Comparison of the Neural Basis for Imagined Writing and Drawing

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Abstract: Drawing and writing are complex processes that require the synchronization of cognition, language, and perceptual-motor skills. Drawing and writing have both been utilized in the treatment of aphasia to improve communication. Recent research suggests that the act of drawing an object facilitated naming, whereas writing the word diminished accurate naming in individuals with aphasia. However, the relationship between object drawing and subsequent phonological output is unclear. Although the right hemisphere is characteristically mute, there is evidence from split-brain research that the right hemisphere can integrate pictures and words, likely via a semantic network. We hypothesized that drawing activates right hemispheric and left perilesional regions that are spared in aphasic individuals and may contribute to semantic activation that supports naming. Eleven right-handed subjects participated in a functional MRI (fMRI) experiment involving imagined drawing and writing and 6 of the 11 subjects participated in a second fMRI experiment involving actual writing and drawing. Drawing and writing produced very similar group activation maps including activation bilaterally in the premotor, inferior frontal, posterior inferior temporal, and parietal areas. The comparison of drawing vs. writing revealed significant differences between the conditions in areas of the brain known for language processing. The direct comparison between drawing and writing revealed greater right hemisphere activation for drawing in language areas such as Brodmann area (BA) 46 and BA 37. *Hum Brain Mapp* 28:450–459, 2007.

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INTRODUCTION

Drawing and writing are complex processes that require the synchronization of cognition, language, and perceptual-motor skills. Drawing [Beeson and Ramage, 2000; Lyons, 1995; Rao, 1995; Sacchetti et al., 1999] and writing [Beeson et al., 2003b; Hillis, 1989; Robson et al., 2001] have been used successfully by some individuals with aphasia for commu-

nication and both can be used to augment communication or substitute for speech when speech is limited or nonfunctional. Farias et al. [2006] investigated the effects of drawing and writing on naming in individuals with aphasia. They found that in this population the process of drawing an object facilitated the name of the object, whereas writing the word diminished accurate naming responses. Based on these findings and prior research that has shown a conceptual link between drawing and language [Gainotti et al., 1983; Kirk and Kertesz, 1989; Swindell et al., 1988], these researchers hypothesized that drawing may access the semantic system in a manner different than writing, thereby improving naming.

There is a widely distributed semantic network that supports naming and access to this semantic system may po-

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tentially improve verbal output in individuals with aphasia [Coelho et al., 2000; Drew and Thompson, 1999; Howard et al., 1985, 1986; Nickels and Best, 1996]. The semantic system is thought to have access to object knowledge from various representations of meaning including structural, perceptual, and associative [Humphreys et al., 1999]. To name an object, a number of processing stages occur. Early visual processes encode the structural aspects of the object, such as shape and size, and the perceptual details of the objects, such as color. This in turn accesses the functional and associative properties of the object, such as category. This information is matched to the stored knowledge of the object and ultimately activates the phonological representations for its name.

Drawing may facilitate a deeper level of semantic processing through increased attention to the structural and perceptual aspects of the object. If each level of processing depends on excitatory and inhibitory connections for accurate target word selection, then the strength of activation of the target must exceed its semantic competitors to successfully progress to phonological encoding. Drawing an object may aid in this refining process through ongoing attention to structural and perceptual details of the object, thereby eliminating competitors that do not contain the appropriate attributes.

Writing involves lexical recall to access the name of the object, the correct letter form and graphic motor control for output [Beeson et al., 2003a; Roeltgen, 1993]. Writing requires lexical access to initiate the process of writing; in contrast, drawing requires knowledge of the perceptual aspects of the object and can be initiated without access to the word form [Makuuchi et al., 2003].

