

Semantic processing of living and nonliving concepts across the cerebral hemispheres

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Abstract

Studies of patients with category-specific semantic deficits suggest that the right and left cerebral hemispheres may be differently involved in the processing of living and nonliving domains concepts. In this study, we investigate whether there are hemisphere differences in the semantic processing of these domains in healthy volunteers. Based on the neuropsychological findings, we predicted a disadvantage for nonliving compared to living concepts in the right hemisphere. Our prediction was supported, in that semantic decisions to nonliving concepts were significantly slower and more error-prone when presented to the right hemisphere. In contrast there were no hemisphere differences for living concepts. These findings are consistent with either differential *representation* or *processing* of concepts across right and left hemispheres. However, we also found a disadvantage for nonliving things compared to living things in the left hemisphere, which is not consistent with a simple representation account. We discuss these findings in terms of qualitatively different semantic processing in right and left hemispheres within the framework of a distributed model of conceptual representation.

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1. Introduction

Category-specific semantic deficits have provided insights into how semantic knowledge may be organised in the human brain. Since the seminal work of Warrington and colleagues (Warrington & McCarthy, 1983, 1987, 1994; Warrington & Shallice, 1984) various category-specific dissociations have been reported. For example, between concrete and abstract words (Breedin, Saffran, & Coslett, 1994; Tyler, Moss, & Jennings, 1995; Warrington, 1981) and between nouns and verbs (e.g., Damasio & Tranel, 1993; Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994). However, the most commonly reported category-specific semantic deficit, is the

double dissociation between living and nonliving things. The more usual pattern is that knowledge of living things is found to be disproportionately impaired in relation to nonliving things (e.g., Hillis & Caramazza, 1991; Moss & Tyler, 1997; Sartori & Job, 1988; Warrington & Shallice, 1984). However, a few patients have also been reported with deficits for nonliving things in contrast to their relatively preserved knowledge of living things (e.g., Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Hillis & Caramazza, 1991; Sachett & Humphreys, 1992; Tranel, Damasio, & Damasio, 1997; Warrington & McCarthy, 1983).

Several competing models have attempted to account for this pattern of preserved and impaired knowledge. For example, the Sensory-functional model (e.g., Warrington & McCarthy, 1983, 1987, 1994; Warrington & Shallice, 1984) argues that the dissociation between

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living and nonliving concepts can be explained in terms in their properties, e.g., visual, functional, tactile, etc. Thus, living concepts are more reliably differentiated by their sensory properties, whereas discriminating among nonliving concepts relies more on their functional properties. The Sensory-functional model makes several testable predictions. For example, the model predicts that damage to sensory properties should result in a deficit for living things whereas damage to functional properties should result in a deficit for nonliving things. However, not all patients show this pattern; some patients have difficulty processing sensory information but do not show a specific deficit for living things (e.g., Lambon-Ralph, Howard, Nightingale, & Ellis, 1998). Furthermore, patients with living things deficits should have more difficulty with sensory compared to functional properties. However, this prediction has not always been supported (e.g., Caramazza & Shelton, 1998) and some patients have shown a contradictory pattern, with greater problems for the functional properties of living things (e.g., Lambon-Ralph et al., 1998).

Partly in response to the limitations of the Sensory-functional account, it has been argued that category rather than type of property is the first-order organising principle in semantic memory. Caramazza and Shelton (1998) hypothesised that evolutionary pressures have resulted in specialised mechanisms for animals, plants, and perhaps some nonliving concepts (e.g., tools) and that this has led to such knowledge being categorically organised in the brain. They argue that semantic knowledge is organised into broad categories reflecting evolutionarily salient distinctions in semantic knowledge, supported by distinct neural structures that may be damaged independently of one another.

Both the Sensory-functional and Category-specific accounts assume a differentiated semantic system, either as a function of feature type or category. However, deficits tend not to be so clearly dissociable; patterns of deficits are generally complex and impairments to categories or properties tend to be graded rather than all-or-none. Moreover, the vulnerability of concepts may vary as a function of variables such as frequency (Funnell & Sheridan, 1992) or manipulability (Tranel et al., 1997; Tranel, Logan, Frank, & Damasio, 1997). In response to these phenomena, researchers have asked whether distributed systems, undifferentiated by domain or type of knowledge, may be better able to account for patterns of spared and impaired knowledge. Thus, rather than focal damage affecting a specific store of knowledge, damage to a unitary system affects domains of knowledge differently because of underlying differences in the structure and content of concepts within these domains. One such model, the conceptual structure account (CSA), argues that it is the distribution of distinctive and shared properties, and the correlations between them, that are the key to the pattern of spared and impaired knowledge

