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AN fMRI INVESTIGATION OF CATEGORY-SPECIFIC EPISODIC ENCODING

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ABSTRACT

Determining whether certain categories of words have discrete neural representations (processing dedicated to different brain regions) is the pursuit of this thesis. Twelve participants were scanned using functional magnetic resonance imaging (fMRI) to discriminate between the neural correlates of words representing either animals or objects during episodic encoding. Consistent with semantic retrieval studies, neural activity associated specifically with objects was encoded predominantly in the posterior portion of the left hemisphere: the superior frontal gyrus, parahippocampal gyrus, fusiform gyrus, posterior cingulate cortex, occipitotemporal cortex, precuneus, and occipital cortex. Activity associated specifically with animals, however, was encoded predominantly in anterior portion of the right hemisphere: the dorsolateral prefrontal cortex (DLPFC), ventrolateral prefrontal cortex (VLPFC), medial prefrontal cortex, and the posterior midline. Although the regions for animal activity are inconsistent with previous studies, data show that each category exhibits its own processing regions, suggesting that category specificity occurs not only during semantic retrieval, but also during episodic encoding of words.

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Introduction

Because most neuroscientific evidence suggests that the animal brain operates on principles governed by physical laws, it is particularly unusual that the capabilities of the animal brain, chiefly the human brain, extend beyond such principles. The continuous progression of time illustrates a physical law that is defied by human thought. For everything in nature, the passing of time is constant and irreversible, with only one exception. Via thought, the human brain is able to break from the present and retrieve stored memories of past events. These memories are snippets of time, timeless in themselves, and, according to modern evidence, are perceived from the activity of specific neural networks in an individual's brain. This thesis is concerned with this neuronal basis of memory and how different types of memory are processed in distinct regions of the brain.

Memory research is a core aspect of cognitive psychology and has modeled human memory into several divisions. Long-term and working memory are the primary divisions, having temporal differences but sharing characteristics such as encoding, consolidation, and retrieval. Long-term memory (LTM) is considered an archive of memory with a duration lasting from just beyond the length of working memory to indefinite. Furthermore, as a subset of LTM, declarative memory serves as the basis of remembering facts and events experienced throughout life.

A final division differentiates declarative memory into episodic and semantic memory. Episodic memory is the memory for personal experiences and events, which gives rise to the possibility of mental time travel. Alternatively, semantic memory is the memory subserving the knowledge of concepts and facts that one has accrued throughout his or her lifetime. Remembering the event of eating waffles for breakfast is an example of episodic memory, whereas remembering

that waffles are breakfast foods is an example of semantic memory. Episodic memory, with emphasis on its neural substrates, is the memory subsystem of focus in this thesis.

One of the major questions that has arisen in the domain of semantic memory is how semantic memory processing is distributed throughout the brain. Is all semantic memory processing accomplished in a single, isolated brain region, or is each partition of knowledge processed in discrete areas? Until the advent of neuroimaging, which has helped reveal latent brain function during performance tasks, the main approach to this category-specific research was limited to behavioral methods from patients with brain lesions.

Specialization of brain function has thus been identified by the behavioral deficits in individuals with brain damage. One such example of specialization is seen in patients with prosopagnosia. Individuals with prosopagnosia suffer from lesions in bilateral inferior occipitotemporal lobes, the fusiform face area (FFA), and are unable to recognize particular faces (Geschwind, 1979; Sergent, Ohta, & MacDonald, 1992). Although these individuals are able to discern the image of a face, they are impaired in associating a face with the identity of a person. This deficit suggests that the neuronal functions of face processing have a unique home in the FFA. Thus the specialization of brain function in the case of prosopagnosia serves to illustrate how specific lesions can result in processing deficits of particular visual stimuli.

Similarly, patients with aphasia, or word processing deficits, reveal a comparable finding. Because they can exhibit particular deficits from picture identification, auditory identification, and comprehension naming, patients suffering from brain damage have provided valuable behavioral insight into the neural divisions of verbal processing and memory tasks. An aphasia in which verbal processing is intact except for one category of stimuli is called a category-specific aphasia. Individuals

with category-specific aphasia may exhibit superior or inferior performance in recognition and comprehension tasks from one of number of different categories of stimuli such as animals, tools, jobs, places, foods, body parts, etcetera (Warrington & McCarthy, 1987; Gainotti, Silveri, Daniele, & Giustolisi, 1995; Warrington & Shallice, 1984; Suzuki, Yamadori, Fuji, 1997; Thompson-Schill, 2003). One example of a patient with category-specific differences in comprehension is F.C., who exhibited superior comprehension performance for the category countries when compared to his performance in colors, objects, body parts, and animals (McKenna & Warrington 1978). Another example of category-specificity is the concreteness effect. In healthy individuals, comprehension for concrete words is greater than comprehension for abstract words (Paivio, 1991). Many aphasic individuals, however, show the opposite effect; studies have demonstrated superior comprehension for abstract words over concrete words (Breedin *et al.*, 1994). This finding suggests that neural processing of conceptual verbal information is distinct from the processing of concrete information.

