NOTES ON CORTICAL AREAS IN MAMMALS
Martin I. Sereno (1996, unpublished)

The past two centuries of work on the structure and function of the cerebral cortex have been characterized by recurring debates—often too often forgotten and re-argued—involving several basic oppositions. Two of these are: (1) "field" *versus* "localization" theories of cortical function, and (2) higher-level, abstract (linguistic) facilities *versus* lower-level, less abstract, sensorimotor functions. In the following sections, we first briefly consider the history of ideas about cortical areas rehearsing debates about those two issues. Second, we present the current picture of our understanding of visual areas in primates (which occupy over half of the entire primate neocortex). In the third section, we consider the evidence for auditory, somatosensory, motor, and frontal limbic areas which take up most of the remaining half of the cortex. In the fourth section, we introduce the very old idea of a "common sensorium" as a preface to recent evidence against the idea of a centrally located polymodal association cortex. Finally, we turn to recent attempts to identify monkey cortical areas in humans, and draw out the implication of these results with respect to the long-standing debates identifed above.

Early Ideas About Cortical Areas

In the beginning of the nineteenth century, the physician Franz Gall argued that there were regional differences among the cortical convolutions that reflected their different function. Though the localization of 30 odd "primitive forces" on those convolutions was never studied *in vivo*, the surrogate study of skull shape gained immediate scientific and public notoriety. It even penetrated the self-help literature of the time—one might have a particularly well-developed innate "instinct for cruelty", but one could rein it in with hard work (more recent discussions of left/right hemispheric function come to mind here). The phrenologists were the quintessential localizationists; but it is important to recognize that their "primitive forces" were actually high level, abstract functions like "circumspection" and "sarcasm".

The phrenologists' position had its scientific and philosophical critics from the start. Jean-Pierre-Marie Flourens, citing both his lesion experiments on animals as well as arguments for the unity and moral freedom of the soul described a complete functional distribution of higher and lower functions: "all sensations, all perception, and all volition occupy concurrently the same seat in [the cerebral hemispheres]" (Flourens, 1824). The phrenologists' critics prevailed, academically, at least, and after the mid-century, we find Broca (1861) arguing the minority position for cortical functional localization in the context of a then orthodox field theory. Nevertheless, it is important to realize that Broca, very much like the phrenologists, localized only higher mental functions to the cortex—like the ability to produce articulate language and to think; lower level sensorimotor processing was still confined to the brainstem and spinal cord in this scheme.

Given this context, it should be clearer why it was a surprise when more sophisticated techniques for stimulating the brain electrophysiologically revealed a 'non-mental' map of localized muscle movements in what came to be called motor cortex (Fritz and Hitzig, 1870;

Ferrier, 1874). Lesion studies parcelling the cortex into primary and association areas for audition, somatosensation, vision, and olfaction soon followed. The tables were temporarily turned back in favor of functional localization, but now of non-phrenological, lower level sensorimotor functions. The lower level functions apparently revealed in large regions of the cortex prompted some like Ferrier to wonder if "mental operations in the last analysis must be merely the subjective side of sensory motor substrata" (see Young, 1970, and the second chapter of James' *Principles of Psychology*, 1890, for an informative contemporary review). Wernicke (1874) made similar points about the importance of sensory and motor "memories" and their recombination, and argued against direct phrenological attribution of higher level psychological categories and functions to brain regions.

There was another line of localizationist research, more purely anatomical, that dates at least to Meynert's recognition in 1867 of regional anatomical (macroscopically visible) differences in the cortex. The work of Campbell (1905), Brodmann (1909), and Economo and Koskinas (1925) represented the golden age of "cortical architectonics"—the microscopic study of regional differences in cell and fiber density and lamination patterns in the cortex. Brodmann in particular studied many mammalian species, including several primates, in addition to humans. Though Brodmann explicitly referred to his book as "a cortical organology" (words often used by Gall), he was hesitant to associate specific functions with specific areas. It is, of course, Brodmann's 1909 map and areal numbering scheme that appear to this day in texts and research papers concerning the human brain—decades after Brodmann's parcellation had to be revised as a result of modern research on non-human primates (see below).

