The effects of handwriting experience on functional brain development in pre-literate children

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ABSTRACT

In an age of increasing technology, the possibility that typing on a keyboard will replace handwriting raises questions about the future usefulness of handwriting skills. Here we present evidence that brain activation during letter perception is influenced in different, important ways by previous *handwriting* of letters versus previous *typing or tracing* of those same letters. Preliterate, five-year old children printed, typed, or traced letters and shapes, then were shown images of these stimuli while undergoing functional MRI scanning. A previously documented "reading circuit" was recruited during letter perception only after handwriting—not after typing or tracing experience. These findings demonstrate that handwriting is important for the early recruitment in letter processing of brain regions known to underlie successful reading. Handwriting therefore may facilitate reading acquisition in young children.

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1. Introduction

Reading is a relatively recent development for citizens in general in the history of human cognition, but it has become a crucial skill for functioning in modern society. Thus, understanding the mechanisms underlying reading acquisition during development is an important endeavor for education and public policy as well as for basic science. Individual letter processing is an especially important component of both reading acquisition and skilled reading [57]. In preliterate children, letter recognition is a precursor to proficient reading. Speed and accuracy in naming letters in the preschool years is a better predictor of later reading skill than measures such as letter–sound knowledge [45,21,67]. Early delays in letter recognition significantly predict reading disabilities in later grades [52] and contribute to the diagnosis of literacy delays [12]. In accomplished readers, individual letter identification remains a major stage of processing in visual word recognition [8,63]. In short, the ability to recognize individual letters of the alphabet is a crucial skill for reading.

The processes involved in letter recognition are not well understood, but as in learning to recognize many visual images, letter learning requires that many perceptually dissimilar instances be grouped together in a single, abstract category. For instance, we must learn that: A, a, a and a all refer to the same category of the letter A. During letter perception, we must process and use visual information specifying the relative sizes, locations, orientations and angles of lines in the stimuli, because these features define letter identity. We often use global shape information to categorize non-letter objects, but letter recognition cannot rely only on differences in global shape because different letters – for example, lower case 'b' and 'd' – may have the same global shape and differ only in the orientation of that shape. Thus, whereas most objects can be recognized from a range of different orientations, a change in the orientation of a letter can change the letter's identity. Similarly, whereas we can usually recognize familiar objects despite partial occlusion, even a small amount of occlusion can change the identity of a letter. Therefore, letter recognition is unlike recognition of other objects because we cannot rely solely on global shape information, we are obliged to code and use orientation information, and we cannot ignore even small changes in appearance due to occlusion.

There is substantial evidence that letter perception relies both on global shape and on local feature perception. For instance, the well-known 'global precedence effect', which demonstrates that global shape is processed before local features during letter perception, also demonstrates that local features are still processed, and can interfere with global shape processing—in this case, letters (for review see [40]). Neuroimaging research further suggested that the right hemisphere processes the low spatial frequencies required for global perception, while the left hemisphere processes higher spatial frequencies used for local feature processing [15] and that this specialized processing occurs after a preliminary visual processing stage of the stimuli, and is therefore affected by top-down processes such as attention [30]. The high spatial frequency information so important in letter recognition

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can be thought of as reflecting the importance of features and their relationships to one another. This hypothesis fits well with the findings that letter processing is a more left hemisphere function (e.g. [33]) processing that requires an emphasis on local feature processing. Further, substantial research by Sanocki and his colleagues has shown that letter recognition relies on defining a set of features whose membership relies on distinctiveness as well as commonalities (e.g. [61]). In addition, commonalities may be important for defining a category of letter, while distinctive-ness may help to process sub-ordinate categories, such as type-face or font [61].

However, letter recognition by the literate adult is affected minimally or not at all by variation such as changes in font, size, or case. How do children who are just learning to distinguish among and recognize letters sort out which perceptual properties of letters are important to attend to and which can be ignored? We and others have proposed that it is the creation of letter forms in writing that allows children to gain an understanding of which perceptual properties are crucial for identity and which are not [31,34,44,53]. When children begin to print, their motor output (a letter) does not conform to prototypical lettering: each output (which is also the perceptual input) can be said to be noisy relative to the model. In addition, different instances of the same letter produced by the child are highly variable and thus the percepts are variable too. Interestingly, children can still accu-rately recognize their atypical printed forms as the intended letters—presumably because the children themselves created them (unpublished data). In other sensori-motor activities that produce letters – in particular, tracing and typing – children succeed in producing forms similar if not identical to the target shapes (non-noisy). However, we propose that the experience of producing accurate copies of letters by tracing or typing does not contribute to the child's knowledge of letters like the experience of printing less accurate copies of letters does—that in fact, the highly variable output of early free-form printing may be a crucial component of emerging letter recognition and understanding.

It has been established that variation across exemplars of a category can lead to better abstraction of the invariant features of the category (cf. [55]). Recent support of this idea in cognitive development comes from a study in which children were taught a set of highly similar category exemplars vs. highly variable category exemplars and tested on their generalization ability within the learned category as well as outside of that category [54]. Perry and colleagues showed that teaching children the same category label (e.g., Bucket) for very different looking exemplars led to a broader and more accurate use of the category label for other, unlearned instances. Such findings suggest that a child's production of many different forms of a single letter in his or her printing – which results in variable exemplars of a category – may broaden that letter category in the developing letter recognition system and enhance recognition of a broader range of instances.

The ability to use categories for grouping visual information is thought to be crucial for the fast visual recognition ability observed in human behavior (see [28], for review). Thus, learning abstract categories is beneficial for recognition [27], and learning perceptually variable exemplars enhances category learning. Therefore, learning through perceiving variable instances may enhance recognition. It is by this logic that we believe that printing letters may improve letter recognition. However, we are also interested in the mechanisms that underlie this learning – in particular, how the brain changes its responses as we become proficient at assigning instances to categories.

Research in cognitive neuroscience has demonstrated that once exemplars of abstract categories are successfully classified, left hemisphere structures dominate visual recognition [64].