across domains. Correlated properties are those which frequently occur together; they are more robust to damage because they support one another with mutual activation. Living and nonliving domains differ in terms of the kinds of properties which are correlated. Living things tend to have shared properties which are strongly correlated, while their distinctive properties are relatively weakly correlated. The pattern for nonliving things is different; they tend to have fewer shared properties which are generally not highly correlated and strong form-function correlations among distinctive properties (see Randall, Moss, Rodd, Greer, & Tyler, 2004; Tyler & Moss, 2001; Tyler, Moss, Durrant-Peatfield, & Levy, 2000).

The functional dissociation between living and nonliving domains of knowledge has implications for the way in which these domains are thought to be instantiated in the brain. For example, data from patients with category-specific semantic deficits have primarily been used to investigate whether living and nonliving concepts are represented in different brain regions. A related issue, which we address in this study, is whether living and nonliving concepts are differentially represented or processed across the left and right hemispheres. The pattern of damage associated with deficits for either living or nonliving domains suggests that there may be differential involvement of right and left hemispheres in the processing of these domains. For example, patients with deficits for living things frequently exhibit bilateral temporal lobe damage, often as a result of herpes simplex encephalitis (HSE) which targets antero-medial temporal lobes (Gitelman, Ashburner, Friston, Tyler, & Price, 2001; Moss, Rodd, Stamatakis, Bright, & Tyler, *in press*; Moss, Tyler, Durrant-Peatfield, & Bunn, 1998). Deficits for living things are also seen in patients with widespread damage affecting both cerebral hemispheres; for example, in patients with traumatic brain injuries (e.g., Farah, Hammond, Mehta, & Ratcliff, 1989; Laiacina, Barbarotto, & Capitani, 1993; Samson, Pillon, & De Wilde, 1998), or progressive neurological disease such as Alzheimer's disease (AD) in which cortical damage is arguably patchy and widespread, involving both hemispheres (Gonnerman, Andersen, Devlin, Kempler, & Seidenberg, 1997; Mazzoni, Moretti, Lucchini, Vista, & Muratorio, 1991; Silveri, Daniele, Giustolisi, & Gainotti, 1991; but see Garrard, Patterson, Watson, & Hodges, 1998).

With far fewer reported cases of semantic deficits for nonliving things there is less agreement about the neural underpinnings of nonliving concepts, although deficits for nonliving things tend to be associated with damage to left hemisphere (LH) brain regions. For example, Saccett and Humphreys (1992) report a nonliving deficit patient with Broca's aphasia (CW) who has left temporo-parietal damage. Patients VER and YOT reported by Warrington and McCarthy (1983, 1987) also have

damage confined to the LH in fronto-parietal and temporo-parietal regions. Hillis and Caramazza (1991) report a Wernicke's aphasic patient (JJ) with damage to left temporal lobe and basal ganglia. Furthermore, a study of over 100 patients with focal lesions showed maximum lesion overlap in LH regions for tool recognition. In contrast maximal lesion overlap for deficits in recognition of animals occurred in both hemispheres (Tranel et al., 1997).

Findings from neuroimaging studies of healthy volunteers have shown mixed findings (for a review see Price & Friston, 2002). For example, in a recent study, Pilgrim, Davis, Fletcher, Rodd, Stamatakis, and Tyler (2003) combined split visual-field presentation with event-related fMRI and found no evidence for differential activation for living compared to nonliving concepts, either within or between hemispheres. In contrast other studies have reported bilateral activation for living compared to nonliving concepts. For example, Mummery, Patterson, Hodges, and Wise (1996) found activation primarily in temporal and frontal regions, with more bilateral temporal activation for living things compared to nonliving things. Devlin, Moore, Mummery, Gorno-Tempini, Phillips, and Noppeney (2002) also found bilateral activation for living compared to nonliving concepts, while activation for tools was confined to LH regions.

