Neural substrates of sensorimotor processes: letter writing and letter perception

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Vinci-Booher SA, James KH. Neural substrates of sensorimotor processes: letter writing and letter perception. *J Neurophysiol* 115: 1–4, 2016. First published July 22, 2015; doi:10.1152/jn.01042.2014.—Writing and perceiving letters are thought to share similar neural substrates; however, what constitutes a neural representation for letters is currently debated. One hypothesis is that letter representation develops from sensorimotor experience resulting in an integrated set of modality-specific regions, whereas an alternative account suggests that letter representations may be abstract, independent of modality. Studies reviewed suggest that letter representation consists of a network of modality-responsive brain regions that may include an abstract component.

handwriting; letter perception; sensorimotor processing; neural representations

WRITING INDIVIDUAL LETTERS begins as an effortful task and, with experience, becomes a skilled and nearly automatic sequential visual-motor skill. Letter writing, then, is a sensorimotor experience, and fluent letter writing is characterized by efficient integration between motor output and sensory input. Similarly, letter perception also may be thought of as a sensorimotor experience in which fluent letter perception is characterized by efficient integration between sensory and motor systems based on prior experience. In this view, it would be expected that sensorimotor components associated with modality-specific experience with letters, such as motor programs for letter writing, visual-spatial properties of letterform, and phonological properties of lettersound, would have corresponding neural substrates that, together, comprise a network that may be thought of as a neural representation of letters (James and Gauthier 2006). Indeed, early neuropsychological case studies have shown that damage to dorsal premotor areas results in an inability to write letters (Exner 1881) and damage to ventral premotor areas results in an inability to articulate lettersounds (Broca 1861). It also has been shown that damage to inferior parietal areas results in writing misshapen letterforms (Sukarai et al. 2007) and deficits in written spelling (Rapp and Caramazza 1997). However, a recently published article has provided evidence that the representation of letters extends beyond modality-specific sensorimotor representation and includes an abstract component, which exists independently of sensory and motor systems (Rothlein and Rapp 2014).

This mini-review will consider the nature of the neural representation of letters by examining four neuroimaging studies. The first study examines the neural substrates associated with writing letters. Longcamp et al. (2014) found that letter writing is associated with increased neural responses in left premotor and supplementary motor brain regions when compared with digit writing. The second study examines the neural substrates associated with the unique shape trajectory of a written letter, or letterform. Kadmon Harpaz et al. (2014) found that letter writing is associated with activation patterns specific to each unique letterform in left primary motor and left parietal regions. The third study examines the effect of experience with writing letters on brain activity during phonological processing in the developing child. Gimenez et al. (2014) found that letter writing ability was negatively correlated with activation in right hemispheric premotor areas during a phonological processing task, indicating a shift to a left-lateralized neural representation of letters that is specific to lettersound and affected by motor experience with writing letters. Finally, the fourth study suggests that the cortical representation of letters is marked by an abstract letter representation in addition to modality-specific letter representations that correspond to the motor execution of letter writing, letterform, and lettersound (Rothlein and Rapp 2014).

Letter Writing: Motor Control During Letter Writing

Longcamp et al. (2014) investigated the extent to which activation in motor brain regions during letter writing is specific to letters, as opposed to digits. They hypothesized that activation in motor brain regions during letter writing would be specific to letters, given the accumulation of evidence that visual brain regions exhibit letter specificity during letter perception (James et al. 2005; James and Engelhardt 2012; James and Gauthier 2006; Polk et al. 2002). Their conclusions support their hypothesis and indicate that the sensorimotor integration between the visual and motor systems required during letter writing results in letter-specific processing in visual and motor brain regions, with the degree of specificity being related to experience level.

