

The role of sensorimotor learning in the perception of letter-like forms: Tracking the causes of neural specialization for letters

Karin H. James & Thea P. Atwood

To cite this article: Karin H. James & Thea P. Atwood (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, DOI: [10.1080/02643290802425914](https://doi.org/10.1080/02643290802425914)

To link to this article: <https://doi.org/10.1080/02643290802425914>



Published online: 07 May 2009.



Submit your article to this journal [↗](#)



Article views: 884



View related articles [↗](#)



Citing articles: 18 View citing articles [↗](#)

The role of sensorimotor learning in the perception of letter-like forms: Tracking the causes of neural specialization for letters

Karin H. James and Thea P. Atwood

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

Functional specialization in the brain is considered a hallmark of efficient processing. It is therefore not surprising that there are brain areas specialized for processing letters. To better understand the causes of functional specialization for letters, we explore the emergence of this pattern of response in the ventral processing stream through a training paradigm. Previously, we hypothesized that the specialized response pattern seen during letter perception may be due in part to our experience in writing letters. The work presented here investigates whether or not this aspect of letter processing—the integration of sensorimotor systems through writing—leads to functional specialization in the visual system. To test this idea, we investigated whether or not different types of experiences with letter-like stimuli (“pseudoletters”) led to functional specialization similar to that which exists for letters. Neural activation patterns were measured using functional magnetic resonance imaging (fMRI) before and after three different types of training sessions. Participants were trained to recognize pseudoletters by writing, typing, or purely visual practice. Results suggested that only after writing practice did neural activation patterns to pseudoletters resemble patterns seen for letters. That is, neural activation in the left fusiform and dorsal precentral gyrus was greater when participants viewed pseudoletters than other, similar stimuli but only after writing experience. Neural activation also increased after typing practice in the right fusiform and left precentral gyrus, suggesting that in some areas, any motor experience may change visual processing. The results of this experiment suggest an intimate interaction among perceptual and motor systems during pseudoletter perception that may be extended to everyday letter perception.

Keywords: Letters; fMRI; Pseudoletters; Writing; Development; Neural activation.

Functional specialization, the propensity for neural systems to be active more to one category of stimulus than to a seemingly similar category, has been thought to reflect efficient, sometimes expert,

neural processing (Downing, Jiang, Shuman, & Kanwisher, 2001; Gauthier, Williams, Tarr, & Tanaka, 1997; Tanaka & Gauthier, 1997). Functional specialization has been shown to exist

Correspondence should be addressed to Karin H. James, Department of Psychological and Brain Sciences, Indiana University, 1101 East 10th Street, Bloomington IN, 47405, USA (E-mail: khjames@indiana.edu).

The authors would like to acknowledge Thomas James for helpful comments on the manuscript and for scholarly discussion on this topic.

for several stimulus categories including faces (Kanwisher, 2000; Kanwisher, Chun, & McDermott, 1996), body parts (Downing et al., 2001), places (Kanwisher, 2000), biological motion (Grossman & Blake, 2002), words (Cohen et al., 2000), and individual letters (Flowers et al., 2004; James, James, Jobard, Wong, & Gauthier, 2005; Garrett et al., 2000; Longcamp, Anton, Roth, & Velay, 2003). In one survey of functional specialization of 20 stimulus categories in the visual cortex, Downing, Chan, Peelen, Dodds, and Kanwisher (2006) found that there were a small number of regions that were actually category selective, indicating that this is not a typical response profile for the ventral visual stream (Downing et al., 2006). Functional specialization was revealed only for faces, body parts, and places—categories of stimuli with which we are very efficient at processing. Another category of stimuli (that was not tested in the aforementioned work) that we learn to recognize extremely efficiently is composed of the written characters of our native writing system. Written characters are a particularly interesting category of stimuli because the recency of such stimuli in our evolutionary history suggests that there has been no change in our innate neural architecture that would support stimulus-specific efficiency of processing. Nonetheless, with sufficient exposure and training, individuals become extremely efficient at processing their native characters in many formats over the course of just a few years. Functional specialization for the written character has been shown in a number of studies (e.g., Flowers et al., 2004; Garrett et al., 2000; James et al., 2005). However, why this specialized neural response pattern occurs is still a topic of speculation. First we consider a set of theories that are not necessarily mutually exclusive, but that intend to offer explanations as to why functional specialization for letters occurs. We then show evidence that suggests that motor learning may play a part in the emergence of neural specialization for letters in the ventral stream.

There are several theories that have been proposed to explain why different regions become specialized for processing particular categories of stimuli. One attempt to account for functional

specialization in high-level visual areas concerns the eccentricity biases associated with different object categories (Hasson, Harel, Levy, & Malach, 2003; Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Levy, Hasson, Avidan, Hendler, & Malach, 2001; Levy, Hasson, Harel, & Malach, 2004; Malach, Levy, & Hasson, 2002). Based on results from a variety of functional magnetic resonance imaging (fMRI) studies, the authors suggested that functional specialization is a result of different resolution demands associated with different object categories. Face perception is associated with centre-biased visual areas for the detailed discrimination required, while perception of buildings is associated with periphery-biased visual areas for the large-scale integration involved. Words and letters, because of their small size, represent the extreme case of object perception requiring high resolution and foveation.

Another proposal based on stimulus processing requirements contends that specialized processing in the ventral visual processing stream may also be due to the level of categorical analysis that is required for a given task. For example, during face perception one often has to identify the face of an individual (e.g., Al Gore). Such discrimination within a homogeneous class (e.g., among other faces) requires consideration of not only the fine-grain, metric differences of features (e.g., lip thickness), but also the second-order relations among face features (e.g., interocular distance; Diamond & Carey, 1986). However, face identification at this level does not require coarse discrimination, for example whether a feature is present or absent—that is, we do not have to discern whether or not Al Gore has a nose in order to distinguish him from other people. Letter perception, in contrast, relies on the use of coarse information like feature presence/absence (e.g., an oblique stroke in “N”) and first-order relations (e.g., the oblique stroke is in between the two vertical strokes in “N”), as well as second-order relations (the angle of the oblique line is also important to distinguish an “N” from an “H”). Analyses of the stimulus properties of characters across different languages have

also shown that a high level of redundancy is introduced in their creation, such that one can perceive only part of a character and be able to distinguish it from the other alternatives (Changizi & Shimojo, 2004). Therefore, letter identification involves processing of different types of stimulus information when compared with other stimulus categories.

Other theories of ventral visual stream organization and specialization couch the problem in terms of a continuous object-form topography, such that neighbouring neural substrates tend to represent features that are more similar to each other (Carlson, Schrater, & He, 2003; Cox & Savoy, 2003; Haxby et al., 2001; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; O'Toole, Jiang, Abdi, & Haxby, 2005). An important idea of this theory is that there is no absolute neural specialization for certain object categories. Instead, there is relative preference of certain substrates for certain categories based on features, and object information is widely distributed and overlapping across the high-level visual areas. Support for this theory comes from finding that activity in category-specific areas (e.g., face-selective regions in the fusiform gyrus) contains diagnostic information for the categorization of nonpreferred categories (Haxby et al., 2001), and activity patterns over a wide region of the inferior temporal cortex correlate with physical properties of objects (O'Toole et al., 2005). It should be noted, however, that object representations in the occipito-temporal cortex are probably not completely distributed, as some regions (e.g., the face- and scene-selective areas) still enjoy a greater discriminatory power for their preferred categories than other objects (O'Toole et al., 2005; Spiridon & Kanwisher, 2002).

Another theory maintains that different parts of the ventral visual processing stream are suited for different processes. The observed object selectivity is a result of the prolonged recruitment of different substrates to fulfil specific recognition demands for different objects (Bukach, Gauthier, & Tarr, 2006; Gauthier, Skudlarski, Gore, & Anderson, 2000; Tarr & Gauthier, 2000). Accordingly, "recognition demand" and "experience" are therefore

the key factors determining the use of different substrates for different categories. This theory gains support from findings of recruitment of the face-selective areas for other types of objects like cars, dogs, birds, fingerprints, and novel objects, which are claimed to require a common perceptual demand of fine-grained discrimination and common holistic manner of processing that results from extensive experience (Gauthier et al., 2000; Xu, 2005).

These ideas allow speculation as to why the ventral visual stream may demonstrate functional specialization for letters, but how would this develop? We propose that functional specialization for letters may be caused by the way that we learn to recognize letters and, more specifically, that specialization for letters may reflect the sensorimotor integration that is required when we learn to write letters (James & Gauthier, 2006; Longcamp et al., 2003). Sensorimotor experience in the form of learning to print and write letters allows the interplay between motor production and visual perception to broaden the stored representation of letters. That is, motor construction of forms may lead to motor programmes that are stored with visual information. Because, during writing, these programmes are variable, they may serve to augment visual information, allowing very different-looking exemplars to be categorized as the same letter. Grouping visually dissimilar letters into a single category occurs before children are exposed visually to a large variety of handwriting styles or fonts, but after they learn to print. In support of the idea that sensorimotor experience may lead to functional specialization in the visual processing stream, recent work has shown that when participants view letters, a sensorimotor network becomes engaged (James & Gauthier, 2006). That is, areas in the ventral visual processing stream become active during visual perception but, more interestingly, so do motor and premotor regions of the brain (perhaps part of the dorsal stream of visual processing). This finding was interpreted as showing that neural circuits for writing letters (premotor cortex) were automatically activated upon seeing letters, implying that motor experiences were stored and reactivated

upon subsequent encounters. In addition, ventral visual areas—specifically, the left fusiform gyrus—were engaged when participants wrote letters (without seeing them), but not when they drew shapes (James & Gauthier, 2006). Thus, coactivation of brain regions that process both visual and motor information during either perceptual or motor interaction with familiar letter stimuli was shown, suggesting a sensorimotor representation of letters.

