

# Organization of Semantic Knowledge and the Origin of Words in the Brain

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**What does it mean to claim that a nonhuman species has words? Recent evidence from cognitive neuroscience indicates that meaning or semantic information about a particular object is represented as a distributed network of discrete cortical regions. Within this network the features that define an object are stored close to the sensory and motor regions of the brain that were active when information about that object was acquired. These semantic representations are active whenever the object is perceived and when its name is produced or heard. The organization of semantic information parallels the organization of the sensory and motor systems in the primate brain. Evidence of similarities in the way object information is stored in the cerebral cortex of human and nonhuman primates may provide a means for assessing the referential status of nonhuman vocalizations.**

Until very recently, our understanding of the organization of language in the brain has come from the study of adult humans with deficits in specific language abilities as a result of focal brain damage. For example, it has been known since the latter half of the 19th century that damage to the posterior region of the left temporal lobe (now referred to as Wernicke's area) can produce impaired speech comprehension, whereas damage to the inferior region of the left frontal cortex (now referred to as Broca's area) can produce impaired speech production. These observations have held-up remarkably well (Figure 1) and during the hundred years following Broca and Wernicke we have learned a great deal about how language is represented in the brain from the study of language-impaired individuals (for an excellent review and synthesis see Caplan 1992).

The recent advent of functional brain imaging technologies (*e.g.*, positron emission tomography, PET; and functional magnetic resonance imaging, fMRI) have ex-

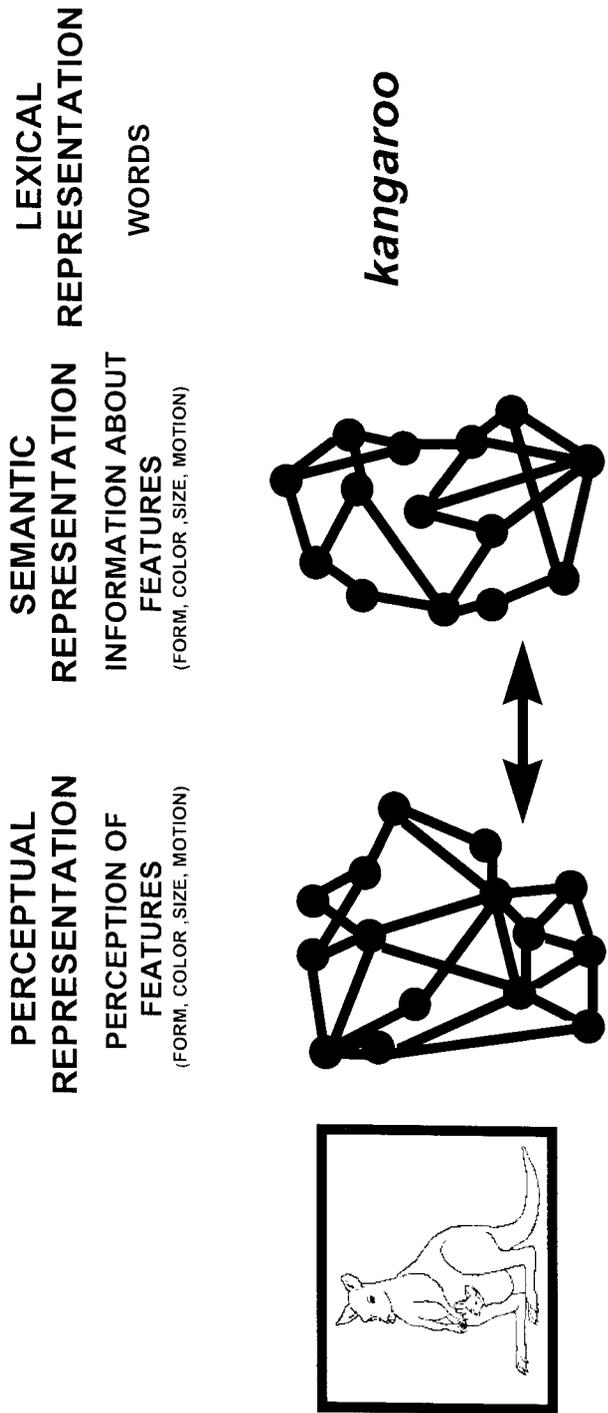


FIGURE 2. Hypothesized neural networks mediating object naming. Perceptual and semantic representations are shown as discrete but interacting networks activated prior to word retrieval.

perienced them together (*i.e.*, they co-occur in time during perception). This binding constitutes a network of discrete cortical regions: a semantic network.