Though the organization of primary visual cortex in humans had been revealed early on through the use of patients with localized occipital damage (Holmes, 1912), it wasn't until the studies of Marshall et al. (1937) that architectonics and electrophysiology were finally explicitly brought together. In these studies, in which surface macroelectrodes were used to record local field potentials, an unexpectedly stable somatotopic projection of the body surface was discovered to correspond to Brodmann's areas 3, 1 and 2. Within several years, a second somatotopic area had been found (Woolsey, 1943). Though Marshall et al. speak of "functional analysis", they were actually using cortical physiology to elucidate cortical structure, not cortical function in the usual sense of the word. The question of a specific area's function in all but the most basic sense remained untouched, as Lashley and others were quick to point out. In 1946, Lashley and Clark delivered a blistering critique of the architectonic method. Using a single set of spider monkey brain sections, they independently subdivided the cortex into areas and got very different results, concluding that there were only a handful of areas (about 10) in all mammals, including humans.

Even professional anatomists much more familiar with the material were swayed; in a wonderful example of theory-driven observation, Bailey and Bonin (1951) blurred even the razor sharp border of primary visual cortex in their summary diagram.

Beginning in the late 1950's, modern microelectrode mapping techniques made it possible to routinely record from one or a few neurons and to stimulate much smaller groups of neurons than was possible with surface electrodes. In an interesting conceptual parallel with the discovery of an unexpectedly lower level movement representation in motor cortex amost a century before, studies in visual cortex revealed unexpectedly lower level feature detectors (Hubel and Wiesel, 1962, following closely upon the related work of Lettvin et al., 1959, in the frog tectum). These same techniques made it possible to explore the topographic organization of cortical sensory and motor representations in much greater detail than ever before (Welker and Campos, 1963). Such studies began in earnest in a number of species in the 1960's and have continued to the present. We now turn to these results.

Visual Areas in Primates

Modern Definition of a Cortical Area

Cortical sensory areas remain best defined by multiple converging criteria (Van Essen, 1985; Kaas, 1987; Sereno and Allman, 1991). Criteria for the definition of a visual area presently include *architectonic features* (e.g., degree of myelination, cell size/morphology/packing density in cortical layers, histochemical features), *connection patterns* (e.g., input and output areas, laminar origins and targets of connections), *receptotopic organization* (e.g., mirror-image or non- mirror-image map of the sensory field, bounding areas, pattern of map discontinuities, degree of receptotopy), and *physiological properties* (e.g., excitatory receptive field size, direction selectivity, attention-related modulation). Areas radically 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 (note that MT was not recognized by Brodmann in monkeys using anatomical techniques alone— Brodmann included MT and a number of other currently recognized visual areas in a single area 19). Other areas—e.g., in inferotemporal cortex—are less well studied. There is, however, no evidence to suggest that they are any less distinct.

Primitive Primates

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. Extrastriate cortical areas have so far been studied in detail in two primitive primates—the bush baby, *Galago*, and the dwarf fat-tailed lemur, *Cheirogaleus*.

Galago has on the order of 16 distinct visual areas including a well-defined area V1, V2, and MT (Allman and McGuinness, 1983; Sereno et al., unpublished studies). Recently Krubitzer and Kass (1991) provided evidence of visual processing streams like those initially revealed in monkeys (see below). 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.