Right-handed adults were asked to write letters and digits on a functional magnetic resonance imaging (fMRI)-compatible tablet during fMRI scanning. In this study, auditory stimuli were presented to indicate which letter or digit the subjects were expected to write, and they were able to see the letters and digits as they wrote. Writing letters showed increased activation in left dorsal premotor (L-PMd) and supplementary motor areas (SMA) compared with writing digits; however, writing digits showed increased activation in these same areas compared with rest. Furthermore, writing duration for both letters and digits modulated activity in several other brain regions. Longer writing duration correlated with heightened activation in primary motor and premotor regions [including bilateral precentral gyri (PrG) and right inferior frontal gyrus (R-IFG)], visual processing regions [including bilateral fusiform gyri

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(FuG)], phonological processing regions [including right middle temporal gyrus (R-MTG)], and parietal regions [including bilateral superior parietal lobe (SPL)].

Results are interpreted as evidence that L-PMd and SMA show preferential activation for letter writing compared with digit writing. Other studies have shown that areas of the L-FuG show preferential activation for letter perception compared with digit perception (Polk et al. 2002), pseudo-letter perception (James et al. 2005), and shape perception (James and Engelhardt 2012). Thus activations observed in premotor, supplementary motor, and visual perceptual areas have a general property of responding to several stimulus categories, although they might show a stronger response to one particular category (i.e., letters). The authors posit that the reason for the preferential response to letters over digits is that participants typically have more experience writing and perceiving letters than digits. Taken together, these results indicate that letter writing is supported by a distributed experience-based neural representation for letters composed of regions that also respond to other stimulus categories (i.e., digits). Notably, L-PMd and SMA are modality specific, although they are also letter specific; only premotor and supplementary motor regions show activation specific to letter writing.

Letterform: Movement Trajectory for Individual Letterforms

Kadmon Harpaz et al. (2014) investigated motor control of letter writing and focused on neural populations that were recruited for specific letter-writing trajectories (letterform) regardless of the size of the written letter (scale). They hypothesized that the motor representation of letter writing is essentially a motor plan that encodes letterform and relies on primary motor and parietal regions, given evidence from nonhuman primates that these regions are involved in producing complex movement trajectories. The authors' conclusions support their hypotheses and indicate that activation within primary motor and parietal regions during letter writing reflects unique movement trajectories associated with each individual letter.

Right-handed adults were asked to write three letters (a, s, n) in two sizes (small, large) during fMRI scanning. In this study, auditory stimuli were presented to indicate which letter the subjects were expected to write, and they were unable to see the letter as they wrote. Letter-writing regions of interest (ROIs) were defined as brain regions that showed higher activation levels during letter writing than rest and included left primary motor cortex (L-PMC), left anterior intraparietal sulcus (L-aIPS), left ventral premotor (L-PMv), L-PMd, and SMA. Note the absence of visual processing regions, suggesting that writing letters without seeing them did not automatically recruit letter-specific visual processing, contrary to previous results (James and Gauthier 2006).

A pattern classification algorithm was trained on the averaged activation from each letter-writing ROI to learn to decipher what letterform had been written and in what scale it had been written. The classifier was then applied to each ROI to decode the dimension of interest (letterform, scale). Further analysis investigated differences in activation patterns within these ROIs by performing the same pattern classification steps to each voxel within each ROI. Training the classifier on the averaged activation across all voxels within an ROI was sufficient to train the classifier to decode scale; however, training the classifier on the voxel-by-voxel activation within the ROI was required to train the classifier to decode letterform. Only activation within L-PMC and L-aIPS could be used to reliably detect the letterform being written, regardless of scale. Importantly, letter writing duration was significantly longer for the large scale than for the small scale, and increased letter writing duration correlated with increased average activation in L-PMC and L-aIPS (Kadmon Harpaz et al. 2014; Longcamp et al. 2014). Thus, although a particular area may be routinely recruited for letter writing across letter categories (i.e., a vs. n), the activation patterns within that ROI are specific to the individual letterforms.