In addition to lesions studies and behavioral evidence that suggests discrete processing for different categories of words, recent studies using functional neuroimaging techniques have been able to assess these different functions in healthy individuals. Neuroimaging studies of semantic retrieval provide a non-invasive approach to study brain function, identifying the category-specific semantic impairments exhibited by aphasic patients in non-compromised brains.

From the many studies that have utilized neuroimaging techniques, one common finding that has emerged is the difference in activated regions between living and non-living stimuli, elicited by pictures of animals and pictures of objects or tools (Caramazza & Shelton, 1998; Saffran, 2000; Perani *et al.*, 1995; Martin *et al.*, 1996). Object recognition was associated with a certain set brain regions and animal recognition activated a different set of brain regions (Perani *et al.*, 1995; Martin *et al.*,

1996; Moore and Price 1995; Mummery *et al.*, 1996). Although the exact correlation between category and its associated region has been somewhat inconsistent, this animate/inanimate category-specific effect has been demonstrated in a number of studies and is also the main contrast in this thesis.

Neuroimaging studies targeting brain activity associated specifically with animals have revealed common activations in temporal and occipital areas. In a study using positron emission topography (PET) participants were asked to identify black and white visual stimuli that were either animals, objects, or nonsense (Perani *et al.*, 1995). Results showed that, compared to baseline, activity for selective to animals was located in occipital and inferior temporal areas, bilaterally. Similarly, Martin and colleagues (1996) found that identifying pictures of animals activated the medial occipital lobe, which is known to be associated with early-stage visual processing. Additionally, Mummery and colleagues (1996) also found temporal lobe activity when participants generated words that belonged to the category natural entities. Furthermore, Moore and Price (1999) found bilateral anterior temporal and right posterior middle temporal activity for picture naming and word-picture matching tasks. Hence, both temporal and occipital activity, without lateralization, appears to be specifically associated with animal processing. Activity in the occipital areas may be representative of visual imagery elicited by participants when viewing pictures of animals, and temporal activity may represent visual discriminatory perception contributed by the ventral stream (Gooddale & Milner, 1992).

Studies targeting brain activity specifically associated with objects have revealed that objects commonly elicit left hemisphere activity. Perani and colleagues (1995) found that naming picture of objects elicits left hemispheric networks, including the dorsolateral prefrontal cortex (DLPFC).

Mummary and colleagues (1996) found that generation of objects activated left hemispheric posterior regions, including the left posterior temporal cortex. Additionally, Moore and Price (1999) also found left posterior medial temporal cortical activity in response to object picture naming and word-picture matching tasks. Furthermore, Martin and colleagues (1996) found that identifying pictures of objects activated the left premotor area, which has been implicated in imagined hand movements, and left middle temporal gyrus, which has been implicated in generation of action words. Thus, object representation is predominantly located in the left hemisphere. Additionally, object processing is distributed in frontal areas, which are responsible for manipulation of thought and movement, as well as occipital and temporal areas, which are associated with visual and memory processes.

Thus, although neuroimaging provides evidence for semantic category specificity as suggested by case studies from aphasiac individuals, the data is somewhat inconsistent among various studies, limiting the specificity of a category to either a hemisphere or two adjacent lobes. Furthermore, this inconsistency is even more complicated when predicting the neural correlates of episodic encoding. Neuroimaging studies involving episodic encoding extend beyond semantic retrieval studies and seek to identify brain regions which contribute to memory formation that are active during a semantic retrieval task, which activates regions associated with stimuli identification and naming tasks only. During episodic encoding, semantic retrieval of information functions as a means for interacting with and processing the to-be-learned stimuli (Tulving, 2002). In a study by Prince, Tsukiura, & Cabeza (2007) the neural correlates between episodic encoding and semantic retrieval were found to be dissociable, although activity for both tasks was common to the middle region of the left inferior prefrontal cortex when semantic retrieval was high. This suggests that neuroimaging results of

category-specific episodic encoding tasks may elicit different brain regions than semantic retrieval tasks.

Furthermore, studies have shown differences in neural activity due to differences in modality (Engel *et al.*, 2009; Tyler *et al.*, 2001). Because the present study examines encoding for words representing animals and objects, the results will most likely differ from retrieval studies which used pictures as stimuli. Instead of a visual modality, the present study examines a verbal modality. Studies investigating the neural correlates of verbal encoding tasks have revealed left-lateralized activation for (Kelley *et al.*, 1998; Wagner *et al.*, 1998). Thus, such lateralization should be reflected in the present study as well.

