CENTER FOR RESEARCH IN LANGUAGE

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Paper: *Language and the Primate Brain*
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EDITOR'S NOTE

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LANGUAGE AND THE PRIMATE BRAIN

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Abstract

Psychologists, neuropsychologists, and primate neurobiologists have studied human language comprehension and its relation to the primate brain in almost complete isolation from each other. Recent developments provide grounds for a new attempt at drawing some preliminary connections across the levels of organization spanned by these fields. New data on the large number of modality-specific areas in the post-central cortex of several non-human primates, and recent anatomical and functional studies of the human brain suggest that very little of the cortex consists of poly-modal 'association' areas. These observations are used to reinterpret psychological and neuropsychological data on language comprehension in normal and brain-damaged humans. I argue that language comprehension in sighted people might best be thought of as a kind of code-directed scene comprehension that draws heavily upon specifically visual, and probably largely prelinguistic processing constraints. The key processes of word-recognition and the assembly of visual word meaning patterns into interacting chains, however, may be mediated in part by species-specific activity patterns in secondary auditory cortex similar to those generated by uninterpreted speech-sound sequences.

One obvious reason to study non-human primate brains is that they resemble the human primate brain in many ways. Yet humans exhibit behaviors--especially the comprehension of linguistic discourse--that are qualitatively very different from behaviors of primates and other animals. Because of this, some have concluded that animal brains may be poor models for the human brain. There are presently quite substantial rifts between psychological, neuropsychological, and neurobiological approaches to language. Recent developments in studying human and animal brains, however, provide a strong impetus to re-open discourse among these disciplines.

The neocortex of all mammals is now known to consist primarily of a mosaic of visual, auditory, somatosensory, motor, and limbic areas. Primitive mammals have a small number of areas in each of these modalities, while carnivores and primates have many. In monkeys, for example, a mosaic of 25 visual areas occupies more than half of the entire neocortex (Merzenich and Kaas, 1980; Kaas, 1987; Sereno, 1988; Felleman and Van Essen, 1990; Sereno and Allman, 1990). The traditional site for higher-level functions--"polymodal association cortex"--has been reduced to a few diminutive strips in between large expanses of unimodal visual, auditory, and soma-tosensory areas. The potential significance of this reparcellation of cortex for the study of language and the brain has hardly been explored. The aim of this paper is to re-introduce a thoroughly comparative perspective into the evolutionary acquisition of the capacity for language, but one that does not back away from the obvious cognitive differences between humans and other animals. The anatomical and physiological organization of cortical areas in primates, including recent work on human cortex, is reviewed first. The implications of this work for theories of human language comprehension are then explored.

Cortical Sensory Areas in Primates

Definition of a Visual Area. Cortical sensory areas are best defined by multiple converging criteria (Van Essen, 1985; Sereno and Allman, 1990). I begin here with visual areas, since they constitute the largest of the primary subdivisions of the cortex. Criteria for the definition of a visual area presently include *architectonic features* (e.g., degree of myelination, cell size, cell morphology, and cell packing density in cortical layers, histo-chemical features), *connection patterns* (e.g., input and output areas, laminar origins and targets of connections), *visuotopic organization* (e.g., mirror-image or non-mirror-image map of hemifield, bounding areas, pattern of map discontinuities, degree of retinotopy), and *physiological properties* (e.g., excitatory receptive field size, direction selectivity, attention-related modulation). Areas differ in the degree to which these criteria have been explored. V1 (primary visual cortex) and MT (middle temporal area) are distinct, well-

studied areas in primates that are convergently identified by many of these criteria. Other areas--e.g., in inferotemporal cortex--are less well studied. There is no evidence to suggest that they are any less distinct.

Visual Areas in Prosimians and Monkeys. The first primates were probably nocturnal, judging from the large size of their orbits (Szalay and Delson, 1979). The primates living today most closely related to these early primates are also nocturnal or crepuscular. The bush baby or galago, the only prosimian primate studied in detail (Allman and McGuinness, 1983; Sereno et al., unpublished studies), has on the order of 16 distinct visual areas. Almost all visual areas in galagos exhibit a substantial degree of retinotopic organization, including areas in the inferotemporal cortex. In these studies, the entire extent of visual cortex was physiologically mapped in detail for the first time. In a passive animal, visual areas only respond to visual stimuli, auditory areas only to auditory stimuli, and somatosensory areas only to somatosensory stimuli. Visual cortical areas border almost directly upon somatosensory areas (dorsally) and auditory areas (ventrally). The transitional strip between, for example, auditory and visual areas (in which neurons have both a visual and an auditory receptive field) is less than one millimeter wide.