Research suggests that writing activation is strongly left-lateralized [Beeson et al., 2003a; Katanoda et al., 2001; Menon and Desmond, 2001; Nakamura et al., 2000; Tokunaga et al., 1999]. Beeson et al. [2003a] attributed activation in the left posterior inferior temporal cortex to lexical-orthographic processing and activation in the left superior parietal and frontal premotor cortex to graphic motor control. Conversely, drawing involves more in-depth processing of the spatial features of objects, which has been shown to activate a distributed network of cortical regions including right hemisphere regions [Chao et al., 1999; Faillenot et al., 1999; Gerlach et al., 2000; Tyler et al., 2003]. In particular, previous studies have shown right hemisphere activation in the posterior inferior temporal cortex [Makuuchi et al., 2003] and the inferior frontal cortex [Imamura et al., 1996]. We suspect that the differences in the focus of drawing and writing and their associated activation patterns may explain Farias et al.'s [2006] clinical observations.

This project was undertaken in an effort to elucidate the differential effects of writing and drawing on naming. Although there have been several imaging studies that have investigated the neural substrates of writing [Beeson et al., 2003a; Katanoda et al., 2001; Menon and Desmond, 2001; Nakamura et al., 2000; Petrides et al., 1995; Seitz et al., 1997; Tokunaga et al., 1999], only a few have studied drawing [Ino

et al., 2003; Makuuchi et al., 2003; Suchan et al., 2002]. This research was designed to identify the brain regions that are recruited in normal healthy adults for drawing and writing and to compare the differences in activation using functional magnetic resonance imaging (fMRI). We hypothesized that: 1) writing activation will lateralize left, while drawing will be bilaterally distributed and thereby less lateralized; and 2) compared to writing, object drawing would yield more right hemisphere (RH) activation associated with the semantic network and this RH activation will contribute to the facilitation of naming for aphasic individuals with left hemisphere (LH) damage.

MATERIALS AND METHODS

Subjects

Written informed consent was obtained from all subjects to participate in the study as approved by the UC Davis Human Subjects Protection Committee. Eleven right-handed subjects (six female) with no history of neurological illness participated in Experiment 1 (ages 22–61, mean 37.1). Six subjects (four female) from Experiment 1 participated in Experiment 2 (ages 26–54, mean 39.0). Right-handedness was assessed with the Edinburgh Handedness Inventory [Williams, 1991].

Task Design: Experiment 1

In order to reduce head motion, subjects mentally imagined drawing and writing instead of executing the full motor movements. Before scanning, the subjects were trained to visualize drawing the picture or writing the word as if they were actually drawing or writing. In order to directly compare the activation differences between drawing and writing, the tasks alternated between writing names of objects and drawing objects within each fMRI acquisition run. During the experiment, the subject viewed a picture for 2 s and at the end of the 2 s either heard the command “draw” or “write.” The picture was removed from the screen and the subject mentally imagined drawing the object or writing the name of the object until they heard the command “stop.” This procedure was similar to that used with aphasic patients in the clinical study [Farias et al., 2006]. To control for time on task differences that may occur due to the speed at which a subject drew or wrote, the subject was instructed to redraw or rewrite until the stop instruction was heard (subjects therefore drew or wrote for the entire trial). The experimental paradigm was 6 min, 32 s in duration with 11 blocks of the “drawing” objects condition and 11 blocks of the “writing” object names condition. A different object was presented for each block and the same set of objects was used for all subjects. Each block of the drawing or writing condition lasted 8 s and was separated by variable durations (4–8 s) of a baseline rest condition in which the subject was instructed to attend to the screen in preparation for the next stimulus. Two runs of the experiment were acquired for each subject and the objects for each condition were counterbalanced between runs.

The picture stimuli used to represent objects were line drawings from the Snodgrass and Vanderwart [1980] set. All pictures were concrete nouns and they were matched for concreteness and frequency. The picture stimuli were projected through an LCD projector (XG-G20XU, Sharp Electronics, NJ) outside the scanning room to a screen located at the end of the scanner bed using Presentation software (www.neurobs.com). The subject viewed the screen via a mirror on top of the head coil and special MRI-compatible headphones (Resonance Technologies, Northridge, CA) were used to deliver the auditory stimuli. The subject's head was restrained with a moldable airbag (Vac-Fix, Bionix, Toledo, OH) to help reduce head motion.