Evidence for category-specificity has thus progressed from case studies of individuals with focal lesions and supported by semantic retrieval tasks in neuroimaging studies. In the current study we seek to identify category-specific activation additionally for episodic encoding. A difference between our current study and most previous studies is that stimuli are presented as words instead of pictures. Despite this difference in stimuli, we predict category-specific activation will be preserved. However, because the present study seeks to identify encoding activity, we expect to find different regions than activated by semantic retrieval tasks, as found in Prince, Tsukiura, and Cabeza (2007). Furthermore, we predict that the regions elicited by episodic encoding of animals and objects when presented by words will be localized to the left hemisphere, which has been identified as the dominant hemisphere in verbal semantic processes (Kelley *et al.*, 1998; Wagner *et al.*, 1998).

Methods

Participants

Twelve healthy young participants (eight male and four female students; mean age = 22.2 yrs, SD = 3.5) from Duke University were scanned and paid for their participation. Informed consent was obtained for all participants according to and approved by Duke University Institutional Review Board.

Stimuli

Stimuli included 304 words equally divided four categories: jobs, objects, places, and animals. Each word presented belonged to exactly one of the four categories. Of the 304 words presented, 224 were presented in the scanner during encoding and 80 additional words were presented on a computer during retrieval only.

Procedure

During encoding each word was presented visually, one at a time, centered on the scanner projection. Four letters (j, o, p, a) were displayed below each word to remind the participant of the four word categories. Participants were asked to categorize each word by pressing a button corresponding to the appropriate category. They were also asked to make this semantic judgment as quickly and as accurately as possible. Participants were unaware of the subsequent memory test. Retrieval occurred approximately 20 minutes following the encoding session wherein participants completed a recognition test outside the scanner. Participants were presented on a computer 208 old words from encoding and 80 new words. At retrieval, participants were asked to judge whether the words were old or new (indicating whether they had seen the word during encoding) and to rate the confidence of their judgment (Definitely Old, Probably Old, Probably New, Definitely New). Words

were presented one at a time for three seconds each, and participants were asked to press the key corresponding to their judgment and confidence.

Scanning

Images were collected using a 4T GE scanner. Stimuli were presented using liquid crystal display goggles (ResonanceTechnology, Northridge, CA) and behavioral responses were recorded using a four button fiber optic response box (Resonance Technology). Scanner noise was reduced with earplugs and head motion was minimized using foam pads and a headband. Anatomical scans began by first acquiring a T1-weighted sagittal localizer series. The anterior (AC) and posterior commissures (PC) were identified in the midsagittal slice and 34 contiguous oblique slices were prescribed parallel to the AC-PC plane. High resolution T1-weighted structural images were acquired with a 12ms repetition time (TR), a 5 ms echo time (TE), 24 cm field of view(FOV), 68 slices, 1.9mmslice thickness, 0mmspacing, and 256×256 matrix. Echoplanar functional images were acquired using an inverse spiral sequence with a 1500 ms TR, 31 ms TE, 24 cm FOV, 34 slices, 3.8mm slice thickness, resulting in cubic 3.8mm³ isotropic voxels, and 64×64 image matrix.

fMRI analyses

All image preprocessing and statistical analyses were performed using Statistical Parameter Mapping software implemented in Matlab (SPM2; Wellcome Department of Cognitive Neurology, London, UK). After discarding the first six volumes, images were corrected for slice-timing and motion, then spatially normalized to the Montreal Neurological Institute (MNI) template and smoothed using a Gaussian kernel of 8mm FWHM. For each subject, item-related activity was modeled with a stick function corresponding to stimulus onsets, convolved with a canonical hemodynamic response function (HRF) within the context of the GLM, as implemented

in SPM2. Confounding factors (head motion, magnetic field drift) were also included in the model. According to our motion parameters no participant moved more than 3mm in any direction either within or across runs. Thus, no data was eliminated due to motion artifacts. To further address this issue we calculated both the mean and maximum value for each motion parameter for each subject for each direction (x, y, z, pitch, roll, and yaw). We then performed unpaired t-tests on each motion parameter across age groups. No test approached significance (p ranged from 0.1 to 0.96 across all tests).¹