Although by no means conclusive, the contrasting patterns of damage associated with deficits for living and nonliving things, plus neuroimaging findings, suggest that right and left hemispheres may be differentially involved in the representation and/or processing of different domains of knowledge. Such that there may be greater involvement of the right hemisphere (RH) in the semantic processing of living things compared to nonliving things. The simplest version of this *representational* claim would be to assume that the type of semantic processing undertaken by the RH is the same as that undertaken by the LH, and that living and nonliving concepts are represented in a qualitatively similar way, e.g., by the same kinds of properties and with similar relationships between those properties. On this type of account the only difference across the hemispheres would be that the RH semantic system duplicates a subset of the full repertoire of concepts available in the LH.

An alternative possibility is that the same concepts are available in both hemispheres, but the type of *processing* performed by each hemisphere is qualitatively different. For example, it has been argued that the RH weakly activates broad semantic fields (Beeman & Chiarello, 1998; Beeman et al., 1994). On this account, a large number of semantic properties associated with a given concept, including those that are less central to its meaning, are only weakly activated in the RH (often referred to as *coarse* processing). In contrast, the LH strongly activates semantic fields which are more narrowly focused and sensitive to fine details (*fine* processing).

As it stands, the distinction between coarse and fine processing in the RH and LH, respectively, does not account for apparent hemisphere differences in the processing living and nonliving domains of knowledge. However, if we combine these claims about hemisphere processing differences with the representational claims of the conceptual structure account (CSA), a novel hypothesis emerges. Specifically, the consequences of coarse processing may be different for concepts with many shared correlated properties and those with few such properties.

As we outlined above, the CSA argues that living things have more shared, highly correlated properties, while their distinctive properties are weakly correlated. In contrast, nonliving things have relatively few shared properties and some distinctive properties which tend to be highly correlated (see Randall et al., 2004; Tyler & Moss, 2001; Tyler et al., 2000). Thus, if the RH is processing at a coarse level with weak activation for any given property, there will be a considerable advantage for those properties that are shared by many concepts and are also supported by mutual activation from correlated properties. Properties that are not strongly correlated may be obscured due to weak activation, even if they are highly informative/distinctive. This pattern of activation will have more impact on nonliving concepts than on living concepts, due to their intrinsic conceptual structure (e.g., living things having more shared correlated properties compared to nonliving things), making nonliving things more difficult to process in the RH. If the RH is processing at a coarse level then distinctive properties may not be activated above some threshold due to weak activation and thus not be accessible. In contrast, the LH is capable of finer-grained semantic processing, therefore both living and nonliving concepts may be processed similarly as the LH is able to access the distinctive properties of both.

If this account is correct then it has implications for the processing of living and nonliving domains of knowledge in the normal system, as well as in patients with left versus right hemisphere damage. Although domain of knowledge has been pivotal in neuropsychological accounts of semantic deficits, there is scant data from healthy participants regarding semantic representation or processing across the hemispheres. In this study, we ask whether there are hemisphere differences in terms of domain of knowledge in the normal system. To test this hypothesis we use a split visual-field paradigm in which words representing living and nonliving concepts are presented in the left visual field (lvf) or right visual field (rvf) for semantic decision. If healthy participants hold their gaze on a central fixation point and stimuli are then presented briefly to either the right or left side of this central point, stimuli are first perceived by the contralateral hemisphere (Bradshaw, 1990). Therefore, presenting stimuli for semantic decision to a

single visual field can be used to draw inferences about semantic representation/processing in the contralateral hemisphere, if presentation of stimuli is sufficiently rapid (i.e., under 200 ms; [Hardyck, Dronkers, Chiarello, & Simpson, 1985](#)). Although lateralised stimuli will eventually be available via inter-hemisphere transfer (via corpus callosum and subcortical structures) to both hemispheres, the initial stimulation of the contralateral hemisphere allows us some insight into the processing capabilities specific to either the RH or LH.

To summarize, we predict a disadvantage for nonliving things compared to living things presented to the RH (i.e., slower reaction times and possibly higher error rates with lvf presentation). Both the representation and processing models could account for a disadvantage in the RH for nonliving things, but would interpret them in different ways. However, we may be able to dissociate these two accounts if we find a main effect of domain as well as the predicted interaction between domain and visual field. For example, if living and nonliving concepts show a different pattern of responses in the LH—this would not be predicted by a representational account which argues that living and nonliving concepts are represented in a similar way in the LH. However, accounts which argue for qualitatively different types of processing across the hemispheres, coupled with varying conceptual structure across domains, can accommodate dissociations in both the LH as well as the RH. Thus, this study investigates whether there is an interaction between living/nonliving domain and hemisphere. Furthermore, it will also help dissociate between representation and processing accounts.