For example, Seger et al. [64] tracked neural response patterns as individuals became more proficient at classifying instances into categories. As participants learned how to classify checkerboard-like patterns, they showed a shift from right lateralized activation in the frontal, parietal and occipital cortices, to bilateral, and then to left lateralized activation [64]. This shift in lateralization may underlie the left hemisphere dominance for letter and word processing seen in most literate individuals. In a majority of adults, a predictable set of left-lateralized neural regions respond during reading ([13,48,66]; for review see [16]). Individual letter processing engages the left fusiform gyrus, a cortical region that spans the ventral portion of the temporal lobe at the occipital-temporal junction, in close proximity to visual association areas [20,24]. Words are processed in a different region along this gyrus (cf. [13,48,34]). The process of reading in general recruits left occipital, ventral temporal, posterior parietal and inferior frontal gyri (e.g. [66]). A region that is seen during letter perception, but not during reading in most studies, is the premotor cortex ([33]; but see the special case of verb reading, e.g. [56]). Why letters are processed in different neural regions than words – specifically, in the fusiform gyrus and premotor cortex – is not known, but some hypotheses have been eliminated. For example, length of stimulus alone does not affect the region of processing [34], nor does readability: non-words (groups of letters) are processed in 'word regions' rather than in 'letter regions' [17,18,6]. One interesting hypothesis that has emerged from this literature is that letters may be processed differently than words partially because of our motor experience with them [31,33,41,44]. When we write, we write one letter at a time, so there should be motor information affiliated with the stored visual information about individual letters, and perhaps not with representations of the changeable combinations of those individual letters. In fact, researchers have asserted that there are at least two aspects to writing letters—an internal code that specifies the letter form arising from the superior parietal lobe (Basso et al., 1978 [3]) and a graphomotor code that recruits the premotor cortex (Brain, 1967 [4]). Further, an area in the dorsal lateral premotor cortex, termed Exner's area, is well known to be important for writing (e.g. Anderson et al., 1990 [1]), completing a possible circuit for writing letters that comprises the poterior parietal lobe, prefrontal cortex and pre-motor cortex. But does this writing circuit then provide input to letter perception? How would our experience of writing affect visual processing of letters?

Recent studies have investigated the role of motor practice on subsequent letter recognition [41,32]. Behavioral studies with adults show that letter recognition benefits from handwriting practice more than from typing practice [44,32], and adult neuroimaging studies indicate that visual letter perception recruits motor systems that are typically dedicated to the execu-tion of writing movements ([33,41,50]). Importantly, James and Atwood [32] demonstrated that adults who had handwriting experience with novel letter-like stimuli developed functional cortical specialization for these stimuli. Specifically, after hand-writing experience, adults showed greater activation in the left fusiform gyrus to pseudo-letters that they had previously drawn than to pseudo-letters that they had studied visually, but not previously drawn [32]. These findings suggest that motor experi-ence, by virtue of producing variable exemplars, may change visual processing during subsequent letter recognition in adults.

The first step in investigating this hypothesis was to demon-strate that learning letters through printing results in different neural processing than learning letters through visual practice alone. We chose to address this issue, and to attempt to replicate the previous findings, in an fMRI study of pre-school-aged children [31]. The children learned letters either through printing or through visual practice. Both groups of children learned to

recognize the letters. However, imaging results showed that children who had printed the letters had greater activation in the left fusiform gyrus during letter perception than children who had learned the letters without printing practice.

The findings from adults and children are the same. Together, they provide evidence that handwriting experience results in the recruitment of letter-specific neural processing regions, and may be important for setting up the neural system that will be responsible for processing letters once an individual becomes literate [31]. However, the results do not establish that handwriting is the only kind of motor experience that would produce this effect. The current work seeks to address the *type* of motor experience that is required for the creation of this writing-perception network. It is possible that motor acts during learning simply engage attention – in this case, attention to letter shapes – more effectively than visual learning without a motor component does. If this is the case, then any motor movement that accompanies visual learning – for example, hunt-and-peck typing of the letters to be learned – should facilitate neural specialization for letters. Alternatively, it might be that letter-specific motor activity (forming each letter shape with an effector) might be required for the emergence of specialization. In this case, copying a letter by tracing might be as effective as printing free-form. Finally, it is possible that the letters must be free-form creations of the child himself (as discussed above), resulting in varied and non-stereotypical letter-forms. If this is the case, then only printing practice (and not tracing or typing) will result in neural specialization.

The current study was designed to test all of these possibilities by comparing the effects of each of these different kinds of motor experience during letter learning on children's development of neural specialization for letters. Preliterate children in this study produced letters and simple shapes by handwriting (printing free-form or tracing) or single-key typing. A note on terminology is required here: handwriting in this case is free-form printing of manuscript letters that are presented on a computer screen but does not involve writing cursive letters. After one of these three types of training, participants underwent a functional imaging session (fMRI) in which they passively viewed the letters and shapes that they had learned along with additional letters and shapes not included in training. The presentation was blocked according to training and stimulus category (letters or shapes), and the resultant blood-oxygen-level-dependent (BOLD) activations were measured. By comparing these conditions and their effects on neural regions engaged in visual letter perception, we directly assessed whether the effect of handwriting on activation in the regions reported in James [31] can be obtained through experience with *any* motor act with letters, and so is equal after handwriting (printing), tracing, and typing; or requires the stroke-by-stroke creation of a letter form by hand, and so is greater after handwriting and tracing than after typing; or results from the perception of variable, self-created letter forms, and so is greater after handwriting than after typing or tracing experience.

2. Materials and methods

2.1. Participants

Fifteen children (8 females; ages 4 years 2 months to 5 years 0 months) with right-hand dominance as determined by a revised Edinburgh questionnaire [14] were recruited from the Bloomington, Indiana community to participate in the study. All were native English speakers, and parents reported normal vision, hearing, and motor development. Parents reported no known neurological impairments, birth trauma, or ongoing medications. Children were pre-literate at the time of testing according to parental report.

All research was approved by the Indiana University Protection of Human Participants board. Children were compensated with a small toy and gift card as well as a gift certificate.

2.2. Stimuli and apparatus

In each condition, children were shown a letter or shape on an index card and asked to draw, trace or type the item without it being named by the experimenter. Participants were provided with squares with dotted outlines of the letters for the tracing condition, a page of blank squares for the drawing condition, or a blank white 8.5×11 page on a computer screen for the typing condition. Typing was performed via Microsoft PowerPoint 12.1 on a Mac OSX 10.4.2 laptop. The laptop was connected to a modified keyboard so that children could easily identify the shapes and letters in these conditions. Letter and shape stimuli were counterbalanced across all conditions. In total, each participant had direct motor experience with twelve letters (Y, U, D, T, S, W, P, L, C, H, R, K) and twelve shapes (flower, crescent, circle, parallelogram, leaf, rectangle, semicircle, triangle, star, raindrop, arrow, pentagon)—four of each in each condition. An additional 12 letters and shapes were used as controls, in that they were not practiced during training, but were shown during the imaging session.

2.3. Procedure

2.3.1. MRI acclimation

After screening and informed consent, children were acclimated to the MRI environment by watching a cartoon in an artificial scanner. We performed this exposure prior to training to identify children who could not stay still for long enough, or who were uncomfortable in the environment, so that those participants did not have to undergo training. Participants heard simulated scanner sounds and were instructed to inhibit head and body motion while inside the scanner. A replica head coil was also used and children were packed securely with foam to acclimate them to this experience. If participants were comfortable and could stay still in the artificial scanner, they moved on to the training session. Five children were excluded from the study at this stage due to discomfort in the artificial scanner.

