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Generating animal and tool names: An fMRI study of effective connectivity

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Abstract

The present fMRI study of semantic fluency for animal and tool names provides further evidence for category-specific brain activations, and reports task-related changes in effective connectivity among defined cerebral regions. Two partially segregated systems of functional integration were highlighted: the tool condition was associated with an enhancement of connectivity within left hemispheric regions, including the inferior prefrontal and premotor cortex, the inferior parietal lobule and the temporo-occipital junction; the animal condition was associated with greater coupling among left visual associative regions. These category-specific functional differences extend the evidence for anatomical specialization to lexical search tasks, and provide for the first time evidence of category-specific patterns of functional integration in word-retrieval.

Keywords: fMRI; Neuroimaging; Effective connectivity; Functional integration; Psychophysiological interaction; Semantic memory; Semantic fluency; Semantic categories; Living and non-living; Tools and animals

1. Introduction

Disorders of identification and/or naming, which display selectivity for a specific category of entities, such as animals or people, have been repeatedly described in patients with brain damage, and may be expected to contribute to the understanding of the organization of conceptual knowledge and of its neurological substrate.

At the cognitive level of analysis, several models have attempted to account for category-specific disorders (see Caramazza & Shelton, 1998; Forde & Humphreys, 1999; Tyler & Moss, 2001 for extensive reviews). Broadly summarising, there are two classes of models.

The "reductionist" class of interpretations proposes that category-specific impairments emerge because of the peculiar processing demands of, respectively, living and non-living entities. The multiple-semantic systems hypothesis (Warrington & McCarthy, 1987; Warrington & Shallice, 1984) and its computational variant (Farah & McClelland, 1991) are both based on the hypothesis that the identification of living and non-living entities depends on specific features, referring to perceptual/visual aspects (e.g., "has small ears"), or to functional properties (e.g., "can cut paper"). Perceptual/visual features are considered to play a crucial role for the representation of living entities, whereas functional-associative features

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are more important in the representation of non-living entities. According to one of the most popular versions of this view, category specific impairments then emerge when the visual, or, respectively, the verbal semantic system are selectively affected (McCarthy & Warrington, 1988; Warrington & Shallice, 1984). It has also been suggested that perceptual features are particularly vulnerable to the effects of brain damage, thus explaining why deficits for living entities are more frequently observed.

An alternative reductionist account has been proposed by Tyler and Moss (2001), on the basis of a connectionist model of conceptual structure. These authors propose a unitary, distributed system, in which concepts are defined in terms of properties with different degrees of intercorrelation. The specific prediction of this model is that severity of brain damage is a major determinant of category specificity. Mild disorders should be associated with living impairments, while non-living impairments should be observed only with diffuse, severe damage. Additional predictions include the presence of graded effects, and interaction with task demands, with more severe impairment in tasks associated with the retrieval of distinctive, rather than shared, features (Tyler & Moss, 2001).

According to the second class of interpretations, category-specific semantic disorders reflect a genuine segregation of knowledge pertaining to different entities. Caramazza and Shelton have proposed a 'domain-specific knowledge' hypothesis, essentially based on the theory that evolutionary pressures have resulted in specialized mechanism for perceptually and conceptually distinguishing living and non-living entities, leading to a 'separated' categorical organization of the corresponding knowledge in the brain (1998). A selective dysfunction of one of these domain-specific knowledge systems might result in a selective category-specific impairment.

At the neurological level, it has been proposed, on the basis of lesion location evidence, that category-specific disorders might be associated with different lesion sites in the brain. As underscored by Gainotti (2000), the models discussed above are associated with a different set of predictions about the underlying neurological substrates. In particular, the sensory-functional account predicts that damage to high-order visual processing areas should be associated with an impairment of living entities. Models based on feature intercorrelations emphasize the importance of the extent of brain damage. On the other hand, the domain-specific hypothesis suggests a link between damage to evolutionary salient categories and limbic area involvement. Patients with bilateral inferomedial temporal lobe damage secondary to herpes simplex virus encephalitis often show a significant impairment for living entities. In Gainotti's detailed review (2000), bilateral damage to the anteromesial and inferior temporal lobes was consistently associated with semantic impairments for living entities, whereas a selective lexical disorder for the plant category was found in patients with unilateral damage to the left infero-mesial temporo-occipital areas. Tranel, Damasio, and Damasio (1997) found that defective knowledge about animals was associated with medial occipito-temporal lesions, more extensive on the right. In the case of impaired performance for non-living entities, the most frequently described lesions were in the left hemisphere, usually involving the perisylvian areas (Saffran & Schwartz, 1994).

A more direct method to investigate the correlates of categorical semantic knowledge has been provided in recent years by functional neuroimaging in normal subjects. Perani et al. (1995) using a visual picture-matching task, have shown for the first time different locations of brain activation according to the semantic category (animals vs. tools). Animal identification was associated with activations in the inferior temporo-occipital areas, bilaterally. On the other hand, the identification of non-living entities engaged the activation of a predominantly left hemispheric network involving the left dorsolateral frontal cortex, and the left middle temporal gyrus (Perani et al., 1995, 1999). Soon afterwards, activations in separate locations were observed during naming of pictures of animals and tools. In particular, greater activation for non-living entities than for living entities was found in left temporal or temporo-parietal areas (Damasio, Grabowski, Tranel, Hitchwa, & Damasio, 1996; Martin, Wiggs, Ungerleider, & Huxby, 1996) and also in a left inferior frontal area (Grabowski, Damasio, & Damasio, 1998; Martin et al., 1996). In general, these category-specific effects appear to represent differential profiles of activation, rather than all-or-none activation differences. It has been suggested that they reflect the retrieval of category-specific features and attributes (Chao, Weisberg, & Martin, 2002). In particular, the activation in the left inferior frontal gyrus and middle temporal gyrus repeatedly observed for tools is considered to reflect the retrieval of action knowledge related to tool motion and/or manipulation (Beauchamp, Lee, Haxby, & Martin, 2002; Martin et al., 1996; Perani et al., 1995; Phillips, Noppeney, Humphreys, & Price, 2002).

There is also evidence that the type of task interacts with semantic category effects in determining the pattern of brain activation. Most of the studies summarized above involved matching or naming of picture stimuli. Word generation in response to a semantic cue (semantic verbal fluency) is a widely used task in brain imaging research, which can be expected to be sensitive to semantic variables. While the anterior part of the left inferior prefrontal cortex seems to be related to the executive/strategic requirements of lexical search, the comparison of phonological with semantic fluency indicated that the latter task is more dependent from the left temporal regions (Paulesu et al., 1997). Similar results have been reported, contrasting semantic with phonological decision, by Gold and Buckner (2002). In a PET study