspects of production. These four conditions were not the focus of the present study and were, therefore, not analyzed.

2.3 | Materials and stimuli

2.3.1 | Apparatus

All stimuli were recorded and presented using the MRItab as displayed in Figure 1 (for a full description, see Vinci-Booher, Sturgeon, James, & James, 2018). Auditory instructions and letter prompts were presented through MR-safe headphones. Boom™ was used to enhance audio clarity. An in-house Matlab program using the Psychophysics Toolbox extensions interfaced with the MRItab and MRI-compatible headphones to record and present all stimuli (Brainard, 1997; Pelli, 1997). A Wheaton® elastic shoulder immobilizer and inflatable head immobilization padding were used to restrict motion.

2.3.2 | Stimuli

All stimuli were presented in white on a black background. A box that subtended 10 by 10 degrees of visual angle was displayed on the tablet at all times. A singular dot was presented in the center of the screen during the initial and final fixations. Stimuli presented within the box changed according to condition.

A set of 12 single upper-case letters of the Roman alphabet were selected: A, B, C, D, G, H, J, L, Q, R, U, and Y. Typed letters were always presented in 120-point Arial font and subtended 4 by

4 degrees of visual angle. Stimuli for the Watch Handwritten Other condition were recorded from age-matched controls. Stimuli in the Watch conditions were previously recorded (within the same experimental session) productions of their own handwritten forms. In the Watch Dynamic Own condition, participants viewed their own previously recorded production of their letter unfolding in real time. In the Watch Handwritten Own condition, participants viewed the final, static handwritten letter that they produced.

Each block contained six letters. The six letters for each block were selected randomly from the full stimulus set at the beginning of each run, with the restriction that a particular set may not contain letter names that are easily confused (Conrad, 1964; Hull, 1973). Note that in the Watch Handwritten Own and Watch Dynamic Own conditions, participants viewed their own handwritten productions—recorded on the MRItab just before the scanning session. The six letters used for these blocks were necessarily the same set of six letters. For this reason, the same set of six letters was also displayed in the Watch Handwritten Other and Watch Typed Letter conditions.

In all conditions, block instructions and letter names were pre-recorded from a female native English speaker and played at the beginning of each block and trial, respectively. For the conditions of interest in this study, the block instruction was always 'Watch'.

2.4 | Procedure

2.4.1 | Children

After the consenting process was completed, children were first asked to write the 12 single upper-case letters of the Roman alphabet to dictation using the MRItab. This step was necessary for the collection of handwriting samples and in familiarizing with the MRItab. It also served as an additional screening criterion. Only

children who produced a form to dictation within 4 s for at least 10 of the 12 letters were permitted to continue in the study. We did not require that their production was accurate or legible.

After a short movie in the MRI simulator, children performed an abbreviated version of the stimulation protocol also in the simulator (see Figure 2). If they made an error of any sort (e.g. tracing the statically presented letters instead of watching them), they received feedback and were asked to try again. Once it was apparent that they understood their tasks and if they appeared comfortable in the MRI simulator, they continued to the actual MRI environment.

During the initial anatomical scan, children were allowed to watch a movie, listen to an audio book, or simply rest. Following the anatomical scan, each functional run contained a complete set of experimental conditions: four perceiving blocks and four motor blocks (see Figure 2) and lasted 344 s (5:44 min). The present study focuses on the four perceiving blocks. We acquired up to four functional runs, depending on the comfort and compliance of the participant. A trained research assistant remained in the MRI room with the child during all runs to help them remain still and to ensure that they paid attention to the tasks. A second trained research assistant observed through a video camera placed just outside the bore of the MRI to ensure that children were paying attention to the task.

Block orders were pseudo-randomized and counter-balanced across participants. Each block within the functional runs contained six 4-s trials. Blocks were separated by 14-s inter-block intervals, the last 2 s of which were auditory instructions for the following block. Initial fixation and final fixation times were 20 s and 10 s, respectively. Before each block, auditory instructions alerted the participant as to what would be expected of them throughout the next block. At the start of each trial, participants heard one letter name before they were visually presented with the letter. The letter name was provided as a prompt for the motor conditions and was, therefore, also provided for the visual conditions in order to control for the auditory input.

2.4.2 | Adults

The neuroimaging procedure for adults was the same as the procedure for children, except that adults were not required to undergo training in the MRI simulator. Adult participants were still required to write the 12 upper-case letters of the Roman alphabet one at a time to dictation using the MRItab outside of the MRI environment before they began the imaging session. The stimulation protocol for the imaging session for adults was the same as the stimulation protocol for children.

2.4.3 | Scanning parameters

Neuroimaging was performed at the Indiana University Imaging Research Facility, housed within the Department of Psychological and Brain Sciences with a Siemens Magnetom Prisma 3-T whole-body MRI system. High-resolution T1-weighted anatomical volumes were acquired using a MPRAGE sequence: TI = 900 ms, TE = 2.98 ms, TR = 2,300 ms, flip angle = 9°, with 176 sagittal slices of 1.0 mm thickness, a field of view of 256 × 248 mm, and an isometric voxel size of 1.0 mm^3. For functional images, the field of view was 220 × 220 mm, with an in-plane resolution of 110 × 110 pixels and 72 axial slices of 2.0 mm thickness per volume with 0% slice gap, producing an isometric voxel size of 2.0 mm^3. Functional images were acquired using a gradient echo EPI sequence with interleaved slice order: TE = 30 ms, TR = 1,000 ms, flip angle = 52° for blood-oxygen-level-dependent (BOLD) imaging.

2.4.4 | Behavioral procedure

Behavioral scores were collected at a second session to determine group differences in literacy, visual-motor, and/or fine-motor skills. The behavioral session consisted of a battery of standard assessments designed to assess visual-motor integration (Beery VMI: green, blue, and brown), fine motor skill (Grooved Pegboard), and literacy level (WJ-IV Achievement: Letter-Word Identification, Spelling, Word Attack, Spelling of Sounds). Children and adults completed the same battery of assessments. A composite score quantified the abilities of each participant on these three criteria. Group means and standard errors for the behavioral measures and composite scores are reported in Table 1.

2.5 | Analyses

All neuroimaging analyses were conducted using Brain Voyager QX, Version 2.8 (Brain Innovation).

2.5.1 | Neuroimaging preprocessing

Preprocessing of functional data included slice scan time correction, 3D motion correction using trilinear/sinc interpolation, and 3D Gaussian spatial blurring with a full-width-at-half-maximum of 6 mm. Temporal high-pass filtering was performed using a voxel-wise general linear model (GLM) with predictors that included a Fourier basis set with a cutoff value of 2 sine/cosine pairs and a linear trend predictor. To account for head motion, rigid body transformation parameters were included in the design matrix as predictors of no interest (Bullmore et al., 1999; Weissenbacher et al., 2009) along with spike regressors for each time point at which the relative root mean squared (RMS) time course exceeded 2.0 mm (Satterthwaite et al., 2013; Van Dijk, Sabuncu, & Buckner, 2012). Entire runs were removed from the analysis if the number of spike regressors in that run was greater than or equal to 7 and/or if visual inspection of the rigid body motion parameters indicated a large amount of non-spiking motion in at least one parameter. This resulted in the removal of 22 runs from the younger children, 23 runs from the older children,

TABLE 1 Descriptive statistics

	Group		
	Younger children (*n* = 14)	Older children (*n* = 13)	Adults (*n* = 11)
	M (SD)	*M (SD)*	*M (SD)*
Age (months)	65.5 (5.6)	92.1 (5.6)	242.9 (11.9)
Woodcock Johnson IV			
Letter Word Identification	21.7 (13.9)	50.3 (16.9)	70.8 (3.6)
Spelling	9.6 (2.5)	23.8 (9.0)	47.1 (4.4)
Word Attack	9.5 (4.7)	21.5 (5.2)	27.8 (2.8)
Spelling of Sounds	6.1 (2.9)	15.6 (4.3)	25.4 (2.4)
Beery			
VMI	15.2 (1.6)	20.5 (2.8)	27.6 (2.2)
Visual perception	18.8 (3.7)	22.3 (3.0)	27.7 (2.2)
Motor coordination	14.5 (2.6)	19.5 (4.4)	25.4 (3.1)
Grooved Pegboard			
Right	45.5 (2.6)	36.5 (12.5)	58.3 (7.5)
Left	54.0 (10.1)	37.2 (9.3)	64.4 (7.7)
Composite scores			
Literacy	11.8 (6.0)	26.7 (8.9)	42.7 (2.6)
Visual motor	16.2 (1.4)	20.7 (2.5)	27.0 (2.0)
Fine motor	4.1 (0.6)	5.7 (1.1)	8.2 (0.9)