A very similar picture has recently emerged in another primitive primate, *Cheirogaleus*, that shows a striking resemblance to fossil primates (e.g., *Tuetonius*) from the Paleocene. Again, there was clear evidence for V1, V2, and MT, as well as topographically organized parietal and inferotemporal areas (Sereno et al., 1994).
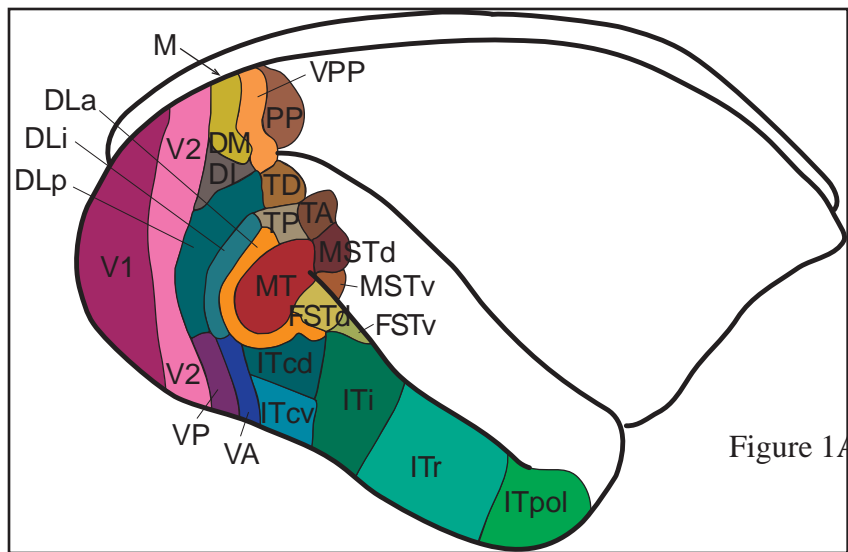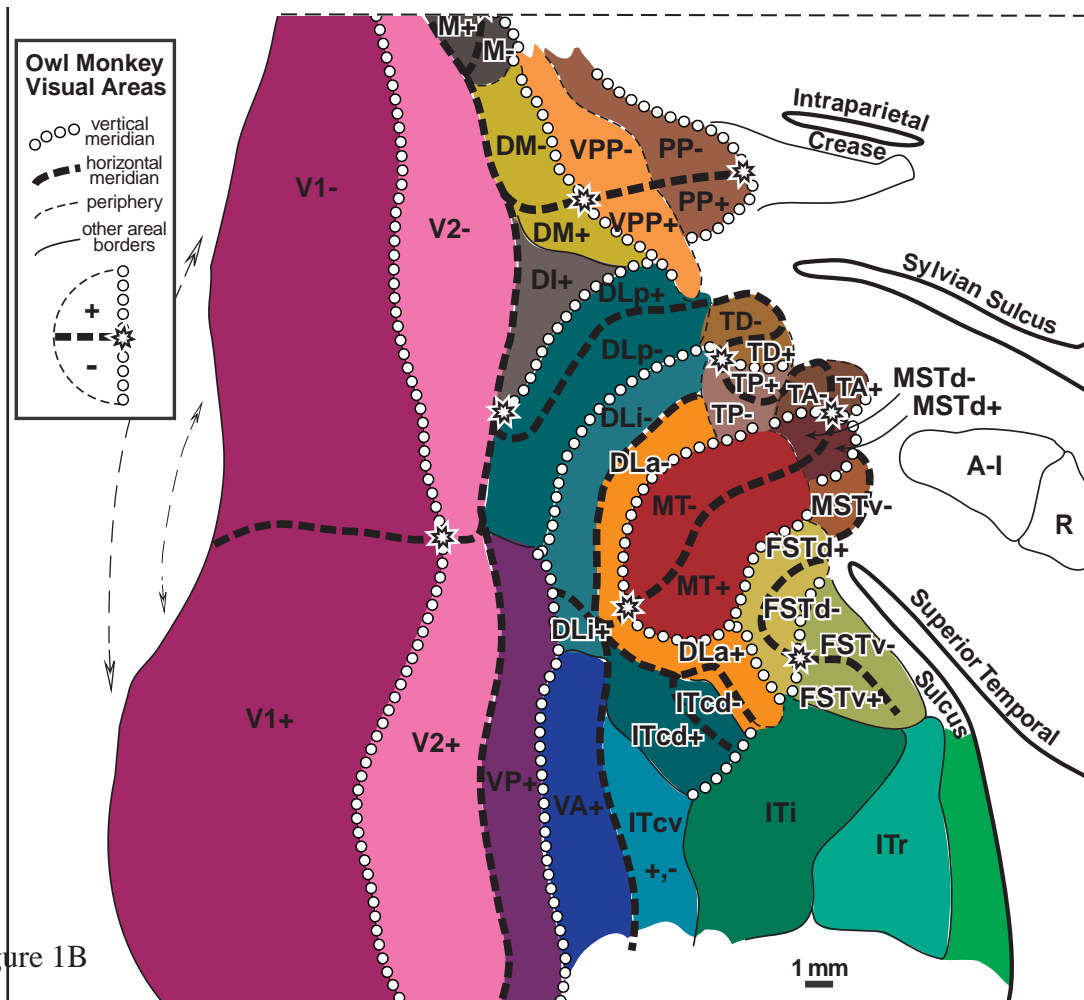
Owl Monkey

