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Research Report

Action selectivity in parietal and temporal cortex

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Abstract

The sensory–action theory proposes that the neural substrates underlying action representations are related to a visuomotor action system encompassing the left ventral premotor cortex, the anterior intraparietal (AIP) and left posterior middle temporal gyrus (LPMT). Using fMRI, we demonstrate that semantic decisions on action, relative to non-action words, increased activation in the left AIP and LPMT irrespective of whether the words were presented in a written or spoken form. Left AIP and LPMT might thus play the role of amodal semantic regions that can be activated via auditory as well as visual input. Left AIP and LPMT did not distinguish between different types of actions such as hand actions and whole body movements, although a right STS region responded selectively to whole body movements.

Theme: Neural basis of behavior
Topic: Cognition

Keywords: Functional imaging; Category-specificity; Semantic memory; Action retrieval

1. Introduction

Among the many cognitive models that describe how semantic memory might be organized, the sensory–action theory [52] has received particular attention. The sensory–action theory predicates category-specific effects (e.g., tools vs. animals) on anatomical segregation for different semantic features (e.g., action vs. visual). The neural substrates underlying these semantic representations are assumed to be functionally and anatomically linked to the sensory and motor areas that are active when they are experienced. In particular, the feature-based account [29] proposes that the neural substrates underlying action representations are related to brain regions taking part in a visuomotor action system encompassing the left ventral premotor cortex, the anterior intraparietal (AIP) and left posterior middle temporal gyrus (LPMT).

The AIP and ventral premotor circuitry is thought to play a crucial role in retrieving the appropriate action for a particular object and the associated visuomotor transformations. In the macaque, neurons in areas F5 and AIP have been identified that respond selectively to action execution, observation and presentation of graspable objects [24,40–42]. Similarly, in humans, premotor cortex and the supramarginal gyrus/AIP have been implicated in action observation, simulation, imitation and execution [4,5,15,16,18,44,46,47]. A recent study has shown somatotopically selective activation along the (pre)motor cortex for action words referring to face, arm or leg actions (e.g., lick, pick, kick) in a passive reading task [20].

In addition to AIP and ventral premotor areas, the left posterior middle temporal region (LPMT) has been associated with action semantics. As LPMT is just anterior to motion area MT/V5, its role in action semantics might be engendered by its functional relation to action/motion perception mediated by afferents from area MT/V5. Consistent with this conjecture, LPMT is activated for observing grasping movements relative to static objects [37,43], hands [17,18] or random motion [2,3,19]. While these activation differences might be due to specific motion characteristics of the stimuli at the perceptual

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level, LPMT activation was also increased for static pictures or sentences with implied motion/action relative to similar stimuli that did not imply motion [25,45,48,51]. Most importantly, in semantic decision or generation tasks, LPMT is activated for retrieval of action (e.g., "Do you twist this object?") relative to retrieval of visual semantics (e.g., "Is the object bigger than a kiwi?"), when the stimuli are written words or pictures referring to real world objects [27,38].

This study pursues two main aims: first, we tried to identify the action retrieval system that is common to different types of actions. For this, we compared action semantics to a range of other semantic types such as sounds, visual attributes or abstract semantics using (1) a semantic decision task on spoken words and (2) a semantic association task on triads of written words. This allowed us to identify action-selective responses that emerge at the semantic level and do not depend on the stimulus modality or the particular task instructions. Testing for activations that are common to the visual and auditory modality seems to be particularly important because of the anatomical proximity between the MT/V5 complex and satellites (e.g., KO, i.e., kinetic occipital area) that process biological motion. Thus, a recent study comparing words referring to actions and pictures with implied actions demonstrated enhanced activation in motion area MT/V5 for pictures, but for words in an area slightly anterior to MT/V5 [22] suggesting that the area referred to as LPMT might actually encompass several functionally distinct areas.

Second, within this more general aim, we embedded a more focused question and investigated whether any regions within or beyond the action retrieval system responded selectively to particular types of actions. For this, we compared hand actions with whole body movements. Although hand actions and body movements are both classified as actions, they differ in terms of their semantic and perceptual characteristics. At the semantic level, hand manipulations are more strongly associated with tools and utensils, while whole body movements are primarily linked with humans and animals. Different neural substrates for these two action types at the perceptual level (i.e., using movies) have recently been suggested [2]. Using words rather than pictures or movies, this study enables us to identify regions that respond selectively to hand actions or whole body movements at the semantic level.

In brief, we report two fMRI experiments using auditory and visual input modalities respectively. In the first fMRI experiment, subjects made semantic decisions on spoken words referring to hand actions, body motions, visual attributes and sounds. In the second fMRI experiment, they were engaged in a semantic association task on triads of written words referring to hand actions, abstract concepts, visual attributes and sounds. Collectively, Experiments 1 and 2 allow us to investigate action-selective responses irrespective of the input modality and the particular task instructions. In addition, Experiment 1 enables us to further characterize them by comparing hand actions and whole body movements.

2. Methods

The two fMRI experiments were conducted with different subjects in each experiment. In both experiments, subjects were presented with blocks of (a) spoken or written words with different types of meaning (matched for word frequency and number of syllables); and (b) a non-lexical baseline condition that controlled for non-linguistic sensorimotor processing. Subjects engaged in decisions that explicitly focused their attention on the semantic content of each word (Experiment 1) or made semantic similarity judgements on triads of stimuli (Experiment 2). Details of each experimental design are given below and details of the stimuli are provided in the Appendix.

2.1. Experiment 1: fMRI. Semantic decisions on heard words

In the activation conditions, subjects made semantic decisions on spoken words with four different types of meaning and performed a semantic decision task that explicitly directed their attention to the semantic content of each word:

1. Words referred to hand actions. Subjects decided if the hand action involved a tool.
2. Words referred to body motion. Subjects decided if the body movement was slow.
3. Words referred to visual features. Subjects decided if the visual form was curved.
4. Words referred to auditory features. Subjects decided if the sound was usually loud (see stimulus Appendix for more details).

The decisions involved an alternate forced choice response—yes/no (see Appendix). For each activation condition, there was a matched baseline condition that employed the same stimuli after they had been reversed to remove lexical and semantic content. The task was to decide if the reversed words were recorded in a male voice. For all 8 (4 semantic and 4 baseline) conditions, there were 30 stimuli. one-third of the stimuli were targets. Yes/No responses to all conditions were indicated (as quickly and as accurately as possible) by a two-choice key press. All stimuli were presented at a rate of one per 4 s. There were five stimuli per block (20 s per block), and each block was preceded by a short spoken instruction period (5 s). The order of semantic conditions was counterbalanced within and across subjects, and each semantic condition was followed or preceded by its matched baseline condition.