Additional evidence for coactivation of the visual processing areas and motor regions comes from a study showing common repetition suppression profiles in ventral and dorsal stream regions (Mahon et al., 2007). In this study, repetition suppression (RS), the tendency for neural activity to be reduced upon repeated stimulus presentation (Grill-Spector, Henson, & Martin, 2006), was shown to emerge for “tools” in areas in the ventral visual processing stream as well as in dorsal stream structures. In addition, the authors use a functional connectivity analysis to show that areas in the left middle temporal gyrus and the left inferior parietal lobule both show RS for tool stimuli. Here, “tools” were defined as objects whose function (how to interact with them) was apparent in their structure—arguably, objects with “affordances” (Gibson, 1979). Interestingly, objects that did not have a systematic relationship between structure and function, termed “arbitrarily manipulated” objects (e.g., book, envelope), overlapped in their RS functions with “tools” in right hemisphere ventral (middle fusiform) and dorsal stream (right caudal inferior parietal lobule) systems, but not in left hemisphere systems. This work suggests that motor information (how to interact with objects) is associated with visual object processing.

This idea is supported by behavioural work as well. There is now a substantial body of evidence that motor experience—that is, our history of interactions with some objects—can facilitate visual recognition (Harman, Humphrey, & Goodale, 1999; James, Humphrey, & Goodale, 2001; James et al., 2002) and mental rotation (Wexler, Kosslyn, & Berthoz, 1998; Wohlschläger & Wohlschläger, 1998), as well as the development of spatial maps

(Bai & Bertenthal, 1992; Campos et al., 2000; for review see Wexler & Boxtel, 2005). For example, visual recognition of novel objects is facilitated by actively moving the objects compared to watching the same movement performed by another person (Harman et al., 1999; James et al., 2001, 2002). Such behavioural facilitation supports the idea that the dorsal motor and ventral visual systems are interacting during object processing.

In addition, several neuroimaging studies have found that motor systems are automatically activated upon visual perception of some objects (Chao & Martin, 2000; Gerlach, Law, Gade, & Paulson, 2002; Grezes & Decety, 2002; James & Gauthier, 2006; Longcamp et al., 2003; Longcamp, Anton, Roth, & Velay, 2005a; Longcamp, Zerbato-Poudou, & Velay, 2005b; Mecklinger, Gruenewald, Besson, & von Cramon, 2002). This literature suggests that motor systems are active when we visually perceive objects that we regularly interact with motorically—for example, tools and utensils (Chao & Martin, 2000; Mahon et al., 2007; Mecklinger et al., 2002). Interestingly, these objects also invoke, by their appearance alone, specific ways to interact with them. That is, they contain “affordances” (Gibson, 1979) that can be used to specify motor interactions (potentially independent of our experience), and these affordances are visually perceptible. By investigating the effects of prior motor experience on visual recognition of objects without affordances, one can more directly attribute the recruitment of motor systems to experience.

Letters, by their appearance alone, do not “suggest” how we must interact with them—in this way, they are similar to the arbitrarily manipulable objects in the Mahon et al. (2007) studies. Perceiving letters, however, does seem to invoke the associated history of letter-specific motoric interactions. For instance, in a series of studies, Freyd and colleagues (Babcock & Freyd, 1988; Freyd, 1983) found that the way that a subject is taught to write a letter-like symbol directly affects their subsequent recognition of that symbol. In addition, writing experience can alter the perception of movement illusions in written symbols (Tse & Cavanagh, 2000), and knowledge of cursive stroke directions affects anticipated

letter identity (Orliaguet, Kandel, & Bois, 1997). Longcamp et al. (2005b) have demonstrated that children recognize letters more efficiently after being trained to print letters versus being trained to type letters. This latter study suggests that motor experience may be generative—the motor experience that is important for visual recognition is through constructing the form of the letter, not by the simple motor act of typing. A study conducted by Cunningham and Stanovich (1990) found similar results. They used three different modalities to teach children how to spell words. Children were presented with a word both visually and orally and were asked to spell words by writing, arranging a set of tiles, or typing the word. After spending 30 minutes training over the course of four days, children were asked to spell out each of the words on a sheet of paper, by using a computer keyboard and by arranging tiles. Results demonstrated that there were significantly more correct responses for those words learned in the writing condition versus the typing and tile conditions, and this effect emerged regardless of the format in which the children spelled the words in the test session.

Furthermore, research on individuals with literacy disabilities has also suggested a link among motor and visual systems in letter processing. Writing movements can facilitate letter recognition in patients with pure alexia—the inability to identify letters and words (Bartolomeo, Bachoud-Levi, Chokron, & Degos, 2002; Seki, Yajima, & Sugishita, 1995). Although these patients cannot recognize a letter visually, if they are allowed hand movements while they are looking at the letter, they will often trace out the shape of the letter as if writing it—and this movement (that is unseen by them) facilitates their visual recognition of letters. In addition, some dyslexic adults are delayed in motor tasks; it is possible that in such cases motor difficulties affected their letter-learning ability (Stoodley, Fawcett, Nicolson, & Stein, 2005). Similarly, children exhibiting developmental dyspraxia, a disorder that can manifest in reduced fine motor skills (including writing), often have difficulty in

letter identification and in learning to read—this disorder is highly comorbid with dyslexia (e.g., Portwood, 2000). Furthermore, a patient has been reported with agraphia (inability to write) with alexia that has resulted from damage to the left premotor cortex (Anderson, Damasio, & Damasio, 1990). Although this patient cannot read or identify letters and cannot write letters or words, she can draw complex shapes, and she can write numbers. This case provides some evidence that damage to the motor system can affect not only writing, but also visual processing of letters. It also shows that the motor deficit can be very circumscribed to one particular category of stimuli.

The neuroimaging, patient, and behavioural results outlined above have revealed an interesting aspect of letter recognition—while we ultimately spend a lot of time reading words, it is the isolated letter that we need to learn first, and we learn this stimulus by seeing and writing. The work presented here investigates whether this aspect of letter processing—the integration of sensorimotor systems—leads to functional specialization in the visual system. The left fusiform gyrus of the literate adult is already specialized for processing letters more than other, similar characters (Flowers et al., 2004; Garrett et al., 2000; James & Gauthier, 2006; James et al., 2005). Therefore, it is difficult to assess the effects of writing experience on the development of this specialization. We therefore conducted a training study that directly compared the effects of writing experience, typing experience, and visual-only experience on visual “letter” processing. Because adults have already learned letters, however, we trained them on a group of letter-like characters, referred to here as “pseudoletters”. In this way we investigated the effects of motor experience on visual recognition and on neural processing.

Method

Participants

A total of 18 participants gave informed consent according to the guidelines of the Indiana University Human Participants Review Board and were paid for their participation. All were undergraduate or graduate students enrolled

at Indiana University. All participants were right-handed and reported normal or corrected-to-normal vision, had English as their first language, and had no known history of neurological or psychiatric disorders. A total of 10 females and 8 males participated, and they were between the ages of 21 to 31 years with a median age of 23.5 years.

Stimuli

Stimuli were 96×96 pixels and were presented in isolation, in the centre of a computer screen. Stimuli included a group of 18 capital letters (H, A, F, C, S, U, K, N, T, B, D, G, R, J, L, P, Z, Y), 18 shapes and symbols (e.g., clover, heart, percentage sign, pound sign, treble clef, star, etc.), 18 pseudoletters (studied), and another set of 18 pseudoletters (unstudied; see Figure 1). Each of these groups had four more subsets—an Arial font group, a serif-type font group, a cursive-type font group, and a rotation group (consisting of each stimulus rotated 0, 45, 90, and 180 degrees). Stimuli that lacked noticeable difference when rotated were not used—for example, the letter “O” and the shape of a square were not used because each of these symbols, when rotated 180 degrees, are no different from their counterparts oriented at 0 degrees rotation. Different formats of the stimuli were used to add variation to the stimulus sets and to attempt to make

matching tasks more difficult in the behavioural portion of the experiment. All orientations and font types were used in the matching task, both within the scanning environment and outside.

General procedure

There were four sessions in total, and each session was separated by one day of rest: First, there was a pretraining imaging session (a “pretrain scan”), which helped to determine the participant’s initial blood-oxygen-level-dependent (BOLD) activation to the novel (pseudoletter) alphabet as well as to letters and simple shapes. Participants then took part in two training sessions, separated by one day. The training sessions consisted of training procedures, followed by behavioural testing. We included testing in these training sessions to (a) assess whether or not the training had any effect from Day 1 to Day 2 and (b) to motivate the participants to learn the stimuli. All testing procedures involved visual tasks only. After training, participants took part in a final posttraining imaging session (a “posttrain scan”) to determine whether any change in BOLD activation patterns had occurred as a result of the training sessions.