6) This semantic/cortical network is activated automatically (*i.e.*, obligatorily, quickly, and outside of conscious awareness) when an object is viewed. This point becomes evident when we consider that “seeing” as we commonly use the term, refers to “seeing as.” To perceive an object is to identify it as a member of some class (*i.e.*, a “dog,” “chair,” “word,” or even a “shapeless form”). Perception, in this everyday usage of the term, cannot occur without the automatic activation of previously acquired information. Typically, for example, it takes less than 700 msec for subjects to name line drawings of common objects, even though the drawings have not been seen previously by the subjects. How could we quickly recognize or identify an object as being of a particular type (*e.g.*, a chair, pencil, or kangaroo) if we did not have prior knowledge of chairs, pencils, and kangaroos?

7) In humans, semantic networks are activated not only when objects are seen, but also when the object’s name is read, heard, or retrieved in the service of writing and speech. The name serves as a powerful, economical, shorthand description of just those features that uniquely define the object.

Based on these claims, then, to argue that the alarm calls of the vervet monkey function like words, is to argue that the semantic representation of “martial eagle” is activated not only by perception of the eagle, but also by the sound of the alarm call. This is the critical claim. The alarm call represents the martial eagle because both the perception of the eagle and the alarm call activate a common semantic network in the brain. Presumably, as with the learning of feature-object associations (*i.e.*, learning about the form, color, pattern of motion, *etc.* that define “martial eagle”), the learning of the alarm call-object association may be dependent on the cocurrence of environmental events. In this case, the association between hearing the call and the perception of the eagle, and perhaps also the association between hearing the call and the perception of the call’s affect on the behavior of other monkeys.

What is the evidence to support these claims? Before turning to that question it is necessary to briefly describe the organization of the primate visual system.

## **Organization of the Primate Visual System**

The visual system evolved to solve the problem of representing the world. We remain quite far from a formal understanding of how perception is accomplished (*i.e.*, understanding the computations performed in enough detail to build a device that could accomplish the type of simple visual recognition tasks — such as identifying objects from multiple viewpoints — that we accomplish quickly and effortlessly). Nevertheless, we have gained considerable knowledge about the locations and functional properties of the brain regions that mediate vision.

An important starting point for understanding complex brain systems like those that mediate vision is the “principle of modular design” (Simon 1962; Marr 1982). This principle asserts that complex problems are solved by breaking them down into smaller, and presumably more manageable parts. The main idea is that complex systems are composed of subsystems that are as nearly independent of one another as the overall function of the system will allow. If such independence did not exist then even a small change in one part of the system would change the entire system. Thus, in order for evolution to occur in a nonmodular scheme, each change would need to be accompanied by numerous and simultaneous changes throughout the entire system.

Modular design allows for the possibility of modifying or creating new subsystems without necessitating change in all other subsystems.

Until the recent advent of functional neuroimaging in man, the bulk of our knowledge about the modular design of the visual system has come from investigation of one of our closest living relatives, the Old World monkey. Studies of the cortical surface of the macaque have revealed at least 30 separate visual areas occupying nearly one half of monkey cortex (Felleman & Van Essen 1991). These regions are broadly organized into two functional processing streams (Figure 3). An occipitotemporal stream that subserves object vision and an occipitoparietal stream that subserves spatial vision and visual guidance of movements towards objects in space (for recent review see Ungerleider & Haxby 1994). These processing streams are organized hierarchically, with increasingly complex neuronal response properties as one proceeds from primary visual areas in occipital cortex to more anterior sites in the temporal lobe (for the object processing) and parietal lobe (for spatial processing).

