

Distinct and shared cortical regions of the human brain activated by pictorial depictions versus verbal descriptions: an fMRI study

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Received 26 April 2004; revised 6 August 2004; accepted 13 August 2004

Available online 11 November 2004

Using fMRI, we observed that there were functionally disjunctive regions in the human brain that were specifically activated during the silent reading of sentences (i.e., the symbolical representation at the propositional level) but not during the perception of arranged objects (i.e., analogical representation), or vice versa: Parts of the left and right lingual gyri, the left fusiform gyrus, the left and right inferior occipital gyri, the right cuneus, and the left middle occipital gyrus were activated exclusively during the silent reading of sentences, whereas perception of the arranged objects activated distinct regions in the lingual gyrus, the declive, the fusiform gyrus, and the cuneus in the right hemisphere. A large proportion (86% in cortical volume) of the occipito-temporal regions was functionally conjunctive: these neural structures were activated during both silent reading of sentences and perception of arranged objects. We observed a similar trend of functional disjunction and conjunction between single words (the symbolical mode at the lexical level) and single objects (analogical mode): the degree of functional conjunction in the latter case was about 96%. These results suggest that the degree of functional disjunction between the pictorial depictions and the verbal descriptions tended to increase as the complexity of mental representation increased from the single word (lexical) level (4%) to the sentence (propositional) level (14%).

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Keywords: fMRI; Pictures; Words; Sentences; Analogical; Symbolical

Introduction

The human brain possesses versatile capabilities for various modes of mental representations. The analogical mode involves direct perceptual experiences such as seeing, hearing, and touching

concrete objects and states of affairs. This is a phylogenetically common mode by which other primates and some higher mammals may be capable of representing with various degrees of complexities. In contrast, the ability to use the logical combinations of symbols (e.g., language) that stand for something else to represent real and/or imagined objects and various external and/or internal states of affairs (i.e., the symbolical mode of mental representations) must be unique to the human brain. Furthermore, we can communicate such symbolical representations (e.g., thoughts, ideas, emotions, imaginations, etc.) with others by use of a conventional system of symbols such as the linguistic signs (Saussure, 1915/1983) in accordance with a set of rules (e.g., grammars, pragmatic conventions, etc.) as you witness it by reading what is written here. The main objective of the present fMRI work is to study which parts of the human brain are involved in the analogical mode of representation, and which neural structures are concerned with symbolical representations.

Previous neuroimaging experiments on visual perception (Gauthier et al., 1997, 1999, 2000; Grill-Spector et al., 1999; James et al., 1999; Kanwisher et al., 1996, 1997; Kourtzi and Kanwisher, 2000; Kraut et al., 1997; Malach et al., 1995, 1998; Mendola et al., 1999) showed that the ventrolateral occipitotemporal regions in the human brain were activated during perception of integral objects, but not to their scrambled montages. These neuroimaging results for the human brain were consistent with more direct and concrete results of neurophysiological studies in the monkey (Gallant et al., 1993; Logothetis and Sheinberg, 1996; Pasupathy and Conner, 1999; Tanaka, 1996; Vogeles, 1999): Neurons in the ventral visual pathways (e.g., V4, the occipitotemporal regions) were selective for shapes of objects. These results strongly suggest that the ventrolateral occipitotemporal regions of the brain are involved in the analogical representation of objects both in man and in monkey. Furthermore, Epstein and Kanwisher (1998) found that a particular area within human parahippocampal cortex was selectively activated by viewing the scenes that depict the spatial layouts of objects (the local visual environment), but only weakly to single objects and not at all to faces.

The cognitive processing of single words was extensively studied with PET scanning methods: Petersen et al. (1989) found

Abbreviations: BOLD, blood oxygenation level dependent; fMRI, functional magnetic resonance imaging.

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Available online on ScienceDirect (www.sciencedirect.com).