Monkeys (anthropoids) are thought to have diverged from the ancestors of galagos at least 40 million years ago (Szalay and Delson, 1979). All but one of the anthropoids are diurnal (day- living), suggesting strongly that day-living habits evolved early in the monkey lineage. The one nocturnal monkey, the New World owl monkey, lacks a tapetum, suggesting that its ancestors had diurnal habits. The organization of visual cortex has been studied in detail in two different monkeys--the owl monkey and the macaque monkey. Figure 1A (hard copy only) shows a flattened summary map of visual areas in the owl monkey (Allman and Kaas, 1976; Weller and Kaas, 1985; 1987; Sereno and Allman, 1990). As in galagos, V1 is the largest area, followed by V2. There appear to be at least three somewhat separate 'streams' of information passing through V1 and V2--the magnocellular, parvocellular interblob, and parvocellular blob streams (named after their relay structures in the dorsal lateral geniculate nucleus and area V1)--that remain somewhat separated as one moves on to higher areas (Ungerleider and Mishkin, 1982; Livingstone and Hubel, 1984; DeYoe and Van Essen, 1988; Zeki and Shipp, 1988). These pathways process different aspects of the visual signal in parallel--roughly,

motion, location, and depth in the magnocellular pathway, and color, shape, and shading in the parvocellular pathways. The pathways pass through layer 4B, layer 2-3 interblobs, and layer 2-3 blobs in V1, and the thick stripes, interstripes, and thin stripes in V2, respectively. There is a broad subdivision of the more rostral visual areas into parietal (e.g., TP, ST--receiving primarily magnocellular stream input) and inferotemporal (e.g., ITcd, ITr--receiving primarily parvocellular interblob and parvocellular blob input). Retinotopy is only lost in the most anterior members of these two streams. One can define a hierarchy of visual areas based on the laminar targets of corticocortical projections; feedforward projections synapse mainly in layer 4 of the target area, while feedback projections avoid layer 4 (Rockland and Pandya, 1979; Maunsell and Van Essen, 1983; Felleman and Van Essen, 1990). The border between different modalities appears to be as sharp as in galagos; detailed mapping experiments at the anterior border of visual cortex reveal that the transitional strip between visual and somatosensory areas in parietal cortex as well as the strip between visual and auditory areas in temporal cortex is less than one millimeter wide (Sereno and Allman, 1990; unpublished studies).

Figure 1B (hard copy only) shows a similar summary map for the macaque monkey (an Old World monkey) (based on Van Essen, 1985; Desimone and Ungerleider, 1986; Felleman et al., 1986; 1987; and personal communication; Colby et al., 1988). Although many of the areal names are not the same, and though the relative sizes of similar areas differ, the overall configuration of the map, the retinotopic and functional organization of individual areas, and the interareal connection pattern is remarkably similar to our results in the owl monkey. New and Old World monkeys diverged over 30 million years ago. The main difference between the maps is the reduced size of the areas between V2 and MT in owl monkeys, the shape of V3 (owl monkey DM, its probably homologue, is much less elongated than the macaque area), and the somewhat larger size of several inferotemporal areas. Most of these differences reflect the reduced emphasis on the center of gaze in the retina of the secondarily nocturnal owl monkey. An important point is that there does not appear to be any substantial increase in the area of overlap between modalities. The zone in the dorsal bank of the superior temporal sulcus that responds to more than one modality is several millimeters wide (Seltzer and Pandya, 1989); this is in line with the greater overall area of the primary cortical areas in the macaque compared to the owl monkey.

Auditory and Somatosensory Areas in Monkeys. Auditory and somatosensory areas have been studied in parallel with visual areas. The main differences are the basis for topography (tonotopy and somatotopy vs. retinotopy), the one-dimensional nature of tonotopy (in contrast to two-dimensional retinotopy and somatotopy), the smaller overall size of auditory and somatosensory cortex, and the greater diversity of types of information collected by somatosensory receptor types (light touch, pain and temperature, muscle length changes, force on tendons, joint position). In both New and Old World monkeys, there are about 9 auditory cortical areas (Merzenich and Brugge, 1973; Pandya and Yeterian, 1985) and about 9 somatosensory cortical areas (Merzenich et al., 1978; Burton, 1986; Cusick et al, 1989). As in visual cortex, one can define a hierarchy of areas based on the laminar targets of between-area projections, and, as in vision, there is a successive loss of receptotopy as one progresses to higher levels in the two systems. Most of the somatosensory maps are based on responses to cutaneous stimulation (it is difficult to stimulate muscle and tendon receptors without also stimulating the skin).