Results are interpreted as evidence that both L-PMC and L-aIPS contain neural populations responsible for distinct movement trajectories associated with letterform, regardless of scale. The classifier analysis was also applied to the whole brain, in lieu of restricting investigation to the preselected letter-writing ROIs, to determine if there were regions that showed similar patterns outside of the areas recruited for letter writing. This follow-up analysis revealed similar results, which indicates that these results were not biased by ROI selection and that only regions associated with the motor component of letter writing showed characteristic activation patterns for each letterform. Notably, L-PMC and L-aIPS are modality specific, although they are also letterform specific; only motor and parietal regions show patterns specific to writing unique letterforms.

Lettersound: Phonological Processing

Gimenez et al. (2014) investigated developing neural substrates of phonological processing in children and their relationship to letter writing ability. They hypothesized that activation in phonological processing brain regions would be correlated with letter-writing ability, given the accumulation of evidence that the specificity of visual brain regions during letter perception is related to letter-writing experience (James and Engelhardt 2012; James and Gauthier 2006). The authors' conclusions support their hypothesis and indicate that the recruitment of phonological processing regions is related to experience writing letters.

Right-handed children (ages 5–6 yr) were asked to decide whether or not the name of two simultaneously presented visual stimuli began with the same sound during fMRI scanning. In this study, no auditory stimuli were presented and visual stimuli consisted of images of common objects (i.e., banana, butterfly). Children neither saw letters nor were asked to write letters. Contrasting brain activation during the phonological processing task to rest revealed that children engaged primary motor and premotor areas [including L-PrG, SMA, bilateral IFG, bilateral middle frontal gyrus (MFG)], visual processing areas (including R-FuG), and a parietal area (L-SPL). Outside of the scanner, children completed phonological processing assessments along with an assessment of handwriting ability as a measure of experience with writing letters. Handwriting ability scores correlated neither with the out-of-scanner phonological processing assessments nor with accuracy of the in-scanner phonological processing task. Brain activity in the R-IFG and R-MFG during phonological processing was negatively correlated with handwriting ability; as

experience with letter writing increased, activation in right hemispheric premotor regions decreased.

Results are interpreted as evidence that experience with letter writing promotes left-lateralization for phonological processing, a ubiquitous characteristic of the adult neural profile of letter writing and letter perception. Critically, this study shows the heterogeneity in function within premotor regions, because they are indicated in phonological processing of lettersound but are modulated by experience with letter writing. Many of these same areas were indicated in Longcamp et al. (2014) during letter writing with visual feedback: motor and premotor areas (L-PrG, R-IFG), visual processing areas (R-FuG), and a parietal region (L-SPL). Many of these same areas were indicated in Kadmon Harpaz et al. (2014) during letter writing without visual feedback: motor areas (L-PMC) and parietal areas (L-aIPS). Notably, Gimenez et al. (2014) indicate that R-IFG and R-MFG are lettersound-specific, although they are modulated by letter-writing ability.

Letter Perception: Modality-Specific and Abstract Letter Representations

Despite the presence of modality-specific neural representations for letters, the question concerning how a human knows that the letter "a" is the letter "A" across letter case, letter font, and letter input-modality (e.g., visual vs. auditory) has prompted continued work in search of an abstract letter representation capable of unifying the concept of the letter a along its many dimensions. One such study sought to localize brain areas that correspond to an abstract representation of letters (Rothlein and Rapp 2014). Here, the term "abstract" refers to neural representation in an amodal and symbolic sense, meaning that the abstract letter representation exists independently of sensorimotor input and is not based on experience with writing letters. The authors conclude that an amodal and abstract letter representation exists in the L-FuG and may work in concert with modality-specific brain regions responsible for letter writing, letterform, and lettersound.

An orthographic localizer task and a symbol detection task were administered to right-handed adults during fMRI scanning. In the orthographic localizer task blocks, participants passively viewed words, consonant strings, and checkerboard rectangles. Brain areas that showed increased neural activity to words and consonant strings relative to checkerboard rectangles were chosen as orthographic ROIs. In the symbol-detection task blocks, participants viewed 12 uppercase and lowercase letters and 4 non-letter symbols, for a total of 28 visual stimuli types, and were asked to press a button when they saw one of the non-letter symbols. In this study, the participants were not asked to write letters and were not presented with any auditory stimuli but did visually perceive letters.