Scanning protocol. Both pre- and posttraining scanning sessions proceeded in the same manner. All stimuli were back-displayed with a Mitsubishi XL30 projector onto a screen that was viewed through a mirror from the bore of the Siemens Trio 3T scanner. Stimuli were presented with SuperLab Pro 2.0.4 software with Dell Inspiron 6000 laptops. Each scanning session consisted of six runs. The first five runs were functional scans that measured activation to our stimulus conditions, and the final run was a high-resolution anatomical scan. Conditions were presented in a blocked design: Each block contained 16 different presentations of the stimulus condition. Each run consisted of the same stimulus blocks, but the order of the blocks was randomized across runs. Order of runs was varied across participants. Each run began and ended with a 16-s fixation cross and, in addition, consisted of 16 blocks of experimental trials: 4

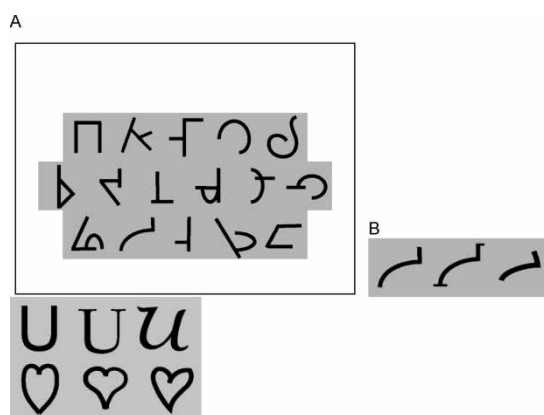


Figure 1. A: Example of pseudoletter stimuli. B: Font types: sans serif, serif, cursive.

stimulus types (letters, studied pseudoletters, unstudied pseudoletters, and shapes) \times 2 change conditions (font or rotation) \times 2 repetitions. Within each block, participants were required to perform a one-back matching task by pressing a button with their right index finger when two stimuli presented consecutively possessed the same category identity (an identity that is shared regardless of font type or orientation). That is, participants had to detect whether an “A” was an “A” regardless of font or orientation. Stimuli in each block were pseudorandomized such that there were at least two repetitions (one-back match) of a stimulus in each block. The one-back perceptual match task was used to maintain attention. Participants pressed a button with their right index finger when an image was repeated irrespective of font or orientation. This task was described to the participant prior to scanning. Stimuli were presented in the centre of the screen for 500 ms, followed by a Gaussian noise mask presented for 500 ms. There were 16 presentations of stimuli within each block, and the ratio of repetitions to nonrepeats was 1:7 (making this a very easy task). The stimuli that were presented within a block were randomly selected such that not every Rotation \times Stimulus combination was presented, the only requirement being that an average of two repetitions occurred in each block. Each block was separated by a 10-s fixation cross.

Training Sessions 1 and 2

Both training sessions were run in the same manner, although the order of the behavioural tests varied. All stimulus presentations were run on a Dell Optiplex GX 280 desktop computer, via SuperLab Pro 2.0.4 software, and response time and accuracy data were collected via a computer keyboard. Participants were randomly assigned to one of three conditions: a writing condition, a typing condition, or a visual condition. Each condition consisted of four training exposures and six behavioural tests. The training exposure varied according to the condition (writing, typing, or visual). The six behavioural tests were constant for all participants, although

the order of the presentation of the tests varied per training session (1 or 2). A training session consisted of a training exposure, followed by two recognition tests, followed by another training exposure, until a total of four training exposures were completed.

Training exposure conditions. For the writing condition, participants were given a pad of paper and a pen and were asked to copy pseudoletters presented on the computer screen to the best of their ability. For the typing condition, participants were asked to find and type the pseudoletter that was presented on the screen. A keyboard was modified for this purpose (pictures of the pseudoletters were affixed to a regular keyboard). When the participant typed the key, the presentation of the pseudoletter on the screen disappeared and was not replaced. Thus, the screen was blank after the participant typed their response. For the visual condition, participants were asked to look at the presented stimulus and to try to memorize its form. All participants were notified that they would be tested on these stimuli after training. No feedback was given for any of the training conditions. In each training task, each of the 18 stimuli were presented a total of three times in their proper orientation, for a total of 54 stimulus presentations per training task. This was repeated four times per training day (for a total of eight repetitions). Each stimulus was presented for the same amount of time (4 seconds) for each training condition. This resulted in the visual condition having a greater amount of visual exposure to each stimulus, because they were not required to divert their gaze to write or type. However, in the typing condition, participants would find and then see the pseudoletter on the keyboard. In the writing condition, they would write and then see the written pseudoletter. For each training group the stimulus was presented on the screen for the entire trial. Although we did not measure the amount of time that each person required to type or write, both conditions were easily completed in the time allotted, and one did not appear to take longer than any other.

Behavioural testing. The tests did not change from participant to participant, although the order of the tests did vary. A total of six tests were presented in one training session. Three of these were standard visual search tests. The participant was presented with a target (trained pseudoletter) stimulus, followed by a Gaussian noise mask, followed by a field of stimuli. The fields were 2×2 (small array), 3×3 (medium array), or 6×6 (large array). The participant's task was to quickly decide whether the target stimulus was presented in the field of stimuli. The participant pressed the "/" key if the target was present and "z" if the target was absent. Stimuli were presented in roman font and in an upright orientation. The visual search tests were included as a measure of learning that did not require explicit recognition of the target stimulus. However, visual search has been shown to be sensitive to learning effects and even as an effective measure of automaticity in processing (Czerwinski, Lightfoot, & Shiffrin, 1992). We were therefore curious to see whether or not visual search ability became more efficient with our training paradigm.

Two tests required matching of stimuli. The participant was presented with a target stimulus, followed by a Gaussian noise mask, and then a second stimulus, followed by a brief fixation cross. The participant's task was to decide whether the two stimuli were the same or different (serial match task). The first match test incorporated font changes between the two stimuli; the second match test changed orientation of the first and second stimulus presentations. These two matching tasks consisted completely of the trained pseudoletters. Participants pressed the "/" key if the stimuli were the same and the "z" if the stimuli were different. This task was included to assess implicit processing of the pseudoletters and how this may change over time. In addition, this task was a close approximation of the one-back task that was performed in the imaging environment, except that during this task all levels of orientation changes and font changes were used.

The final test was an old/new recognition test: Participants decided whether a presented stimulus

was one that had been previously studied, or if the stimulus was new and had not been studied. Again, this test consisted completely of the trained pseudoletters, as well as 18 novel pseudoletter stimuli (the "new" stimuli). Font and orientation were changed randomly throughout this procedure; thus, not all levels of orientation and font were necessarily used. Participants pressed the "/" key if the pseudoletter had been previously studied and "z" if the pseudoletter was new. The novel pseudoletters presented in the old–new test decision were presented only within the confines of this task. Of the three tasks, this was the only test that required explicit recollection of the studied pseudoletter stimuli.

Because this type of training exposure is virtually untested, we were unsure how it would affect performance. For this reason, we included several behavioural tests that would potentially allow us to determine how our training affected different types of performance (e.g., implicit vs. explicit recognition).

Imaging parameters. Imaging was performed using a 3-T Siemens Magnetom Trio whole-body MRI system and a phased-array eight-channel head coil, located at the Indiana University Psychological and Brain Sciences department. The field of view was $22 \times 22 \times 12.5$ cm, with an in-plane resolution of 64×64 pixels and 25 slices per volume that were 4 mm thick with a 1.0-mm gap among them. These parameters allowed us to collect data from the entire brain. The resulting voxel size was $3.4 \text{ mm} \times 3.4 \text{ mm} \times 5.0 \text{ mm}$. Images were acquired using an echo-planar technique (echo time, TE = 30 ms; time to repetition, TR = 2,000 ms; flip angle = 70°) for BOLD based imaging. High-resolution T1-weighted anatomical volumes were acquired using a 3D Turbo-flash acquisition. Functional data underwent slice time correction, 3D motion correction, linear trend removal, and Gaussian spatial blurring (FWHM 4 mm) using the analysis tools in Brain VoyagerTM. Individual functional volumes were coregistered to anatomical volumes with an intensity-matching, rigid-body transformation algorithm. Individual anatomical volumes were

normalized to the stereotactic space of Talairach and Tournoux (1988) using an eight-parameter affine transformation, with parameters selected by visual inspection of anatomical landmarks. Applying the same affine transformation to the coregistered functional volumes placed the functional data in a common brain space, allowing comparisons across participants. Voxel size of the normalized functional volumes was standardized at $1\text{ mm} \times 1\text{ mm} \times 1\text{ mm}$ using trilinear interpolation.

fMRI data analysis procedures. The functional data were further analysed with a random effects general linear model (GLM) using Brain Voyager'sTM multisubject GLM procedure. The GLM analysis allows for the correlation of predictor variables or functions with the recorded activation data (criterion variables) across scanning sessions. The predictor functions were based on the blocked stimulus presentation paradigm of the particular run being analysed and represent an estimate of the predicted haemodynamic response during that run. Regions of interest were determined based on group statistical parametric maps (SPMs) that were considered above threshold if they met the following criteria in our random-effects analysis: (a) significant at $p < .001$, uncorrected, with a cluster threshold of 270 contiguous 1-mm isometric voxels; (b) peak statistical probability within a cluster at least $p < .0001$, uncorrected.

To localize regions of the brain that were engaged during letter processing, we performed a letters versus fixation contrast in the group data combined across the pretrain and posttrain scans. Results of this contrast are presented in Figure 2 and produced 12 regions of interest (ROIs). We then extracted percentage BOLD signal change values for all participants within these ROIs for both pretrain and posttrain scans. Using peak activation from each participant as our dependent measure, we then performed an omnibus analysis of variance (ANOVA) for each ROI. However, we only compared trained and untrained pseudo-letters with one another, these being our stimuli

of interest (that is, we did not extract BOLD signal change to shapes).

Results and discussion

Behavioural results

Two separate 2×3 mixed measures ANOVAs (one for reaction times and one for accuracy) were performed for each test type with training day (1 or 2) as a within-subjects variable and training condition (write, type, or visual) as a between-subjects variable.

