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Lexical retrieval constrained by sound structure: The role of the left inferior frontal gyrus

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Abstract

Positron emission tomography was used to investigate two competing hypotheses about the role of the left inferior frontal gyrus (IFG) in word generation. One proposes a domain-specific organization, with neural activation dependent on the type of information being processed, i.e., surface sound structure or semantic. The other proposes a process-specific organization, with activation dependent on processing demands, such as the amount of selection needed to decide between competing lexical alternatives. In a novel word retrieval task, word reconstruction (WR), subjects generated real words from heard non-words by the substitution of either a vowel or consonant. Both types of lexical retrieval, informed by sound structure alone, produced activation within anterior and posterior left IFG regions. Within these regions there was greater activity for consonant WR, which is more difficult and imposes greater processing demands. These results support a process-specific organization of the anterior left IFG.

Keywords: PET; Word retrieval; Vowel; Consonant; Left inferior frontal gyrus; Lexical; Word generation

1. Introduction

The retrieval of words into working memory involves activation of, and selection among, alternative candidates from the mental lexicon (Cutler & Clifton, 1999). The left inferior frontal gyrus (IFG) and adjacent premotor cortex (PMC) are involved in this process (Milner, 1964; Petersen, Fox, Posner, Mintun, & Raichle, 1989; Warburton et al., 1996), but the functional organization of these regions remains controversial (Gold & Buckner, 2002; Poldrack et al., 1999). One hypothesis proposes a domain-specific organization, where the anterior left IFG (Brodmann's areas (BA) 45/47) is specialized for the controlled processing of semantic information, whereas the more posterior left IFG and PMC (BA 44, extending into BA 6) processes only phonological information (Poldrack et al., 1999; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). Alternatively, a process-specific organization has been proposed, where processing demands that are associated with the maintenance and the retrieval/selection of verbal information governs neural recruitment (Barde & Thompson-Schill, 2002; Gold & Buckner, 2002).

Evidence in favor of a domain-specific organization includes the observations that the anterior left IFG is activated during the processing of semantic information e.g. (Poldrack et al., 1999) and that the level of activation in this region is modulated by the extent of semantic processing (Wagner et al., 2001). In addition, activation of the posterior left IFG (BA 44) and PMC (BA 6) has been observed during tasks which depend upon processing the sound structure of information held in working memory, such as word-stem completion (Buckner, Raichle, & Petersen, 1995; Poldrack et al., 1999). A strict domain-specific organization for the IFG predicts that

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tasks that exclusively involve the controlled processing of non-semantic information should not activate the anterior left IFG and a number of studies have reported patterns of activation in keeping with this prediction, e.g. (Buckner et al., 1995; Poldrack et al., 1999).

However, activation of the anterior left IFG has been observed during phonological processing (Devlin, Matthews, & Rushworth, 2003) and similar levels of activation have been seen within this region when phonological and semantic processing have been directly compared (Barde & Thompson-Schill, 2002; Gold & Buckner, 2002). These results suggest that the anterior left IFG does not exclusively process semantic information and provide evidence in favor of a process-specific organization within the left IFG. Further evidence in favor of this type of organization comes from other studies which have shown that activation within the left IFG reflects the processing demands associated with many types of non-verbal as well as verbal stimuli, e.g. (Chein & Fiez, 2001; D'Esposito et al., 1998; Owen, 1997; Thompson-Schill, 2003).

Explicit lexical retrieval produces activation within the left IFG, e.g. (Warburton et al., 1996), and when word choice is determined by semantic criteria this activation includes the anterior left IFG (Raichle et al., 1994). Although this result has been interpreted as supporting a domain-specific organization, it may reflect processes that are common to processing both lexical and sub-lexical information. The observation of activation within the anterior left IFG during a verbal task that requires lexical retrieval—guided specifically by attention to surface sound structure and not word meaning—would provide further evidence for a process-specific organization.

To this end a laboratory task was chosen that required the subjects to retrieve a familiar word from memory where the correct response demanded attention to sound structure rather than meaning. The task, word reconstruction (WR), has been used to investigate the way in which the processing of vowels and consonants constrains lexical access in an overt lexical activation task (van Ooijen, 1996). In WR, listeners hear non-words and generate a real word by changing a single sound segment (phoneme). The non-words were constructed so that a real word could be generated by the substitution of either a vowel or a consonant; for example, *eltimate* can be changed into either *ultimate* or *estimate*. Such an experimental design was readily adapted to investigate the neural basis of cognitive processes involved in lexical retrieval based on sound structure but not meaning.

In the experiments of van Ooijen, English-speaking subjects showed asymmetric response patterns: WR proved more difficult when consonants rather than vowels had to be replaced, indexed by longer reaction times (RT), more errors and more omissions (van Ooijen, 1994). Furthermore, when allowed a free choice, subjects used vowel substitution more frequently than consonant substitution. There are many vowel sounds in English, and they vary with regional accent (for example, contrast *bath* in Northern English vs Southern English pronunciations, or *not* in British vs North American English). Since vowels might simply be more variable in spoken English, further studies were carried out with other languages, where there are fewer vowels or the regional accent is not mainly expressed on the vowels. The same behavioral asymmetry was shown for speakers of Spanish, Dutch, and Japanese, languages which have widely differing phonemic repertoires (Cutler & Otake, 2002; Cutler, Sebastian-Galles, Soler-Vilageliu, & van Ooijen, 2000). The robustness of the effect across languages suggests that it is not simply a product of variability in the proportion of vowel and consonant sounds. Further, its presence in speakers of languages such as Spanish and Japanese, in which vowel sounds are acoustically very distinct (because there are fewer of them), argues against an explanation based on the acoustic closeness of vowels compared to consonants. Nor can the difference be explained in terms of the number of sounds which can potentially be changed, given that, in English, although the majority of words contain more consonants than vowels; changing consonants is still harder when the number of vowels and consonants in the non-words is equated (van Ooijen, 1996).

The advantage for vowel over consonant substitution is held to reflect two asymmetries, both of which are observed across languages. First, there is asymmetry in the number of lexical neighbours resulting from substitution of a single sound: on average, across the vocabularies in which WR experiments have been conducted, consonant substitution produces about twice as many existing lexical neighbours as vowel substitution (Cutler et al., 2000). However, the actual number of possible answers was strictly controlled in the experiments, and equated across vowels and consonants. Second, the acoustic variability within vowels and consonants is asymmetric. In general vowels have a greater intrinsic variability, that is the range of realizations for vowels in natural speech is far larger than the range of realizations for consonants, and perceptual confusion experiments show that this variability often produces misidentification (Hillenbrand, Getty, Clark, & Wheeler, 1995). As Rosner and Pickering put it, "the variability that a speaker accepts exceeds the variability of productions identified with high accuracy by a listener" (Rosner & Pickering, 1994). In consequence, listeners accrue greater experience of varying realizations for vowels and, potentially, more experience of initially mistaken categorization of vowels requiring revision of an initial hypothesis. This experience then translates into a greater readiness to alter vowels than consonants in a WR task.