Figure 1A

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,B shows a lateral brain view and a flattened summary map of visual areas in the owl monkey (Allman and Kaas, 1976; Weller and Kaas, 1985; 1987; Sereno and Allman, 1991, Sereno et al., in preparation). 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

Owl Monkey Visual Areas

ooooo vertical meridian
▬▬▬ horizontal meridian
- - - periphery
——— other areal borders

Figure 1B

broad subdivision of the more rostral visual areas into parietal (e.g., TP, MST—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 *Galago*; 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, 1991; Sereno, MacDonald, and Allman, 1994; unpublished studies).

Macaque Monkey

A similar summary map has been generated for the macaque monkey (an Old World monkey) (Figure 2, based on Van Essen, 1985; Desimone and Ungerleider, 1986; Felleman et al., 1986; 1987; and personal communication; Colby et al., 1988; Felleman and Van Essen, 1991). Although several 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,

VISUAL CORTICAL AREAS

PO
Non-Mirror

MDP

--

--

V1
Mirror

V2
Non-Mirror

--

PIP

VIP

LIP

V3
Mirror

+

7a

-

-

V3a

- -

DPL

MSTd

--

MT
Non-Mirror

MSTl

V4
Non-Mirror

V4t

- +

STP

FST

V1
Mirror

PITd

CITd

+

PITv

VOT
Mirror

CITv

AIT

36

+

+

+

VP
Mirror

V4v
Non-Mirror

++

TF

ER

TH

HC

V2
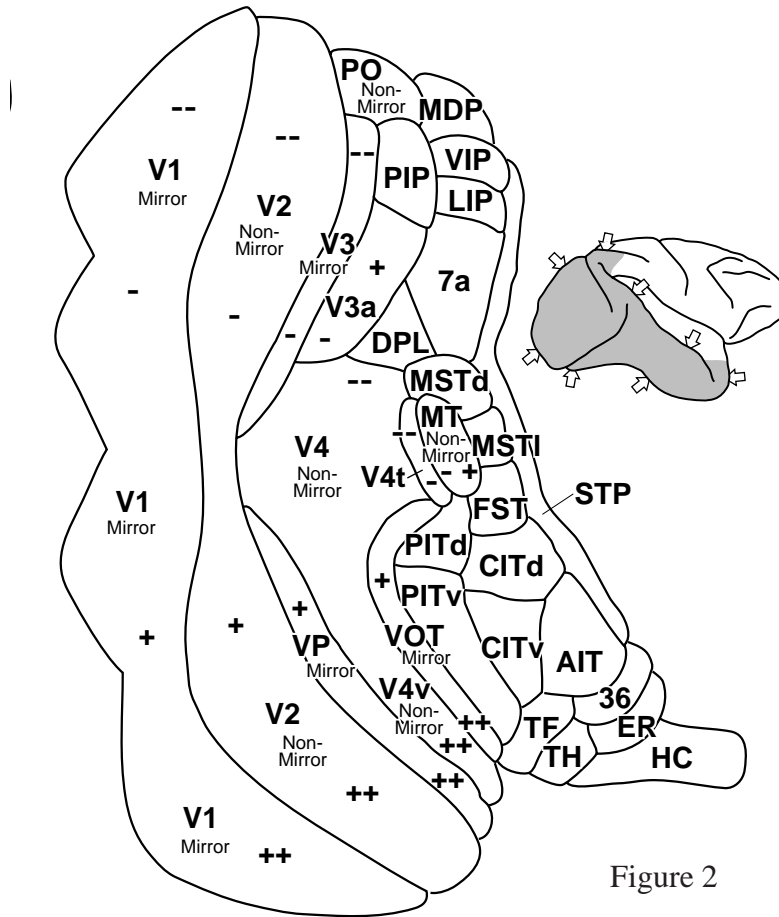Non-Mirror

++

++

++

V1
Mirror

++

Figure 2

and the interareal connection pattern is remarkably similar to ours and others results in the owl monkey. New and Old World monkeys diverged at least 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.