Reaction times. For each test type there was no significant effect of training group: Match 1 (font change), $F(2, 15) = 1.4$, *ns*; Match 2 (orientation change), $F(2, 15) = 0.93$, *ns*; Visual Search 1, $F(2, 15) = 1.6$, *ns*; Visual Search 2, $F(2, 15) = 1.03$, *ns*; recognition, $F(2, 15) = 0.85$, *ns*. Thus, the type of training did not affect speed of response in any of these measures. However, each group did improve their performance over training days in the match tasks and in the large-array visual search task: Match 1, $F(1, 15) = 23.4$, $p < .0001$; Match 2, $F(1, 15) = 13.9$, $p < .002$; Visual Search 2, $F(1, 15) = 8.7$, $p < .01$. There was no improvement with training in the small-array visual search task, $F(1, 15) = 1.8$, *ns*; and only a trend towards significance in the recognition task, $F(1, 15) = 3.9$, $p < .06$. There were no significant interactions between training day and training condition.

Accuracy. There were no significant effects on accuracy as a function of training, or training group (all $F_s < 2.8$, *ns*). This is a surprising result given the expectation that motor training would facilitate both reaction time and accuracy. Accuracy, however, was quite high in these tests prior to any training, which may have contributed to the insignificant change in performance. In addition, it is not unusual to show reaction time effects without accuracy effects in many cognitive tasks (e.g., Harman et al., 1999; Prinzmetal, McCool, & Park, 2005). Another possible explanation for the absence of accuracy differences is the small sample size: In each condition there were only 6

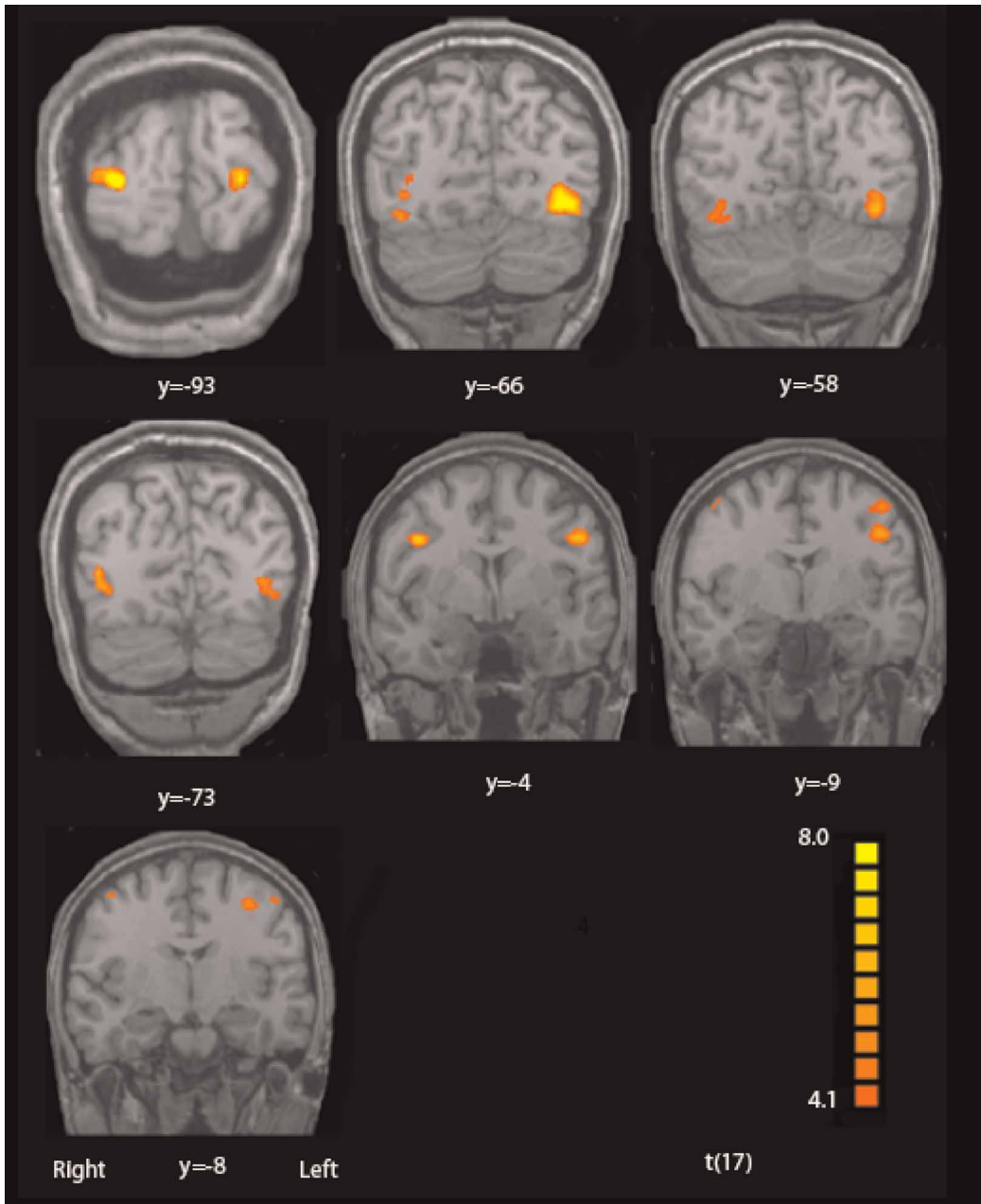


Figure 2. Regions of interest (ROIs) resulting from the contrast of letters greater than fixation baseline combined across pretrain and posttrain scans. Statistical parametric maps (SPMs) depict averaged group data (pre- and postscan data are collapsed for each participant) viewed at an uncorrected statistical threshold of $p < .0001$ (see Table 1 for Talairach coordinates, cluster size, t -values, and p -values for each ROI). Data are depicted in radiological coordinates. Top row, left: bilateral inferior occipital gyrus; centre: bilateral posterior fusiform gyrus; right: bilateral middle fusiform gyrus. Middle row, left: bilateral middle occipital gyrus; centre: bilateral precentral gyrus; right: left dorsal precentral gyrus (seen dorsal to the precentral activation). Bottom row: left medial precentral gyrus (seen medial to bilateral precentral activation). To view a colour version of this figure, please see the online issue of the Journal.

participants. Studies that have shown effects of motor training on behavioural performance have used much larger sample sizes (e.g., Longcamp et al., 2005a, 2005b). More days of training may have facilitated changes in accuracy as well. Prior studies on training participants on novel objects have required 7 hours of training to result in a behavioural change (Gauthier et al., 1997). Thus, the behavioural methods that we used may not have been sensitive enough to reveal the underlying neural changes that were occurring.

fMRI results

Behavioural results from imaging session. Behavioural performance in the one-back perceptual matching task was not analysed beyond computing descriptive statistics, because of ceiling effects. Note that there was an average of only two repetitions of a stimulus per block; therefore, this task was very easy for the participants. Mean responses in the letter task for each group was at ceiling ($99 \pm 0.5\%$ for motor group; $98.3 \pm 1.1\%$ for typing group, and $97.5 \pm 2.1\%$ for visual group), as was performance for studied pseudoletters (motor group, $97.3 \pm 0.5\%$; type group, $98.0 \pm 2.8\%$; visual group, $96.3 \pm 1\%$), unstudied pseudoletters (motor group, $94.4 \pm 2.3\%$; type group, $98.9 \pm 1.7\%$; visual group $99 \pm 1.3\%$), and simple shapes (motor group $99.9 \pm 0.5\%$; type group, $94.5 \pm 2.7\%$; visual group, $95.5 \pm 1.5\%$).

Localizing regions of interest

We compared letters to fixation to localize regions of the brain that were involved in letter processing. This contrast resulted in 12 ROIs (Figure 2): bilateral inferior occipital gyrus (see Table 1 for all Talairach coordinates), bilateral posterior fusiform gyrus, bilateral middle fusiform gyrus, bilateral middle occipital gyrus, bilateral precentral gyrus, left dorsal precentral gyrus, and left medial precentral gyrus. Inferential statistics for each region of interest are reported below, and because figures represent the data in terms of difference scores (trained minus untrained pseudoletters), we also include all raw data (% BOLD signal change mean peaks) in Table 2.