Task Design: Experiment 2

To compare imagined drawing and writing to the actual operation of drawing and writing, a subset of the subjects from the first experiment completed Experiment 2. The stimuli and timing of the experimental paradigm were exactly the same as the first experiment. As in the first experiment, two acquisition runs were acquired for each subject. Subjects used a pencil to draw or write on a pad of paper that was placed on their lap. In order to ensure that each subject was properly performing the task, an experimenter removed the top piece of paper after the subject stopped drawing or writing the name for each object. In this manner the subject used a fresh piece of paper each time and this allowed for an examination of each of the drawing and writing tasks. One limitation of the setup was that the subject was not able to view what they were drawing.

Imaging

For the functional images, 21 contiguous 5-mm axial slices were acquired with a gradient echo, echo-planar imaging sequence (TR = 2 s, TE = 50 ms, flip angle = 90°, FOV = 22 cm, 64 × 64 matrix) using a 1.5T GE Signa NV/I MRI system. High-resolution images for anatomical reference were acquired using a T1-weighted 3D fast SGPR sequence (slice thickness = 1.2 mm, FOV = 22 cm, 256 × 256 matrix, TE = 1.8 ms, TR = 8.7 ms, flip angle = 15°, bandwidth = 15.63 kHz).

Analysis

The echo-planar images were reconstructed using standard Fourier transformation combined with image phase correction [Buonocore, 2003; Buonocore and Gao, 1997] to reduce the N/2 ghost artifact. The images were registered to the third image of each fMRI time series with a 3D registration algorithm [Cox and Jesmanowicz, 1999] and the statistical analysis was performed with Analysis of Functional Neuroimages (AFNI) [Cox, 1996]. Each condition was analyzed using multiple linear regressions with linear trends included as covariates and then a general linear test was applied to compare the effect of drawing vs. writing. Each functional "dataset" contained 196 image volumes and the first four image volumes were removed to allow for the

magnetization to reach dynamic equilibrium. The two datasets were concatenated and the linear trends used in the regression analysis were calculated separately for each run. Activation maps were created by applying a *P* value and cluster size threshold [Forman et al., 1995; Xiong et al., 1995] to the statistical maps. The program AlphaSim (AFNI) was used to estimate the cluster size necessary to achieve a significance level less than 0.05 with an individual voxel threshold of $P < 0.0001$.

The anatomical reference volume obtained using the SPGR sequence was transformed to Talairach space [Talairach and Tournoux, 1988] and regions of interest (ROIs) based on Brodmann areas (BAs) were drawn according to Talairach coordinates utilizing the Talairach atlas [Lancaster et al., 2000]. The six ROIs created were for inferior frontal (BA 44–47), premotor (BA 6), occipital (BA 18/19), inferior parietal (BA 40), superior parietal (BA 7), and posterior inferior temporal (BA 37) regions. The statistical maps were transformed to Talairach coordinates using a nearest-neighbor transformation derived from the anatomical reference and the volume of the activation within each ROI (left and right) was calculated by counting active voxels within the ROI.

To further analyze the difference in the pattern of activation between the draw and write conditions, laterality indices (LIs) were calculated for the ROIs. Since activation maps, and measures generated from these maps such as activation volumes, are highly dependent on the chosen threshold [Adcock et al., 2003], we used a method for calculating LIs that was not dependent on one threshold value. In this method, the F-statistics generated from the regression analysis were used to compare the activation from an ROI in one hemisphere to the contralateral ROI [Fernandez et al., 2003]. Each LI was calculated by subtracting the sum of F-scores above a given threshold in the right ROI from the sum in the left ROI and dividing by the sum from both ROIs: $(\text{SUM}_{\text{left}} - \text{SUM}_{\text{right}}) / (\text{SUM}_{\text{left}} + \text{SUM}_{\text{right}})$. For each subject, LIs were calculated for a range of thresholds progressing from a low threshold ($P = 0.01$) to a high threshold ($P = 1.0 \times 10^{-6}$) and the LI assigned to each ROI was the average LI over the range of thresholds. The LIs ranged from 1.0 to -1.0 and LIs less than -0.2 were classified as right lateralized, LIs greater than 0.2 were classified as left lateralized, and all LIs in between ($-0.2 \leq \text{LI} \leq 0.2$) were classified as bilateral.