Trial types included High Hits (correct retrieval from high-confidence encoding), Low Hits (correct retrieval from low-confidence encoding), Low Misses (incorrect retrieval from low-confidence encoding), and High Misses (incorrect retrieval from high-confidence encoding). High and Low Hits were combined into the single trial type All Hits. Likewise, High and Low Misses were combined into the single trial type All Misses. Successful encoding was defined as a difference in memory (Dm), where activity for subsequently forgotten items was subtracted from subsequently remembered items. Dm was calculated by comparing All Hit > All Miss activity for both animals and objects. The threshold for this contrasts was set to $p < .05$ and $K = 10$ contiguous voxels.²

From this Dm contrast an addition contrast was formed between the categories animals and objects. Specifically we looked for regions where Animal Dm was greater than Object Dm, (DmA > DmO). Likewise, we looked for regions where Object Dm was greater than Animal Dm, (DmO > DmA). Contrasts were created using a threshold of $p < .05$ and 10 voxels, masked with the main effect of interest at $p < .05$ and 10 voxels.

¹ Neuroimaging and data acquisition were performed in a previous study. Methods for scanning and fMRI analysis were taken from Dennis *et al.* 2007.

² This threshold is lenient for most neuroimaging studies but was necessary to identify pertinent differences in the current analysis.

Results

Behavioral Results

To examine memory differences among categories, t-tests were performed. No significant differences were found between categories for high hit rate ($t = -0.814$, $p < .4241$), low hit rate ($t = -0.528$, $p = .6029$), miss rate ($t = -0.098$, $p = .9232$), FA rate ($t = 0.686$, $p = .5672$). Encoding RT revealed no differences for time-on-task ($t = 1.026$, $p = .3936$). Thus, any differences in neural activity are due to a category-specificity effect alone.

Neuroimaging Results

Table 1 lists activated regions Animal Dm, and Table 2 lists activated regions Object Dm. Table 3 lists regions active where Animal Dm is greater than Object Dm ($DmA > DmO$), which include the right dorsolateral prefrontal cortex (DLPFC), right ventrolateral prefrontal cortex (VLPFC), right medial prefrontal cortex, and the right posterior midline. Thus, Animal Dm activations are lateralized to the right hemisphere. Also included in Table 3 are region active where Object Dm is greater than Animal Dm ($DmO > DmA$), which include the left superior frontal gyrus, left parahippocampal gyrus, left fusiform gyrus, left posterior cingulate cortex, right occipitotemporal cortex, left precuneus, and right occipital cortex. Thus, in contrast to $DmA > DmO$ activation and with the exception of the occipitotemporal and occipital cortices, $DmO > DmA$ activation is lateralized to the left hemisphere.

Table 1
Episodic encoding activations for animal Dm

	H	BA	Coordinates (T&T)				Voxels
			x	y	z	T	
<i>Animal Dm</i>							
Medial PFC	L	10	-15	45	8	2.43	17
Dorsolateral PFC	R	45/46/10	53	37	5	3.44	28
	R	9/44	34	5	31	2.65	10
Ventrolateral PFC	R	47/11	26	29	-14	5.59	88
Medial PFC	L	10	-23	37	-2	3.14	14
Medial	R	24	19	2	35	3.43	12
Anterior Parahippocampal Gyrus	L	21	-30	-1	-29	2.63	17
Parahippocampal Gyrus	L	37	-30	-48	-4	3.05	25
Posterior Midline	R	31	15	-32	33	2.56	24
Inferior Parietal Cortex	R	40	45	-35	30	2.58	13
Superior Parietal Cortex	L	7	-19	-52	66	3.38	10
	R	7/19/39	30	-57	38	3.98	120
Precuneus	L	7	-11	-57	48	3.78	45
Occipital Cortex	L	17/18	-15	-76	21	2.90	11
	L	18	-30	-96	2	3.50	32
	R	18	23	-99	5	2.74	18

Notes: PFC = prefrontal cortex, BA = Brodmann Area, H = Hemisphere, T= statistical *t*-value, T&T = Talairach and Tournoux

Table 2
Episodic encoding activations for object Dm

	H	BA	Coordinates (T&T)				Voxels
			x	y	z	T	
<i>Object Dm</i>							
Orbitofrontal Cortex	L	10	-19	48	-6	2.76	32
Superior Frontal Cortex	L	8/9	-8	32	51	3.5	78
Inferior Lateral PFC	R	47	45	32	-18	3.95	18
Ventrolateral PFC	L	47	-49	25	-8	3.52	15
Inferior Temporal Cortex	R	20	38	-9	-32	3.09	11
Anterior Parahippocampal Gyrus	L	28/35	-34	-9	-28	3.16	26
Parahippocampal Gyrus	L	27/28	-11	-23	-8	3.28	27
Thalamus	L	—	-23	-25	12	2.72	14
Precuneus	L	7	-8	-53	41	3.29	12
Lateral Inferior Parietal Cortex	L	39	-41	-58	31	2.36	10
Posterior Cingulate Cortex	L	30/31/23	-4	-62	17	3.67	72
Occipitotemporal Cortex	R	18/19/37	41	-81	4	3.89	135
Occipital Cortex	M	17	0	-92	5	2.44	15
	L	18	-19	-95	12	4.16	41
Fusiform Gyrus	L	27/30	-34	-60	-23	5.36	263