ROI results

Left inferior occipital gyrus (Figure 3). A 3 (training group, TG: writing, typing, visual) \times 2 (scan day, SD: pretrain scan, posttrain scan) \times 2 (pseudoletter, PL: untrained or trained) mixed-model ANOVA revealed three significant interactions. The two 2-way interactions, one between TG and SD, $F(2, 15) = 5.3, p < .01$, and the second between TG and PL, $F(2, 15) = 8.5, p < .01$, are better interpreted by looking at the significant 3-way interaction, $F(2, 15) = 3.8, p < .05$. The significant 3-way interaction was due to no differences between the untrained and trained pseudoletters in the pretrain scan session for any of the groups—writing, $t(5) = 1.3, ns$; type, $t(5) = 1.4,$

Table 1. Talairach coordinates, cluster size, peak t value, and significance level of each region of interest

Region of interest	Talairach coordinates (peak) (x, y, z)	Cluster size (1-mm voxels)	t(17) peak	p < (uncorrected)
Left inferior occipital gyrus	-29, -93, -1	353	8.2	.000003
Right inferior occipital gyrus	27, -92, -1	496	11.3	.000004
Left posterior fusiform gyrus	-43, -66, -12	657	9.4	.000002
Right posterior fusiform gyrus	38, -66, -15	275	7.0	.000001
Left middle fusiform gyrus	-43, -58, -10	680	8.2	.000003
Right middle fusiform gyrus	36, -59, -13	560	6.3	.000002
Left middle occipital gyrus	-46, -73, -9	290	9.3	.000002
Right middle occipital gyrus	46, -73, -5	487	8.7	.000002
Left precentral gyrus	-45, -4, 34	675	7.4	.000001
Right precentral gyrus	40, -4, 32	409	7.9	.000001
Left dorsal precentral gyrus	-46, -8, 51	275	5.6	.0001
Left medial precentral gyrus	-34, -9, 50	270	5.8	.0001

Table 2. Peak BOLD percentage signal change averaged across all participants in each ROI

ROI	Motor				Typing				Visual			
	Pretrain		Posttrain		Pretrain		Posttrain		Pretrain		Posttrain	
	New PL	Tr. PL	New PL	Tr. PL	New PL	Tr. PL	New PL	Tr. PL	New PL	Tr. PL	New PL	Tr. PL
L. inf. occipital gyrus	0.95 (0.08)	0.92 (0.11)	0.95 (0.08)	1.10 (0.17)	0.95 (0.30)	0.99 (0.25)	0.87 (0.23)	1.31 (0.23)	0.98 (0.31)	0.93 (0.22)	0.95 (0.24)	0.73 (0.13)
R. inf. occipital gyrus	1.13 (0.10)	1.18 (0.10)	1.19 (0.08)	1.33 (0.15)	1.15 (0.28)	1.13 (0.23)	1.14 (0.12)	1.31 (0.15)	0.89 (0.18)	0.83 (0.25)	0.90 (0.27)	0.88 (0.09)
L. post. fusiform	0.11 (0.06)	0.10 (0.05)	0.12 (0.09)	0.35 (0.07)	0.09 (0.04)	0.11 (0.06)	0.11 (0.06)	0.14 (0.13)	0.12 (0.09)	0.10 (0.08)	0.14 (0.11)	0.13 (0.11)
R. post. fusiform	0.57 (0.05)	0.59 (0.05)	0.59 (0.04)	0.67 (0.07)	0.58 (0.14)	0.56 (0.11)	0.57 (0.06)	0.85 (0.17)	0.45 (0.09)	0.41 (0.12)	0.45 (0.14)	0.44 (0.04)
L. middle fusiform	0.56 (0.04)	0.53 (0.09)	0.58 (0.04)	0.67 (0.07)	0.58 (0.14)	0.56 (0.11)	0.57 (0.06)	0.58 (0.21)	0.45 (0.09)	0.41 (0.12)	0.45 (0.14)	0.44 (0.04)
R. middle fusiform	0.65 (0.14)	0.67 (0.25)	0.65 (0.22)	0.67 (0.11)	0.63 (0.18)	0.63 (0.17)	0.65 (0.22)	0.67 (0.25)	0.65 (0.14)	0.63 (0.16)	0.65 (0.14)	0.63 (0.17)
L. middle occipital	1.26 (0.14)	1.21 (0.17)	1.33 (0.10)	1.19 (0.18)	1.18 (0.18)	1.20 (0.19)	1.25 (0.13)	1.26 (0.13)	1.18 (0.18)	1.16 (0.09)	1.23 (0.13)	1.22 (0.13)
R. middle occipital	1.57 (0.10)	1.57 (0.10)	1.57 (0.10)	1.58 (0.10)	1.56 (0.10)	1.53 (0.17)	1.56 (0.11)	1.56 (0.10)	1.54 (0.10)	1.55 (0.15)	1.57 (0.10)	1.55 (0.15)
L. precentral	0.53 (0.07)	0.51 (0.09)	0.53 (0.06)	0.83 (0.16)	0.51 (0.10)	0.52 (0.08)	0.51 (0.10)	0.72 (0.18)	0.50 (0.06)	0.50 (0.07)	0.45 (0.14)	0.50 (0.07)
R. precentral	0.36 (0.03)	0.31 (0.07)	0.34 (0.08)	0.42 (0.12)	0.37 (0.05)	0.31 (0.07)	0.37 (0.05)	0.36 (0.03)	0.35 (0.03)	0.38 (0.04)	0.36 (0.03)	0.39 (0.02)
L. dorsal precentral	0.71 (0.24)	0.73 (0.29)	0.69 (0.21)	0.86 (0.12)	0.74 (0.20)	0.74 (0.20)	0.75 (0.14)	0.73 (0.17)	0.71 (0.24)	0.73 (0.25)	0.71 (0.24)	0.74 (0.24)
L. medial precentral	0.35 (0.95)	0.35 (0.92)	0.35 (0.95)	0.39 (1.10)	0.35 (0.95)	0.33 (0.99)	0.34 (0.87)	0.34 (1.31)	0.34 (0.98)	0.34 (0.93)	0.31 (0.95)	0.40 (0.73)

Note: Standard deviations in parentheses. BOLD = blood-oxygen-level-dependent. ROI = region of interest. PL = pseudoletter. Tr. = trained. R. = right. L. = left. inf. = inferior. post. = posterior.

ns; visual, $t(5) = 1.7$, *ns*—with significant differences between the two PL types in the postscan session for two (writing and typing) of the three groups: writing, $t(5) = 2.6$, $p < .05$; type, $t(5) = 2.3$, $p < .05$; visual, $t(5) = 0.65$, *ns*. Thus, in this early visual area, the PL training had an effect on percentage BOLD signal change in the motor and typing training groups.

Right inferior occipital gyrus. The results of the ANOVA in this region revealed one significant main effect, that of the group variable, $F(2, 15) = 11.9$, $p < .001$. This effect was driven by lower overall peak percentage signal change in the visual group ($M = 0.87$) than in the typing group ($M = 1.2$), $t(5) = 5.4$, $p < .001$, and in the

motor group ($M = 1.15$), $t(5) = 4.1$, $p < .001$. The writing and typing groups were not significantly different from one another, $t(5) = 1.2$, *ns*.

Left posterior fusiform gyrus (see Figure 4). The $3 \times 2 \times 2$ ANOVA revealed several significant differences in this region. First, there were main effects of SD, $F(1, 15) = 17.4$, $p < .001$, and PL, $F(1, 15) = 5.6$, $p < .05$; the main effect of group was not significant, $F(1, 15) = 1.3$, *ns*. The significant main effects must be interpreted in light of the three 2-way interactions and one 3-way interaction. The three 2-way interactions, between TG and SD, $F(2, 15) = 5.7$, $p < .01$, TG and PL, $F(2, 15) = 4.7$, $p < .05$, and SD \times PL, $F(1, 15) = 18.4$, $p < .0001$, are better

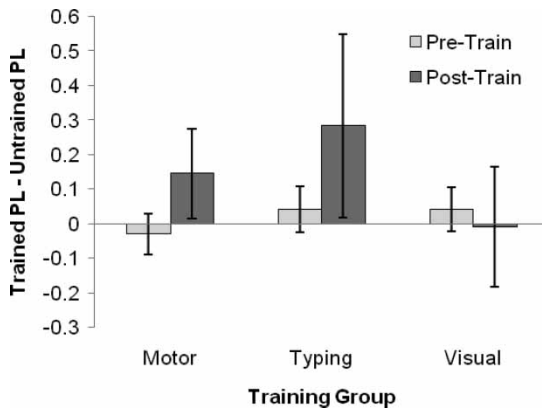


Figure 3. A depiction of the significant three-way interaction among pseudoletters (PLs), training group, and scan day in the left inferior occipital gyrus. All interaction graphs depict peak blood-oxygen-level-dependent (BOLD) activation of untrained pseudoletters subtracted from trained pseudoletters as a function of training group and scan day. Error bars depict 95% confidence intervals, and therefore overlap with the x-axis depicts nonsignificance, while nonoverlap depicts a significant difference between trained and untrained pseudoletters (see text for inferential statistics and Table 2 for mean % BOLD signal change values). Note that there are no differences between trained and untrained PLs before training (light grey bars), but significant differences after training for the motor and typing training group.

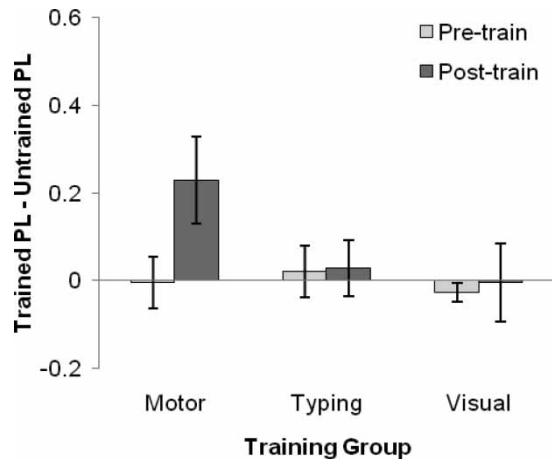


Figure 4. A depiction of the significant three-way interaction among pseudoletters (PLs), training group, and scan day in the left posterior fusiform gyrus. There is no significant difference between trained and untrained pseudoletters prior to training and no difference in activation to these two stimulus sets after typing and visual training. There is, however, a large difference in blood-oxygen-level-dependent (BOLD) percentage signal change (greater to trained than to untrained) after motor training.

understood when we consider the three-way interaction, $F(2, 15) = 13.2, p < .0001$. The 3-way interaction revealed that for the writing training group, there was a significant difference only in the posttraining scan between trained and untrained pseudoletters, $t(5) = 4.02, p < .005$, but not between trained and untrained PLs prior to training, $t(5) = 1.9, ns$. In the typing training group, there were no significant differences between trained and untrained PLs during the pretrain scan, $t(5) = 0.21, ns$, or during the post-train scan, $t(5) = 0.26, ns$. For the visual training group, again, there were no significant differences between the trained and untrained PLs in the pre-train scan, $t(5) = 1.97, ns$, or in the posttrain condition, $t(5) = 0.47, ns$. Thus, in the left posterior fusiform gyrus, we find that percentage BOLD signal change increases as a function of training, but only when the training involves writing the pseudoletters, not after typing or purely visual

training. When letters are compared to other visual stimuli, the left fusiform gyrus has been shown to be engaged more during letter processing than during processing of other, similar shapes (Flowers et al., 2004; James et al., 2005; Longcamp et al., 2003). Here we show that activation before and after training with pseudoletters changed activation patterns in this region, suggesting that the sensitivity to letters in this region may be due to sensorimotor interactions as well.