For the group analysis the statistical maps were smoothed (without threshold) with a 6-mm full-width at half-maximum (FWHM) Gaussian kernel to compensate for residual differences after normalization. Group averages were performed by calculating the mean of the regression coefficients for each voxel and the corresponding *t*-statistic of the mean. Group averages were calculated for both imagined drawing and imagined writing compared to baseline and for imagined drawing compared to imagined writing. In addition, for the six subjects that performed both experiments drawing and writing were compared to their respective imagined conditions. Functional maps for the group data were created by applying a threshold of $P < 0.0001$ and cluster size $> 50 \text{ mm}^3$.

Figure 1.

Laterality analysis: imagined drawing and imagined writing. Average laterality index (LI) within each ROI for imagined drawing and imagined writing compared to baseline for all 11 subjects. Conditions: black = imagined drawing, gray = imagined writing. ROIs: InfFnt = inferior frontal, PreMot = premotor, SupPar = superior parietal, InfPar = inferior parietal, InfSupTemp = inferior superior temporal, Occip = occipital.

RESULTS

Experiment 1: Individual Results

Figure 1 displays the average LI within each ROI for imagined drawing compared to baseline and imagined writing compared to baseline.

ing compared to baseline. Imagined writing was left-lateralized (LI > 0.2) in all ROIs and this lateralization was significantly more asymmetric compared to drawing in the superior parietal and premotor ROIs. Imagined drawing was left lateralized in all ROIs except within the superior parietal ROI.

Experiment 1: Group Results

Imagined drawing and imagined writing.

Table I lists the Talairach coordinates and z-score corresponding to the group analyses of imagined drawing compared to baseline, imagined writing compared to baseline, and imagined drawing compared to imagined writing. Imagined drawing and writing produced similar group activation maps, especially in the LH (Fig. 2). This is expected, as the imagery of both drawing and writing involve motor planning, visuospatial mapping, and language processing that strongly activate premotor, inferior frontal, posterior inferior temporal, and parietal areas. Areas active for imagined drawing compared to baseline but not for imagined writing compared to baseline included the insular cortex bilaterally (BA 13), RH posterior inferior temporal (BA 37), middle/inferior frontal cortex (BA 46/9), and LH anterior inferior frontal cortex (BA 47). The z-scores for imagined drawing compared to writing were greater than for imagined drawing compared to baseline.

TABLE I. Group analysis for imagined conditions: local maxima in Talairach coordinates

BA	Area	Write		Draw		Draw vs. write	
		<i>x, y, z</i>	<i>z</i> -score	<i>x, y, z</i>	<i>z</i> -score	<i>x, y, z</i>	<i>z</i> -score
6/44	Inferior Frontal	-51, 5, 26	5.1	-50, 3, 30	6.0		
46/9	Middle/Inferior Frontal	-37, 34, 24	4.3	-45, 29, 22	6.9	-43, 34, 13	4.7
11/47	Inferior Frontal			27, 38, -11	4.9		
6	Middle Frontal	-21, -7, 58	6.5	-24, -3, 46	13.0	-24, 6, 51	6.7
6	Precentral	-42, -6, 41	6.1	-54, -2, 31	6.9		
37	Posterior Temporal	-50, -63, -6	5.0	-48, -59, -7	7.4	-48, -60, -4	6.9
40	Inferior Parietal	-57, -22, 28	5.3	-37, -39, 38	13.0	-43, -32, 38	7.5
7	Superior Parietal	-22, -64, 49	6.2	-14, -61, 53	13.0	-11, -57, 54	6.5
19	Middle Occipital					-33, -86, 11	4.7
13	Insula			-30, 19, 7	5.7	-39, 13, 10	4.7
	Putamen			-19, 4, 10	4.8		
6*	Medial Frontal/SMA	-5, -2, 52	7.5	-4, -3, 52	7.3		
44	Inferior Frontal	51, 8, 20	5.1	51, 8, 25	5.9	44, 11, 20	6.2
	Middle/Inferior Frontal						
46/9	Frontal			48, 40, 16	4.6	45, 41, 16	5.3
6	Middle Frontal	24, -2, 52	7.1	25, -3, 45	13.0	25, -2, 48	7.2
6	Middle Frontal			48, 4, 43			4.5
6	Precentral	49, 0, 46	4.7	48, 1, 44	4.8		
9/10	Superior Frontal				31	45, 34, 4.9	
37	Posterior Temporal			55, -55, -9	4.9	48, -57, -13	5.7
7	Superior Parietal	17, -56, 58	5.6	13, -63, 54	13.0	11, -61, 57	7.2
40	Inferior Parietal	33, -35, 39	6.5	33, -28, 36	13.0	38, -30, 41	7.6
19	Middle Occipital				33	-77, 18, 4.9	
13	Insula			47, 7, 16	5.2		
	Clastrum/Insula			33, 1, 4	4.9		
	Putamen			16, 9, 9	4.9		
	Thalamus					12, -17, 8	4.7