Notes: PFC = prefrontal cortex, BA = Brodmann Area, H = Hemisphere, T= statistical *t*-value, T&T = Talairach and Tournoux

Table 3
Episodic encoding activations animals compared to objects

	H	BA	Coordinates (T&T)				Voxels
			x	y	z	T	
<i>Animal Dm > Object Dm</i>							
DLPFC	R	46	45	45	8	3.29	13
VLPFC	R	47/11	30	36	-18	2.87	17
Medial PFC	R	24	19	5	35	3.70	11
Posterior Midline	R	31	15	-31	37	3.26	14
<i>Object Dm > Animal Dm</i>							
Superior Frontal Gyrus	L	8	-8	36	51	2.67	11
Parahippocampal Gyrus	L	28/35	-8	-19	-12	4.15	13
Fusiform Gyrus	L	20/37	-34	-38	-17	4.35	47
Posterior Cingulate	L	31	-4	-62	21	3.91	39
Occipitotemporal Cortex	R	19/37	38	-66	0	2.51	10
Precuneus	L	7	-8	-79	49	2.85	12
Occipital Cortex	R	18/19	41	-88	4	3.56	34

Notes: DL = dorsolateral, VL = ventrolateral, PFC = prefrontal cortex, BA = Brodmann Area, H = Hemisphere, T= statistical *t*-value, T&T = Talairach and Tournoux

Discussion

The purpose of this thesis was to determine whether the neural substrates of successful episodic encoding for words representing animals and objects are category specific. Previous studies have shown that specific brain regions are activated by each category during semantic retrieval tasks, and this study focused on whether such neural differences also exist during the encoding phase of learning.

In accord with semantic retrieval studies, neural differences between animals and objects were also found during episodic encoding. Results showed that each category activated discrete brain regions (See Table 3). For areas active for animals (DmA > DmO), see Figure 1. For areas active for objects (DmO > DmA), see Figure 2.

Animal and Object Dm

Successful encoding activations for Animal Dm and Object Dm were consistent with literature on the neuroimaging of encoding. Activated in both categories was the medial temporal lobes (MTL) and the prefrontal cortex (PFC). More specifically, the left prefrontal cortex, which has been implicated in a number of successful memory encoding studies (Tulving *et al.*, 1994; Nyberg, Cabeza, and Tulving, 1996; Prince, Daselaar, & Cabeza, 2005) was activated in both Animal Dm and Object Dm. Likewise, areas of the MTL, such as the parahippocampal gyrus, which has also been identified as a key region in memory encoding (Wagner *et al.*, 1998; Schon *et al.*, 2004) was also activated by both Animal Dm and Object Dm. These findings indicate normal activity for memory encoding processes.

Animal-specific processing

In addition to Animal Dm and Object Dm, discrete neural activations selective to animals (DmA > DmO) were found. This category-specificity is consistent with literature suggesting discrete processing areas for different categories of words. However, although consistent in the sense that each category is discrete, the findings are inconsistent with the areas suggested to be associated with each category. For example, semantic retrieval studies have identified temporal and occipital areas with recognition of animals (Moore & Price, 1995; Perani *et al.*, 1995; Martin *et al.*, 1996; Mummery *et al.*, 1996). In the present study, neither temporal nor occipital areas were activated selectively for animals.

Activated regions specific to successful encoding of animals are isolated to the right hemisphere. These areas include the right DLPFC, right VLPFC, medial prefrontal cortex, and the posterior midline. These findings are inconsistent with the literature studying the neural processing specific to animals, which has implicated temporal and occipital areas in animal processing. Furthermore, prefrontal areas are associated with working memory, attention, and executive functions (Blumenfeld & Ranganath, 2006; Tanji & Hoshi, 2008; Asplund *et al.*, 2010). Thus, it may be that successful animal encoding requires heightened activation in working memory systems or demands increased attention compared to object stimuli. One might be able to support or dismiss this hypothesis in a follow-up study by comparing encoding performance for each category under cognitively demanding conditions. If, under these conditions, memory performance for objects is more successful than animals, then this difference provides evidence that successful animal encoding requires greater attention or working memory.