Note: Behavioral testing occurred within 3 weeks of the neuroimaging session. Grooved Pegboard is reported in seconds to completion. All others are reported in number of correct items. The literacy composite score was calculated by averaging the raw score on the Woodcock Johnson IV Letter–Word Identification, WJ-IV Spelling, WJ-IV Word Attack, and WJ-IV Spelling of Sounds. The visual-motor composite score was calculated by averaging the raw score on the Beery VMI, Beery VP, and Beery MC. The fine motor skill composite score was calculated by averaging the time taken on the Grooved Pegboard for both hands, dividing by the number of rows completed (i.e. the children only complete two rows, whereas the adults complete five rows), taking the inverse to make higher scores correspond to higher skill, and, finally, multiplying by one hundred to scale the score. One younger child and one adult did not complete the Fine Motor tasks. The Right and Left Grooved Pegboard and Fine Motor Composites are, therefore, calculated from 13 younger children, 13 older children, and 10 adults.

and 12 runs from adults. All runs were removed for four younger children, five older children, and four adults, effectively removing these participants from the analysis. Individual anatomical volumes were normalized to Talairach space (Talairach & Tournoux, 1988). Coregistration of functional volumes to anatomical volumes was performed using a rigid body transformation.

2.5.2 | Analyses

The statistical analyses began with a voxel-wise GLM with one predictor of interest for each condition and seven predictors of no interest that were included for motion correction purposes only. Each predictor of interest was convolved with a double-gamma hemodynamic response function (Boynton, Engel, Glover, & Heeger, 1996). The resulting design matrix was subjected to a random-effects GLM analysis for planned contrasts.

We performed several whole-brain contrasts *within* each participant group to observe activation associated with the different visual experiences associated with letter production. Comparing Watch Dynamic Own with Watch Handwritten Own revealed areas associated with seeing a form unfold over time, a contrast that we will refer to as the *dynamic unfolding* contrast; comparing Watch Handwritten Own with Watch Handwritten Other revealed areas associated with the perception of one's own handwritten form, the *ownership* contrast; comparing Watch Handwritten Other to Watch Typed Letter revealed areas associated with variability in letter form, the *variability of letterform* contrast; contrasting Watch Typed Letter with fixation revealed areas associated with the perception of typed letters, the *typed letter* contrast. The resulting t-maps were subjected to a voxel-wise threshold of $p_{voxel} < .01$ with a cluster threshold of 60 contiguous 2-mm isotropic voxels.

We then investigated the interaction between the conditions and the groups by comparing the contrast maps among groups. For

each contrast map, we performed a one-way ANOVA at the whole-brain level. The analysis proceeded in a voxel-wise fashion, with one model for each voxel that included one between-participant factor, GROUP, with three levels: younger children, older children, and adults. The dependent variable was the voxel's *t* value for the contrast of interest. We followed each whole-brain ANOVA with post hoc between-group comparisons that were also performed at the whole-brain level. Resulting statistical maps for the overall ANOVA and post hocs were subjected to a corrected voxel-wise threshold of $p_{vox} < .001$ with a cluster threshold of six contiguous 2-mm isotropic voxels. We applied a more conservative threshold for the between-groups contrasts than for the within-groups contrasts because the threshold used for within-groups contrasts led to significant results in nearly every part of the brain, making inference at the relatively liberal threshold used for within-groups contrasts impossible.

3 | RESULTS

3.1 | Typed letters

We compared activation during the perception of typed letters to activation during fixation to identify the entire letter processing system, as has been performed in prior work (James & Atwood, 2009; Longcamp et al., 2003; Longcamp, Hluschchuck, & Hari, 2011). We found no significant responses during passive typed letter perception in the younger children (Table 2). Both literate groups, older children and adults, demonstrated a response to typed letters (Tables 4 and 5; Figure 3).

Older children recruited three major clusters, all within ventral-temporal cortex (Table 3). Two clusters covered regions of cortex often referred to as the lateral occipital complex (LOC) (Grill-Spector

et al., 1999) and the third cluster was located in the left fusiform gyrus, anterior to the left LOC response. Adults recruited four major clusters during letter perception (Table 4; Figure 3). The first and second clusters covered posterior portions of lateral temporal lobe and lateral occipital cortex, including LOC, and extended down into the fusiform gyrus in the left, and right hemispheres, respectively. The third cluster included left ventral premotor cortex, including posterior middle frontal gyrus and posterior inferior frontal gyrus. The fourth cluster included left intraparietal sulcus. These results are consistent with a large number of prior works that demonstrate a similar ventral-temporal response during passive letter perception in children with handwriting experience (James, 2010; James & Engelhardt, 2012; Kersey & James, 2013) and ventral-temporal and motor responses in adults (James & Atwood, 2009; James & Gauthier, 2006; Longcamp et al., 2003, 2008; Longcamp, Tanskanen, & Hari, 2006; Longcamp, Zerbato-Poudou, & Velay, 2005).

The between-group whole-brain contrasts indicated significant differences among groups during the perception of typed letters in the left inferior frontal gyrus, left dorsal precentral gyrus, left posterior intraparietal sulcus, left fusiform gyrus, right fusiform gyrus, right occipital cortex, and an anterior portion of the right superior parietal lobe (Table 5; Figure 5). Post hoc between-group comparisons revealed that the left fusiform gyrus response was greater in the older children than in the younger children, consistent with prior work indicating that the onset of a left fusiform response during letter perception is related to developmental changes in letter recognition ability and experience with handwriting (James, 2010; James & Engelhardt, 2012; Kersey & James, 2013) (Table 5; Figure 5). The right dorsal postcentral gyrus was also more responsive in the older children than in the younger children during typed letter perception (Table 5). Post hoc comparisons also revealed several responses that were greater in the adults than in the younger children, including the left inferior frontal gyrus, left dorsal precentral gyrus, left posterior intraparietal sulcus, and the right

TABLE 2 Whole-brain contrasts within groups: younger children

| Contrast | No. of clusters | Cluster size (voxels) | Talairach Coordinates | | | Peak T | Anatomical location |
			Peak x	Peak y	Peak z		
Watch Dynamic Own > Watch Handwritten Own	1	3,463	12	−76	37	4.87	Right precuneus
Watch Handwritten Own > Watch Handwritten Other	0	—	—	—	—	—	—
Watch Handwritten Other > Watch Typed Letter	3	31,789	30	−70	10	8.16	Right posterior cingulate cortex
			12	−91	−2	6.69	Right lingual gyrus
			−12	−67	16	5.77	Left posterior cingulate cortex
			39	−76	−5	5.72	Right inferior occipital gyrus
			−24	−73	−18	5.17	Left posterior fusiform gyrus
			42	−61	−14	4.73	Right posterior fusiform gyrus
		3,811	−27	−76	7	4.15	Left cuneus
		2,433	−42	−55	−41	5.23	Left cerebellum
Watch Typed Letter > Fixation	0	—	—	—	—	—	—