Boldface entries represent right hemisphere activation.

*Activation cluster that crosses hemispheres.

Figure 2.

Group analysis: imagined drawing and imagined writing. Axial slices are in radiological view, Talairach coordinates $z = 50$ to $z = -13$, 7 mm gap. Color key: yellow = areas active for just drawing vs. rest, red = areas active for just writing vs. rest, blue = overlap of activation from the drawing and writing conditions.

ined writing compared to baseline in all areas except for the activation in the medial frontal gyrus.

Imagined drawing vs. imagined writing.

All of the significant differences detected by the direct comparison of imagined drawing to imagined writing revealed greater activation for imagined drawing (Fig. 3). These areas include the RH inferior frontal gyrus and bilaterally in the middle frontal, inferior frontal, parietal, and posterior inferior temporal gyri. Clusters of activation specific only to the drawing vs. writing analysis were detected in the superior frontal (BA 9) gyri of the RH and bilaterally in the occipital cortex (BA 19).

Experiment 2: Individual Results

Figure 4 displays the average LI within each ROI for drawing compared to baseline and writing compared to

baseline and the average LI of the same six subjects for imagined drawing and imagined writing. There were no significant differences in laterality between the actual and imagined conditions.

Experiment 2: Group Results

Figure 5 shows the group results for the subjects who participated in both Experiments 1 and 2. In both comparisons between the tasks with motor output and the imagined tasks (drawing vs. imagined drawing, writing vs. imagined writing), the tasks with motor output produced more activation in BA 4 within the precentral gyrus (Talairach: $-34, -26, 57$). For drawing vs. imagined drawing there was also significant activation in BA 6 within the superior frontal gyrus (Talairach: $-9, 0, 65$). There were no other significant differences between the tasks with motor output and the imagined tasks.

Figure 3.

Group analysis: imagined drawing vs. imagined writing. Axial slices are in radiological view, Talairach coordinates $z = 50$ to $z = -13$, 7 mm gap. All activation represents drawing > writing. Key: red = $P < 1 \times 10^{-4}$, orange/yellow = $P < 1 \times 10^{-6}$.

Figure 4.

Laterality analysis: actual and imagined. Average laterality index (LI) within each ROI for drawing and writing with motor output compared to baseline for all six subjects from Experiment 2 and the average LI for the same six subjects for the imagined drawing and imagined writing conditions. Conditions: D = drawing, ID = imagined drawing, W = writing, IW = imagined writing. ROIs same as for Figure 1.

DISCUSSION

To limit the artifact of head motion induced by actual drawing and writing, mental imagery of drawing and writing was used in the first experiment. Previous studies have compared mental imagery of motor processes vs. actual motor processes [Decety, 1996; Gerardin et al., 2000; Grezes and Decety, 2001; Jeannerod, 2001; Stippich et al., 2002] and provide converging evidence that mental imagery of motor function requires the same association cortices that are used in motor execution. The results from the second experiment in this study provide further evidence. The largest significant difference between drawing and writing with motor output compared to the imagery tasks was in the primary motor cortex. Seitz et al. [1997] compared actual drawing of ideograms to imagined drawing in a PET study. They found that imagined drawing produced greater bilateral activation within BA 7, while actual drawing produced more activation within the motor sensory regions.