2. Methods

2.1. Participants

Thirty participants from the Centre for Speech and Language (CSL) participant panel were tested (21 women and 9 men). Ages ranged from 18 to 36 years. All were native English speakers, with no vision or language problems. All were classified as right handed according to the Edinburgh Handedness Inventory ([Oldfield, 1971](#)).

2.2. Materials

Words that were unambiguously nouns were selected from the Celex Lexical database ([Baayen, Piepenbrock, & Gulikers, 1995](#)), i.e., all items had zero ratings as verbs. There were 80 words, half from the domain of living concepts (animals, birds, fruit, vegetables, flowers, and trees) and half from the domain of nonliving concepts (vehicles, tools, furniture, and clothing). All words were between three and six letter long. See in the Appendix A for complete stimulus list.

Table 1
Item means (and standard deviations)

	Living	Nonliving
Imageability	562 (57)	577 (34)
Frequency	16 (15)	12 (10)
Length	5.00 (.88)	4.93 (.97)
Neighbours	4.47 (4.26)	3.60 (4.70)

Imageability ratings and number of neighbours¹ were taken from the MRC psycholinguistic database ([Coltheart, 1981](#)). A one-way ANOVA showed no significant difference between living and nonliving concepts in terms of imageability, frequency, letter length or number of neighbors. See [Table 1](#) for means and standard deviations.

The experiment was divided into two versions so that each participant saw each word once. The design was fully rotated so that if a word was presented in the left visual field in version one, it appeared in the right visual field in version two and vice versa. Participants were asked to make a living/nonliving decision to nouns. Items were pseudo-randomized within the study and matching was maintained within the first and second half of the study, ensuring an equal distribution of items throughout.

2.3. Procedure

Words were presented in lower case in Courier New font (12 point), with a viewing distance of 60 cm. To ensure that stimuli were perceived initially by the contralateral hemisphere only, words were presented at an eccentricity of approximately 2° from the central fixation point to the inner edge of the word in line with previous laterality research (e.g., [Beeman et al., 1994](#); [Burgess & Simpson, 1988](#)). Visual angles to the outer edge of each 3-, 4-, 5-, and 6-letter word were 3.34°, 3.81°, 4.29°, and 4.76°, respectively. A fixation point appeared in the centre of the screen 500 ms before each word appeared and remained on while the word was presented. Words were presented for 100 ms pseudo-randomly to the left or right visual field. A short presentation rate (i.e., <200 ms) ensures that words are first perceived by the contralateral hemisphere as participants do not have time to move their eyes to fixate on words in the left or right visual field. Recording of responses began at the onset of stimulus presentation and there was a time-out 2500 ms after stimulus presentation. A chin rest ensured limited head movement and a fixed viewing distance.

Participants were asked to respond as quickly and as accurately as possible. At the start of each block they

¹ The number of neighbours a word has is defined as the number of words differing from it by one letter ([Coltheart, Davelaar, Jonasson, & Besner, 1977](#)).

Table 2
Mean RTs and errors (with 95% CIs) in each condition

	lvf-RH		rvf-LH		RH and LH combined	
	Errors	RTs	Errors	RTs	Errors	RTs
Nonliving	22% (16–28)	808 ms (868–756)	10% (6–13)	741 ms (789–698)	16% (12–19)	773 ms (824–728)
Living	16% (13–19)	695 ms (742–654)	12% (8–16)	681 ms (714–652)	14% (11–17)	688 ms (725–655)
All concepts	19% (16–22)	747 ms (798–703)	11% (8–14)	710 ms (747–676)	15% (12–18)	728 ms (770–690)