Note: Local peaks with a T-statistic greater than 4.0 are reported for large clusters that spanned several anatomical locations.
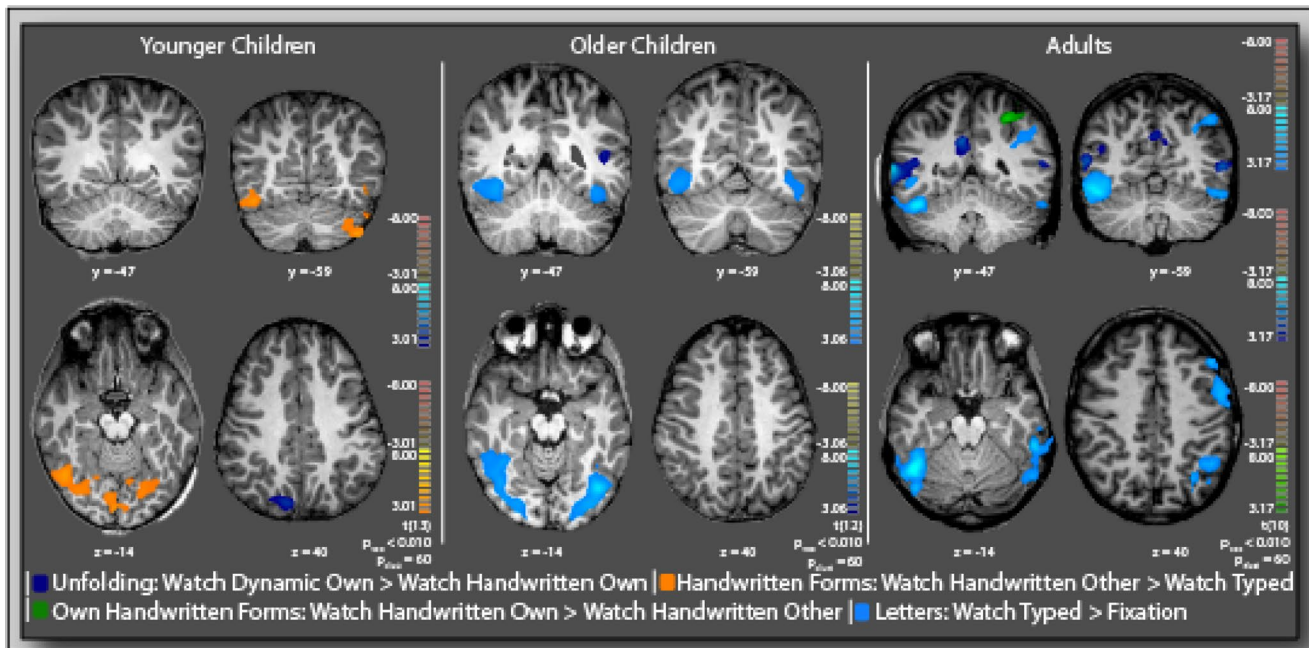
FIGURE 3 Results of whole-brain contrasts for each group. Results of all contrasts are presented on a representative participant's brain for each age group. The results of each contrast are displayed in different colors (see figure legend). Younger children (left) responded to variability in form (orange) and to the unfolding (dark blue) while demonstrating no significant response to the perception of typed letters (light blue). Older children (center) and adults (right) responded to typed letters and to the unfolding. Adults demonstrated an additional response to the perception of one's own handwritten forms (green). Talairach coordinates for each slice are displayed. Results are presented a $p_{vox} < .01$ with a cluster threshold of 60 contiguous 2-mm isotropic voxels

TABLE 3 Whole-brain contrasts within groups: older children

Contrast	No. of clusters	Cluster size (voxels)	Talairach coordinates			Peak T	Anatomical location
			Peak x	Peak y	Peak z		
Watch Dynamic Own > Watch Handwritten Own	1	1,684	−42	−43	10	4.65	Left middle temporal gyrus
Watch Handwritten Own > Watch Handwritten Other	0	—	—	—	—	—	—
Watch Handwritten Other > Watch Typed Letter	0	—	—	—	—	—	—
Watch Typed Letter > Fixation	2	9,498	39	−64	−12	4.69	Right fusiform gyrus
		7,367	−42	−70	−13	7.0	Left fusiform gyrus

fusiform gyrus (Table 5; Figure 5). There were no significant differences between the adults and the older children.

3.2 | Handwritten letters

3.2.1 | Dynamic unfolding

We compared activation during the perception of one's own handwritten letter dynamically unfolding to activation during the perception of the static handwritten letter that they produced to identify regions that were sensitive to the dynamic unfolding of a letter. A response to dynamic unfolding was present in all groups (Tables 3–5; Figure 3). In the younger children, activity in the right precuneus

was associated with the perception of dynamic unfolding. In the older children, activity in the left temporal cortex was associated with the perception of the dynamic unfolding. Adults demonstrated a response to dynamic unfolding in bilateral temporal cortex, right posterior cingulate cortex, and left posterior middle frontal gyrus. The between-group whole-brain contrasts revealed no significant differences among groups (Table 4).

3.2.2 | Variability of letterform

We compared activation during the perception of letters written by an age-matched control to typed versions of those same letters to identify neural regions that were sensitive to the variability of

TABLE 4 Whole-brain contrasts within groups: adults

| Contrast | No. of clusters | Cluster size (voxels) | Talairach Coordinates | | | Peak T | Anatomical location |
			Peak x	Peak y	Peak z		
Watch Dynamic Own > Watch Handwriting Own	3	6,231	60	−46	10	8.02	Right middle temporal gyrus
		2,236	−51	−61	7	7.00	Left middle temporal gyrus
		1,718	6	−52	31	5.78	Right precuneus
Watch Handwritten Own > Watch Handwritten Other	1	2,030	−27	−46	49	6.90	Left precuneus, along intraparietal sulcus
Watch Handwritten Other > Watch Typed Letter	0	—	—	—	—	—	—
Watch Typed Letter > Fixation	4	12,189	45	−52	−16	9.72	Right fusiform gyrus
		5,068	−51	8	25	5.90	Left inferior frontal gyrus
			−51	−1	40	5.30	Left dorsal precentral gyrus
			−51	20	34	4.63	Left posterior middle frontal gyrus
		4,290	−54	−37	−17	6.81	Left fusiform gyrus
		3,332	−45	−55	43	6.04	Left inferior parietal lobe, along the intraparietal sulcus

Note: Local peaks with a T-statistic greater than 4.0 are reported for large clusters that spanned several anatomical locations.

letterforms that occurs during handwriting. Younger children demonstrated a response to variability of letterforms in bilateral ventral-temporal cortex (Table 2; Figure 3). Neither the older children nor the literate adults demonstrated a significant response (Tables 4 and 5).

The between-group whole-brain contrasts revealed a difference among groups in the left posterior fusiform gyrus and in the left intraparietal sulcus (Table 5; Figure 4). Post hoc between-group comparisons revealed that the response in the left posterior fusiform gyrus was greater in the younger children than in the older children. The left intraparietal sulcus response was greater in younger children than in adults. There were no significant differences between the adults and the older children.

3.2.3 | Ownership

We compared activation during the perception of one's own handwritten letters to activation during the perception of letters written by an age-matched control to identify neural regions that were sensitive to the perception of one's own handwritten forms. Neither the younger children nor the older children demonstrated a neural response associated with the perception of one's own handwritten forms (Tables 3 and 4). Literate adults, however, responded to the perception of one's own handwritten letters in left superior parietal cortex along the intraparietal sulcus (Table 4; Figure 3). The between-group whole-brain contrasts revealed no significant differences among groups (Table 5).

3.3 | Behavioral assessments

We performed three one-way ANOVAs with one between-participants factor, GROUP, that included three levels, younger children, older children, and literate adults, to confirm group differences in literacy and

to quantify any group differences in visual-motor and/or fine-motor skill. The one-way ANOVA for literacy confirmed group differences in literacy, $F(2, 35) = 69.845$, $p < .001$, and also indicated group differences in visual-motor ability, $F(2, 35) = 88.171$, $p < .001$, and fine motor skill, $F(2, 33) = 69.980$, $p < .001$. All post hoc independent samples t tests were significant, $p < .001$, Bonferonni-corrected. In all cases, the scores were greater for the literate adults than the older children and greater for the older children than the literate adults, indicating that the adults had more experience than the older children and that the older children had more experience than younger children in terms of literacy, visual-motor skill, and fine-motor skill.