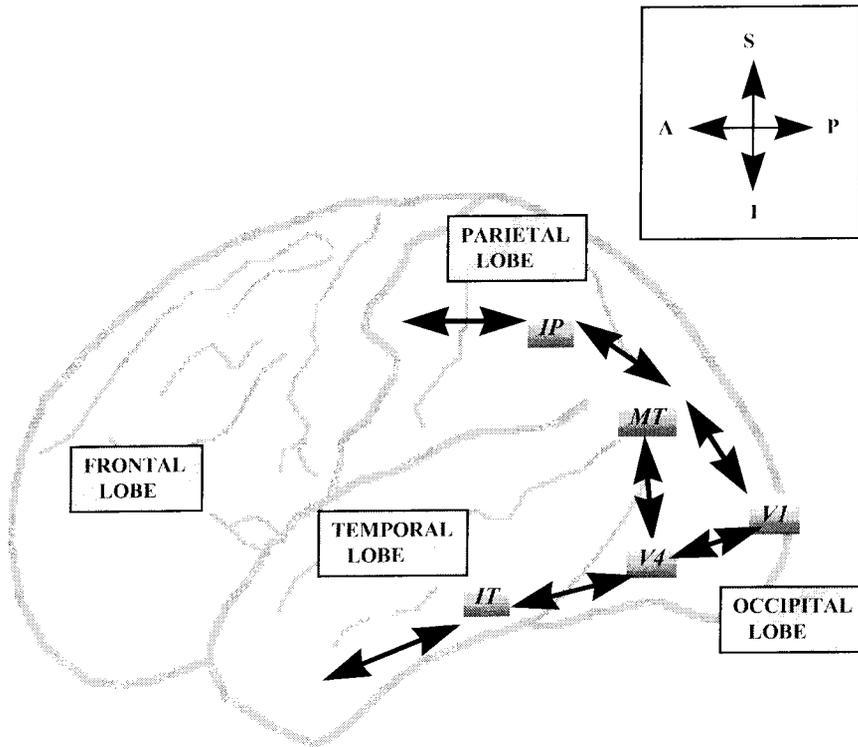


FIGURE 3. Schematic diagram of the two cortical visual systems. Visual information is received in primary visual cortex in the occipital lobe (V1) and then brought forward along two separate processing pathways. An occipitotemporal pathway that mediates object vision (from V1 towards the inferior temporal cortex, IT) and an occipitoparietal pathway that mediates spatial vision (from V1 towards inferior parietal cortex, IP). Each processing stream has extensive feedforward and feedback connections (bidirectional arrows), as well as connections between regions assigned to different processing streams. In the monkey over 30 visual processing regions have been identified, only a few of which are shown here. MT is critical for motion perception and V4 is critical for perception of form and of color (for details see Ungerleider & Haxby 1994).

The need for this separation of function becomes apparent when one considers the work that each system is required to perform. The object recognition system must be designed in such a way as to allow recognition of a particular object as the same object regardless of its position in the visual field. Consistent with this requirement, whereas neurons in the primary visual cortex (in the occipital lobes) have small visual fields, neurons further up stream (in the temporal lobes) have large visual fields (*i.e.*, they respond to a particular object over a large region of space). As a result, information about the exact location of an object is sacrificed in the service of object recognition. While this neural architecture is perfectly suited for visual recognition, it is particularly ill-suited for the job of object localization. Therefore another system, with a different architecture, is needed to keep track of position in space. This job is accomplished by the occipitoparietal spatial processing stream.

Studies of brain-damaged patients have documented a similar organizational scheme in the human brain. For example, damage to the parietal lobes (especially the right parietal lobe) can produce disorders of spatial cognition, including selective deficits in perceiving object location and orientation (Newcombe & Ratcliff 1989), while temporal lobe lesions can produce deficits in object recognition and object naming (especially after left temporal lobe lesions) (Damasio *et al.* 1989).

At a more specific level of analysis, modular design extends to functioning within each processing stream as well. For example, regions in the lower, or inferior aspect of the occipital lobes respond to an object's form and color, whereas other more superiorly located regions respond to an object's direction and speed of movement through space (Desimone & Ungerleider 1989; see Figure 3). Again similar findings have been documented in humans. Damage to the inferior region of the occipital lobe can produce the syndrome of achromatopsia (acquired color blindness; Damasio *et al.* 1980), whereas a more superiorly located lesion at the junction of the occipital, temporal, and parietal lobes can produce akinetopsia (acquired motion blindness; Zeki 1991). Thus, within the cortex, the beginning stages of object recognition are mediated by relatively independent neural modules that subservise perception of specific features of the visual scene. The previously mentioned perceptual representation of an object is mediated by these regions of the brain.

## **Investigating the Organization of Semantic Attributes**

The idea that information about the attributes that define an object may be distributed among different regions of the brain is not new. Wernicke, for example, argued that word forms were stored in one location and received input from visual and other sensory modalities in which modality-specific images of the object concept were stored (as discussed in Head 1926). More recent formulations of the idea that information about different object attributes and features are stored in separate cortical regions has been championed, in somewhat different forms, by Elizabeth Warrington and her colleagues (Warrington & Shallice 1984), Antonio Damasio (1989), and Glynn Humphreys (Humphreys & Riddoch 1987), among others (for review see Saffran & Schwartz 1994; and see Allport 1985 for an influential formulation of distributed semantic representations from a cognitive view). Evidence for this claim, however, has been rather indirect, based almost exclusively on single-case studies of patients with unusual and rare syndromes resulting from focal brain damage and disease.