2.3.2. Training in the visual–motor tasks (tracing, drawing and typing letters and shapes)

Participants were seated at a desk with the experimenter seated beside them. Children participated in a single training session involving six conditions presented in random order. Participants were asked to trace, draw, and type capital letters and shapes. They repeated each action eight times with a single stimulus before advancing to a different stimulus within the same visual–motor condition. For example, a child might start with drawing the letter 'T'. This would be repeated eight times, while the experimenter held up the index card model throughout the trials. Then the child might proceed to drawing a circle, which they would draw eight times. Once four letters and four shapes were drawn, the child would move on to the next visual–motor condition, for example, typing. The stimuli presented within a condition were shown in a random order, but no stimulus was repeated for a child. Throughout a given stimulus condition, the index card would be held up by the experimenter such that the child could refer to the stimulus at all times. The stimulus was not named by the experimenter, and if the child named the stimulus the experimenter did not give explicit feedback as to whether the name was correct or not. The training session took approximately 30 min to complete.

2.3.3. Evaluation

Prior to scanning, guardians filled out the *Movement Assessment Battery for Children 2* [29] to determine the participants' motor competence and non-motor factors that might affect movement. After scanning, participants completed a series of inventories that evaluated their verbal and spatial knowledge. Selected subtests of the *Bader Reading and Language Inventory* [5] assessed phonemic awareness, letter identification, and visual word discrimination. We used one subtest of the *Beery–Buktenica Developmental Test of Visual–motor Integration* [7] to evaluate the translation of visual shape information into a written form. Children were also asked to identify the shapes presented during scanning.

2.3.4. Imaging session

Prior to actual scanning, parents filled out a medical questionnaire to assess possible safety issues and parents and children were again asked for their consent verbally to continue with the experiment (they had already signed a consent form). Once the child was placed in the actual MRI scanner, they watched a cartoon to get comfortable; that also allowed us to gather a high-resolution anatomical brain scan. This scan took 3.5 min, after which the child was given instructions for the functional runs, and they commenced.

We conducted 3–4 functional runs, depending on the child's comfort level. Throughout functional scanning, children were told to look at the stimuli, resulting in a passive viewing task. Each run was 4 minutes, 55 s long, and contained 8 blocks (six training and 2 control). Control blocks contained letters or shapes that had not been experienced in the training session. Prior to the first block, a 20 s fixation cross was presented that children simply watched. Each block consisted of 16 stimuli from one of the conditions, and blocks were separated by a 10 s interval where children saw only a fixation cross. Because each condition only consisted of 4 training stimuli, these were repeated 3 times in random order within each block. Stimuli within the block (from a single condition) were randomized, and each stimulus was presented for 1 s with 0.5 s between stimulus presentations, thus each block was 24 s long. Each run contained the same blocks reflecting all 8 conditions, but in a different order for each run. The entire imaging session took approximately 20 min. A researcher stood in the scanner room touching the child's leg to ensure that the participants felt safe and were sufficiently inhibiting movement.

2.3.5. fMRI data acquisition

Imaging was performed using a 3-T Siemens Magnetom Trio whole body MRI system and a phased array twelve channel head coil, located at the Indiana University Psychological and Brain Sciences department. Images were presented via SuperLab Pro 4.0.7.b software on a Mac OSX 10.6.4 laptop. All stimuli were then back-displayed by a Mitsubishi XL30 projector onto a screen that participants viewed through a mirror in the bore of the MRI scanner. Whole Brain axial images were acquired using an echo-planar technique ($TE = 30$ ms $TR = 2000$ ms, flip angle $= 90°$) for BOLD based imaging. The field of view was $22 \times 22 \times 9.9$ cm³, with an in plane resolution of 64×64 pixels and 33 slices per volume that were 4 mm thick with a 0 mm gap among them. The resulting voxel size was 3.0 mm × 3.0 mm × 4.0 mm. Functional data underwent slice time correction, 3D motion correction, linear trend removal, and Gaussian spatial blurring (FWHM 6 mm) using the analysis tools in Brain Voyager ™. Individual functional volumes were co-registered to anatomical volumes with an intensity-matching, rigid-body transformation algorithm. Voxel size of the functional volumes was standardized at 1 mm × 1 mm × 1 mm using trilinear interpolation. High-resolution T1-weighted anatomical volumes were acquired prior to functional imaging using a 3D Turbo-flash acquisition (resolution: $1.25 \times 0.62 \times 0.62$ mm³, 128 volumes).

2.3.6. Data analysis procedures

A Regions-of-interest (ROI) analysis was performed using anatomical localization of the anterior and posterior fusiform gyri as reported previously [31], in each individual brain. The fusiform gyrus is bounded by the lateral occipital sulcus laterally, by the collateral sulcus medially, and by the anterior and posterior collateral sulci rostrally and caudally [19]. The distance between the lateral occipital sulcus and the collateral sulcus was on average 10 mm—this provided the extent of the ROI in the X dimension. In the Z dimension, our ROIs began on the ventral surface of the temporal lobe and extended 10 mm dorsally. In the Y dimension, we acquired a 20 mm distance from the anterior to the posterior collateral sulcus, then split this region into two equal segments, 10 mm each. Thus, both the anterior and posterior ROIs were $10 \times 10 \times 10$ mm³. The data from these regions was then extracted from each individual, and peak activation within each region was used as a data point in subsequent analyses. We also calculated average activation for each condition, but these data are not reported here because the results were consistent with the peak-based analyses. A 4 (visual–motor training condition and control) $\times$ 2 (shapes and letters) repeated measures omnibus ANOVA was performed on the resultant data, and simple effects analyses and a priori *t*-tests were performed on conditions of interest.

In addition to the ROI analysis, we also performed whole-brain contrasts within each individual and across the combined group. The functional data were analyzed with a random effects general linear model (GLM) using Brain Voyager's™ multi-subject GLM procedure for the group, and with a fixed affects GLM (FDR corrected) for the individuals. The GLM analysis allows for the correlation of predictor variables or functions with the recorded activation data (criterion variables) across scans. The predictor functions were based on the blocked stimulus presentation paradigm of the particular run being analyzed and represent an estimate of the predicted hemodynamic response during that run. Any functional data that exceeded 5 mm of motion on any axis were excluded from the analyses. Out of 1872 volumes collected, only 10 were omitted due to movement. Exclusion of these data does not significantly alter the power of the present analyses. To further limit the effects of movement in the data, we used 3 axes motion parameters as regressors in the General Lineal Model applied to the data—these were not included in the analyses. Data were left in native space for individual contrasts, and were also transformed into a common stereotactic space (e.g. [69]) for group whole-brain comparisons. In our group data, we used the BrainVoyager Cluster-Level Statistical Threshold Estimator plugin to control for multiple tests. The plugin estimates the cluster-size threshold necessary to produce an effective alpha < 0.05, given a specific voxel-wise *p*-value, using Monte Carlo simulation. The statistical significance of clusters in a given contrast was first assessed using a random-effects between-groups ANCOVA model. Voxel-wise significance was set at $p = 0.001$. The Cluster-Level Statistical Threshold Estimator plugin estimated a cluster-size threshold of six 3 mm³ voxels. Only clusters that exceeded this threshold were considered for interpretation.