Additionally, right prefrontal activity has been implicated in facial processing (Nyberg, Cabeza, & Tulving, 1996; Kelley, 1998). Activation of this area may be a reflection of visual imagery provoked by animal stimuli. When presented with words representing animals, participants may be imagining the faces of the animals during the encoding process. Although this is speculative, further investigation could compare the conditions in the study, where the task is to categorize stimuli, with a task where participants are specifically asked to visually imagine the same stimuli. If similar areas are activated, then such findings may support the hypothesis that participants are imagining the faces of animals during episodic encoding.

Object-specific processing

Activated regions specific to successful encoding of objects (DmO > DmA) were located in the left hemisphere, with the exception of the occipital and occipitotemporal cortices. These include the superior frontal gyrus, parahippocampal gyrus, fusiform gyrus, posterior cingulate cortex, occipitotemporal cortex, precuneus, and occipital cortex. This activation dominant in the left hemispheric is consistent with the literature on object recognition processing (Perani *et al.*, 1995; Martin *et al.*, 1996).

Although there are some common findings among studies, much of the data reveal different regions activated for slightly different tasks. This difference in task-specific activation may be responsible for the inconsistency in findings. One such difference is presentation modality. In semantic retrieval studies, participants were scanned while viewing pictures. In the present study, however, participants were presented with words. Although the meaning of the stimuli is common in each study, the stimuli presentation modality may nonetheless have activated different brain regions, causing this inconsistency in the activated areas specific to each category.

Another unique finding in this study is the lateralization effect between categories. Although previous studies have identified the left hemisphere as being dominant in semantic retrieval tasks associated specifically with objects (Perani *et al.*, 1995; Martin *et al.*, 1996), to our knowledge, no studies have noted right hemisphere dominance for processing of animals.

Limitations and Future Directions

One limitation of this study may be a consequence of how episodic encoding was defined during analysis. Because episodic encoding was defined by the Dm effect as subsequent misses subtracted from subsequent hits, data analysis reflects activity merely when both encoding and retrieval were successful. However, unsuccessful memory may also be due to failure to retrieve, and not failure to encode alone. Therefore, the results of this study cannot be generalized to overall encoding processes, but merely successful, subsequently remembered episodic encoding.

Another weakness of this study is the definition of animal and object specificity. Because no baseline conditions were measured during encoding, active regions specific to each category were identified by a category-to-category contrast, instead of a category-to-baseline contrast, as was performed in category-specific semantic retrieval tasks (Moore & Price, 1995; Perani *et al.*, 1995; Martin *et al.*, 1996; Mummery *et al.*, 1996). In future studies category activity should first be contrasted with baseline encoding conditions and then contrasted between categories to properly reflect category-specific activity.

From these findings there are many possible avenues for further investigation. Future studies could examine semantic processing involved in the processing of this same stimuli. Instead of analyzing memory processes, new studies could investigate semantic retrieval processing of words representing each category. This could help elucidate whether right-hemisphere animal lateralization

in the present study is due to episodic encoding conditions. Alternatively, a follow-up study could investigate episodic memory using pictures as stimuli instead of words. This would elucidate the role of modality on the results of this study and provide a closer comparison to semantic retrieval studies which also use picture stimuli.

Furthermore, patients with category-specific aphasias could be used in future studies to determine if the regions associated with their deficits correspond to the neuroimaging results of healthy individuals. Moreover, if these patients were to relearn their aphasic categories, neuroimaging studies could identify how these categories were represented anew throughout the brain, revealing the extent of neuroplasticity in episodic encoding.

By studying the neural correlates of verbal encoding tasks, researchers can identify the neural representation of knowledge throughout the brain. Studies like the present can elucidate how knowledge is constructed and distributed throughout neural networks. The present study, finding category-specific activations for animals and objects, has provided evidence that the representation of semantic knowledge is not simply stored in differing brain regions, but is also encoded in different brain regions. This provides further evidence into the specialization of brain regions, where processing differences are found not only between categories, but also between components of memory tasks.

In summary, fMRI was used to determine the neural processes of healthy individuals during category-specific episodic encoding task. Successful encoding for both categories activated the PFC and MTL, which is consistent with encoding literature. Analysis further differentiated between the encoding animals and objects to determine whether each category was processed in discrete brain regions, and results showed that category-specificity exists. Activated regions associated specifically

with animals are lateralized to the right hemisphere, and activated regions associated specifically with objects are, with exceptions, predominantly lateralized to the left hemisphere.