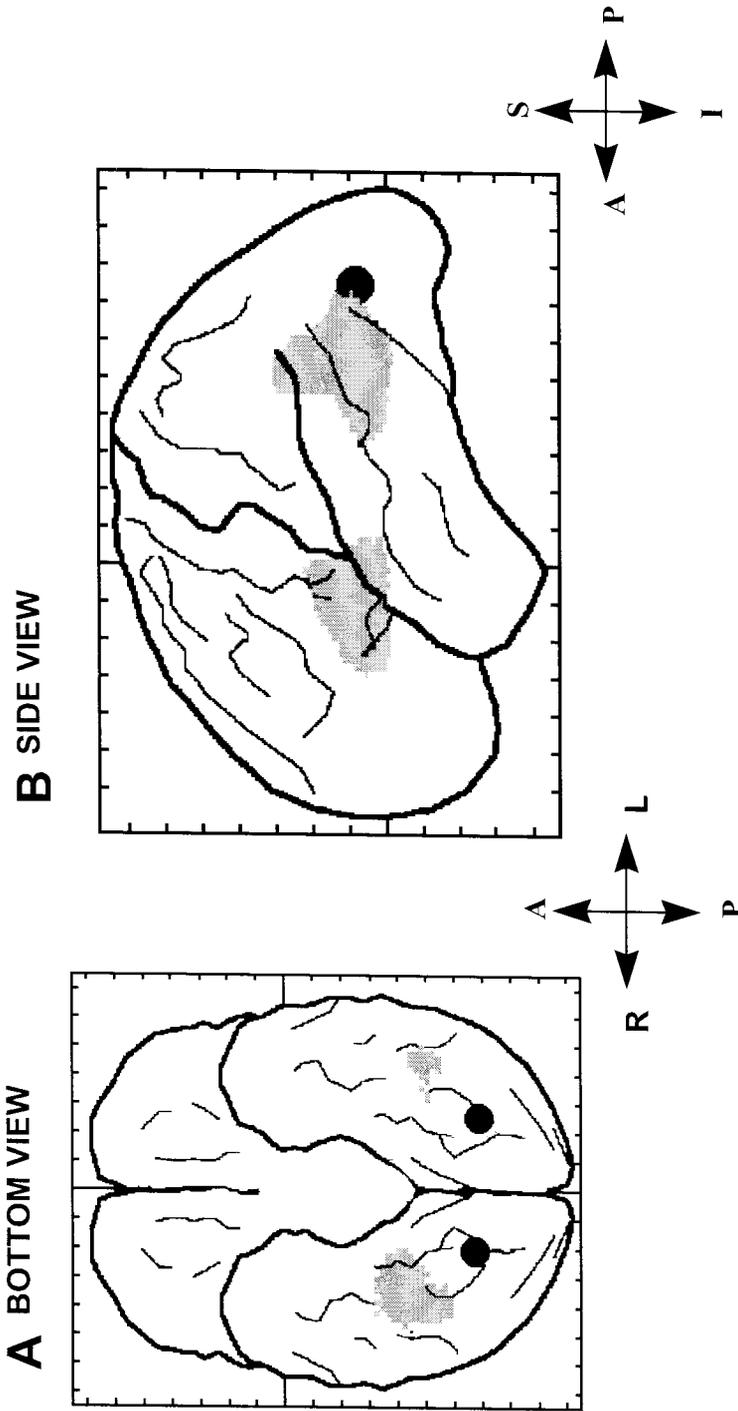


FIGURE 4. (a) Bottom view of the brain showing regions (in gray) more active when subjects retrieved words denoting object-associated colors than when they retrieved words denoting object-associated actions. Black circles show location of areas active when perceiving color. (b) View of the left side of the brain showing regions (in gray) more active when subjects retrieved words denoting object-associated actions than when they retrieved words denoting object-associated colors. Black circles show location of area active when perceiving motion (adapted from Martin *et al.*, 1995). R = right, L = left.

rately. In addition, the sites of storage are near the areas active during the perception of, and therefore when we learned about, those attributes.

More recent work from our laboratory has suggest that brain regions specifically associated with perception are themselves not reactivated when perceptually-based information is retrieved (Chao & Martin submitted). Thus it appears that retrieving information about a specific object attribute like color requires activation of a region of the brain situated close to, but not including, the neural circuitry involved in the perception of color. This finding is consistent with reports of patients with cortical lesions that can no longer see colors, yet retain the ability to imagine colors (Shuren *et al.* 1996), and patients who can no longer see objects, yet retain the ability to imagine objects (Behrmann *et al.* 1992). Taken together, the available evidence suggests that information about object features are stored near, but not in, the tissue active during perception of those features.

### Category-Specific Knowledge

The PET studies established three important points with regard to earlier claims about the organization of semantic information. First, retrieving information about different object-associated features is associated with activity in different regions of the brain. Second, the locations of these regions are close to, but do not include, areas associated with the perception of those features. And, third, these regions are active during word retrieval. Retrieving words in appropriate context requires activation of a semantic representation.

To perform these tasks correctly, however, required an appreciable amount of work or effort on the part of the subjects. Specifically, they had to focus attention on previously acquired information about a specific object feature and then find the right word to express that knowledge, all under considerable time pressure (a new stimulus appeared every two seconds). In the model of object recognition sketched previously, however, semantic representations are activated automatically, without effort, whenever an object is seen. Therefore, the next question became: Could we find evidence for the automatic activation of a semantic/cortical network during object identification?