Other Modalities in Primates

Somatosensory Areas

Just as visual areas have been individuated by retinotopy, somatosensory areas have been distinguished by somatotopy. The nine currently recognized somatosensory areas in the macaque monkey are illustrated in Figure 3. The modern picture of somatosensory areas dates to the detailed studies of Merzenich et al. (1978) on the owl monkey somatosensory cortex. Similar studies followed in the macaque monkey. These studies showed that classical "S-I" actually
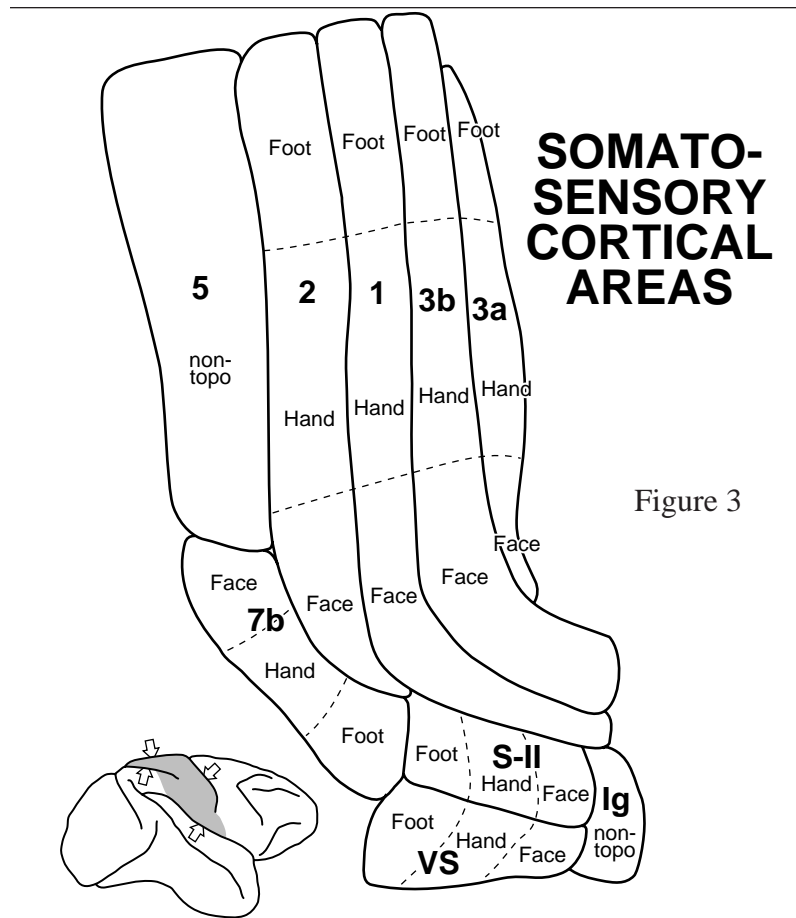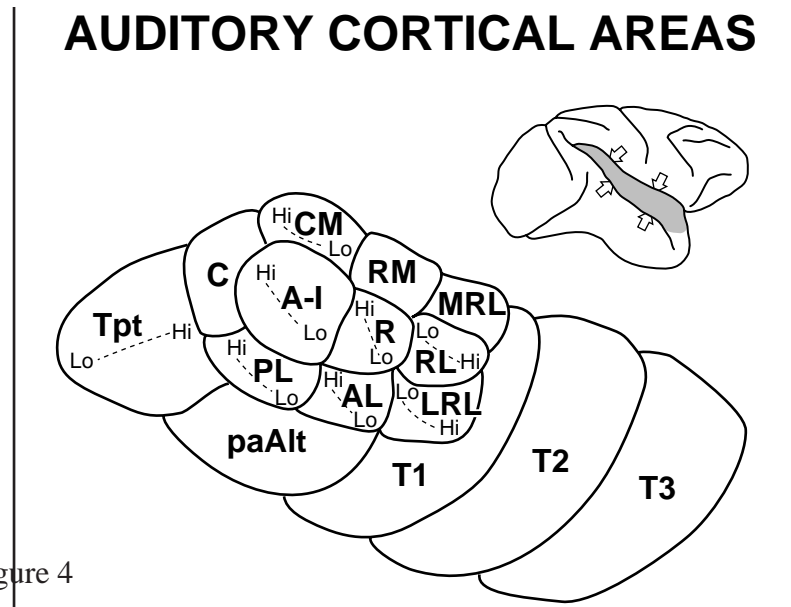
Figure 3