4 | DISCUSSION

To better understand how the visual experiences produced during handwriting might affect neural activity in children in early and later stages of learning about letters and in adults, we characterized the neural responses associated with the perception of various letters. By exposing participants to the visual percepts that result from handwriting as well as typed letters, we have shown that different types of visual percepts of a single category—letters—recruit different neural systems and that these systems change with experience. Our results make two crucial contributions: (a) Adult-like letter processing emerges earlier in ventral-temporal cortex than in parietal and frontal motor regions and (b) The perception of variability of letterform that occurs during letter production may contribute to this developmental trajectory.

4.1 | Perception of typed letters

A large body of literature has reported letter-selective neural responses in ventral-temporal cortex with a focus on sensitivity to

TABLE 5 Results of whole-brain contrasts between groups

Statistical Map	No. of clusters	Post hoc comparison	Cluster size (voxels)	Peak x	Peak y	Peak z	Peak T	Anatomical location
				Talairach Coordinates				
Watch Dynamic Own > Watch Handwritten Own	0	—	—	—	—	—	—	—
Watch Handwritten Own > Watch Handwritten Other	0	—	—	—	—	—	—	—
Watch Handwritten Other > Watch Typed Letter	2	Younger Children > Older Children	612	−48	−67	−10	4.50	Left fusiform gyrus
		Younger Children > Adults	267	−39	−40	49	4.50	Left inferior parietal lobe, along intraparietal sulcus
Watch Typed Letter > Fixation	6	Adults > Younger Children	1,517	−45	11	13	4.81	Left inferior frontal gyrus
		Adults > Younger Children	288	−48	−7	46	4.81	Left dorsal precentral gyrus
		Adults > Younger Children	384	−32	−64	43	4.46	Left precuneus, along intraparietal sulcus
		Adults > Younger Children	910	48	−58	−9	4.66	Right fusiform gyrus
		Older Children > Younger Children	1,591	−39	−70	−11	4.90	Left fusiform gyrus
		Older Children > Younger Children	540	60	−22	46	5.09	Right dorsal postcentral gyrus

Note: Local peaks with a T-statistic greater than 4.0 are reported for large clusters that spanned several anatomical locations.

letters as an object category in the left fusiform gyrus (e.g. Cohen et al., 2000; Dehaene, Cohen, Sigman, & Vinckier, 2005; Dufor & Rapp, 2013; Flowers et al., 2004; Garrett et al., 2000; Gauthier et al., 2000; James et al., 2005; Rothlein & Rapp, 2014). Neural responses that are greater to letters than other similar objects have also been observed in the posterior parietal cortex, the dorsal and ventral motor cortex, and the middle frontal and inferior frontal gyri (James & Atwood, 2009; James & Gauthier, 2006; Longcamp et al., 2003). In the current study, adults recruited this well-known system during typed letter perception (James & Gauthier, 2006; Longcamp et al., 2014; Yuan & Brown, 2014). The older children recruited only the ventral-temporal portion of this neural system and the younger children showed no significant activation to typed letters compared with fixation. Directly comparing between groups revealed that the fusiform gyrus response was greater in the older children than in the younger children and, further, that responses that were greater in the literate adults compared to the younger children were predominately located within the dorsal motor system.

Our findings—that only adults recruited the full parietal-frontal system—suggest that an extensive amount of experience may be required for parietal-frontal regions to develop a response during letter perception. We have, nonetheless, found activation in these regions in young children during letter perception after a short amount of within-experiment handwriting training in prior studies (James & Engelhardt, 2012; Kersey & James, 2013). Although not empirically

tested yet, we would propose that the small amount of within-experiment training may result in a temporary, short-lived increase in the neural system that supports letter perception. For this response to become stable and permanent, however, more extensive experience would be required. That the dorsal visual processing stream takes extensive experience to develop a stable response is consistent with work that suggests a more prolonged trajectory for the functional development of the dorsal relative to the ventral visual stream (for review, see Stiles, Akshoomoff, & Haist, 2013).

4.2 | Perception of handwritten forms

4.2.1 | Dynamic unfolding

Our whole-brain contrasts revealed a bilateral response in temporal cortices as well as a response in right precuneus in the parietal cortex in adults during the perception of a letter dynamically unfolding as if it were being written relative to the final, static versions of those handwritten letters. The bilateral temporal response was near anatomical regions commonly associated motion perception, often referred to as MT/V5 (Tootell et al., 1995; Zeki et al., 1991). The right precuneus has also been associated with motion perception and more specifically with directing visual attention for tracking purposes (for review, see Cavanna & Trimble, 2006). Our whole-brain ANOVA found no
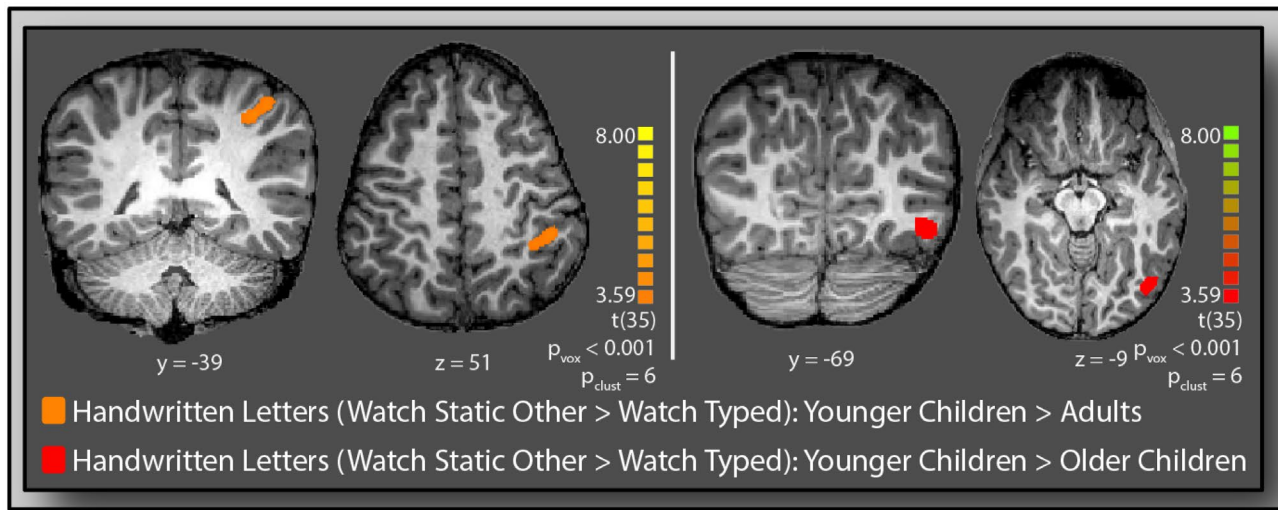
FIGURE 4 Group differences for the perception of handwritten forms. A whole-brain one-way repeated measures ANOVA revealed that activation in the left posterior fusiform gyrus and the left intraparietal sulcus differed among younger children, older children, and literate adults. Post hoc between-group comparisons at the whole-brain level indicated that the difference in the left intraparietal sulcus could be attributed to more sensitivity to variability in form in the younger children than in the literate adults (orange) and that the differences in the left posterior fusiform gyrus could be attributed to more sensitivity to variability in form in the younger children than in the older children (red). There were no differences between older children and literate adults. Talairach coordinates for each slice are displayed. Results are presented a $p_{vox} < .001$ with a cluster threshold of six contiguous 2-mm isotropic voxels

differences between groups for the dynamic unfolding contrast, suggesting that the responses in bilateral temporal cortices and right precuneus in the children were precursors to the adult response.

Prior works in adults have suggested that knowledge concerning how an object moves benefits recognition (Babcock & Freyd, 1988; Orliaguet et al., 1997) and that, in the specific case of letter recognition, seeing a letter unfold as it is normally experienced unfolding during handwriting facilitates recognition (Freyd, 1983b; Schubert et al., 2018). Schubert et al. (2018) demonstrated that the influence of this dynamic information does not depend upon ventral-temporal regions associated with object perception and suggested that it may be associated with either premotor or visual motion perception regions. Our results are consistent with those of Schubert et al. (2018) and add that the influence of dynamic information is likely mediated by motion perception regions (i.e. MT/V5), as opposed to premotor regions. Motion perception regions may participate in letter recognition by conveying information about an object's typical movement pattern, though additional research is needed to make such a claim, given the extensive work that indicates that MT/V5 responds to motion in a domain-general fashion (Tootell et al., 1995; Zeki et al., 1991; for review see Cavanna & Trimble, 2006), no indication of MT/V5 participation in letter recognition in non-clinical populations (James & Gauthier, 2006; Longcamp et al., 2003), and the absence of a similar effect for the same unfolding contrast in a prior study (Vinci-Booher et al., 2019).