3. Results

3.1. Literacy evaluations

Participant performance on the *Movement Assessment Battery for Children, Bader Reading and Language Inventory* [5], and the *Beery–Buktenica Developmental Test of Visual–motor Integration* [7]

was all within the typical range for all children tested and there were no outliers detected in any of our measures (by ESD method) (see Table 1 for scores). Note that these tests were administered only to ensure that our participants were performing within a normal range and were not included for data analyses. In addition, all children were able to identify the shapes that were used during scanning.

3.2. fMRI

Two types of analyses were performed. The first, a region-of-interest analysis, provided an in-depth look at processing in the fusiform gyrus. This neural region is known to be engaged in letter processing in the literate individual [20,24,34] and it was affected by children's letter printing experience in James [31]. The second analysis probed whole brain functioning to see how the different training conditions engaged other regions of the brain.

3.3. Region-of-interest analyses

The fusiform gyrus was localized in each individual with anatomical markers described in detail below and in James [31]. The data from four $10 \times 10 \times 10$ voxel regions were extracted and repeated-measures analyses of variance – 4 (visual–motor training condition and control) $\times$ 2 (shapes and letters) – were run on the resultant data in each region of interest. Following this analysis, simple effects analyses (one-way repeated measures ANOVAs) were performed contrasting overall effects of letters verus shapes in each region; then *a priori* t-tests were performed comparing the effects of the letters in each possible pairing of different visuo-motor training conditions.

3.4. Right anterior fusiform gyrus

In the right anterior fusiform, the ANOVA revealed a significant main effect of training condition ($F(1,14)=3.2$, $p < 0.05$ (MSe$=0.047$)), but no main effect of stimulus type, and no interaction (see Fig. 1a).

To better understand the main effect of training, t-tests comparing overall (collapsing across stimuli) differences between pairs of training types were performed. These tests revealed a significant difference between activation levels in response to drawn stimuli overall (mean percent BOLD signal change$=0.49$) compared with control stimuli overall (mean$=0.32$: $t(14)=3.2$, $p < 0.005$, Cohens $d=0.84$) and to traced stimuli overall (mean$=0.44$) compared with control stimuli overall (mean$=0.32$: $t(14)=2.5$, $p < 0.01$, $d=0.65$). Because of the lack of interaction, no further tests were performed on these data.

3.5. Left anterior fusiform gyrus

In the left anterior fusiform, the analysis of variance revealed significant main effects of both stimulus type (letters vs. shapes: $F(1,14)=21.5$, $p < 0.0001$ (MSe$=0.01$)), and training condition (draw, trace, or type: $F(3,42)=23.5$, $p < 0.0001$ (MSe$=0.01$)). However, a significant interaction was also revealed ($F(3,42)=7.0$, $p < 0.001$, (MSe$=0.008$)).

Simple effects demonstrated that the main effect of stimulus was due to greater BOLD activation to letters than to shapes in this neural region ($t(14)=4.6$, $p < 0.0001$, $d=1.2$), as letters combined had a percent BOLD change of 0.69 from baseline, whereas shapes overall recruited a 0.55 percent BOLD signal change in this region.

Table 1
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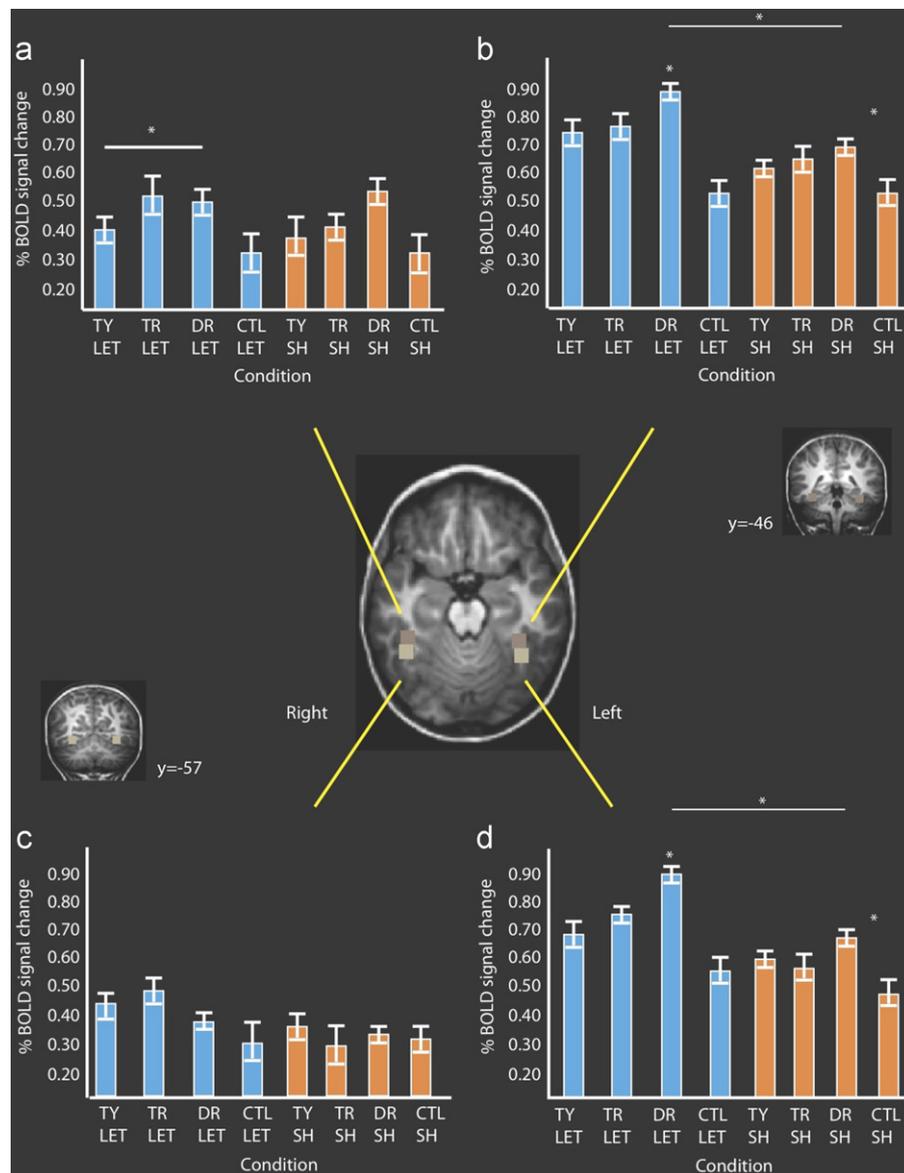| Partic.	Age (mo)	Sex	Phonemic awareness % correct	Letter ID % correct	Visual discrimination % correct	Object discrimination % correct	Object ID % correct
AB	54	f	100	92.3	28.6	55.6	55.6
AM	54.9	f	87.5	88.5	28.6	33.3	66.7
BD	59.7	m	37.5	69.2	28.6	51.9	72.2
DS	53.7	m	75	96.2	42.9	71.4	38.9
EB	58.9	f	37.5	19.2	14.2	55.6	72.2
HM	53.8	f	56.3	100	42.9	59.3	50
JB	60.8	m	37.5	80.8	28.6	44.4	38.9
KJ	60.1	f	43.8	11.5	42.9	59.3	50
MM	48.8	m	37.5	76.9	28.6	37	61.1
NH	58.6	f	56.3	96.2	21.4	22.2	50
PM	61.8	m	93.8	100	42.9	55.6	66.7
SS	53.8	f	43.8	23.1	35.7	44.4	44.4
TB	60.4	m	68.8	100	21.4	59.3	44.4
TM	57.6	f	100	100	35.7	48.1	66.7
Means			62.52	75.28	31.64	49.81	55.56
Stdev			24.63	32.57	9.20	12.71	11.94
Sterr			6.36	8.41	2.38	3.28	3.08
Z-scores using ESD method for outlier detection							
AB			−1.52	−0.52	0.33	−0.46	0.00
AM			−1.01	−0.41	0.33	1.30	−0.93
BD			1.02	0.19	0.33	−0.16	−1.39
DS			−0.51	−0.64	−1.22	−1.70	1.39
EB			1.02	1.72	1.90	−0.46	−1.39
HM			0.25	−0.76	−1.22	−0.75	0.47
JB			1.02	−0.17	0.33	0.43	1.39
KJ			0.76	1.96	−1.22	−0.75	0.47
MM			1.02	−0.05	0.33	1.01	−0.46
NH			0.25	−0.64	1.11	2.17	0.47
PM			−1.27	−0.76	−1.22	−0.46	−0.93
SS			0.76	1.60	−0.44	0.43	0.93
TB			−0.25	−0.76	1.11	−0.75	0.93
TM			−1.52	−0.76	−0.44	0.13	−0.93