consists of four distinct re-representations of the body—area 3a (primarily muscle receptors), area 3b, area 1, and area 2. Subsequent studies of classical "S-II" revealed that it too was composed of two areas—S-II proper and VS (Cusick et al., 1989; Krubitzer, in press). Area 7 is divisible into a dorsoposterior visual part (area 7a) and an ventroanterior somatosensory part (area 7b) containing yet another rough body map (Burton, 1986). As in visual cortex, one can define a hierarchical pattern of connections (Pandya and Yeterian, 1985; Pons et al.,), and there is a gradual loss of receptotopy as one progresses into the system.

The main difference between somatosensory areas and visual areas is that cortical somatotopic maps contain discontinuities—a small movement in somatosensory cortex can sometimes result is a completely non-overlapping receptive field (the receptive field may jump to a different finger, for example). Such discontinuities have not been observed in visual cortex where nearby cortical points virtually always have overlapping visual receptive fields (note that this continuity of receptotopy in the cortex does not imply continuity of sensory surface representation—nearby points on *both* the retina and body surface can be represented far from each other on the cortex: see Sereno et al., 1994). Another difference is the greater diversity of types of information collected by somatosensory receptor types (light touch, pain, heat and cold, muscle length changes, force on tendons, joint position).

Auditory Areas

Auditory areas have been individuated by tonotopy. Nine currently recognized auditory areas

AUDITORY CORTICAL AREAS

Figure 4

in the macaque monkey are illustrated in Figure 4 (based on Merzenich and Brugge, 1973; Pandya and Yeterian, 1985; Morel and Kaas, 1992; Morel, Garraghty, and Kaas, 1993). The more tonotopic primary areas are located on the superior temporal plane while non-tonotopic extend onto the crown of the superior temporal gyrus and into the depths of the central insula. One feature that distinguishes auditory areas from visual and somatosensory areas is that there is only one dimension of receptotopy in the auditory system (frequency, as defined by position along the basilar membrane), in contrast to two dimensions in both the somatosensory and visual system. As in vision and somatosentation, an anatomically-based hierarchy can be defined.

Frontal motor cortex

As noted above, the overall organization of motor cortex was already known at the end of the last century. However, it is only quite recently that the musculotopy of these areas was systematically re-explored with comprehensive microstimulation studies (McGuinness et al., 1980; Gould et al., 1986; Morecraft and Van Hoesen, 1992; Stepniewska, Preuss, and Kaas, 1993; He, Dum, and Strick, 1993). These studies revealed that motor cortex is organized differently than somatosensory cortex. Though there is an parallel tendency for the motor cortex maps to progress from the face to the hand to the foot as one moves from lateral to medial along the central sulcus, there is a much greater degree of mosaicism. Wrist movements, for example, could be elicited from 9 different disjoint regions (Gould et al., 1986). The organization shows a certain resemblance to the 'fractured somatotopy' revealed in maps of the somatosensory representation in the cerebellum (Shambes et al., 1978).