4.2.2 | Variability of letterform

We suggest that the variability in form present in handwritten letters may be a particularly important part of handwriting in young

children who are still learning to produce and recognize letters. Our results demonstrate that the perception of handwritten letters, whether they were written by oneself or an age-matched control, affects the neural activity in the fusiform gyri more than typed letters during the early stages of letter learning. Only the younger children demonstrated this sensitivity to variability in form. When directly compared to older children and adults, younger children had significantly more activation in the left fusiform gyrus for variability.

Variability among instances of visual forms is a known driver of category learning (e.g. Perry, Samuelson, Malloy, & Schiffer, 2010; Twomey, Lush, Pearce, & Horst, 2014; Twomey, Ranson, & Horst, 2014). Compared to typeface letters, handwritten letters are variable in form—each production of a letter is different from the last—especially when produced by young children (Longstaff & Heath, 1997; Wing & Nimmo-Smith, 1987). Letter production may simply be a natural and effective way to present the perceptual system with variable category exemplars, as letter categorization improves similarly whether children learn symbols by handwriting or by visually perceiving the symbols presented in variable fonts (Li & James, 2016).

Our current hypothesis is that the visually variability in handwritten forms leads to the formation of broad category representation, allowing the nascent system to recognize many variable instances as belonging to the same category. This hypothesis receives support from noting that the same region within the left fusiform gyrus that demonstrated greater activity in the younger children for variability in form compared to the older children (Figure 4) also demonstrated greater activity in the older children for typed letters compared to the younger children (Figure 5). This cross-over from sensitivity to variability in the early stages of learning to sensitivity to a stereotypical letter in a later stage of learning suggests that the left fusiform gyrus may develop
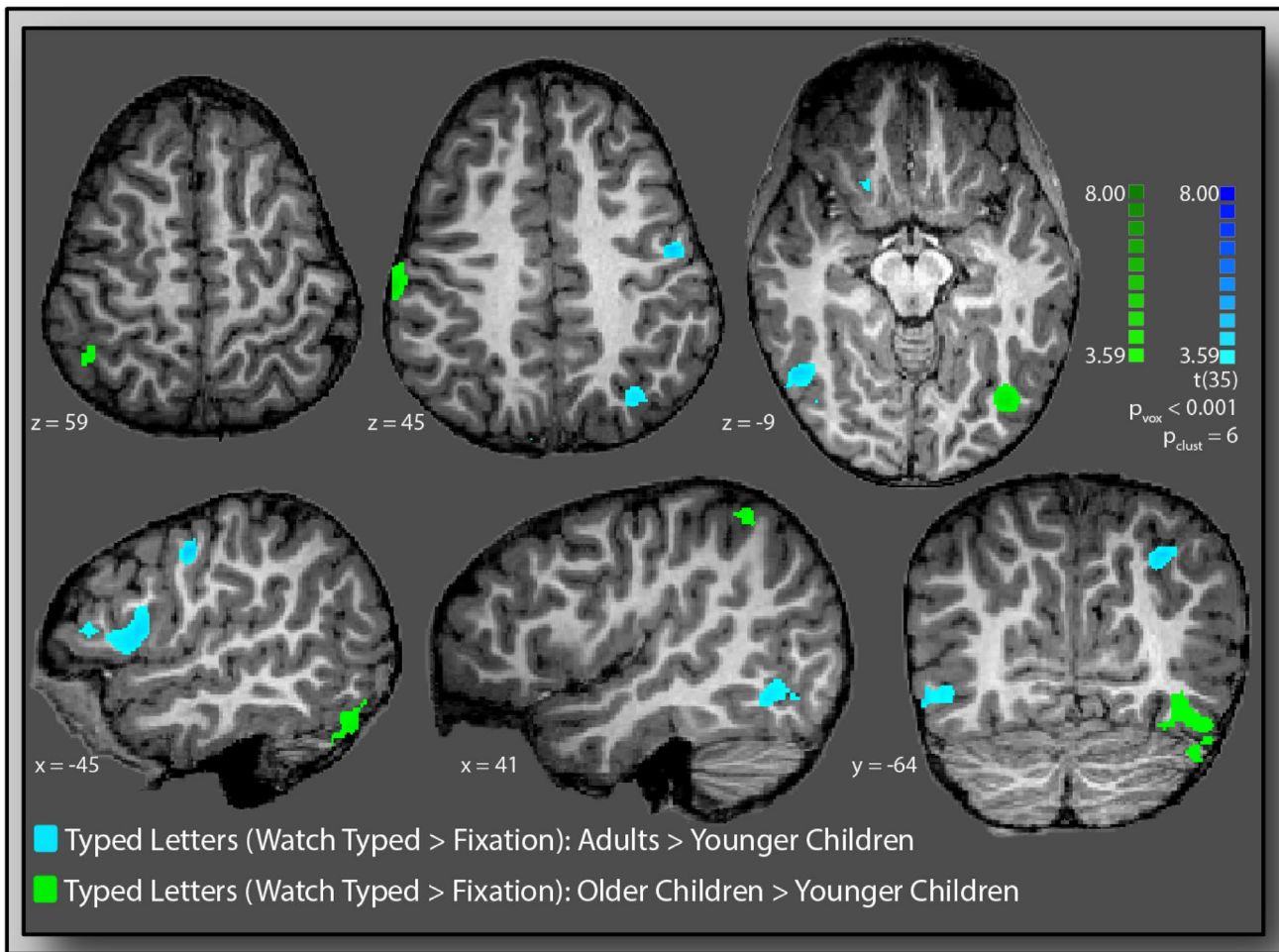
FIGURE 5 Group Differences for the Perception of Typed Letters. A whole-brain one-way repeated measures ANOVA revealed that activation in the left posterior fusiform gyrus, right posterior fusiform gyrus, left posterior intraparietal sulcus, left inferior frontal gyrus, and left dorsal precentral gyrus differed among younger children, older children, and literate adults. Post hoc between-group comparisons at the whole-brain level indicated that the difference in the left posterior fusiform gyrus and the right dorsal postcentral gyrus could be attributed to more sensitivity to typed letters in the older children than in the younger children (green) and that the difference in the other regions could be attributed to more sensitivity to typed letters in the literate adults than in the younger children (turquoise). There were no differences between older children and literate adults. Talairach coordinates for each slice are displayed. Results are presented a $p_{vox} < .001$ with a cluster threshold of six contiguous 2-mm isotropic voxels

sensitivity to object categories by exposure to visual variability. Such a hypothesis would be supported by prior work that has demonstrated that the left fusiform gyrus responds selectively to the category of letters in literate adults (James & Gauthier, 2006; James et al., 2005) across modality and for different allographs (Rothlein & Rapp, 2014) and that experience with handwriting can influence this response in preliterate children (James, 2010; James & Engelhardt, 2012).

The left intraparietal sulcus was also more responsive to handwritten forms in the younger children than in adults. Unlike the group differences for handwritten forms in the left fusiform gyrus, the group differences for handwritten forms in the left intraparietal sulcus did *not* overlap with those that were found for typed letter perception. Younger children were more sensitive than adults to variability in form in the anterior portion of left intraparietal sulcus (Figure 4), whereas adults were more sensitive than younger children to typed letters in the posterior portion (Figure 5). The results of the

whole-brain contrasts (Figure 3) suggest that both of these results were related to a response to typed letters in both anterior and posterior portions of intraparietal sulcus in adults that was not observed in the younger children. Although it is difficult to interpret based on this study alone, it is possible that the anterior portion of the left intraparietal sulcus responds to form variability at an early age, similar to ventral-temporal cortex, and begins to respond to letters as a category with experience. This developmental trajectory is, similar to our other results, indicative of an early sensitivity to variability in letterform before sensitivity to letters themselves.