Only the orthographic ROIs were investigated further for sensitivity and selectivity to each of the four dimensions of interest: letter writing, letterform, lettersound, and abstract letter identity. Modality-specific letter representations included motor programs for letter writing, visual-motor properties associated with the shape trajectory of distinct letterforms, and phonological properties of lettersound. Motor programs for writing letters were said to be represented in brain areas that responded similarly for letter pairs that scored similarly on a "stroke-feature metric" developed by Rapp and Caramazza

(1997) (e.g., T vs. L). Letterform representations were defined as brain areas that responded similarly for letter pairs that have been empirically shown to be similar in form (e.g., o vs. O, or b vs. d). Lettersound representations were defined as brain areas that responded similarly for letter pairs that have been empirically shown to have confusable letter names (e.g., b vs. e). Abstract letter identity representations were defined as brain areas that responded similarly for letter pairs that were of the same letter category but of different letter case (e.g., A vs. a). An area was labeled sensitive to a certain dimension if it responded similarly for letter pairs that shared that feature dimension. An area was labeled selective for a certain dimension if it responded similarly for letter pairs that shared only that feature dimension.

Letters that require similar letter writing motor plans showed similar response patterns in L-IPS, demonstrating sensitivity to motor plans. Letters that have similar lettersounds showed similar response patterns in L-MTG, demonstrating sensitivity to lettersound. Areas that responded similarly for upper- and lowercase letters of the same letter category included premotor regions (including R-IFG and L-MFG), visual processing areas (including bilateral FuG), and a parietal region (L-IPS), demonstrating sensitivity to abstract letter identity. Only one brain region was identified for which all participants demonstrated selective activation for upper- and lowercase letters: the L-FuG. Results are interpreted as evidence that although some aspects of letter representation are sensitive to modality-specific features, an abstract letter representation also exists in the L-FuG that is amodal and independent of sensory and motor systems.

Summary

Looking back to the three previously discussed studies (Gimenez et al. 2014; Kadmon Harpaz et al. 2014; Longcamp et al. 2014) is helpful in understanding the implications of the results from the Rothlein and Rapp (2014) study on the debate concerning the neural representation of letters. Longcamp et al. (2014) and Kadmon Harpaz et al. (2014) are studies in which participants were asked to write letters and in which motor (L-PMC, SMA) and premotor (L-PMd) areas were said to support letter writing; however, they differ in a crucial way. Participants in the Longcamp et al. (2014) study were able to visually perceive each letter as they wrote it, but participants in the Kadmon Harpaz et al. (2014) study were not. Of the studies reviewed, the only other study in which participants visually perceived letters was that of Rothlein and Rapp (2014). Thus it is not surprising that only Longcamp et al. (2014) and Rothlein and Rapp (2014) indicate a role for the L-FuG in letter representation. Furthermore, the L-FuG was indicated as being responsive to letter-writing duration with visual feedback in Longcamp et al. (2014), and the R-FuG was indicated as being responsive during a phonological processing task in children that required visually perceiving pictures of objects in Gimenez et al. (2014), indicating that the fusiform gyri are, in the least, modality responsive.

In conclusion, there is relevant evidence supporting a modality-specific distributed neural activation profile during letter perception that reflects experience with letters, such as motor plans associated with letter writing, characteristics of the shape trajectory of each letterform, and phonological properties of

lettersound. Importantly, the L-FuG indicated by Rothlein and Rapp (2014) as the location of an abstract neural representation for letters also has been indicated as a modality-responsive neural substrate in letter writing and phonological studies, in that it engages preferentially for visual stimuli. Therefore, although the constitution of a shared neural representation for letter writing and letter perception may include an abstract component in the L-FuG, this area is part of a distributed neural network comprising modality-responsive brain regions related to a history of motor and sensory experiences with individual letters.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.A.V.-B. drafted manuscript; S.A.V.-B. and K.H.J. edited and revised manuscript; S.A.V.-B. and K.H.J. approved final version of manuscript.

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