Fig. 1. Results of the region-of-interest analyses in the bilateral fusiform gyrus. Percent BOLD signal change during perception as a function of training condition in all children is depicted. Abbreviations: TY: type; TR: trace; DR: draw (print); CTL: control; Let: letters; SH: shapes. All letter training conditions are depicted in blue, shape conditions in orange. Error bars depict standard error of the mean. Data is depicted from the (a) left anterior fusiform gyrus, (b) right anterior fusiform, (c) left posterior fusiform, and (d) left posterior fusiform. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

A priori t-tests comparing the letter training conditions (see Fig. 1b) revealed significant differences between printing letters (mean % BOLD signal change 0.85) and typing letters (mean % BOLD signal change 0.73: $t(14)=5.6$, $p < 0.0001$, $d=1.5$), and between printing letters and tracing letters (mean BOLD signal change $=0.76$) ($t(14)=4.3$, $p < 0.001$, $d=1.2$). However, there was no difference in this region between typing letters and tracing letters ($t(14)=0.1$, ns). In addition, there was a significant difference between drawing shapes and control shapes ($t(14)=4.0$, $p < 0.001$, $d=1.05$) but no differences in this region among the other shape conditions.

3.6. Right posterior fusiform gyrus

In the right posterior fusiform, the ANOVA revealed no significant main effects or interactions, although a trend towards a main effect of stimulus was shown ($F(1,14)=3.9$, $p < 0.06$, MSe$=0.025$), in that letters (mean percent BOLD signal change$=0.42$) recruited this region more than shapes (mean percent BOLD signal change$=0.36$: see Fig. 1c).

3.7. Left posterior fusiform gyrus

In the left posterior fusiform, the overall ANOVA produced main effects of both stimulus type (letters vs. shapes: $F(1,14)=27.6$, $p < 0.0001$ (MSe$=0.018$)), and training condition (draw, trace, type: $F(3,42)=14.2$, $p < 0.0001$ (MSe$=0.017$)), and an interaction between the two ($F(3,42)=4.7$, $p < 0.01$, (MSe$=0.009$)).

Simple effects revealed that, as in the anterior fusiform, the main effect of stimulus was due to greater BOLD activation in response to letters than to shapes in this neural region ($t(14)=5.3$, $p < 0.0001$, $d=1.4$): letters combined had a percent BOLD change of 0.57 from baseline, whereas shapes combined produced a 0.45 percent BOLD signal change in this region.

A priori t-tests comparing the letter training conditions (see Fig. 1d) revealed a significant difference between printing letters (mean % BOLD signal change 0.86) and typing letters (mean % BOLD signal change 0.76: $t(14)=5.9$, $p < 0.0001$, $d=1.6$), and between printing letters and tracing letters (mean BOLD signal change$=0.73$: $t(14)=3.9$, $p < 0.001$, $d=1.02$), but no difference in

this region between typing letters and tracing letters ($t(14)=0.9$, ns). There was also a significant difference between drawing shapes and control shapes ($t(14)=4.2$, $p < 001$, $d=1.1$), but no other significant differences among shape conditions.

3.8. Whole-brain analyses

Although our hypotheses centered on visual processing changes due to training, and specifically changes in processing in the fusiform gyrus, we also wanted to see whether the training conditions differed from one another in other regions of the brain. To this end, we performed contrasts of interest in individual brains and also averaged activation together using Talairach transformations on each individual prior to grouping. Preliminary results from our lab have demonstrated that transformations of a group of 5-year-old children's brains into Talairach space are not significantly different from transformations performed on adult's brains (unpublished data). Nonetheless, given the mixed opinions on whether or not transforming brains of 5-year olds into an adult template is a valid procedure (see [11,23,38]), we report only those contrasts that were observed both at the individual *and* at the group level. For brevity, we report and display averaged data here. Results reflect our random-effects analyses, and all results are reported at $p < 0.001$, FDR corrected. Talairach coordinates and ranges are reported in Table 2.

3.9. Letter vs. shape processing

Our first contrast of interest was to test the hypothesis that viewing untrained letters versus shapes will not recruit different regions in the child's brain, this is a measure of how the child's brain reacts to these stimuli without any of our training. There were no significant differences in the group contrasts of activations in the control letters and control shapes conditions—without any practice, letters and shapes were not processed differently in the brains of these children. We then tested whether or not our specific training experiences would alter this pattern—would the training result in different neural recruitment of regions processing letters versus shapes? There were no differences in brain activation patterns to letters versus shapes after typing or tracing experience.