In the current study, there was strong bilateral activation within BA 7 for the drawing task requiring actual motor output as well as for imagined drawing. This was expected, since the actual drawing tasks still contained the same degree of visuospatial imagery as the imagined drawing task since both the pictures on the screen and the drawings made on the paper were not viewable during the drawing process.

Another study just using drawing with motor output produced similar results as the imagined object drawing in the current study [Makuuchi et al., 2003]. The experimental condition in this study involved drawing watercolor pictures with the subject's right index finger while naming the objects and the baseline condition was object naming. The major differences in activations between these two studies were in areas associated with object naming and semantics, not in traditional motor areas. Makuuchi et al. [2003] did not report activation in the left posterior inferior temporal gyrus or within the anterior portions of the inferior frontal gyrus. In the current study these areas were activated by the imagined drawing condition. Most likely, the differences are explained by the baseline condition of naming used in the Makuuchi study. Naming traditionally activates the left posterior inferior temporal gyrus and the anterior inferior frontal gyri and thus activations in this area due to drawing would be cancelled out by the naming baseline condition.

The study shows that imagined drawing produces similar activation patterns as actual drawing. However, a major disadvantage of using motor imagery rather than actual motor function is the inability to independently confirm each subject's activity during each scan. In this study, all of the subjects were trained prior to scanning and the subjects did not report any difficulties in performing the tasks while in the scanner. In cases where drawing or writing output is necessary, drawing or writing can be performed within an MRI scanner without detrimentally influencing the MR images. However, subjects must be trained to move only the hand and lower arm without moving their head. This requires very cooperative subjects and may be too difficult for some patients, especially patients with motor difficulties such as some stroke patients.

Figure 5.

Group analysis: actual vs. imagined. Group comparison for subjects participating in both experiments. Axial slices are in radiological view, Talairach coordinates $z = 64$ to $z = 52$, 4 mm gap. Color key: yellow = areas active for just actual drawing vs. imagined drawing, red = areas active for just actual writing vs. imagined writing, blue = overlap of activation from both actual vs. imagined conditions.

Drawing vs. Writing in Relation to Naming

When comparing the activation maps of drawing and writing compared to baseline (Fig. 3), the areas with the least amount of overlap were in the posterior inferior temporal gyrus and fusiform gyrus corresponding to BA 37. BA 37 is considered a multimodal language area, and both anomia [Foundas et al., 1998; Raymer et al., 1997] and lexical agraphia [Rapcsak et al., 1990; Sakurai et al., 2000b; Soma et al., 1989] have been associated with lesions to BA 37. Moore and Price [1999] divided this region into anterior, middle, and posterior subregions responsible for semantic processing, naming, and object processing, respectively. Both drawing and writing activated a region in the LH encompassing the middle subregion to the posterior subregion. These areas corresponded to those defined by Moore and Price [1999] for naming and object processing. Similarly, Beeson et al. [2003a] reported activation in the posterior region of BA 37, which they proposed was due to the processing of letter shapes.

On the basis of the current study we propose that the overlap of activation for drawing and writing in the posterior BA 37 region is due to the visual processing of the objects in both conditions. The activation patterns for the two conditions differed in the anterior subregion of BA 37, where only drawing caused activation. Moore and Price [1999] proposed that this subregion was involved in semantic processing. Both anterior and middle/posterior subregions of BA 37 were significantly more active for drawing compared to writing, suggesting increased interaction between object features and semantic processing for the drawing condition.