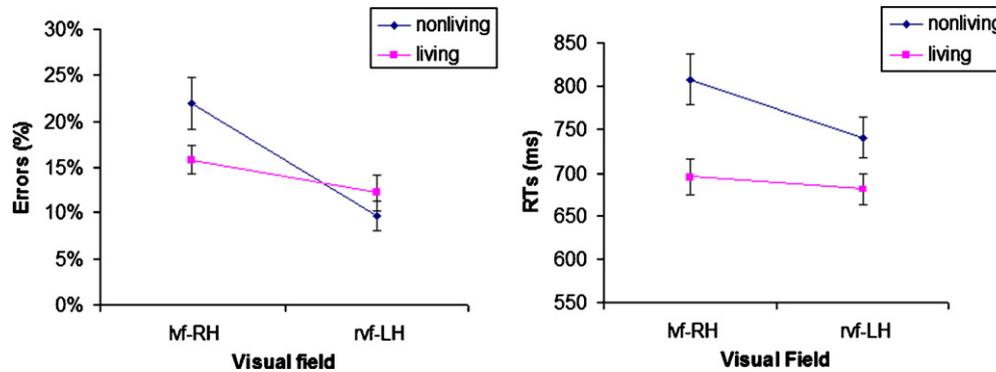


Fig. 1. Mean RTs and error rates (error bars represent SE of the mean).

were reminded of the experimental task followed by 14 practice trials (none of these items were in the main part of the experiment) and given feedback (“correct” and “wrong”). The experimental trials (without feedback) were preceded by six dummy items which were not included in the final analyses. Words appeared pseudo-randomly to either left or right visual fields. Participants were asked to decide whether the word represented a living or nonliving concept. Responses were made via computer mouse using index and middle fingers of the right (dominant) hand.

The experiment was run using DMDX experimental software (Forster & Forster, 2003). All participants were given an information sheet outlining the experimental procedure.

3. Results

Repeated measures ANOVAs were performed on both error rate and reaction time (RT) data. Error rates were arc-sine transformed to stabilise variances (Winer, 1971). RTs were inverse transformed to increase statistical power without introducing truncation biases (see Ratcliffe, 1993; Ulrich & Miller, 1994). For ease of interpretation, all mean RTs have been retransformed. Means, 95% confidence intervals (CI) and effect sizes are calculated across participants’ data.

In the participants analyses (F_1) within-participants factors were Visual field (left and right) and Domain type (nonliving and living). Version (1 and 2) was entered as a between participants dummy variable and will not be discussed further. In the items analyses (F_2)

the within-items factor was Visual field (left and right). Between-items factors were Domain type (nonliving and living) and Version (1 and 2) which was entered as a dummy variable as in the participants analyses.

There was a main effect of Domain which was significant in the analysis of RTs ($F_1(1,28) = 81.83, p < .001$; $F_2(1,76) = 72.68, p < .001$; partial $\eta^2 = .76$). Responses to nonliving things were slower than to living things. This effect was not present in the error rates analyses ($F < 1$). All means and confidence intervals are shown in Table 2.

In addition, as is typically reported, there was a significant main effect of Visual field: there was a left visual field advantage for both error rates ($F_1(1,28) = 28.41, p < .001$; $F_2(1,76) = 30.20, p < .001$; partial $\eta^2 = .50$) and RTs ($F_1(1,28) = 14.60, p < .001$; $F_2(1,76) = 26.09, p < .001$; partial $\eta^2 = .34$).

Critically, there was also a significant interaction between Visual field and Domain for both error rates ($F_1(1,28) = 5.34, p = .028$; $F_2(1,76) = 8.58, p = .004$) and RTs ($F_1(1,28) = 5.72, p = .024$; $F_2(1,76) = 10.63, p < .001$). Although the effect size for this interaction was small (Partial $\eta^2 = .16$ for error rates and $.17$ for RTs), the robustness of the effect is supported by the fact that it was significant at conventional levels in both by-items and by-participants ANOVAs, and showed the same pattern for error rates and RT analyses. The interaction is plotted in Fig. 1.

We explored this interaction further with a number of paired t tests on the by-participants data.² Although

² In addition, we analyzed the data by-items and replicated the by-participants findings.

these were planned comparisons with respect to our predictions concerning the differential role of the hemispheres in processing living and nonliving things, we also applied a Bonferroni correction to reduce the possibility of Type 1 error due to multiple tests (resulting in an α level for significance of $p < .01$).

The first two paired t tests revealed the basis for the interaction: responses to nonliving concepts were markedly different across the hemispheres—error rates were higher and RTs longer in the lvf-RH compared to the rvf-LH (see Table 2 for means). The difference was significant in both error rates ($t_{(29)} = 4.51, p < .001$) and RT analyses ($t_{(29)} = 4.96, p < .001$). In contrast, responses to living concepts were similar across the hemispheres—neither mean error rates ($t_{(29)} = 1.90, p = .067$) nor RTs ($t_{(29)} = 1.08, p = .288$) differed significantly.