Our strategy for pursuing the answer to this question was the same as the one we used in the color and action knowledge studies. Specifically, we pitted two different categories against each other to determine whether different brain areas became active. This time, however, rather than performing a mentally strenuous and attention-demanding task — retrieving words denoting specific attributes of objects, subjects performed a simpler, less demanding task — naming objects. In fact, for the conditions to be discussed below, subjects were not required to overtly produce names, but merely to view objects and name them silently to themselves.

The categories we chose to study were animals and tools (Martin *et al.* 1996). As with our choice to study knowledge about color and action, this choice of categories was motivated by reports of brain-damaged patients. In this case, reports of patients with selective difficulty naming and answering questions about living things (Warrington & Shallice 1984; Farah *et al.* 1991; Silveri & Gainotti 1988; Sheridan & Humphreys 1993), and reports of patients with deficits limited to man-made objects (Warrington & McCarthy 1983; Warrington & McCarthy 1987; Sacchett & Humphreys 1992).

How could such category-specific impairments occur? One approach to this question has been to deny that these selective deficits actually do occur. This is not an unreasonable position given that category-specific disorders are rare, the between-category dissociation often not pure (*i.e.*, naming may be abnormal for members of both categories, but greater for one than the other), and the findings open to alternative interpretations. In particular, it has been argued that the selective deficit in naming living things is an artifact of differences in the visual complexity of the stimuli used to depict living things and man-made objects (Fennell & Sheridan 1992; Stewart *et al.* 1992). Animals, for example, do tend to have more visually complex forms than tools. As a result, pictures of animals may be more difficult to identify than pictures of tools; especially for a brain-damaged subject. However, such physical differences cannot account for the opposite finding (*i.e.*, *more* difficulty naming man-made than living objects) and recent studies controlling for visual complexity have reduced, if not negated, the explanatory power of the visual-complexity criticism (Farah *et al.* 1996).

Given that category-specific disorders do occur after brain damage, most investigators have relied on some form of a semantic feature model to explain their occurrence. In general, it has been argued that the critical feature used to differentiate members of the category "four-legged animals" is knowledge about physical features. We learn to distinguish animals by their physical characteristics. Moreover, the differences between animals can be quite subtle (consider for example, the difference between horses, donkeys, and mules, or leopards, tigers, and jaguars). Tools, in contrast, while differing in physical form, also have specific functional properties, and these functional properties are the critical component of their definition. This difference in the types of attributes that define animals and tools can be easily verified by consulting a dictionary. This has in fact been done and the results showed that the ratio of physical properties to functional properties is much greater in the dictionary definitions of animals than tools (Farah & McClelland 1991).

This difference in the attributes and features that define animals and tools suggests that the developmental histories of animal and tool learning may differ as well. Knowledge about the unique physical features that define each animal would be acquired primarily through object vision, whereas knowledge about tool differences would be acquired through the motor system (patterns of dominant hand movement learned through the use of tools) and motion vision (patterns of motion learned through observation of tool use by ourselves and others). If these are the kinds of information needed to identify objects, then one would predict that naming animals would require greater activation of previously acquired information about shape or form than would tool naming, whereas tool naming would require activation of information about visual motion and motor movements associated with tool use.

To investigate this hypothesis we asked subjects to silently name briefly presented pictures of objects (Martin *et al.* 1996). Animal pictures were presented during one PET scan and pictures of tools were presented during another PET scan. In addition, subjects were scanned while attending to pictures of nonsense object forms, and while staring at visual noise patterns. Several findings emerged from this study. First, the outer or lateral regions of the left and right occipital lobes were active when subjects perceived objects, regardless of whether they were meaningful (animals and tools) or meaningless (nonsense object forms) (see Malach *et al.* 1995 for a similar finding). This finding suggests that this region of occipital cortex is critical for perceiving object form, and therefore associated with the perceptual, but not the semantic representation of an object (Figure 5). Second, in contrast to nonsense objects,