However, there was greater activation in several regions during letter perception than during shape perception following *printing* and *drawing* of letters and shapes. Significant differences were observed in the left intraparietal sulcus/superior parietal lobule and bilateral precentral gyri—activation was significantly higher when viewing letters than shapes (see Fig. 2 and Table 2). These regions are components of a motor system, and their higher levels of activation during letter perception may reflect re-activation of motor systems that are letter specific. Other regions visible in Fig. 2 were not of a significant cluster size.

3.10. Differences resulting from typing, tracing and printing letters on letter perception

Our second contrast was designed to investigate how the different letter training conditions affected letter perception.
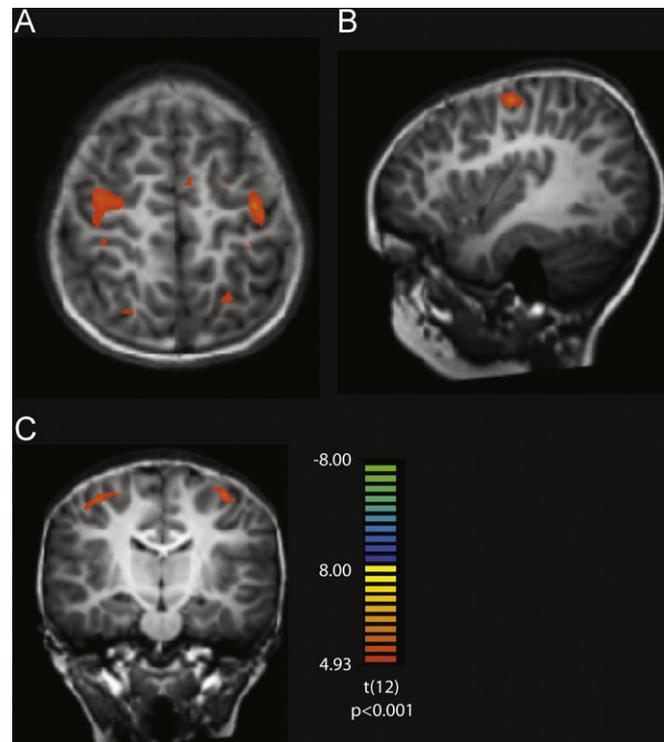

Fig. 2. Voxel-wise whole brain contrast between training printing letters and drawing shapes. Figure depicts significant activation in the bilateral precentral gyri and the bilateral inferior parietal lobe. (A) Horizontal section $Z=55$; (b) sagittal section; (c) coronal section, $Y=-15$. See Table 1 for full Talairach co-ordinates.

Table 2
Whole brain contrast results.

Contrast	Region	Talairach peak (X,Y,Z)	X range	Y range	Z range	Total voxel size
Print letters vs. draw shapes (Fig. 2)	Left IPS	−25, −60, 57	−22…−29	−58…−63	56…0.69	104
	Right IPS	21, −67, 57	20…0.25	−66…−68	57…0.58	40 n/s
	Left precentral gyrus	−38, 16, 57	−34…−41	−11…−24	51…0.61	491
	Right precentral gyrus	39, −11, 53	32…0.44	−7…−24	45…0.57	1497
	Left postcentral gyrus	−35, −35, 57	−33…−36	−34…−38	54…0.58	42 n/s
	Right postcentral gyrus (anterior)	32, −34, 57	31…0.35	−32…−35	54…0.56	41 n/s
	left cingulate	−7, −5, 57	−5…−8	−4…−8	57…0.57	25 n/s
Print letters vs. type letters (Fig. 3a and b)	Left IFG	−41, 31, 6	−38…−46	24…0.37	2…0.13	1857
	Left ACC	−13, 26, 41	−7…−15	21…0.32	38…0.45	486
	Right ACC	10, 29, 36	10…0.13	26…0.36	33…0.38	307
	Left IFG	−46, 20, 13	−43…−50	18…0.25	10…0.15	222
Print letters vs. trace letters (Fig. 3c)	Left IPS	−34, −47, 56	−26…−42	−42…−52	47…0.60	1195
	Left SPL	−17, −53, 60	−13…−21	−51…−58	55…0.60	554
	Left precentral gyrus	−28, −25, 60	−24…−31	−24…−30	58…63	135
Trace letters vs. type letters (Fig. 3d)	Left IFG	−35, 27, 7	−30…−38	23…0.29	5…0.11	521
	Right IFG	41, 27, 7	41…0.44	26…0.31	3…0.5	101

Here, we compared the three letter training conditions with one another. First, we compared letter perception after *printing letters* versus *after typing letters*. There was significantly more neural activation after printing than typing in the left Inferior frontal gyrus (IFG) (pars orbitalis), also known as Broca's area (Fig. 3a). In addition, printing experience recruited the left anterior cingulate cortex more than typing experience (Fig. 3b). There were no areas that were more active after typing experience than after printing experience. Next, we compared letter perception after *printing experience* versus *after tracing experience*. Here, greater neural activation after printing experience was observed in the left IPS, SPL and precentral gyrus (Fig. 3c). Again, there were no regions more active during letter perception after tracing letters than after printing letters. Finally, the comparison of activation during letter perception after *experience tracing letters* versus *after experience typing* letters found greater activation in the bilateral IFG after tracing, but no areas of greater activation after typing (Fig. 3d).

In sum, the results of the whole brain analysis suggest that (a) only after practice printing letters does the brain respond differently during letter versus shape perception; (b) that free-form printing and tracing practice both result in the recruitment of the inferior frontal gyrus during letter perception; (c) that free-form printing experience recruits posterior parietal regions and the precentral gyrus more than tracing experience during letter perception; and (d) that typing experience does not recruit any brain regions more than other sensori-motor conditions during letter perception.

4. Discussion

Overall, the results of this study support the hypothesis that after self-generated printing experience, letter perception in the young child recruits components of the reading systems in the brain more than other forms of sensori-motor practice. Specifically, after self-generated printing experience letter perception recruits the IFG, left ACC and the fusiform gyrus more than after typing; and printing experience recruits posterior parietal cortex and the fusiform gyrus more than does tracing experience. The IFG, fusiform gyrus and the posterior parietal cortex (PPC) are all regions that are known to subserve reading in the literate individual (cf. [66,48]), and the IFG and PPC are also involved in writing [46,50]. Thus, after printing practice, the brain activates a network used for reading and writing.

4.1. Motor cortex activation after self-generated printing

Experience printing letters recruits the motor cortex, specifically the precentral gyrus, more than does experience drawing shapes. The Activation of the motor cortex during perceptual tasks has been well documented, but only occurs if the percept represents an item that has been interacted with previously. The results of the whole brain analyses reported here replicate previous work showing that letter perception activates the motor cortex [33,41]. We, and others [41,42], maintain that this activation is due to our motor experience writing letters that is re-activated during visual perception. That is, the visual and sensori-motor representations of letters are not only associated to one another during learning, but also interact during subsequent letter processing forming a functional network. Our current work further suggests that parts of this network are experience-specific in the young child. That is, the motor regions were recruited more only after self-generated printing practice was performed.