Right posterior fusiform gyrus (Figure 5). Another $3 \times 2 \times 2$ mixed-model ANOVA was run on the data from the right fusiform gyrus, revealing a main effect of SD, $F(1, 15) = 9.8, p < .005$, and of PL, $F(1, 15) = 9.2, p < .005$. Three significant interactions emerged as well: one between TG and PL, $F(1, 15) = 6.8, p < .005$, one between SD and PL, $F(1, 15) = 7.0, p < .01$, and a three-way interaction, $F(1, 15) = 3.4, p < .05$. The three-way interaction was driven by no significant differences in percentage BOLD signal change

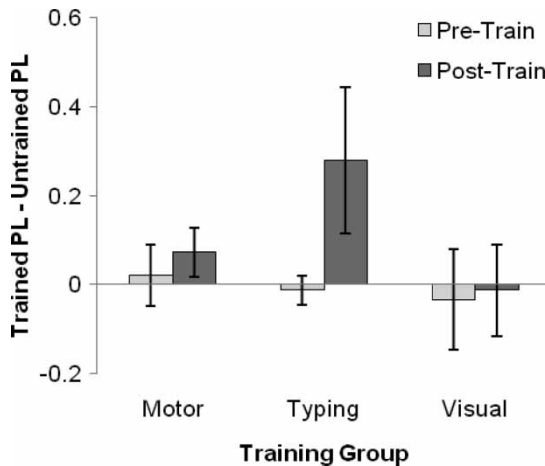


Figure 5. The significant three-way interaction among pseudoletters (PLs), training group, and scan day in the right posterior fusiform gyrus. There is no significant difference between trained and untrained pseudoletters prior to training and no difference after visual training. There is, however, a difference in blood-oxygen-level-dependent (BOLD) percentage signal change (greater to trained than to untrained) after motor and typing training.

for new versus trained pseudoletters in the pretraining scan session for any of the groups (all t values < 1.9), contrasting with a difference between the new and trained PL conditions in the posttraining session after typing training, $t(5) = 3.4, p < .005$, and writing training, $t(5) = 2.75, p < .05$, but not after visual-only training, $t(5) = 0.45, ns$.

Left middle fusiform gyrus. Another $3 \times 2 \times 2$ mixed-model ANOVA revealed a significant main effect of TG in this region, $F(1, 15) = 8.6, p < .005$, with the visual training group producing less percentage signal change than the writing group, $t(5) = 2.8, p < .05$, and less than the typing group, $t(5) = 3.1, p < .05$ (writing, $M = 0.58, SD = 0.07$; typing, $M = 0.57, SD = 0.13$; visual, $M = 0.43, SD = 0.09$). No other effects were significant (all other F values < 2.0). In contrast with the left posterior fusiform, the left middle fusiform was not affected by training in this paradigm. It is curious that the visual training group displayed less activation overall in

this region—a result also found in the right inferior occipital gyrus.

Right middle fusiform gyrus. There were no significant differences among any of the conditions in this region (all F values < 2.0). This result reinforces the idea that the middle fusiform gyrus, although letter sensitive, is not involved in the changes due to training that are seen in the more posterior fusiform.

Bilateral middle occipital gyrus. There were no significant differences among any of the conditions in these regions.

Left precentral gyrus (Figure 6). From the $3 \times 2 \times 2$ ANOVA, we see significant main effects of all three conditions: TG, $F(1, 15) = 8.8, p < .005$; SD, $F(1, 15) = 8.0, p < .01$; and PL, $F(1, 15) = 15.7, p < .001$. There were also two significant interactions, one between TG and SD, $F(1, 15) = 3.7, p < .05$, and one between SD and PL, $F(1, 15) = 16.3, p < .001$. Simple effects demonstrated that the TG \times SD interaction was due to the writing, $t(5) = 2.7$,

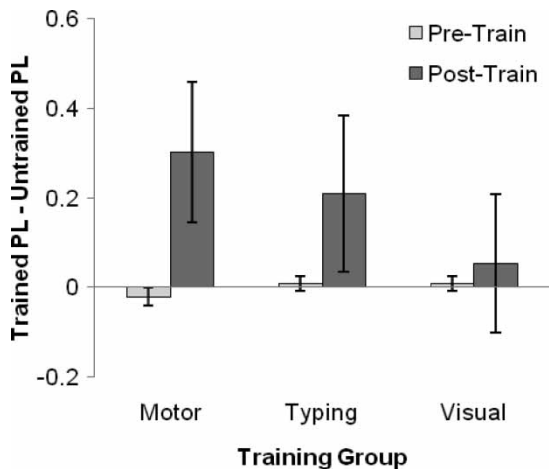


Figure 6. The three-way interaction among pseudoletters (PLs), training group, and scan day in the left precentral gyrus. There is no significant difference between trained and untrained pseudoletters prior to training and, again, no difference after visual training. However, motor and typing training both result in greater activation to trained than to untrained PLs.

$p < .05$, and typing, $t(5) = 2.1$, $p < .05$, groups both showing an increase in percentage signal change after training, whereas the visual training group did not, $t(5) = 0.69$, *ns*. The SD \times PL interaction was due to an increase in percentage signal change after training in the trained pseudoletters only, $t(5) = 3.7$, $p < .005$, that was not present prior to training, $t(5) = 0.25$, *ns*. Taken together, after training, the two groups that interacted with the stimuli using motor systems both showed increases in percentage BOLD signal change. The second interaction suggests that in all three groups, the trained pseudoletters were responded to with greater percentage signal change than were the untrained pseudoletters only after training ($M = 0.49$, $SD = 0.10$ for new PLs, and $M = 0.68$, $SD = 0.19$ for trained PLs after training sessions). The three-way interaction approached significance, $F(1, 15) = 2.9$, $p < .08$, as reflected in Figure 6—the writing and typing groups appeared to be significantly different from the visual group in terms of the change in BOLD response after training. Recent research has found recruitment of the left precentral gyrus during visual letter processing (James & Gauthier, 2006; Longcamp et al., 2003, 2005a, 2005b). The hypothesis that has been brought forth by both groups is that left motor regions are activated because of stored motor programmes that result from experience in writing letters. The current results support this claim and extend it by showing that typing training also results in activation in this region during visual presentation of pseudoletter stimuli. This is the first direct evidence supporting the claim that neural engagement in motor areas during visual tasks is due to motor experience and not specifically writing experience.

Right precentral gyrus. Prior evidence for right precentral gyrus engagement during letter-processing tasks is less compelling than that for the left precentral gyrus. The usual explanation for the lack of activation is that the left hemisphere processes language stimuli more than does the right hemisphere. We did find some right precentral engagement during letter tasks here, though—perhaps

due to the contrast that is used (letters vs. fixation). Although the $3 \times 2 \times 2$ ANOVA performed on the data from this region revealed a significant main effect of SD, $F(1, 15) = 7.4$, $p < .01$, with the posttraining scan resulting in a higher percentage signal change overall ($M = 0.37$, $SD = 0.05$) than the pretraining scan ($M = 0.37$, $SD = 0.06$), there were no other significant effects (all $F_s < 2.5$).

Left dorsal precentral gyrus (Figure 7). This region is similar to that previously found to be engaged during letter perception in some studies (James & Gauthier, 2006). The $3 \times 2 \times 2$ ANOVA that was performed on the data from this region revealed three effects. The first was a main effect of PL, $F(1, 15) = 5.7$, $p < .03$. Perceiving new PLs resulted in a lower percentage signal change ($M = 0.71$, $SD = 0.12$) than did trained PLs ($M = 0.76$, $SD = 0.14$). There were also two interactions, one 2-way interaction between TG and PL, $F(2, 15) = 3.5$, $p < .05$, and a 3-way interaction among TG, SD, and PL, $F(2, 15) = 3.8$, $p < .05$. Simple effects analyses revealed that there was an increase in percentage signal change between the new and trained PLs only after writing training, $t(5) = 2.7$, $p < .05$ (all other t values < 2.0 ; see Figure 7).

Left medial precentral gyrus. The results of our localizer contrast also revealed a region in the medial portion of the precentral gyrus that was involved in letter perception. A $3 \times 2 \times 2$ ANOVA in this region revealed one significant interaction among the conditions: that between SD and PL, $F(1, 15) = 5.1$, $p < .05$. This interaction was due to a significant difference between new and trained PLs only after training, $t(5) = 2.5$, $p < .05$, but not before training, $t(5) = 0.33$, *ns*. Thus, there was an effect of training in this region, but it was not specific to a given type of training.