We then compared responses for living and nonliving concepts within each hemisphere separately. We found slower and more error-prone responses to nonliving compared to living concepts in the lvf-RH. The difference in error rates was marginally significant ($t_{(29)} = 1.98, p = .057$). In the RT analysis the difference between means was highly significant ($t_{(29)} = 8.62, p < .001$). With rvf-LH presentation we found no difference between nonliving and living concepts in terms of error rates ($t_{(29)} = 1.05, p = .301$). However, although noticeably smaller, there was a significant difference in mean RTs ($t_{(29)} = 4.83, p < .001$). Thus, it seems that there is a disadvantage for nonliving things, not only in the RH, but also in the LH.

4. Discussion

The aim of this study was to determine whether there are hemisphere differences in the representation and/or processing of concepts from living/nonliving domains of knowledge. On the basis of neuropsychological and neuroimaging data, we predicted that the RH would show a disadvantage for concepts referring to nonliving, but not living things. The results clearly support this prediction. We found a significant interaction between visual field and semantic domain: responses were slower and more error-prone for nonliving things than living things in the RH; responses to living things did not significantly differ across hemispheres.

So, how then do the contrasting accounts stand in light of our findings? To recap, *representational* accounts would argue that living things are bilaterally represented whereas nonliving things are represented solely in the LH. In contrast, *processing* accounts would contend that there are no differences in terms of the way concepts are represented in each hemisphere. However, the interaction between differences in conceptual structure and the different processing characteristics of the two hemispheres result in disadvantages for particular types of concepts in the RH.

Although the observed interaction between living/nonliving domain and visual field (i.e., longer latencies and more errors for nonliving things in the RH) is consistent with both representation and processing accounts, it needs to be interpreted within the context of the significant main effect of domain that was also observed. Responses were slower to nonliving than living things in the LH as well as the RH—although the differences were less pronounced. On a simple representational account, living and nonliving concepts are represented in a qualitatively similar way in the LH, and there would be no reason to expect nonliving things to be at a disadvantage there. However, if we adopt a *processing* framework and argue for bilateral representation of both living and nonliving domains, and assume that these domains are differently structured, this main effect can be accommodated. The CSA (e.g., Tyler & Moss, 2001; Tyler et al., 2000), outlined in the introduction, can parsimoniously account for both the main effect of domain and the interaction between domain and visual field. This account predicts that if a task requires identification of concepts at the domain level (as is the case here, since participants had only to indicate whether a word referred to a living or a nonliving thing) and therefore requires access only to shared properties, living things should show an advantage over nonliving things (Moss et al., in press; Tyler & Moss, 2001). This is because the numerous correlations between the shared properties of living things lead to increased activation and quick settling times—and therefore to shorter latencies and fewer errors. However, for nonliving things there would be no such advantage, as they have very few shared, correlated properties. On this account, the advantage for living over nonliving things should disappear (and may even be reversed) on tasks that require access to distinctive properties such as unique naming of living things or discrimination among them (see also Randall et al., 2004).

In summary, we contend that it is the interaction between differences in the internal structure of concepts within living/nonliving domains of knowledge, and the processing characteristics of the left and right hemispheres which results in hemisphere asymmetries. In this way, we are bringing together two theoretical approaches and two sets of data that have previously been developed in isolation; on the one hand, the living/nonliving distinction and the CSA, which were primarily developed to address issues of category-specificity in neuropsychological patients, and on the other hand, the laterality literature and the coarse/fine processing account, which have been critical in addressing how the RH may uniquely contribute to semantic processing. Thus, the framework outlined here provides an integrated and parsimonious account of hemisphere differences in the semantic processing of living and nonliving concepts.

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Appendix A

Nonliving concepts		Living concepts	
broom	tongs	rat	goat
dagger	kettle	toad	camel
mallet	trowel	otter	rhino
belt	cape	sheep	tiger
kilt	apron	zebra	beaver
beret	frock	monkey	walrus
glove	scarf	owl	wren
shawl	shirt	eagle	robin
tunic	blouse	canary	pigeon
helmet	jacket	moth	snail
sandal	shorts	spider	clam
rug	sofa	shark	squid
bench	stool	trout	mussel
stove	lamp	oyster	pear
oven	pram	grape	cherry
vase	basin	pea	leek
saucer	teapot	onion	carrot
bangle	brooch	potato	tomato
van	tank	elm	lily
truck	wagon	daisy	willow

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