In the RH, there was only a small activation cluster for writing compared to baseline near the posterior subregion of BA 37, while the larger drawing activation cluster extended from the posterior subregion toward the middle subregion. The difference between the drawing and writing activation within the RH of BA 37 was even more pronounced with the direct comparison of drawing to writing (see Fig. 2). The activation for drawing was significantly stronger than writing for all of the BA 37 subregions including the semantic subregion in the RH. Makuuchi et al. [2003] speculated that the right inferior temporal sulcus, BA 37, subserves drawing by using the knowledge of the structural and perceptual aspects of the object. The magnitude of the signal changes for writing in the RH anterior subregion of BA 37 was slightly negative, which suggests that writing inhibits this area and may explain why this area was only significantly active for the drawing vs. writing contrast. The increased activation for drawing throughout the middle and anterior regions of BA 37 bilaterally may facilitate naming through increased lexical-semantic interaction. The significant difference between activation detected in the draw vs. write condition within the RH may be especially important for patients with aphasia with LH damage.

Further support for the critical involvement of BA 37 in lexical-semantic integration comes from research comparing Japanese Kanji writing to Kana writing [Sakurai et al., 2000a;

Soma et al., 1989; Tokunaga et al., 1999; Usui et al., 2003]. Similar to drawing vs. writing, Kanji writing is thought to require more spatial imagery and semantic components compared to Kana writing. Kanji characters are visual figures that are strongly associated with the semantics of the object they represent [Usui et al., 2003]. Tokunaga et al. [1999] compared the mental imagery of writing Kanji characters to Kana letters and found greater activation in the left inferior temporal cortex for Kanji writing. The study by Usui et al. [2003] compared Kanji and Kana writing with object naming and found that when BA 37 was impaired (via electric stimulation), both object naming and Kanji writing were impaired, although recognition of the structural features of the characters was retained. The majority (70%) of the naming errors were interruption of naming, while the remainder of the errors were semantic. Usui et al. [2003] proposed that BA 37 is involved in the "conversion of visual stimuli carrying semantic information into their phonological representations." The increased activation of BA 37 for drawing may help facilitate the conversion of semantic information into their phonological representations, further supporting the relationship between semantic-lexical integration and drawing, as first suggested by Gainotti et al. [1983].

Another possible reason for the facilitation of naming while drawing could be the increased inferior frontal activation found in drawing compared to writing. Previous studies have shown BA 46 involvement in tasks involving willed action [Frith et al., 1991] and language tasks that involve selection of semantic knowledge [Cappa et al., 1998; Martin et al., 1995; Thompson-Schill et al., 1997] and object naming [Price et al., 1996]. The increase in bilateral activation of BA 46 coupled with the bilateral increase of activation in BA 37 revealed in the drawing vs. writing group analysis could be the result of increased semantic-lexical interaction.

Drawing vs. Writing: Other Areas

It is plausible that facilitation of naming while drawing is the byproduct of the activation induced by the motor aspects of drawing. There was activation in BA 44 of the RH for the drawing vs. writing comparison. Motor imagery has been shown to activate Broca's areas [Binkofski et al., 2000; Stephan et al., 1995] and Binkofski et al. [2000] argue that BA 44 is important for the execution and imagery of skilled forelimb movements. BA 44 is believed to be the homolog of area F5 in the monkey, which represents the hand, arm, and mouth motor area in the monkey [Rizzolatti et al., 2002]. Area F5 is vital for transforming visual properties of 3D objects into hand orientations appropriate to interact with them [Rizzolatti et al., 2002]. In relation to this study, the drawing condition involved transforming visual properties of 2D objects and using this information for appropriate hand motor action.

The superior parietal cortex (BA 7) is a critical area for both drawing [Makuuchi et al., 2003] and writing [Menon and Desmond, 2001]. However, drawing produced significantly stronger and less lateralized activation in BA 7 com-

pared to writing. BA 7 has been implicated in spatial processing and it has been conjectured that the role of BA 7 in writing is to provide graphic images that are passed on to the premotor regions for motor planning [Brain, 1967]. We propose that the differences between drawing and writing, both in strength of activation and laterality, are due to increased imagery and spatial demands for drawing. Visual imagery tasks with spatial components normally produce bilateral activation in BA 7 [Kosslyn et al., 1997, 2001; Mellet et al., 2000; Sack et al., 2002; Trojano et al., 2002] and previous drawing studies consistently found bilateral activation [Ino et al., 2003; Makuuchi et al., 2003] in BA 7.