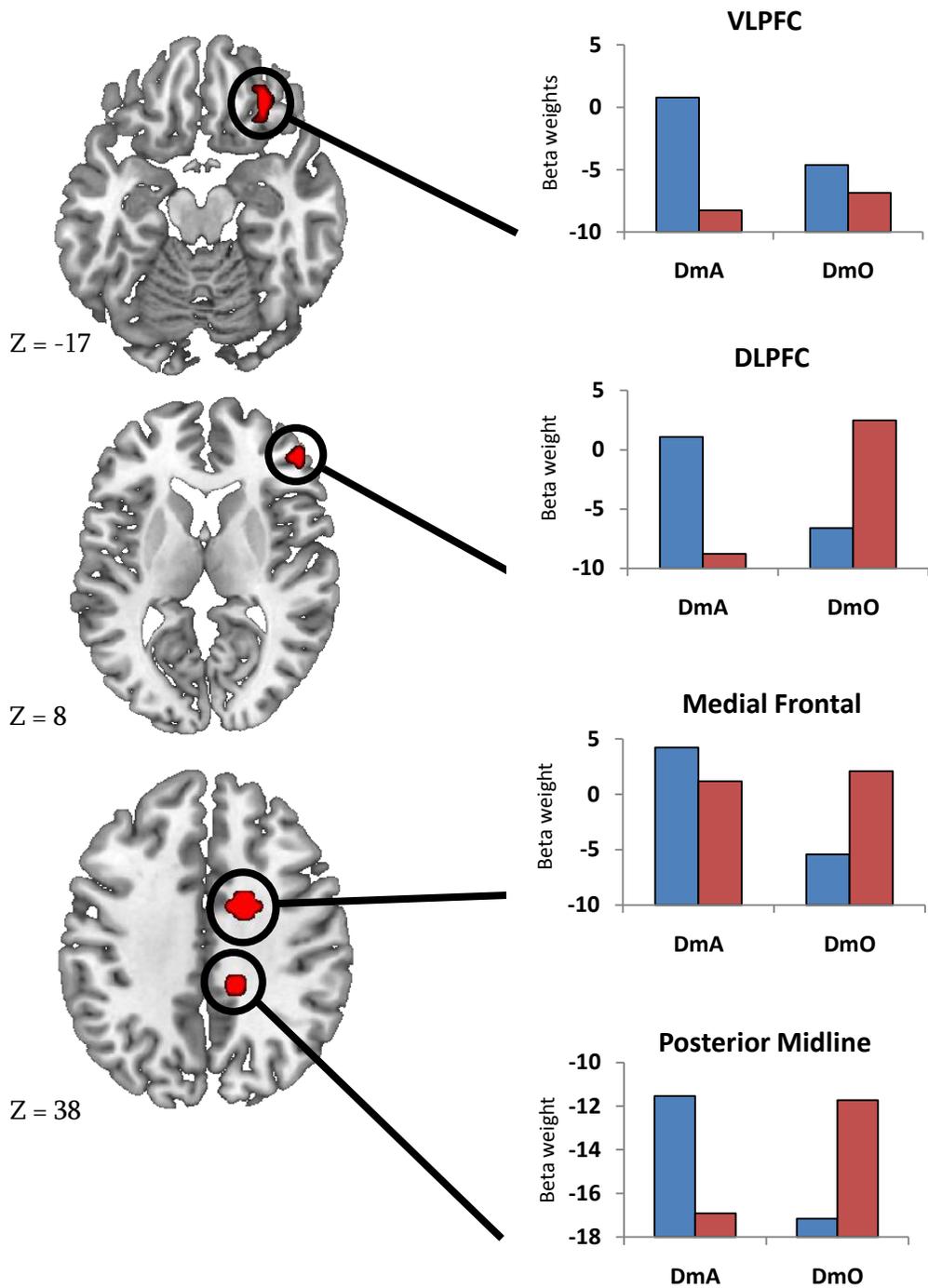


Fig. 1. Activations associated with DmA greater than DmO. See Table 1 for coordinates. The bar graphs represent differences in functional activation (e.g., beta weights) between Hits (blue bars) and Misses (red bars) for Animal Dm and Object Dm.