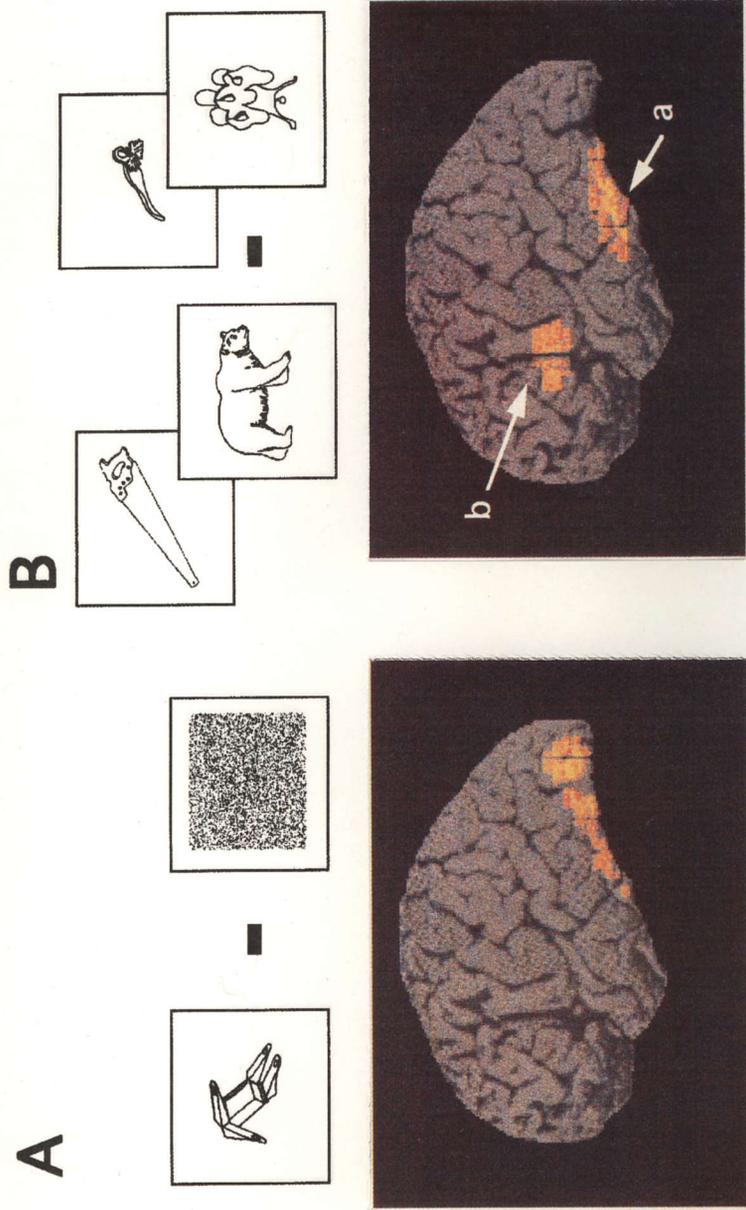


FIGURE 5. A. View of the left side of the brain showing region more active when subjects viewed nonsense objects than when they viewed visual noise patterns. Activation was bilateral, strongest in the occipital lobes, and extended anteriorly into the temporal lobes. B. View of the left side of the brain showing the inferior temporal (a) and inferior frontal regions (b) that were more active when subjects silently named real objects (both animals and tools) than when they viewed nonsense objects (adapted from Martin *et al.* 1996).

naming meaningful objects (animals and tools) activated the inferior region of the temporal lobes (*i.e.*, a more anterior aspect of the object vision pathway) suggesting that this portion of the temporal lobe may be the site for stored information about object form. Third, naming meaningful objects (animals and tools) activated a region of the inferior frontal lobe known to be associated with speech (Broca's area, Figure 5). Fourth, in addition to areas active when naming both animals and tools, other regions of the brain were selectively activated by naming objects from one category or the other.

In comparison to naming animals, tool naming activated a region of the left temporal lobe that was nearly identical to the region active in the previously discussed studies of action word retrieval (Figure 6). As discussed previously, this region is situated just anterior to (in front of) the area known to be active during motion perception. This finding provides additional evidence that this region of the left temporal lobe may be a critical site for stored information about object motion. In addition, tool naming was associated with activation of a region of the left premotor cortex situated just anterior to the primary motor cortex that controls right-sided body movement (Figure 6). The region of premotor cortex active during tool naming was nearly identical to an area previously found to be active when subjects imagined manipulating objects with their right hand (Decety *et al.* 1994). Thus this region of left premotor cortex may be the site for stored information about patterns of hand movements associated with tool use.

In contrast, the only brain region more active for animal naming than tool naming was on the inner or medial surface of occipital cortex, greater on the left than on the right (Figure 6). This region includes the calcarine cortex which is the first cortical area to receive visual information from the eyes. This finding might be viewed as supporting the idea that category-specific impairments are simply a byproduct of the visual complexity of the pictures, as discussed previously. This explanation, however, was eliminated by the results of a separate study that again found greater medial occipital lobe activity for animal than for tool naming even though the pictures were equated for visual complexity by transforming them into silhouettes (see Martin *et al.* 1996 for details). These results suggest that this early-stage, occipital visual processing area may be reactivated in top-down fashion by regions higher up in the object vision pathway (perhaps via feedback connections from the inferior temporal region associated with identifying meaningful objects). Reactivation of the medial occipital region may be necessary to uniquely identify an object when relatively subtle differences in physical features are the primary means by which the object can be distinguished from other members of its category. Converging evidence for these findings has been provided by a recent study of brain-damaged patients with category-specific naming deficits (Tranel *et al.* 1997).