The left precentral gyrus has also been shown to be recruited during letter writing [39,58] and letter perception [33]. Thus, we show here that letter perception activates regions that are recruited during letter writing, similar to Longcamp et al. [41] and James and Gauthier [33], but only if the observer has practice printing letters.

Further, our results show *bilateral* activation of the precentral gyrus rather than unilateral as demonstrated in previous work [39,58]. However, these previous findings tested seasoned readers and writers [41,33]. Because the children in the present study have immature fine-motor systems and are just starting to write, their handedness may not be well established. Degree of handedness increases between ages 3 and 7 and sometimes continues to strengthen up to 9 years of age [49]. In addition, the bilateral activation shown here may reflect early cortical involvement that is less focal than later involvement, supporting the "interactive specialization" theory (cf. [36,37,62]).

4.2. Inferior frontal gyrus activation after printing and tracing

Experience forming letters through self-generation as well as through tracing activated the IFG more than experience typing
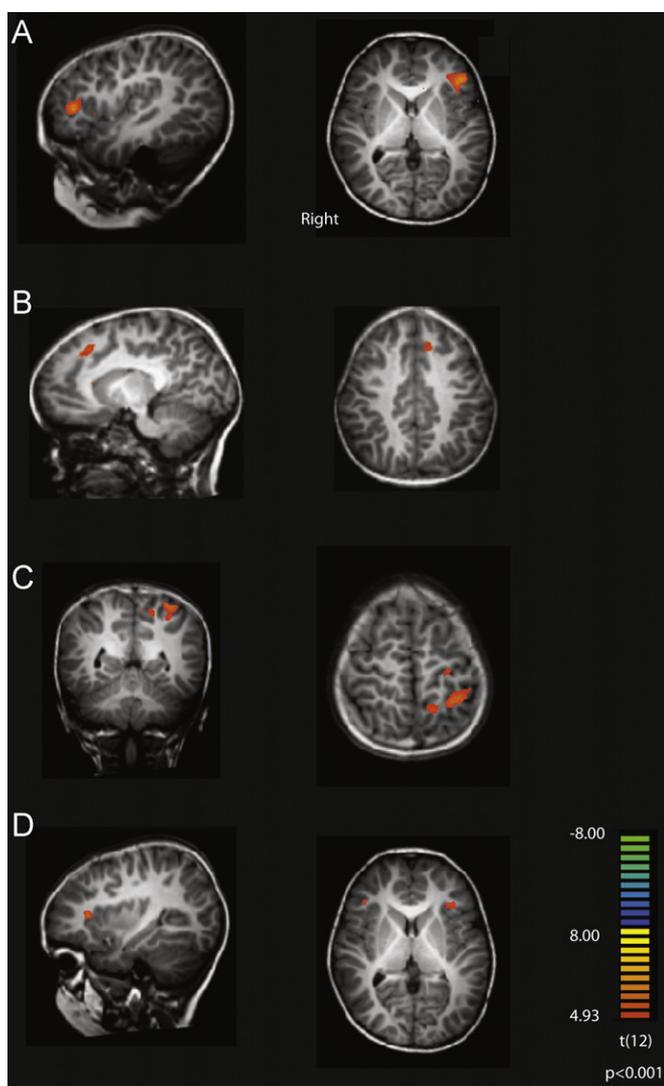

Fig. 3. Voxel-wise whole brain contrast of (a) printed letter trainings > typed letter training, depicting the left IFG activation and (b) the left ACC activation. Contrast of printed letter training > traced letter training is depicted in (c) showing the IPL and SPL activation and (d) depicts the traced letter training > - typed letter training. See Table 1 for Talairach coordinates.

letters. Thus the IFG appears to be involved in motor generation of letters, feature-by-feature. The IFG is a heterogenous area that has been linked to numerous cognitive functions, one of its best-known functions, however, is in language production. Here we demonstrate that experience with language production by hand—printing, also recruits this region. This finding could reflect sub-vocal rehearsal of the letter names prior to printing them, although one would expect that this letter naming may also occur during our other conditions, especially typing, where the letter name is probably kept in mind while the letter is searched for on the keyboard. Interestingly, an electrophysiology study also found involvement of the IFG during writing, and although this region does not usually emerge as active during writing using fMRI (e.g. [50,58]), it has been shown to be active during letter perception [20,33], although not as commonly as other premotor regions in the frontal lobe. Interestingly, in the present study, the IFG does not emerge as significantly active during all letter perception conditions, only during perception of letters that were printed or traced—perhaps this specificity may account for why the recruitment of the region is variable among studies. The difference among these conditions could only emerge from the training episode, copying and tracing involving a feature-by-feature construction of a letter compared to the search and type procedure in typing. Linking features together in an organized way to form a whole is also important in forming words and sentences (a well-known function of the IFG); therefore it may be this particular aspect of printing experience that requires the IFG. Accessing a stored motor program of a letter-form may also be important for letter identification. We suggest that the IFG is maybe required to access stored information regarding fine motor skill plans and those that organize features together in a meaningful way; thus it is involved with motor planning, control and execution. Typing does not require a fine motor plan, as the movement is the same for all letters. The sequence of movements required for printing a particular letter (the motor plan) may be (a) activated due to the association formed during learning, or (b) used during visual perception to augment visual letter processing. In either scenario, activation in the IFG during letter perception may reflect activation of letter specific motor plans.

4.3. Posterior parietal cortex (PPC) recruitment during letter perception

The posterior parietal cortex was recruited during letter perception after self-generated printing practice more than drawing shapes and tracing letter practice. Thus, the IPL and, to a lesser extent, the SPL appear to be specifically recruited after printing but not after any other type of practice. Interestingly, others have shown recruitment of the IPL and SPL during writing ([47,50,58]). Here we can begin to understand what part of the writing process requires the PPC because of our differential effects of printing vs. tracing. Both free-form printing and tracing experience involved copying a letter that was always displayed (either on a card in front of child for copying, or on a sheet of paper for tracing), constructing a visual image of the letter was not necessary in either type of practice. However, the two tasks differ in at least two important ways: (a) self-generated printing that does not follow a visual guide (as in tracing) requires fine motor execution that is quite different from tracing. That is, the printer must keep track of strokes being performed, and link them in a way that forms the letter in question. This task requires more vigilance in terms of fine motor skill as well as adhering to learned spatial relationships among features. And (b) that the output of the two types of practice are visually very different. We will discuss these two hypotheses in turn below.

Research has pointed towards an important role of the anterior intraparietal sulcus (AIP) in attention directed towards motor activities. Termed 'motor attention' [59], because the mechanisms seem to underlie attention to limb movements independently of visual cueing. Further, left AIP and the supramarginal gyrus are involved more with motor attention to hand movements than is right AIP, that is recruited more during ocular motor attention [60]. It is quite possible that during printing, motor attention is engaged more than during tracing and this increased activity is reactivated during visual perception of letters.