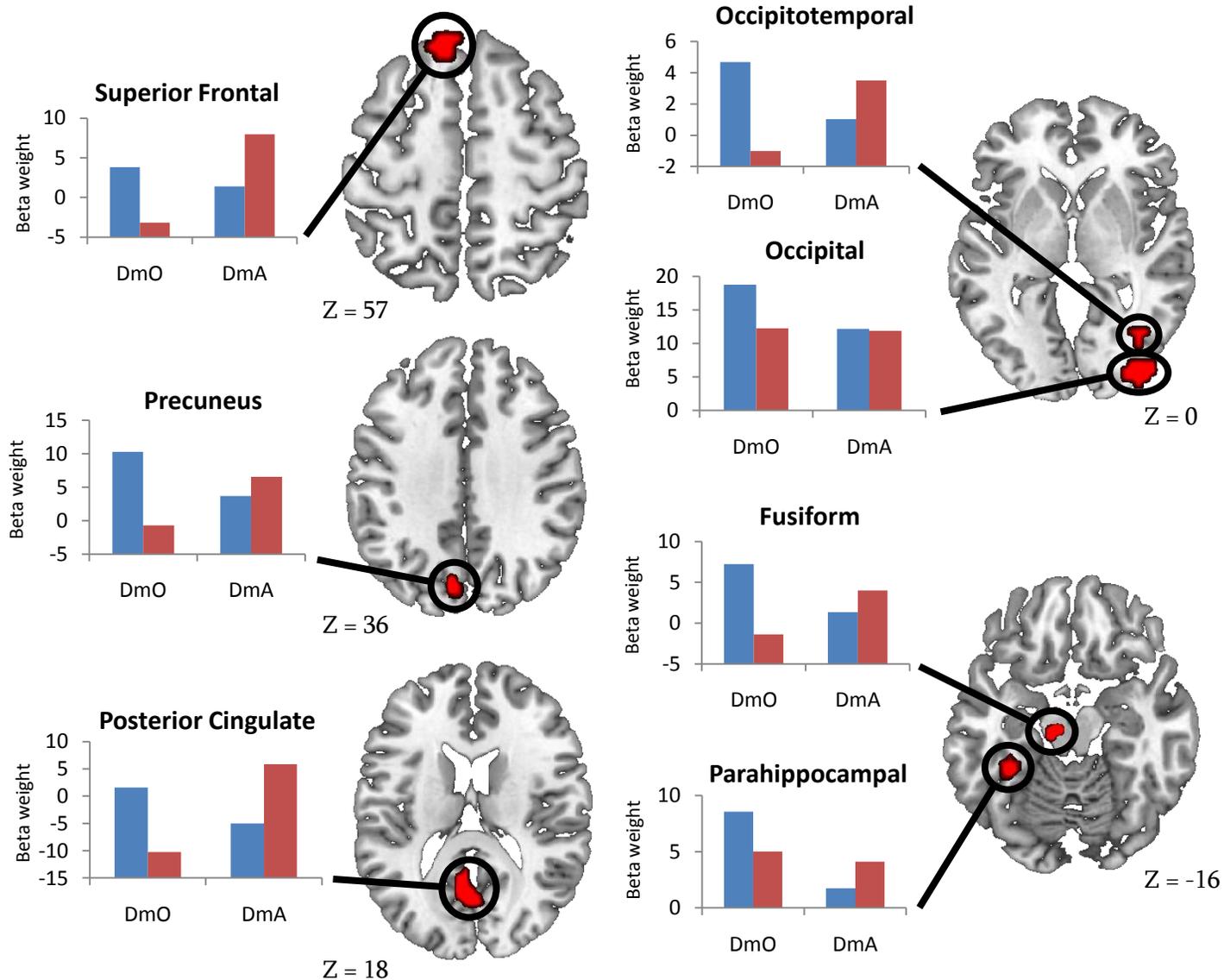


Fig. 2. Activations associated with DmO greater than DmA. See Table 1 for coordinates. The bar graphs represent differences in functional activation (e.g., beta weights) between Hits (blue bars) and Misses (red bars) for Object Dm and Animal Dm.

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ACADEMIC VITA

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Education

Pennsylvania State University, University Park, PA

Bachelor of Science in Psychology, Expected May 2010

Minor in Neuroscience

Schreyer Honors College

Honors Thesis: *An fMRI investigation of category-specific semantic encoding*

Research Experience

Research Assistant

Cognitive Aging and Neuroimaging Lab, Department of Psychology, Penn State

Research conducted under Nancy Dennis, PhD

Responsibilities included:

- Participant recruitment (younger and older adults)
- Administration of neuropsychological tests to older adults including the MMSE and subtests from the WAIS III and WMS
- Scoring of neuropsychological tests
- Administration of participant health screenings for fMRI experiments
- Stimuli development, creation, norming, and quality assessment
- Experimental/behavioral testing of memory paradigms including subsequent data collection and analysis of results
- Analysis of fMRI data with SPM2 implemented in Matlab

Honors, Awards, and Funding

Schreyer Honors College Scholar

Psi Chi International Honors Society in Psychology

Undergraduate Summer Discovery Grant (\$2500)

Edward M. Elias Award

President Sparks Award

President's Freshman Award

Penn State York Honors Program

Volunteerism

Pianist

Entertained visitors at York Hospital, PA

Entertained and taught psychiatric patients on the piano at York Hospital, PA

Patient Transporter

Shuttled patients at York Hospital, PA