### Object-Associated Affect

The evidence reviewed so far relates to some of the cognitive aspects of object meaning. However, in addition to information about physical and functional features, object meaning can also be emotionally laden. Viewing scenes of accidents, surgical procedures, and the like have an aversive component (and have measurable affects on the autonomic nervous system), whereas pleasant feelings can be elicited by pictures of puppy dogs, flowers, and tranquil environments, *etc.* Moreover, many individuals seem to have an instinctive fear of certain animals (spiders, rats, bats)

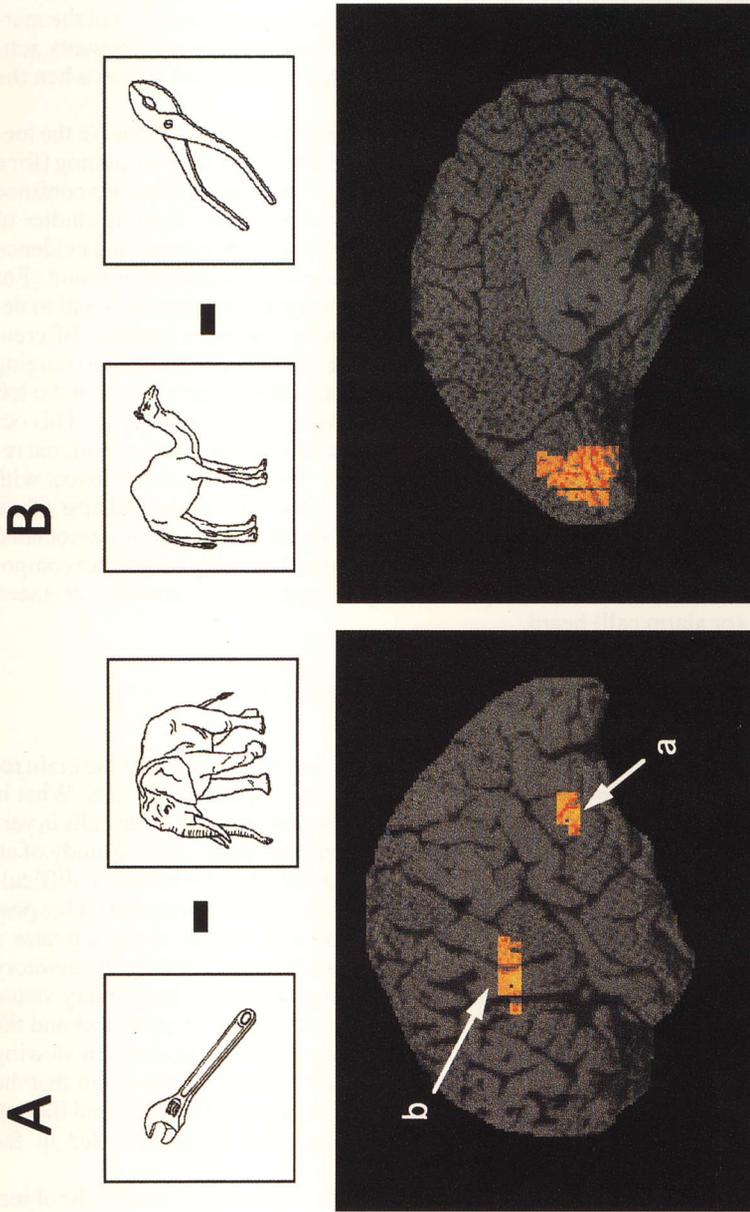


FIGURE 6. A. View of the left side of the brain showing areas in the left posterior temporal lobe: (a) and left premotor cortex (b) and that were more active when subjects silently named pictures of tools than when they silently named pictures of animals. B. View of the inner (medial) surface of the left side of the brain (right side removed) showing the region of the occipital lobe that was more active when subjects silently named pictures of animals than when they silently named pictures of tools (adapted from Martin *et al.* 1996).

and situations (public speaking, heights) and the negative feelings associated with these experiences can be elicited by viewing pictures. Alarm calls must have an affective component to serve as warnings. In order to function as a warning the sight of a predator (e.g., the martial eagle), and the alarm call that represents it, must elicit an emotional response that signals danger and the appropriate avoidance behavior. Therefore, in addition to feature information, the semantic representation of the martial eagle should include affective information. Similarly, the semantic network activated in the brain of the monkey should include regions that were active when the martial eagle-fear association was established.