These maps (and more fragmentary data from other species) suggest that the parcellation of most of the cortex has not changed radically during the evolution of the primate order (Sereno and Allman, 1990). Notably, there does not seem to be any significant increase in the areas where several modalities overlap; rather, modality-specific areas have increased in size, and quite moderately in number; the number of cortical areas has probably not changed in New and Old World monkeys, which have evolved independently for over 30 million years.

Visual Areas in Apes and Humans. The organization of the cortex in a variety of mammals including humans was studied extensively by Brodmann and others at the beginning of the century using stains for cell bodies and myelin (Brodmann, 1909). Since then, anatomical and physiological studies have revised many of Brodmann's conclusions with respect to non-human primate brains (e.g., Brodmann's area 18 in Old World monkeys is twice as wide as it should have been; Brodmann's area 19 actually contains many distinct cortical areas). But it is only very recently that human cortex has been approached from a modern perspective. Preliminary results suggest that human visual cortical areas are organized quite similarly to those of other primates.

The human visual area whose borders are best known is V1--by far the most distinct visual area on architectonic grounds. Fixed- tissue injections of membrane-intercalating dyes suggest that local circuit connections within, and long range connections between, human areas V1 and V2 are very similar to those of other primates (Burkhalter and Bernardo, 1989). There is a densely myelinated, ellipsoidal area in a dorsolateral occipital sulcus that may correspond to human visual area MT, an area found in all primates (Sereno et al., 1988; Sereno and Allman, 1990) (see Figure 2). Studies using PET to monitor blood flow and a stimulus designed to selectively activate MT (based on animal studies) have uncovered an active locus near the densely myelinated region (Miezin et al., 1987).

Now clearly, there is a great deal of 'additional' non-primary cortex in humans. Despite the fact that monkeys, apes and humans all have about the same number of cells in the retina, the dorsal lateral geniculate nucleus, and in V1 (Frahm et al., 1984; Tolhurst and Ling, 1988), V1 comes to occupy a smaller and smaller proportion of the total neocortex--about 10-12% or the neocortex in monkeys, about 6% of the neocortex in apes, but only about 2.5% of the total neocortex in humans. The preliminary studies cited above suggest a new answer to the problem of this 'extra' cortex in humans--it may be occupied mostly by larger versions of areas already familiar from work in monkeys (as opposed, for example, to an evolutionarily unprecedented 'language organ'). V2 in humans, for example, is much wider than would be expected when normalized with respect to the area of V1. Similarly, there is much more area between V1 and the putative human MT than would be expected (this region is mostly occupied by area V4 in Old World monkeys). Finally, the area of the putative human MT is about 3 to 4 times as big as would be predicted on a macaque model. If the other 25 or so extrastriate areas in human visual cortex increased in size (relative to V1) as much as this preliminary data suggests that V2, V4, and MT have, we could almost completely account for the 'extra' non-primary cortex in humans relative to monkeys. These observations, combined with the lack of any trend toward increased polymodal cortex in neocortical evolution, suggest a radical revision of current neuropsychological theories of human cognitive processing.

Language Processing in the Context of the Primate Brain.

Modularity and Levels of Explanation. The question of what language processing looks like in the brain is a contentious one, especially given the

preliminary state of our current knowledge in this area. A certain tradition in cognitive science and neuropsychology seems to have taken as its goal, the isolation of higher levels of explanation from their lower level implementation. Such a so-called 'functional' approach is quite curious from a biological perspective. Surely, biologists are interested in function (e.g., the heart serves as a pump for blood). But the goal there is to try to explain how it is that the structure of the heart gives rise to its function--not to ignore that structure and build an independently motivated theory in a different language (a language of 'heart'?!). The fact that the same program can run on somewhat differently designed von Neumann machines (e.g., Fodor and Pylyshyn, 1988) seems an insufficient reason to abandon a biological and evolutionary approach to the functional organization of the human brain.