that the silent reading of written words (compared with the fixation on the crossbar as a baseline) activated bilaterally the striate and the extrastriate areas and inferior lateral occipital cortex, whereas the listening to spoken words activated bilaterally the posterior superior temporal gyri, the left anterior superior temporal gyrus, and the left temporoparietal area. In further experiments, Petersen et al. (1990) observed that concrete nouns (common names of animals and household objects) and pronounceable non-words activated bilaterally the lateral extrastriate regions, and the left medial extrastriate areas when compared with the crossbar as a baseline condition. But the inferior left frontal region was activated only by the real words. Viewing of consonant strings and false fonts (a series of abstract designs with structural similarity to letters) activated only the primary visual areas. The fact that only the meaningful words but not other word-like stimuli activated the left inferior frontal region suggests that the frontal region is involved in lexical semantic representation. Bookheimer et al. (1995) found that the silent reading of concrete nouns activated the left posterior inferior temporal region and the nearby fusiform gyrus, when compared with the viewing of complex and meaningless figures made up of line drawings (instead of the simple crossbar) as a baseline condition. Beauregard et al. (1997) examined differential activations of the brain for concrete, abstract, and emotional word lexica: They found that the anticipation of the experimental tasks before the presentation of actual test stimuli activated the left orbital frontal gyrus, the left inferior temporal gyrus, the left caudate nucleus, the anterior cingulate, and the cerebellum. When the anticipatory condition was used as baseline, the silent reading of concrete words activated the left middle temporal gyrus, the left middle occipital gyrus, the left fusiform gyrus, and the right lingual gyrus. The abstract words activated the left middle frontal gyrus, the left inferior frontal gyrus, the middle temporal gyrus, and both lingual gyri. The emotional words activated the left inferior frontal gyrus, the left inferior temporal gyrus, and the left medial frontal gyrus. More recently, Delvin et al. (2002) found that word retrieval and semantic lexical decision tasks for living things activated bilaterally the anterior medial temporal poles, whereas semantic tasks on words for tools activated the left posterior middle temporal region and a network of action representations for the use of tools activated the anterior inferior parietal and ventral premotor cortices.

Neuroimaging of sentence processing was investigated with PET and extensively with fMRI methods. Mazoyer et al. (1993) observed that listening to meaningful stories activated the left middle temporal gyrus, the left and right temporal poles, and the superior prefrontal area in the left frontal lobe. Stromwold et al. (1996) found that syntactically more complex sentences (center-embedded versus right-branching) activated the left pars opercularis. A similar trend was also observed by Just et al. (1996) with fMRI. Bavelier et al. (1997) found that silent reading of English sentences (as contrasted with strings of consonants) activated several small, limited patches along the peri-sylvian cortex including Broca's area, Wernicke's area, the angular gyrus, and the anterior portion of the superior temporal gyrus. Kim et al. (1997) found that a second language acquired in adulthood (late bilingual) was spatially separated from the native language within the frontal lobe language sensitive regions (Broca's area). If the second language was acquired during the early language acquisition stage, however, both the native and the second languages tended to be represented in the common frontal areas. Kuperberg et al. (2000) observed that the left superior temporal gyrus was involved more in pragmatic judgment than in semantic or syntactic

judgment, and the right superior and middle temporal gyri were concerned with semantics rather than syntax. The functional conjunctions and disjunctions of the cortical regions were investigated by Hirsch et al. (2001) with regards to three basic cognitive tasks: object naming, same–different discrimination, and integer computation. They found that all three tasks activated a common cortical region: the left medial frontal gyrus.

Some concrete states of affairs may be mentally represented in both the analogical and the symbolical modes. For example, a simple spatial relation between two objects such as a square and a circle can be pictorially depicted as . This same spatial relation can also be verbally described with various sentences: 'The circle is below the square,' 'The square is above the circle,' 'The circle is not above the square,' 'The square is not below the circle', etc.

Clark and Chase (1972) found that the verification of congruence between the pictorial depiction (analogical mode) and verbal descriptions (symbolical mode) involved different types of mental operations according to the propositional complexity and truth value of each verbal description. In the present study, we aimed to identify the specific cortical regions that were activated exclusively by the analogical mode, and those neural structures activated by the symbolic mode but not both (i.e., functional disjunction). We also tried to estimate the extent of the shared cortical regions that were involved in both the analogical and the symbolical modes of the mental representations (i.e., functional conjunction). To determine the pattern of such differential activations, we scanned the brains of normal subjects using fMRI during the following six contrastive cognitive states (see Fig. 1 for examples of the six types of test stimuli): [A] Fixation at a crosshair (used as the baseline state). [B] Perception of single objects (the basic analogical mode). [C] Perception of non-sense letter strings. [D] Silent reading of single words (the symbolic mode at the lexical level). [E] Silent reading of sentential descriptions of spatial relations among objects (the symbolic mode at the propositional level). and [F] Perception of pictorial depictions of the spatial relations among objects (the compositional analogical mode). The magnetic resonance (MR) signals obtained during each type of cognitive state were compared with those of other contrastive cognitive states for each subject within the same session of the fMRI experiment.

Materials and methods

Subjects

Five male and five female students at Dalhousie University volunteered as subjects. Their ages ranged from 21 to 32 with a mean age of 24. All 10 were right handed and native speakers of English without any history of neurological or psychiatric disorders. The protocol of our experiment was approved by the Research Ethics Committee of the Queen Elizabeth II Health Sciences Centre. All subjects gave written informed consent. The data from one subject were excluded from averaging due to an excessive movement artifact.

Experimental design

For each subject, we presented six types of visual stimuli at the center of the visual field using video goggles (Resonance Technologies Inc.) to induce six contrastive cognitive states: [A]

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