Neurobiological studies have established that the amygdala, a structure in the medial region of the anterior temporal lobe, plays a central role in fear conditioning (for a recent review see Ledoux 1996). In addition, studies of patients with lesions confined to the amygdala (e.g., Adolphs *et al.* 1994), and functional brain imaging studies of normal subjects (Breiter *et al.* 1996; Morris *et al.* 1996), provide converging evidence that the amygdala is involved in the visual recognition of emotional expression. For example, in one study (Morris *et al.* 1996) subjects were shown faces and had to decide whether the individual depicted was male or female. The faces depicted different expressions (happy, fear) and varied according to the intensity of expression (ranging from neutral to most fearful or most happy). The data showed that activity in the left amygdala was significantly correlated with the intensity of expressed fear. This occurred even though the task required only gender discrimination, not an emotional response, nor a judgment about emotional expression. This finding is consistent with the idea that the affective valence associated with an object is represented near, if not in, a region critical for learning object-affect associations. Brain regions associated with establishing relationships between objects and emotions may be another component of the semantic network that is automatically engaged whenever an object is seen or its name (or alarm call) heard.

### **Are Alarm Calls Words?**

In this chapter I have described the locations and functions of some of the brain regions that underlie semantic knowledge about concrete objects in humans. What is the relevance of these findings for assessing the referential status of alarm calls in vervet monkeys? Imagine that we could perform a functional brain imaging study of an alert, vervet monkey (such an undertaking would be fraught with technical difficulties; however, we will ignore these problems for the sake of our discussion). One possible outcome would be that the visual presentation of a martial eagle activates a network of cortical regions, and that this same network is activated by the auditory presentation of the martial eagle alarm call (excluding, of course, the primary visual and auditory processing areas associated with the presentation of the object and the call, respectively). Activation of an identical network of brain regions when viewing the predator and hearing the alarm call would provide support for the claim that the alarm call “stands for” the object. That is, we could argue that the object and the call mean the same thing to the monkey *because* they elicit identical states in the monkey’s brain.

At the other extreme, there may be no overlap in the regions activated by the object and the alarm call. For example, whereas the visual presentation of the eagle might activate a distributed network of cortical areas associated with stored information about form and motion, the alarm call might activate a limited circuit comprised of

auditory cortex and limbic structures associated with learned fear. In this case, the association between the alarm call and the monkey's behavior in the wild would be more like a simple, conditioned fear response (although I think there is good evidence to reject this extreme point of view; see Cheney & Seyfarth 1990). The call would elicit a behavioral response without an intervening stage of cognitive mediation. We could then argue that the call no more "referred" to a martial eagle for the monkey, than the bell referred to a steak for Pavlov's dog.

### **Concluding Comments: Knowledge Primitives and the Embodied Mind**

Writing on the structure of categories, the linguist George Lakoff stated that "Thought is embodied, that is, the structures used to put together our conceptual systems grow out of bodily experience and make sense in terms of it; moreover, the core of our conceptual systems is directly grounded in perception, body movement, and experience of the physical and social order" (Lakoff 1987: xvi). The evidence and arguments presented in this chapter support this view.

The object semantic system discussed here is seen as consisting of learned information about features and attributes that uniquely define an object. This information is represented in the brain as a distributed network of discrete regions in which the attributes that define the object are stored near the regions active when this information was acquired. These include the sensory and motor systems through which we act in, and obtain our experience of, the world. It was further argued that these representations were active not only during object recognition, but during word recognition and production as well. If the alarm calls of the vervet monkeys are referential in the same way as human words, then they would be expected to have semantic representations that follow a similar organizational scheme. Given the similarity between the organization of sensory and motor systems in human and nonhuman primates, the expectation of a similarity in the organization and structure of objects semantics does not seem to be an unreasonable one.

An important remaining question is how do words, and alarm calls, get linked to semantic representations? The idea of cooccurrence of events has limited explanatory power in and of itself because it does not explain why certain events get linked (*e.g.*, words with their referents) and others do not, nor does it explain why this learning happens with ease. Clearly, humans are biologically prepared to establish a link between auditory sounds and object semantics. Perhaps vervet monkeys and other nonhuman primates are prepared to establish such links as well. Nevertheless, humans are prepared to acquire a seemingly unlimited lexicon. The lexical system is both open-ended in capacity and highly flexible in its mapping of words to meaning (*i.e.*, the mapping is many to many). Different words can express the same meaning and the same word can have different meanings. In contrast, the vervet monkey may be prepared to acquire only a limited, genetically determined, lexicon that is closed and rigid in its mappings (one to one).

The type of semantic information discussed in this chapter may be viewed as semantic primitives; as the building blocks out of which more refined shades of meaning could be constructed. The representation of meaning by multiple features stored in different brain regions, rather than as a single entity, provides combinatorial power for representing an infinite number of concepts using a finite number of features. As far as we know, this may be true for both humans and monkeys, but only humans may

have the additional capacity to link a multitude of meanings to arbitrary sounds. I have only touched on a few potential candidates for such semantics primitives: knowledge about form, color, motion, action, and affective valence. To this list others could undoubtedly be added, including knowledge of time, space, and number. Although discussion of these semantic features are outside the scope of this chapter, I believe there is evidence from studies of both nonhuman and human primates that point to the existence of localized neural mechanisms that could form the basis for storing information about each of these concepts as well.

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