This tendency to ignore the structure of the brain is quite unfortunate in light of the recent progress made in primate neurobiology. Most current texts of physiological psychology, neuropsychology, and cognitive neuroscience (e.g., Damasio and Geschwind, 1984; Caplan, 1987; Ellis and Young, 1988) still implicitly employ a model of the organization and evolution of the cortex that dates to the associationists of the late nineteenth century. In this way of thinking, 'primitive' mammals like rats start out with primary visual, auditory, and somatosensory areas almost touching. Next up the rung of an essentially pre-evolutionary *scala natura* come animals like cats, which have a small amount of 'uncommitted' space in between. Finally, at the top, are primates and especially humans, where we find a great deal of uncommitted 'association' cortex, properly situated to integrate and associate the modality-specific information presented to it by visual, auditory and somatosensory cortices (see e.g., Fodor, 1983; Ellis and Young, 1988, on the 'semantic system' postulated in most models of word processing; Damasio, 1989).

Fine-grained mapping experiments in hedgehogs, rodents, cats, and primates, during the past decade have shown this picture of the evolution of the cortex to be incorrect. Cats and primates *do* have more cortex in between the primary sensory areas; but that cortex consists not of polymodal association areas, but rather larger and more numerous modality-specific (i.e., visual, auditory, and somatosensory) areas. The studies discussed above provide no indication that humans are any different in this regard. The problem is, then, in the spirit of biological studies of functional organization, to try to describe how the basic anatomical

modules of primate cortex--namely visual, auditory, somatosensory, motor, and limbic areas--support a new, peculiarly human function.

Language as Code-directed Scene Perception. Vision is very important to primates; in fact, over 50% of the cortex in primates, probably including humans, consists of areas devoted to specifically visual processing. This is not to deny that information about an object perceived via another modality--say the somatosensory system--might be able to enter visual areas in the form of a visual copy of the somatosensory areas' activity pattern (see e.g., experiments by Haenny et al. (1988) in macaque visual area V4 using a somatosensory-visual matching task). But it does suggest that we carefully distinguish a visual copy of a somatosensory stimulus (in a visual area with a visual map) from a somatosensory copy of a visual stimulus (in a somatosensory area with a somatosensory map).

Some linguists have independently suggested that visual representations may be very important in the semantics of natural language (Jackendoff, 1983; 1987; Fauconnier, 1985; Lakoff, 1987; Langacker, 1987). An idea common to several different approaches is that more concrete visual meanings may have been extended by analogical processes to deal with more abstract objects and relations. The present proposal goes further in suggesting a particularly direct relationship between the mechanisms of scene and discourse comprehension.

The integration of successive glances in the comprehension of a visual scene requires a kind of serial assembly operation similar in some respects to the integration of word meanings in discourse comprehension. Primates (but also many other animals) make long series of fixations at the rate of several new views per second during scene comprehension. Each fixation brings the retina to a new part of the visual scene and generates a burst of activity in V1, which largely replaces the burst caused by the previous fixation. Higher visual areas with less precise retinotopy somehow integrate information from these disconnected activity sequences to generate an internal representation of the location and identity of the relevant objects in the current scene (e.g., predators, food items, particular conspecifics, escape routes, suitable sleeping trees, etc.) that can serve as a basis for action. Many aspects of this process are redolent of linguistic integration--e.g., the underspecified, context-free information in an isolated glance is sharpened and focused by context (cf. polysemy); information from temporally distant glances must be tied together (cf. anaphora).

None of this implies that scene representations (or their presumed linguistic fellows) need *look* anything like pictures; the patterns in question would be distributed across many areas, some of which show little retinotopy.

One main difference between scene and discourse comprehension is, of course, that scene comprehension is tied closely to the current scene. Discourse comprehension might best be thought of as a kind of fictive visual scene comprehension directed, in the case of spoken language comprehension, by sequences of phoneme representations in secondary auditory cortex. The advantage of linguistic discourse comprehension is that we are no longer tied to the current scene. However, once the appropriate visual word meaning patterns have been called up and bound together, the nature and interactions of the composite pattern may be conditioned mainly by the prelinguistic rules of interaction of scene representations in primate visual areas networks. In this sense, a large part of what has been called linguistic syntax and semantics might *not* be modular with respect to the neurobiology of vision.