Summary

To summarize these results, our localizer contrast revealed 12 regions in the brain that were active more to letter perception than to a fixation

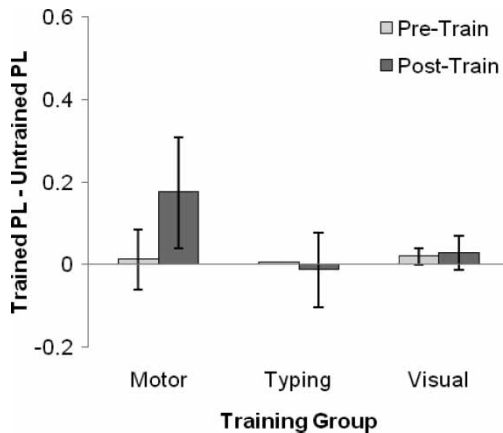


Figure 7. *The three-way interaction among pseudoletters (PLs), training group, and scan day in the left dorsal precentral gyrus. There is no significant difference between trained and untrained pseudoletters prior to training and, again, no difference after typing or visual training. However, motor training resulted in greater activation to trained than to untrained PLs.*

baseline. Of these 12 regions, 5 showed a three-way interaction among our conditions, where new versus trained pseudoletters were responded to differently as a function of scan day and training group. In 3 of these 5 regions (the left inferior occipital gyrus, the right fusiform gyrus, and the left precentral gyrus), writing and typing groups showed an increase in percentage signal change when perceiving trained pseudoletters after training versus perceiving untrained PLs in the same session. In 2 other regions (the left posterior fusiform gyrus and the left dorsal precentral gyrus) there was greater neural activation during trained PL perception than during untrained PL perception only after writing training. Interestingly, these latter regions are the same areas that have been found previously to respond to letter perception and letter writing (James & Gauthier, 2006).

Thus, we have demonstrated that regions of the brain that respond more to letters than to a fixation cross are not necessarily letter specific. These regions are also engaged during perception of other letter-like stimuli after a certain type of experience. Here we tested how writing, typing, and visual experience with previously novel characters would affect neural responses in these

letter-selective regions. Interestingly, the training conditions served to change the response patterns in several of the regions.

GENERAL DISCUSSION

There is abundant evidence that there is neural functional specialization for processing individual letters (Flowers et al., 2004; James & Gauthier, 2006; James et al., 2005; Polk & Farah, 1998; Polk et al., 2002), but, until now, there has not been any work investigating how this specialization may develop. We now present evidence that our experience in writing letters may contribute to the development of functional specialization for letters. We demonstrate that after writing practice, some brain regions that are engaged during letter processing are also engaged more to trained pseudoletters than to untrained pseudoletters, implying that these regions increase their response to these particular stimuli only after a specific type of motor interaction. In other brain regions, activation changed both after writing and after typing training, implying that these regions increase responses after any motor experience. Interestingly, the regions that were found to change response as a result of writing training were the same regions as those found in previous work to respond during letter perception and during letter writing (the left fusiform gyrus and the left dorsal precentral gyrus; James & Gauthier, 2006).

Although performance on some of our behavioural measures improved with training, there was no difference in performance in behavioural tasks as a function of different training conditions. This null behavioural result is in marked contrast to our significant differences in BOLD activation among training groups. Showing a difference in BOLD activation, but not a difference in behavioural measures, is not an uncommon pattern of results (e.g., see James & Gauthier, 2006; McLaughlin, Osterhout, & Kim, 2004; Wilkinson & Halligan, 2003a, 2003b). Such a result can be attributed to the greater sensitivity of measuring changes in BOLD response than response times or accuracy measures (see also

Wilkinson & Halligan, 2003a for further discussion of this view). Such sensitivity is important in revealing neural processing that can inform current cognitive theories and shape future research endeavours.

The imaging results of this work suggest that after experience with certain types of stimuli—in this case, pseudoletters—brain regions change their responses to the learned versus unlearned exemplars of that stimulus set. Because neural activation changes are based on training and not based on stimulus properties (trained and untrained pseudoletters are interchangeable), our results do not support theories of ventral stream organization that focus on eccentricity biases (e.g., Hasson et al., 2003) or stimulus characteristics (e.g., Haxby et al., 2001) as organizing principles of ventral stream activation. We would argue that the functional specialization that has been documented to letters (e.g., Flowers et al., 2004; Garrett et al., 2000; James et al., 2005) in the left ventral stream may be based partially on our motor experience with the stimuli.

We know that motor interactions with objects play a crucial role in learning about the environment, and it makes sense that the brain is organized to reflect this interaction: We see coactivation of visual and motor regions during perception of a variety of different types of objects (e.g., Chao & Martin, 2000; Grezes & Decety, 2002; James & Gauthier, 2006). The present results support this general idea: that after motor experience, seeing a pseudoletter recruits areas of the brain that are specialized for letter processing, comprising a sensorimotor network. But what is it about writing experience that leads to this functional specialization?

Presumably, practised motor experiences set up representations of motor programmes in the frontal cortex, and these representations are activated upon subsequent visual presentation of the object. Efferent copies of such information may project to the ventral visual processing stream, affecting neural activation in these regions. This process may facilitate recognition of the object by augmenting the visual information with sensorimotor information. What then is it about

the motor information that would affect visual processing?

We would suggest that when children learn to write letters, they also learn a very efficient way to group letters into “basic-level” categories (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976) and to perhaps ignore irrelevant changes among exemplars within that category. That is, the category of the letter “A”—presumably a basic, or “entry level” (Jolicoeur, 1985) category—has many exemplars within it that look very different (e.g., A, a, a, A, etc). To become efficient readers, we must learn to identify exemplars that are in the same category, despite irrelevant changes in appearance. Children initially learn to visually recognize and categorize letters that are in a single font type and always appear in the same orientation (the sans serif, capital block alphabet). When children start to write letters themselves however, the motor information that produces that letter is variable. This variability, at first, may conflict with the intent to write a certain letter. With practice, the motor variability may serve to augment visual processing by broadening a visual-motor representation. In this interpretation, motor experience changes stored representations and perhaps then also changes visual processing. In fact, recent research has shown that preliterate children (4–5-year-olds) who are given printing practice with letters have a very different neural response to letters than do children who do not receive such practice. That is, prior to practice, the ventral visual processing stream of both groups of children responds similarly to visually presented letters—neural responses to letters is the same as those to shapes. But after printing practice, the left fusiform gyrus shows a heightened activation to letters compared to simple shapes (James, 2008).

Another possibility as to why the sensorimotor systems interact may be due simply to coactivation. Coactivation of multiple systems during learning could lead to “wiring together” of such systems, leading to future coactivations upon subsequent encounters of the same input. More likely, and not mutually exclusive with the former explanation, activation of sensorimotor systems may

serve to potentiate a motor response. If seeing the item previously required a motor response, then perhaps seeing it again would activate a programme associated with the response to prepare for action.

Our knowledge of the effects of learning experience on functional brain changes in humans is in its beginning stages. The research presented here demonstrates that our sensorimotor interactions with the environment are stored during learning. Furthermore, our motor systems are active during visual presentations, suggesting that the motor system is involved in visual processing at some level and may contribute to functional specialization in the ventral stream. Activation of the motor system during visual processing shown here presumably reflects the behavioural findings that motor information affects visual processing of letters (e.g., Freyd, 1983; Orliaguet et al., 1997; Tse & Cavanagh, 2000). Additional work is needed to uncover why motor interactions during learning influence visual processing and whether this interaction is crucial for normal letter recognition ability to develop.

REFERENCES

- Anderson, S. W., Damasio, A. R., & Damasio, H. (1990). Troubled letters but not numbers: Domain specific cognitive impairments following focal damage in frontal cortex. *Brain*, *113*, 749–766.
- Babcock, M. K., & Freyd, J. J. (1988). Perception of dynamic information on static form. *American Journal of Psychology*, *101*, 111–131.
- Bai, D. L., & Bertenthal, B. I. (1992). Locomotor status and the development of spatial search skills. *Child Development*, *63*, 215–226.
- Bartolomeo, P., Bachoud-Levi, A.-C., Chokron, S., & Degos, J. D. (2002). Visually- and motor- based knowledge of letters: Evidence from a pure alexic patient. *Neuropsychologia*, *40*, 1363–1371.
- Bukach, C. M., Gauthier, I., & Tarr, M. J. (2006). Beyond faces and modularity: The power of an expertise framework. *Trends in Cognitive Sciences*, *10*, 159–166.
- Campos, J. J., Anderson, D. I., Barbu-Roth, M. A., Hubbard, E. M., Hertenstein, M. J., & Witherington, D. (2000). Travel broadens the mind. *Infancy*, *1*, 149–219.
- Carlson, T. A., Schrater, P., & He, S. (2003). Patterns of activity in the categorical representations of objects. *Journal of Cognitive Neuroscience*, *15*, 704–717.
- Changizi, M. A., & Shimojo, S. (2004). Character complexity and redundancy in writing systems over human history. *Proceedings of the Royal Society Britain*.
- Chao, L. L., & Martin, A. (2000). Representation of man-made objects in the dorsal stream. *NeuroImage*, *12*, 478–484.
- Cohen, L., Dahan, S., Naccache, L., Lehéricy, S., Dahan-Lambertz, G., Hénaff, M. A., et al. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal participants and posterior split-brain patients. *Brain*, *123*, 291–307.
- Cox, D., & Savoy, R. (2003). Functional magnetic resonance imaging (fMRI) “brain reading”: Detecting and classifying distributed patterns of fMRI activity in human visual cortex. *NeuroImage*, *19*, 261–270.
- Cunningham, A. E., & Stanovich, K. E. (1990). Early spelling acquisition: Writing beats the computer. *Journal of Educational Psychology*, *82*, 159–162.
- Czerwinski, M., Lightfoot, N., & Shiffrin, R. M. (1992). Automatization and training in visual search. *American Journal of Psychology*, *105*, 271–315.
- Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology: General*, *115*, 107–117.
- Downing, P. E., Chan, A. W.-Y., Peelen, M. V., Dodds, C. M., & Kanwisher, N. (2006). Domain specificity in visual cortex. *Cerebral Cortex*, *16*, 1453–1461.
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, *293*, 2470–2473.
- Flowers, D. L., Jones, K., Noble, K., VanMeter, J., Zeffiro, T. A., Wood, F. B., et al. (2004). Attention to single letters activates left extrastriate cortex. *NeuroImage*, *21*, 829–839.
- Freyd, J. J. (1983). Representing the dynamics of static form. *Memory & Cognition*, *11*, 342–346.
- Garrett, A. S., Flowers, D. L., Absher, J. R., Fahey, F. H., Gage, H. D., Keyes, J. W., et al. (2000). Cortical activity related to accuracy of letter recognition. *NeuroImage*, *11*, 111–123.

- Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, *3*, 191–197.
- Gauthier, I., Williams, P., Tarr, M. J., & Tanaka, J. (1997). Training “greeble” experts: A framework for studying expert object recognition process. *Vision Research*, *38*, 2401–2428.
- Gerlach, C., Law, I., Gade, A., & Paulson, O. B. (2002). The role of action knowledge in the comprehension of artifacts—a PET study. *NeuroImage*, *18*, 928–937.
- Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston: Houghton Mifflin.
- Grezes, J., & Decety, J. (2002). Does visual perception of object afford action? Evidence from a neuroimaging study. *Neuropsychologia*, *40*, 212–222.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Science*, *10*, 18–24.
- Grossman, E. D., & Blake, R. (2002). Brain activity evoked by inverted and imagined biological motion. *Vision Research*, *41*, 1475–1482.
- Harman, K. L., Humphrey, G. K., & Goodale, M. A. (1999). Active manual control of object views facilitates recognition. *Current Biology*, *9*, 1315–1320.
- Hasson, U., Harel, M., Levy, I., & Malach, R. (2003). Large-scale mirror-symmetry organization of human occipito-temporal object areas. *Neuron*, *37*, 1027–1041.
- Hasson, U., Levy, I., Behrmann, M., Hendler, T., & Malach, M. (2002). Eccentricity bias as an organizing principle for human high order object areas. *Neuron*, *34*, 479–490.
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, *293*, 2425–2430.
- Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences, USA*, *96*, 9379–9384.
- James, K. H. (2008). *Sensori-motor experience leads to changes in visual processing in the developing brain*. Manuscript submitted for publication.
- James, K., & Gauthier, I. (2006). Letter processing automatically recruits a sensory-motor brain network. *Neuropsychologia*, *44*, 2937–2949.
- James, K. H., Humphrey, G. K., & Goodale, M. A. (2001). Manipulating and recognizing visual objects: Where the action is. *Canadian Journal of Experimental Psychology*, *55*, 111–120.
- James, K. H., Humphrey, G. K., Vilis, T., Corrie, B., Baddour, R., & Goodale, M. A. (2002). “Active” and “passive” learning of three-dimensional object structure within an immersive virtual reality environment. *Behavior Research Methods, Instruments & Computers*, *34*, 383–390.
- James, K. H., James, T. W., Jobard, G., Wong, A., & Gauthier, I. (2005). Letter processing in the visual system: Different activation patterns for single letters and strings. *Cognitive, Affective, & Behavioral Neuroscience*, *5*, 452–466.
- Jolicoeur, P. (1985). The time to name disoriented natural objects. *Memory & Cognition*, *13*, 289–303.
- Kanwisher, N. (2000). Domain specificity in face perception. *Nature Neuroscience*, *3*, 759–763.
- Kanwisher, N., Chun, M. M., & McDermott, J. (1996). fMRI in individual subjects reveals loci in extrastriate cortex differentially sensitive to faces and objects. *Investigative Ophthalmology & Visual Science*, *37*, S193.
- Levy, I., Hasson, U., Avidan, G., Hendler, T., & Malach, R. (2001). Center-periphery organization of human object areas. *Nature Neuroscience*, *4*, 533–539.
- Levy, I., Hasson, U., Harel, M., & Malach, R. (2004). Functional analysis of the periphery effect in human building related areas. *Human Brain Mapping*, *22*, 15–26.
- 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*, 1492–1500.
- Longcamp, M., Anton, J. L., Roth, M., & Velay, J. L. (2005a). Premotor activations in response to visually presented single letters depend on the hand used to write: A study on left-handers. *Neuropsychologia*, *43*, 1801–1809.
- Longcamp, M., Zerbato-Poudou, M., & Velay, J. L. (2005b). The influence of writing practice on letter recognition in preschool children: A comparison between handwriting and typing. *Acta Psychologica*, *119*, 67–79.
- Mahon, B. Z., Milleville, S., Negri, G. A. L., Rumiati, R. I., Martin, A., & Caramazza, A. (2007). Action-related properties of objects shape object representations in the ventral stream. *Neuron*, *55*, 507–520.
- Malach, R., Levy, I., & Hasson, U. (2002). The topography of high-order human object areas. *Trends in Cognitive Sciences*, *6*, 176–184.

- McLaughlin, J., Osterhout, L., & Kim, A. (2004). Neural correlates of second-language word learning: Minimal instruction produces rapid change. *Nature Neuroscience*, 7, 703–704.
- Mecklinger, A., Gruenewald, C., Besson, M. N., & von Cramon, D. Y. (2002). Separable neuronal circuits for manipulable and non-manipulable objects in working memory. *Cerebral Cortex*, 12, 1115–1123.
- Orliaguet, J.-P., Kandel, S., & Bois, L.-J. (1997). Visual perception of motor anticipation in cursive handwriting: Influence of spatial and movement information on the perception of forthcoming letters. *Perception*, 26, 905–912.
- O'Toole, A. J. O., Jiang, F., Abdi, H., & Haxby, J. V. (2005). Partially distributed representations of objects and faces in ventral temporal cortex. *Journal of Cognitive Neuroscience*, 17, 580–590.
- Polk, T. A., & Farah, M. J. (1998). The neural development and organization of letter recognition: Evidence from functional neuroimaging, computational modeling, and behavioral studies. *Proceedings of the National Academy of Sciences, USA*, 95, 847–852.
- Polk, T. A., Stallcup, M., Aguirre, G. K., Alsop, D. C., D'Esposito, M., Detre, J. A., et al. (2002). Neural specialization for letter recognition. *Journal of Cognitive Neuroscience*, 14, 145–159.
- Portwood, M. (2000). *Developmental dyspraxia*. London: David Fulton Publishing.
- Prinzmetal, W., McCool, C., & Park, S. (2005). Attention: Reaction time and accuracy reveal different mechanisms. *Journal of Experimental Psychology: General*, 134, 73–92.
- Rosch, E., Mervis, C. B., Gray, W. D., Johnson, D. M., & Boyes-Braem, P. (1976). Basic objects in natural categories. *Cognitive Psychology*, 8, 382–439.
- Seki, K., Yajima, M., & Sugishita, M. (1995). The efficacy of kinesthetic reading treatment for pure alexia. *Neuropsychologia*, 33, 595–609.
- Spiridon, M., & Kanwisher, N. (2002). How distributed is visual category information in human occipito-temporal cortex? An fMRI study. *Neuron*, 35, 1157–1165.
- Stoodley, C. J., Fawcett, A. J., Nicolson, R. I., & Stein, J. F. (2005). Impaired balancing ability in dyslexic children. *Experimental Brain Research*, 167, 370–380.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.
- Tanaka, J. W., & Gauthier, I. (1997). Expertise in object and face recognition. In R. L. Goldstone, D. L. Medin, & P. G. Schyns (Eds.), *Psychology of learning and motivation: Vol. 36. Perceptual mechanisms of learning* (pp. 83–125). San Diego, CA: Academic Press.
- Tarr, M. J., & Gauthier, I. (2000). FFA: A flexible fusiform area for subordinate-level visual processing automatized for expertise. *Nature Neuroscience*, 3, 764–769.
- Tse, P. E., & Cavanagh, P. (2000). Chinese and Americans see opposite apparent motions in a Chinese character. *Cognition*, 74, B27–B32.
- Wexler, M., & Boxtel, J. J. A. (2005). Depth perception by the active observer. *Trends in Cognitive Science*, 9, 431–438.
- Wexler, M., Kosslyn, S. M., & Berthoz, A. (1998). Motor processes in mental rotation. *Cognition*, 68, 77–94.
- Wilkinson, D., & Halligan, P. W. (2003a). The relevance of behavioral measures for functional-imaging studies of cognition. *Nature Reviews, Neuroscience*, 5, 67–73.
- Wilkinson, D., & Halligan, P. W. (2003b). Stimulus symmetry affects the bisection of figures but not lines: Evidence from event-related fMRI. *NeuroImage*, 20, 1756–1764.
- Wohlschläger, A., & Wohlschläger, A. (1998). Mental and manual rotation. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 397–412.
- Xu, Y. (2005). Revisiting the role of the fusiform face area in visual expertise. *Cerebral Cortex*, 15, 1234–1242.