The most recent studies revealed that low-stimulation-threshold cortex extends from the central sulcus all the way to the frontal eye fields (Figure 5). There appear to be three main lateral motor fields—M-I proper, premotor cortex (PM), and the ventral premotor area (PMV). The last field contains only representations of face and hand movements and may correspond to 'Broca's area'. There are at least three more motor areas on the medial wall of the hemisphere—the supplementary motor area (SMA), which has a second, dorsomedial frontral eye field appended to it (dmFEF), and

MOTOR CORTICAL AREAS

Figure 5
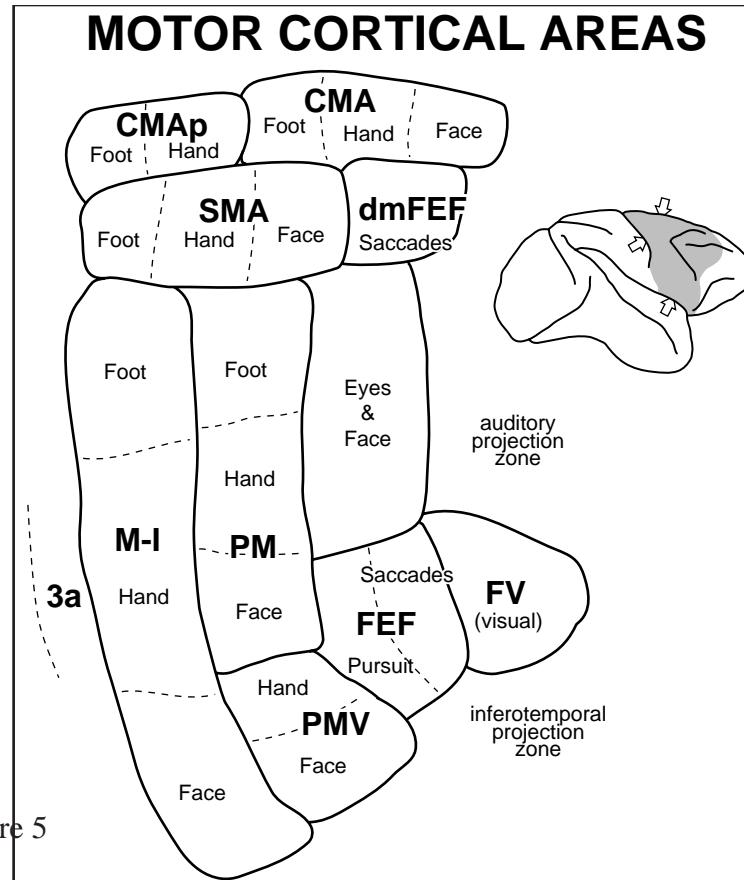
then two cingulate motor areas (CMA, CMAp).

Overview

The most striking observation, rarely explicitly noted by the authors of the individual studies, is the extent to which the large majority of the area of the cortex in monkeys has been shown to be occupied by areas seemingly primarily devoted to a single sensory modality—vision (50%), audition (11%), somatosensation (about 13%), and olfaction (2 %)—or to the control of skeletal musculature and eye movements (12%). The remaining prefrontal cortex that does not appear to be explicitly sensorimotor in function (10%) has mainly connections with the limbic system (as opposed to sensorimotor areas). I think this picture has strong implications for models of human cognition. Nevertheless, this view of how the cortex works has been virtually excluded from most major debates about language and the human brain. In the next section, we try to show how a powerful, intuitive, and very old set of ideas about how cognition works have effectively insulated thought about human cognition from the recent results in non-human primates.

The Search for the Common Sensorium (Polymodal Cortex)

Lashley's "search for the engram" was predicated upon a deep-seated, pre-scientific notion that memories must be stored in some particular region of the cortex. This was really the same kind of intuition that had launched the phrenologists' search for the locus of specific mental faculties a century before. In temporarily dispatching the idea of a localized engram after his long search, however, Lashley's ideas about the equipotentiality of central nervous tissue drew upon a perhaps even more deeply entrenched notion that higher level mental function must somehow involve the

transformation of sense information into a common format that could then be viewed by the mind's eye. This is a very old idea; yet a modern version of it persists at the core of most current neuropsychology. We might call this the 'search for the common sensorium' or more accurately though not as felicitously, 'the search for polymodal cortex'. We turn briefly to its history, and then to modern evidence for and against the idea.