There is in fact substantial evidence that visual areas in humans are involved in specifically linguistic functions. There is a kind of aphasia confusingly called 'transcortical sensory' aphasia (i.e., 'across-from-the-language-cortex' aphasia!) that is generated by a lesion in left human inferotemporal cortex (Rubens and Kertesz, 1983). Many of these lesions are so posterior and ventral that they are associated with overt visual field defects. Transcortical sensory aphasics have poor, "Wernicke's-like" comprehension, yet paradoxically (at least in the context of traditional models of language comprehension), can repeat words effortlessly. Far from being 'across from the language cortex', the visual areas in posterior inferotemporal cortex damaged in these patients may be the primary site of semantic processing in sighted humans. Transcortical sensory aphasics recover more quickly than patients with more dorsal lesions; this may only be an indication that the functions performed by visual cortex in language comprehension are less lateralized than those performed by auditory cortex. This is consistent with what we know about primate visual areas; permanent deficits in visual pattern recognition in monkeys require *bilateral* inferotemporal cortex lesions (Gross, 1973). There is no need to assume that all the cortical areas involved in language comprehension are equally lateralized; for example, the functions performed by the superior temporal gyrus (see below) may be more lateralized than the functions performed by the inferotemporal cortex.

Psycholinguistic experiments using pictures inserted into sentences and picture-word priming (Potter et al., 1986; Vanderwart, 1984) suggest that it is surprisingly easy for visually represented concepts to be integrated into ongoing linguistic discourse comprehension. This may be another indicator of the closeness of visual category representations to linguistic meanings.

Some PET Experiments. Recently, it was suggested on the basis of PET experiments that semantic processing may be localized instead in the frontal lobe, just in front of "Broca's area" (Petersen et al., 1988; Posner et al., 1988). In the key experiment, subjects performed two tasks--1) repeating visually presented nouns, and 2) generating "uses" (related verbs) upon viewing an otherwise comparable series nouns. Upon subtracting these two conditions, an activated locus was uncovered in frontal cortex, just anterior to the representation of face, tongue, and throat muscles in primary motor cortex. Given the ease with which preparation for movement elicits strong activation in premotor areas (see e.g., Roland et al., 1980), however, it seems likely that the activity uncovered in this experiment actually represents the different motor programming demands of the two tasks. In the first case, a motor pattern is called up directly via overlearned connections between visual word shape and articulatory movements. In the second case, by contrast, the subject must make a new motor plan to say a word that is different from that which was viewed. In fact, the subject must also suppress an output that would normally be generated by looking at the first word (in the context of reading words aloud). Frontal cortex lesions in monkeys and man are known to especially impair the ability to make delayed responses. Given that posterior inferotemporal cortex has rarely if ever been selectively activated in a blood flow experiment, and that the PET technique has limited resolution, the activation underlying semantic processing may not yet have been seen. A posterior locus for semantics is more in line with the observation made long ago (and hardly overturned by more recent studies) that patients with large posterior lesions are generally much more impaired in extracting meaning from linguistic discourse--and surely seem to have a much more severe derangement of thought processes--than patients with large anterior lesions.

What's in Wernicke's Area? Wernicke's area has occupied several different gyri over the years. Sometimes it is placed on the angular gyrus;

sometimes it sits more anteriorly on the superior temporal gyrus; and often it sneaks across the superior temporal sulcus (the boundary between auditory cortical areas dorsally and visual cortical areas ventrally in primates) to sit partly in infero-temporal cortex. The left-right asymmetry originally demonstrated by Geschwind and Levitsky (1968) was in yet a different place--on the planum temporale (not even clearly visible in a lateral view). Several architectonic studies (Braak, 1978; Galaburda and Sanides, 1980) have identified a distinct area that shows a considerable left-right asymmetry (Braak's temporal magnopyramidal zone; Galaburda and Sanides' area Tpt) confined entirely to the posterior part of the lateral superior temporal gyrus. By comparison with other primates, this area is very likely to be a unimodal, secondary or tertiary auditory cortical area. Merzenich and Brugge (1973) recorded diffuse auditory responses from a geographically similar area in macaques.