4.2.3 | Ownership

Only the left intraparietal sulcus demonstrated any sensitivity to the perception of one's own handwriting and only in the adult group. Prior

work in adults has found left intraparietal sulcus for letters presented in one's own handwriting compared to typed letters (Vinci-Booher et al., 2019), but it was unclear whether this effect was an ownership effect or whether it was related to variability in form. The results of the current study demonstrate that the parietal response was an ownership effect. We propose that this parietal response is related to the visual processing of the cues for motion present in handwritten letters (i.e. kinematic cues) and that this response is strongest for one's own handwritten forms because they contain visual cues for motion unique to the observer's own handwriting experiences.

The left intraparietal sulcus may be more responsive to one's own handwritten letters than to another's in literate adults because it is responding to visual cues for online modifications of the letter's stored somatomotor plans. Real-time visual cues that point to online changes in the action, such as a curve that went a bit too far to the right while making an 'R', may invoke these parietal responses in expert writers who have acquired their own stereotyped movement patterns for each letter as well as a large amount of experience with them. Several recent neurophysiological studies have suggested that the left intraparietal sulcus does, in fact, store some memory of a past experience of visual-motor coordination (Ferrari-Toniolo, Visco-Comandini, Papazachariadis, Caminiti, & Battaglia-Mayer, 2015; Haar, Donchin, & Dinstein, 2015; Kastner, Chen, Jeong, & Mruczek, 2017), perhaps accumulating evidence for potential motor movements (Tosoni, Galati, Romani, & Corbetta, 2008), and this same region has been associated with visual-motor coordination during letter production in adults (Haar et al., 2015; Kadmon Harpaz, Flash, & Dinstein, 2014; Vinci-Booher et al., 2019).

4.3 | Mechanisms of perceptual learning from motor actions

There are, at least, two non-mutually exclusive explanations of how neural changes associated with changes in perceptual decisions may be caused by motor learning activities. The first of these is that motor activities generate a great deal of efferent neural activity, sending neural output from primary motor cortex to several other brain regions, most notably frontal premotor regions and parietal cortex (for review see Ostry & Gribble, 2016). The second avenue through which motor learning activities affect perceptual changes is that motor activities create environmental realities that are, in turn, processed by sensory systems and, therefore, lead to perceptual changes. Letter production is a learning activity that makes use of both avenues and our results suggest that the mechanisms by which the ventral-temporal cortex undergoes developmental changes during letter production may be different than the mechanisms by which the frontal motor and parietal cortices undergo developmental changes during letter production.

The major environmental change accomplished by letter production is the creation of a handwritten version of a letter that persists after the letter production episode has finished. This visual input may be responsible for the changes in ventral-temporal function after letter production. Ventral-temporal cortex is broadly associated with object categorization processes (for review, see Grill-Spector & Weiner, 2014), and the development of object categorization processes is largely driven by the perceptual differentiation that follows exposure to category variability (Li & James, 2016; Perry et al., 2010; Twomey, Lush, et al., 2014; Twomey, Ranson, et al., 2014). Our results suggest that ventral-temporal cortex may be most sensitive to the variability present in handwritten forms when children are first learning about letters and that this sensitivity to visual variability may be a part of how ventral-temporal cortex undergoes developmental changes that contribute to the formation of category-specific responses.

The response in frontal motor and parietal cortices during letter perception, on the other hand, may be most associated with the strong interconnectivity between these regions during the motor action itself (for review Nakamura & Kouider, 2003; Katanoda, Yoshikawa, & Sugishita, 2001; Rizzolatti, Luppino, & Matelli, 1998; Yuan & Brown, 2014). In younger children, who may not have developed motor plans/programs for motor production, actions themselves may require efficient use of visual and somatosensory feedback throughout the letter production episode (Palmis, Danna, Velay, & Longcamp, 2017). With each letter produced this visual-somatomotor connectivity is strengthened and refined, resulting in somatomotor representation (motor plans/programs) for letters in fronto-parietal cortices, not ventral-temporal cortex, that can be called upon when simply presented with the visual cues for motion that are typically experienced during the visual-motor activity.

The response in ventral-temporal cortex during letter perception might, therefore, develop through the visual perceptual experiences created during letter production, whereas the response in frontal motor and parietal cortices might develop through the experience of the motor movement itself. This suggestion is supported by the two visual steams hypothesis that proposes differing developmental time courses for ventral and dorsal stream processes (Goodale & Milner, 2005; Milner & Goodale, 2006; Stiles et al., 2013) and connectivity between these systems (Lebel, Walker, Leemans, Phillips, & Beaulieu, 2008) in the context of a breadth of literature documenting category-specific responses in ventral-temporal cortex (for review, see Grill-Spector & Weiner, 2014) after handwriting practice (James, 2010; James & Engelhardt, 2012; Kersey & James, 2013) and strong somatomotor interconnectivity between motor and parietal cortices (Andersen, Asanuma, Essick, & Siegel, 1990; for review on written production Nakamura & Koudier, 2003; Ostry & Gribble, 2016; Petrides & Pandya, 1984; Guye et al., 2003). Sensorimotor learning activities are often found to be better at inducing learning effects than other unimodal activities (see Shams & Seitz, 2008 for review), perhaps because of their ability to facilitate developmental changes in perceptual-oriented ventral-temporal regions and, at the same time, in motor-oriented fronto-parietal regions.

CONFLICT OF INTEREST

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, KHJ, upon reasonable request. When we have finished analyzing additional aspects of these data, they will be openly available in brainlife.io.

REFERENCES

Andersen, R. A., Asanuma, C., Essick, G., & Siegel, R. M. (1990). Corticocortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule. *The Journal of Comparative Neurology*, *296*(1), 65–113. https://doi.org/10.1002/cne.902960106

Babcock, M. K., & Freyd, J. J. (1988). Perception of dynamic information in static handwritten forms. *The American Journal of Psychology*, *101*(1), 111–130. https://doi.org/10.2307/1422797

Boynton, G. M., Engel, S. A., Glover, G. H., & Heeger, D. J. (1996). Linear systems analysis of functional magnetic resonance imaging in human V1. *Journal of Neuroscience*, *16*(13), 4207–4221. https://doi.org/10.1523/JNEUROSCI.16-13-04207.1996

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*(4), 433–436.

Bullmore, E. T., Brammer, M. J., Rabe-Hesketh, S., Curtis, V. A., Morris, R. G., Williams, S., ... McGuire, P. K. (1999). Methods for diagnosis and treatment of stimulus-correlated motion in generic brain activation studies using fMRI. *Human Brain Mapping*, *7*(1), 38–48. https://doi.org/10.1002/(SICI)1097-0193(1999)7:1<38:AID-HBM4>3.0.CO;2-Q

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain*, *129*(3), 564–583. https://doi.org/10.1093/brain/awl004

Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M. A., & Michel, F. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain: A Journal of Neurology*, *123*(Pt 2), 291–307. https://doi.org/10.1093/brain/123.2.291

Conrad, R. (1964). Acoustic confusions in immediate memory. *British Journal of Psychology*, *55*(1), 75–84. https://doi.org/10.1111/j.2044-8295.1964.tb00899.x

Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron*, *56*(2), 384–398. https://doi.org/10.1016/j.neuron.2007.10.004

Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: A proposal. *Trends in Cognitive Sciences*, *9*(7), 335–341. https://doi.org/10.1016/j.tics.2005.05.004

Dehaene, S., Le Clec'H, G., Poline, J.-B., Le Bihan, D., & Cohen, L. (2002). The visual word form area: A prelexical representation of visual words in the fusiform gyrus. *NeuroReport*, *13*(3), 321–325. https://doi.org/10.1097/00001756-200203040-00015

Dufor, O., & Rapp, B. (2013). Letter representations in writing: An fMRI adaptation approach. *Frontiers in Psychology*, *4*, 781. https://doi.org/10.3389/fpsyg.2013.00781