Other work has pointed towards the posterior parietal cortex playing a role in graphomotor representation [65]. In this study, writing of letters recruited both the right IPS for newly learned letters and bilateral IPS during execution of well-learned letters. In addition, both the IPS and SPS were recruited during imagery of the motor plan for producing letters, suggesting that both motor plans as well as execution may require the posterior parietal lobe. Our results add to this idea, only self-generation of letters recruited the PPC, suggesting that the motor plans, and not execution per se require the participation of the PPC.

A second hypothesis for the role of the PPC during letter processing is that the output of the motor actions that are then visually processed is very different when comparing self-generated printing vs. tracing. In the case of printing, the child sees the messy, non-stereotypical form of the letter that they are trying to copy, whereas after tracing, the child sees the usual form of the letter. One hypothesis that we have put forth is that viewing these non-stereotypical forms may aid in constructing broad categories of letters that may facilitate letter recognition. The visual processing capacity of the parietal cortex has long been known (e.g. [51]), but most accounts suggest that this role is strictly for visually-guided action in real time. Our results suggest that visual perception without action also recruits the parietal cortex, but this perception may require a history of actions pertaining to the perceived item. Recent work has shown a role for the intraparietal sulcus in categorization of visual information in non-human primates [68], and a significant functional related-ness between ventral temporal reading regions and the posterior parietal cortex in humans has been demonstrated [70]. These recent findings suggest that visual association regions may have an important connection to the PPC. Further, the PPC has important connections to the premotor regions in the frontal lobe (cf. [2]), presumably providing input to the motor system, for planning and execution of movement. Thus, the PPC can be considered to be part of a vision and action system, perhaps providing visual information to motor regions, or integrating visual and motor information. These speculations require further testing in both the visual and motor domains.

4.4. Anterior cingulate recruitment after printing practice

The role of the anterior cingulate cortex is much debated, but is usually observed during tasks that involve cognitive control, and specifically, during conflict monitoring and error detection during decision tasks [9,10]. Interestingly, the participants in our experiment were not required to perform any task during scanning, and thus, we have asserted that the differences seen during letter perception are due to our training conditions. The fact that the ACC is recruited more during the perception of letters that were printed rather than typed suggests that perhaps this region is re-activated after a task that required greater conflict monitoring—that is, printing does require monitoring of performance and comparing that output to stored knowledge. That printing in these young children results in many errors in the resultant form, whereas typing does not, may result in the greater ACC response seen here.

5. The role of the fusiform gyrus in letter processing

Our region-of-interest analysis clearly demonstrates that in a region known to be involved in reading and letter processing—the *left* fusiform gyrus [20,24,34,62] is recruited more after printing experience than experience in typing, tracing or simply perceiving letters (control stimuli). This novel finding extends the results of James [31] by demonstrating that it is specifically experienced in the line-by-line printing of letters, and not just any experience involving attention to, or production of letters, that has an impact on the activation of the fusiform gyrus. In addition, we show activation in the *right anterior* fusiform gyrus that is specific to drawing and tracing letters as well as to drawing shapes. As has been previously proposed, in early readers, letter processing is more bilateral than in more advanced readers [62], supporting the general notion of interactive specialization in the developing brain (cf. [37]).

The current results support previous work regarding the role of the fusiform gyrus while at the same time refining our knowledge of its relationship to motor experience. In this study, as in James [31], activation in the left fusiform gyrus was modulated as a result of motor experience. Because this region was more active after printing experience than typing or tracing suggests that there is something about printing per se that changes visual processing to letters. We believe that it is the production of variable forms of letters that results from printing that produces this change in visual processing. That it is the output from this system—the printed form that serves to create exemplars that are variable, in turn producing input to an abstract category. That is, the motor output from parietal and frontal regions creates the visual input that is processed in the fusifrom gyrus. This input may be stored along with other instances of the stimulus, serving to broaden the perceptual category that refers to a particular letter. Once exemplars of abstract categories are successfully classified, left hemisphere structures dominate visual recognition [64]. It makes sense that classifying exemplars into subordinate level categories (like letters) would recruit this region given the abundance of literature showing that experts classify their objects of expertise in the fusiform gyrus (cf. [25]). In fact we have recent research showing this phenomena with expert categorization in children—those that were experts in a category of visual objects recruited the bilateral fusiform more than novices (James and James, submitted [35]). One interesting difference in the present study and the notion proposed by Seger et al. [64] compared with the adult literature on expertise processing is that we find a greater effect in the *left* fusiform gyrus, whereas most adult experts process their expert category in the right fusiform gyrus (cf. [26]). Presumably, this is because letters are the basis of reading, which is left lateralized in the literate adult, or it may be due to the type of exemplar categorization that is being performed: that is, how diverse the exemplars are in appearance. Lateralization issues aside, the most novel result of our ROI analysis is that visual processing of letters is affected by specific motor experience—the act of printing a letter.

Interestingly, a middle frontal region, called Exner's area that is involved in actual writing in the adult (cf. Katanoda et al., 2001) was not recruited during letter perception in the current study. Previous work has found reactivation of this region during letter perception [41]; thus we expected to see activation here as well. It is possible that Exner's area is not used during letter writing in the young child, or alternatively, it may not be activated during perception in the young child, perhaps due to their lack of writing experience. We are currently investigating the time course of BOLD activation seen during writing in the young child, but currently, it is unknown why Exner's area would not be recruited during letter perception in the current study.

Learning to write letters is not a simple task; children must use their immature fine-motor skills to adopt a specific series of writing strokes for each character [22,43]. Further, the exact location of each stroke relative to other strokes, overlap of strokes and orientation of strokes are all crucial for subsequent letter identification. At the same time, the child must learn that other dimensions, such as size, slant of global form, and small features added to the strokes (as in serifs), are not important for letter recognition. Understanding the important attributes that define letter identity is not a simple task, and printing may be the gateway through which children learn the attributes of letters that are important for successful categorization.

Thus, we argue that construction of letters, stroke by stroke, helps children understand the important components that define a letter. But this creation process is not the whole story, or we would see the same results for printing free-form and for tracing. Although the actual motor tasks of printing and tracing may be very similar, the processes that occur prior to the motor act as well as the output of the motor act are both quite different. Only free-form printing leads to a non-stereotypical, noisy form of a specific letter. We assert here that this variable output is a crucial factor in learning to identify and categorize letters. Categorization based on exemplars that are variable may create a broader letter representation, leading to enhanced letter identification skill, and perhaps greater fusiform gyrus activation.

In summary, when preliterate children perceive letters, only free-form printing experience results in the recruitment of the visual areas used in letter-processing, and the motor regions seen in letter production. This finding adds to previous research showing that letter perception is facilitated by handwriting experience, and it further suggests that handwriting experience is important for letter processing in the brain.

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