If Wernicke's area proper (e.g., of Braak) is in fact a secondary or tertiary auditory area, we are left with something of a conundrum. Why should a lesion in an *auditory* area cause deficits in the assembly of the meaningful units of language? The deficits exhibited by many patients with a lesion in this area seem to extend beyond mere problems with auditory representations of words--their thoughts seem disarranged; often they are unable to manipulate even words with concrete visual meanings. The traditional conclusion has thus been that Wernicke's area must be an evolutionarily new 'language organ' not tied to one modality. A new interpretation more in line with the animal literature, is that the internal representations of speech sound sequences that a primate neurobiologist would expect to find in Wernicke's area proper must have some other function besides merely serving as internal copies of the speech stream; these uninterpreted speech sound representations must also be involved in *word recognition* and *assembly of* (primarily visual) *meanings* into coherent discourse structures. By this account, what distinguishes humans is the ability to use a sequence of symbol patterns from another modality to cause the assembly of meaning patterns in tertiary visual cortex. But the product of that assembly may be very similar to patterns assembled from direct visual inputs arriving via V1 during scene comprehension. The implication is that the trick of language was not to have invented the basic meaningful units but to have found a way of making standardized connections between them (see Sereno, 1986; 1990a; 1990b, for an extended discussion).

In monkeys, the superior temporal sulcus forms, as noted, the border between auditory and visual cortices. Since clinically defined Wernicke's-like aphasics often have lesions that extend into the inferotemporal region on the middle and inferior temporal gyri, a typical 'Wernicke's aphasia' may require damage to both the auditory cortex meaning assemblers and the visual cortex meanings they assemble.

New Routes Between Modalities. In monkeys, one pathway responsible for cross-modal matching performance has been well-defined. Performance on somatosensory-visual matching tasks is catastrophically impaired by lesions to the basolateral amygdala (Murray and Mishkin, 1985). This part of the amygdala receives projections from secondary and tertiary visual, somatosensory, and auditory areas, and projects back to them. There is also a small polymodal strip on part of the upper bank of the superior temporal sulcus (e.g., Seltzer and Pandya, 1989). But this strip cannot by itself support cross-modal matching in monkeys.

The situation in humans must be somewhat different, at least with regard to the relative importance of the amygdala in one particular kind of cross-modal mapping that characterizes human language--the mapping between speech sounds and visual word meanings. The patient H.M. who had his amygdala removed bilaterally is quite unimpaired in recognizing visual objects named for him (or in naming visual objects himself). This suggests that humans must have a more robust connection between areas on either side of the superior temporal sulcus than monkeys do. Cross-modal matching experiments of the kind that amygdala-lesioned monkeys fail to perform have not yet been tried with H.M., and so the cross-modal pathway through the amygdala could very well still be important for some tasks in humans.

Conclusion

Language is recently derived; based on the evidence of stone tools and other more spectacular artifacts like cave paintings, it seems likely that peculiarly human cognition and presumably language use originated rather suddenly less than 50,000 to 100,000 years ago. In view of our knowledge of the strong similarities between the brains of various non-human primates, it seems unlikely that the cortex could have been completely reorganized in so short a time. Surely, there is no positive evidence for such a major reorganization. Recent evidence instead suggests that human and non-human primate brains are

organized quite similarly. We need more attempts to explain the large qualitative differences between animal cognition and human language-based cognition as the result of relatively minor modifications and re-use of pre-existing primate neural circuitry (cf. Bates et al., 1989).

This paper suggests that it might be profitable to view language comprehension in sighted people as a kind of code-directed scene comprehension taking place primarily in unimodal visual areas in posterior inferotemporal cortex. A second suggestion is that internal representation of speech sound chains in secondary auditory cortical areas (Wernicke's area proper) may have other functions besides merely serving as internal copies of the speech code chain; they may be intimately involved in word recognition and the binding together of visual cortex meaning patterns. Code-directed pattern binding is clearly a specifically human faculty; but many of the constraints on the resulting bound-together patterns may reflect prelinguistic (non-modular) constraints on interactions between activity patterns in tertiary visual areas. Studies of the connections of superior temporal sulcus region in humans--just now becoming possible--may throw more light on the presently obscure neural substrate of language and human thought.

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Captions for Figures in hard copy

Figure 1. Cortical visual areas in the owl monkey (A) and the macaque monkey (B). A cut was made in V1 medially to allow the cortex to lie flat. The insets illustrate the location these areas in occipital, parietal, and temporal cortex (after Sereno and Allman, 1990). All areas shown are visual except for area PM (owl monkey) and area STP (macaque), which border on somatosensory and auditory cortices (not shown).

Figure 2. Cortical visual areas in the human (preliminary). A left occipital lobe (reversed here to aid comparison with previous figures) was physically flattened, sectioned, and stained for myelin. The exposed crowns of the gyri are colored black. A cut was made in V1 medially to allow the cortex to lie flat. The insets illustrate the location these areas in the intact brain (after Sereno and Allman, 1990). Note that the scale is now in centimeters.