Emberson, L. L., Cannon, G., Palmeri, H., Richards, J. E., & Aslin, R. N. (2017). Using fNIRS to examine occipital and temporal responses to stimulus repetition in young infants: Evidence of selective frontal cortex involvement. *Developmental Cognitive Neuroscience*, *23*, 26–38. https://doi.org/10.1016/j.dcn.2016.11.002

Ferrari-Toniolo, S., Visco-Comandini, F., Papazachariadis, O., Caminiti, R., & Battaglia-Mayer, A. (2015). Posterior parietal cortex encoding of dynamic hand force underlying hand-object interaction. *The Journal of Neuroscience*, *35*(31), 10899–10910. https://doi.org/10.1523/JNEUROSCI.4696-14.2015

Flowers, D. L., Jones, K., Noble, K., VanMeter, J., Zeffiro, T. A., Wood, F. B., & Eden, G. F. (2004). Attention to single letters activates left extrastriate cortex. *NeuroImage*, *21*(3), 829–839. https://doi.org/10.1016/j.neuroimage.2003.10.002

Freyd, J. J. (1983a). The mental representation of movement when static stimuli are viewed. *Perception & Psychophysics*, *33*(6), 575–581. https://doi.org/10.3758/BF03202940

Freyd, J. J. (1983b). Representing the dynamics of a static form. *Memory & Cognition*, *11*(4), 342–346. https://doi.org/10.3758/BF03202447

Freyd, J. J., & Finke, R. A. (1984). Representational momentum. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *10*(1), 126. https://doi.org/10.1037/0278-7393.10.1.126

Freyd, J. J., & Finke, R. A. (1985). A velocity effect for representational momentum. *Bulletin of the Psychonomic Society.*, *23*(6), 443–446. https://doi.org/10.3758/BF03329847

Garrett, A. S., Flowers, D. L., Absher, J. R., Fahey, F. H., Gage, H. D., Keyes, J. W., ... Wood, F. B. (2000). Cortical activity related to accuracy of letter recognition. *NeuroImage*, *11*(2), 111–123. https://doi.org/10.1006/nimg.1999.0528

Gauthier, I. (2000). What constrains the organization of the ventral temporal cortex? *Trends in Cognitive Sciences*, *4*(1), 1–2. https://doi.org/10.1016/S1364-6613(99)01416-3

Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The fusiform "face area" is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience*, *12*(3), 495–504. https://doi.org/10.1162/089892900562165

Goodale, M. A., & Milner, A. D. (2005). *Sight unseen*. Oxford, UK: Oxford University Press.

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, *10*(1), 14–23. https://doi.org/10.1016/j.tics.2005.11.006

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*, *24*(1), 187–203. https://doi.org/10.1016/S0896-6273(00)80832-6

Grill-Spector, K., & Weiner, K. S. (2014). The functional architecture of the ventral temporal cortex and its role in categorization. *Nature Reviews Neuroscience*, *15*(8), 536–548. https://doi.org/10.1038/nrn3747

Guye, M., Parker, G. J. M., Symms, M., Boulby, P., Wheeler-Kingshott, C. A. M., Salek-Haddadi, A., ... Duncan, J. S. (2003). Combined functional MRI and tractography to demonstrate the connectivity of the human primary motor cortex in vivo. *NeuroImage*, *19*(4), 1349–1360. https://doi.org/10.1016/S1053-8119(03)00165-4

Haar, S., Donchin, O., & Dinstein, I. (2015). Dissociating visual and motor directional selectivity using visuomotor adaptation. *The Journal of Neuroscience*, 35(17), 6813–6821. https://doi.org/10.1523/JNEUROSCI.0182-15.2015

Hull, A. J. (1973). A letter-digit matrix of auditory confusions. *British Journal of Psychology*, 64(4), 579–585. https://doi.org/10.1111/j.2044-8295.1973.tb01384.x

Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences*, 96(16), 9379–9384. https://doi.org/10.1073/pnas.96.16.9379

James, K. H. (2010). Sensori-motor experience leads to changes in visual processing in the developing brain. *Developmental Science*, 13(2), 279–288. https://doi.org/10.1111/j.1467-7687.2009.00883.x

James, K. H., & Atwood, T. P. (2009). The role of sensorimotor learning in the perception of letter-like forms: Tracking the causes of neural specialization for letters. *Cognitive Neuropsychology*, 26(1), 91–110. https://doi.org/10.1080/02643290802425914

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(1), 32–42. https://doi.org/10.1016/j.tine.2012.08.001

James, K. H., & Gauthier, I. (2006). Letter processing automatically recruits a sensory–motor brain network. *Neuropsychologia*, 44(14), 2937–2949. https://doi.org/10.1016/j.neuropsychologia.2006.06.026

James, K. H., James, T. W., Jobard, G., Wong, A. C. N., & Gauthier, I. (2005). Letter processing in the visual system: Different activation patterns for single letters and strings. *Cognitive, Affective & Behavioral Neuroscience*, 5(4), 452–466. https://doi.org/10.3758/CABN.5.4.452

Kadmon Harpaz, N., Flash, T., & Dinstein, I. (2014). Scale-invariant movement encoding in the human motor system. *Neuron*, 81(2), 452–462. https://doi.org/10.1016/j.neuron.2013.10.058

Kanwisher, N. (2000). Domain specificity in face perception. *Nature Neuroscience*, 3(8), 759–763.

Kastner, S., Chen, Q., Jeong, S. K., & Mruczek, R. E. B. (2017). A brief comparative review of primate posterior parietal cortex: A novel hypothesis on the human toolmaker. *Neuropsychologia*, 105, 123–134. https://doi.org/10.1016/j.neuropsychologia.2017.01.034

Katanoda, K., Yoshikawa, K., & Sugishita, M. (2001). A functional MRI study on the neural substrates for writing. *Human Brain Mapping*, 13(1), 34–42. https://doi.org/10.1002/hbm.1023

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, 1–15. https://doi.org/10.3389/fpsyg.2013.00567

Knoblich, G., & Prinz, W. (2001). Recognition of self-generated actions from kinematic displays of drawing. *Journal of Experimental Psychology: Human Perception and Performance*, 27(2), 456–465. https://doi.org/10.1037/0096-1523.27.2.456

Knoblich, G., Seigerschmidt, E., Flach, R., & Prinz, W. (2002). Authorship effects in the prediction of handwriting strokes: Evidence for action simulation during action perception. *The Quarterly Journal of Experimental Psychology Section A*, 55(3), 1027–1046. https://doi.org/10.1080/02724980143000631

Lebel, C., Walker, L., Leemans, A., Phillips, L., & Beaulieu, C. (2008). Microstructural maturation of the human brain from childhood to adulthood. *NeuroImage*, 40(3), 1044–1055. https://doi.org/10.1016/j.neuroimage.2007.12.053

Li, J. X., & James, K. H. (2016). Handwriting generates variable visual output to facilitate symbol learning. *Journal of Experimental Psychology. General*, 145(3), 298–313. https://doi.org/10.1037/xge0000134

Longcamp, M., Anton, J.-L., Roth, M., & Velay, J.-L. (2003). Visual presentation of single letters activates a premotor area involved in writing. *NeuroImage*, 19(4), 1492–1500. https://doi.org/10.1016/S1053-8119(03)00088-0

Longcamp, M., Boucard, C., Gilhodes, J.-C., Anton, J.-L., Roth, M., Nazarian, B., & Velay, J.-L. (2008). Learning through hand- or typewriting influences visual recognition of new graphic shapes: Behavioral and functional imaging evidence. *Journal of Cognitive Neuroscience*, 20(5), 802–815. https://doi.org/10.1162/jocn.2008.20504

Longcamp, M., Hlushchuk, Y., & Hari, R. (2011). What differs in visual recognition of handwritten vs. printed letters? An fMRI study. *Human Brain Mapping*, 32(8), 1250–1259. https://doi.org/10.1002/hbm.21105

Longcamp, M., Lagarrigue, A., Nazarian, B., Roth, M., Anton, J.-L., Alario, F.-X., & Velay, J.-L. (2014). Functional specificity in the motor system: Evidence from coupled fMRI and kinematic recordings during letter and digit writing. *Human Brain Mapping*, 35(12), 6077–6087. https://doi.org/10.1002/hbm.22606

Longcamp, M., Tanskanen, T., & Hari, R. (2006). The imprint of action: Motor cortex involvement in visual perception of handwritten letters. *NeuroImage*, 33(2), 681–688. https://doi.org/10.1016/j.neuroimage.2006.06.042

Longcamp, M., Zerbato-Poudou, M.-T., & Velay, J.-L. (2005). The influence of writing practice on letter recognition in preschool children: A comparison between handwriting and typing. *Acta Psychologica*, 119(1), 67–79. https://doi.org/10.1016/j.actpsy.2004.10.019

Longstaff, M. G., & Heath, R. A. (1997). Space-time invariance in adult handwriting. *Acta Psychologica*, 97(2), 201–214. https://doi.org/10.1016/S0001-6918(97)00015-2

Mattaloni, E. (2013). *Self reference effect in handwriting*. Trieste, Italy: Universita' Degli Studi Di Trieste. Retrieved from https://www.openstarts.units.it/handle/10077/8668

Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action* (2nd ed.). Oxford, UK: Oxford University Press.