The activation within the inferior parietal cortex (BA 40) was significantly left-lateralized for both writing and drawing. Similar to the superior parietal cortex, there was more activation in the inferior parietal cortex for drawing compared to writing. The inferior parietal cortex is consistently activated by motor imagery tasks [Binkofski et al., 2000; Decety, 1996; Gerardin et al., 2000; Grezes and Decety, 2001; Jeannerod, 2001]. The left laterality of the BA 40 activation for drawing and writing can be explained by the requirement of motor attention [Rushworth et al., 2001] for the conditions. However, BA 40 has also been implicated in phonological [Clark and Wagner, 2003; Gold and Buckner, 2002] and working memory [D'Esposito et al., 1998; Jonides et al., 1998; Klingberg et al., 2002] processes. An increased demand for working memory for drawing previously viewed objects, as compared to the reduced demand when writing letters that are familiar, could explain the increased activation in BA 40 for drawing.

The areas that were active for drawing and writing in the frontal cortex superior to the inferior frontal gyrus can be separated into three major subareas: supplementary motor area (SMA), premotor gyrus, and middle frontal gyrus. SMA has been reported to be involved with the selection and preparation of movement [Deiber et al., 1998; Humberstone et al., 1997]. In our studies, significantly greater activation in the SMA occurred for drawing vs. for writing, which suggests that drawing previously viewed objects requires more motor planning compared to writing familiar letters. A portion of the cluster of activation centered in the premotor area was located within the proposed location for Exner's area, which is a language area believed to be specific to writing [Exner, 1881] and responsible for organizing graphic motor images [Longcamp et al., 2003]. The exact location of Exner's area is proposed to be within the premotor cortex (BA 6) of the LH, between Broca's area and the frontal eye fields [Anderson et al., 1990; Matsuo et al., 2003]. Matsuo et al. [2003] compared language tasks to saccadic eye movement tasks in order to separate the frontal eye fields from Exner's area. In Matsuo's study the average coordinates for Exner's area (Talairach: -46, -4, 43) was close to the location of activation in the precentral gyrus for drawing and writing found in this study (Table I). The local maxima z-coordinate of the activation cluster for drawing was slightly inferior to Matsuo et al.'s z-coordinate for Exner's area, but the cluster for drawing encompasses the Matsuo et al.'s [2003] z-coor-

dinate. This suggests that although Exner's area is believed to be responsible for motor programming necessary for producing letters, it may also be responsible for motor programming necessary for drawing objects. Activation also occurred for drawing and writing in the same general area of the RH, although the activation in the LH was much larger for both conditions. However, drawing produced significantly stronger activation than did writing in the RH homolog of Exner's area.

The activation of the frontal eye field can be attributed to the use of the eyes to mentally draw an object. There is evidence that eye movements play a pivotal functional role during visual mental imagery [Laeng and Teodorescu, 2002; Mast and Kosslyn, 2002]. Also, this region has been implicated in working memory tasks [Courtney et al., 1996; D'Esposito et al., 1998; Jonides et al., 1998] and may play a role with the working memory component of the drawing condition. We believe that the increased activation of the frontal eye fields is due to the increased working memory demands for drawing a novel object compared to writing familiar letters. The eyes fields may also be more active specifically for the imagery of drawing compared to actual drawing. Unfortunately, eye-tracking information was not collected in this experiment.

Implications in Patients with Aphasia

Both drawing and writing require cortical areas involved in the processing and control of cognitive, language, and motor functions. Writing, however, employs an exclusively lexical route to phonological output, whereas drawing can utilize a lexical or nonlexical route. Although writing and drawing produce bihemispheric activation, writing may actually inhibit some right hemisphere cortices related to language, while drawing does not. The differences in RH activation, as shown in the draw vs. write group results, are in areas known to be involved in a widely distributed semantic network may contribute to the facilitation of naming in patients with aphasia with LH damage. Drawing also produced strong LH activation within the posterior inferior temporal and anterior inferior frontal cortex, areas known to be activated during naming tasks. Increased activation in these perilesional areas in patients with LH damage may contribute to naming.

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