Nakamura, K., & Kouider, S. (2003). Functional neuroanatomy of Japanese writing systems. *Aphasiology*, 17(6–7), 667–683. https://doi.org/10.1080/02687030344000076

Orliaguet, J. P., Kandel, S., & Boë, L. J. (1997). Visual perception of motor anticipation in cursive handwriting: Influence of spatial and movement information on the prediction of forthcoming letters. *Perception*, 26(7), 905–912. https://doi.org/10.1068/p260905

Ostry, D. J., & Gribble, P. L. (2016). Sensory Plasticity in human motor learning. *Trends in Neurosciences*, 39(2), 114–123. https://doi.org/10.1016/j.tins.2015.12.006

Palmis, S., Danna, J., Velay, J.-L., & Longcamp, M. (2017). Motor control of handwriting in the developing brain: A review. *Cognitive Neuropsychology*, 34(3–4), 187–204. https://doi.org/10.1080/02643294.2017.1367654

Pelli, D.G. (1997). The videotoolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.

Perry, L. K., Samuelson, L. K., Malloy, L. M., & Schiffer, R. N. (2010). Learn locally, think globally: Exemplar variability supports higher-order generalization and word learning. *Psychological Science*, 21(12), 1894–1902. https://doi.org/10.1177/0956797610389189

Petrides, M., & Pandya, D. N. (1984). Projections to the frontal cortex from the posterior parietal region in the rhesus monkey. *The Journal of Comparative Neurology*, 228(1), 105–116. https://doi.org/10.1002/cne.902280110

Rizzolatti, G., Luppino, G., & Matelli, M. (1998). The organization of the cortical motor system: New concepts. *Electroencephalography and Clinical Neurophysiology*, 106(4), 283–296. https://doi.org/10.1016/S0013-4694(98)00022-4

Rothlein, D., & Rapp, B. (2014). The similarity structure of distributed neural responses reveals the multiple representations of letters. *NeuroImage*, 89, 331–344. https://doi.org/10.1016/j.neuroimage.2013.11.054

Satterthwaite, T. D., Elliott, M. A., Gerraty, R. T., Ruparel, K., Loughead, J., Calkins, M. E., … Wolf, D. H. (2013). An improved framework for confound regression and filtering for control of motion artifact in the preprocessing of resting-state functional connectivity data. *NeuroImage*, *64*, 240–256. https://doi.org/10.1016/j.neuroimage.2012.08.052

Sawada, R., Doi, H., & Masataka, N. (2016). Processing of self-related kinematic information embedded in static handwritten characters. *Brain Research*, *1642*, 287–297. https://doi.org/10.1016/j.brainres.2016.03.039

Saygin, Z. M., Osher, D. E., Norton, E. S., Youssoufian, D. A., Beach, S. D., Feather, J., … Kanwisher, N. (2016). Connectivity precedes function in the development of the visual word form area. *Nature Neuroscience*, *19*(9), 1250–1255. https://doi.org/10.1038/nn.4354

Schubert, T., Reilhac, C., & McCloskey, M. (2018). Knowledge about writing influences reading: Dynamic visual information about letter production facilitates letter identification. *Cortex*, *103*, 302–315. https://doi.org/10.1016/j.cortex.2018.03.020

Shams, L., & Seitz, A. R. (2008). Benefits of multisensory learning. *Trends in Cognitive Sciences*, *12*(11), 411–417. https://doi.org/10.1016/j.tics.2008.07.006

Stiles, J., Akshoomoff, N., & Haist, F. (2013). The development of visuospatial processing. In *Neural circuit development and function in the brain: Comprehensive developmental neuroscience* (Vol. *3*, pp. 271–296). Elsevier. https://doi.org/10.1016/B978-0-12-397267-5.00058-3

Talairach, J., & Tournoux, P. (1988). Co-planar stereotaxic atlas of the human brain. 3-Dimensional proportional system: an approach to cerebral imaging.

Tootell, R. B., Reppas, J. B., Kwong, K. K., Malach, R., Born, R. T., Brady, T. J., … Belliveau, J. W. (1995). Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *The Journal of Neuroscience*, *15*(4), 3215–3230. https://doi.org/10.1523/JNEUROSCI.15-04-03215.1995

Tosoni, A., Galati, G., Romani, G. L., & Corbetta, M. (2008). Sensory-motor mechanisms in human parietal cortex underlie arbitrary visual decisions. *Nature Neuroscience*, *11*(12), 1446–1453. https://doi.org/10.1038/nn.2221

Twomey, K. E., Lush, L., Pearce, R., & Horst, J. S. (2014). Visual variability affects early verb learning. *The British Journal of Developmental Psychology*, *32*(3), 359–366. https://doi.org/10.1111/bjdp.12042

Twomey, K. E., Ranson, S. L., & Horst, J. S. (2014). That's more like it: Multiple exemplars facilitate word learning. *Infant and Child Development*, *23*(2), 105–122. https://doi.org/10.1002/icd.1824

Van Dijk, K. R. A., Sabuncu, M. R., & Buckner, R. L. (2012). The influence of head motion on intrinsic functional connectivity MRI. *NeuroImage*, *59*(1), 431–438. https://doi.org/10.1016/j.neuroimage.2011.07.044

Vinci-Booher, S., Cheng, H., & James, K. H. (2019). An analysis of the brain systems involved with producing letters by hand. *Journal of Cognitive Neuroscience*, *31*(1), 138–154. https://doi.org/10.1162/jocn_a_01340

Vinci-Booher, S., Sehgal, N., & James, K. H. (2018). *Visual and motor experiences of handwriting contribute to gains in visual recognition*. Poster presented at the Annual Meeting of the Vision Sciences Society, St. Pete Beach, FL, USA.

Vinci-Booher, S., Sturgeon, J., James, T., & James, K. H. (2018). The MRItab: An MR-compatible touchscreen with video-display. *Journal of Neuroscience Methods*, *306*, 10–18. https://doi.org/10.1016/j.jneumeth.2018.05.018

Weissenbacher, A., Kasess, C., Gerstl, F., Lanzenberger, R., Moser, E., & Windischberger, C. (2009). Correlations and anticorrelations in resting-state functional connectivity MRI: A quantitative comparison of preprocessing strategies. *Neuroimage*, *47*(4), 1408–1416.

Wing, A. M., & Nimmo-Smith, I. (1987). The variability of cursive handwriting measure defined along a continuum: Letter specificity. *Journal of the Forensic Science Society*, *27*(5), 297–306. https://doi.org/10.1016/S0015-7368(87)72768-6

Yuan, Y., & Brown, S. (2014). The neural basis of mark making: A functional MRI study of drawing. *PLoS ONE*, *9*(10), e108628. https://doi.org/10.1371/journal.pone.0108628

Zeki, S., Watson, J. D., Lueck, C. J., Friston, K. J., Kennard, C., & Frackowiak, R. S. (1991). A direct demonstration of functional specialization in human visual cortex. *The Journal of Neuroscience*, *11*(3), 641–649. https://doi.org/10.1523/JNEUROSCI.11-03-00641.1991