The Cell Doctrine

Human thought was for many centuries localized to the ventricles of the brain, which were thought to be filled with air (certainly a more appropriate medium for thought than gelatinous tissue). Building upon ideas from classical antiquity, a coherent theory of the functional specialization of the ventricles was developed by Galen, Avicenna, the early church fathers, and others that persisted well into the 17th century. Clarke and Dewhurst (1972) have termed it the Cell Doctrine of Brain Function. There were innumerable versions, but the basic feedforward topology of the scheme—usually three ventricles or "cells" were connected into a series from front to back—was almost always preserved (there was only a loose correspondence to the real brain ventricles, and they were numbered differently). At the front was the first ventricle, where information from the various senses came together to be presented to the rest of the mind. This was the "sensus communis" or "common sense" or the "common sensorium". The modern meaning of "common sense"—unreflective but reliable knowledge—derives from the notion that the sensations in the "sensus communis" were veridical but remained to be analyzed. Toward the back of the first ventricle, images were created from the sensations in the "sensus communis" by "imaginativa" (imagination) or "fantasia" (fantasy). The second ventricle, which made use of the sense data in the first, was the seat of reasoning ("aestimativa", "cognitiva", "ratio"). The last ventricle was the seat of "memorativa" (memory); it was also generally thought to be the driest, and therefore the well-suited to that task.

This theory of the brain is interesting in that there were no modality-specific areas in it at all; there are many wonderful pictures of the the sense organs (nose, tongue, eyes, ears) connecting up directly to the "common sense" (see Fig. 6, and Clarke and Dewhurst, 1972; Corsi., ed., 1991). Given the self-evidence of a consciousness unified across sensory modalities, this was an eminently reasonable plan. As new data about the organization of cortex has been acquired, however, the notion of a "sensus communis" has turned out to be an exceedingly difficult one to dislodge; it is an immensely appealing notion that has continually re-appeared in new guises, as we shall see.

The Disappearance and Return of the Common Sensorium

Toward the end of the 17th century, thought had been moved from the ventricles into the brain tissue itself. But the search for the common sensorium continued, with debates as to whether it was in the white matter or the gray matter, or in the striatum or the brainstem (Corsi, ed., 1991). By the 19th century, it had been moved back into the cortex. After the decline of the phrenologists and faculty psychology, and the subsequent discoveries of the primary sensory and motor centers of the cortex in mammals, the common sensorium had been all but eliminated by the end of the 19th century. As previously mentioned, classical localizationist-connectionist accounts included

only sensory and motor centers, and tracts connecting them, but often no central, common-format executive in between (Ferrier, 1874; Wernicke, 1874; Meynert, 1874; James, 1890, Chap. II).

But the idea of a central common format for mental events proved difficult to resist. It had very much come back to life for Geschwind in 1964, as he candidly stated in an influential overview of the evolution of the brain and language:

> This region [the angular gyrus] is ideally located for the purposes of our theory [indeed!]. It is placed between the association cortexes of the three non-limbic modalities: vision, audition, and somesthesis. It is thus admirably suited to play the role of acting as the way-station by which associations may be formed between these non-limbic modalities. This area may well be termed 'the association cortex' of the association cortexes. By providing the basis for the formation of non-limbic associations, it provides the anatomical basis for language (1964, p. 165).

Similarly, although Fodor (1983) grants that there are specific input regions (modules) in the cortex specialized for the visual and auditory modalities (as well as the linguistic 'modality'), he holds out for one or more unstructured equipotential "central systems" for symbolic thought and problem solving located, predictably, in "association" cortex, where "neural connectivity appears to go every which way and the form/function correspondence appears to be minimal" (p. 118—no evidence cited to support this last claim).

Evolution of Cortical Areas

There is an oft-rehearsed evolutionary scenario—utterly at odds with modern cortical mapping experiments—that fits well, however, with the notion of the importance of polymodal cortex for higher level cortical function. 'Primitive' mammals like rats start out with primary visual, auditory, and somatosensory areas almost touching. Next up the rung of a *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 polymodal 'association' cortex, properly situated to integrate and associate the modality-specific information presented to it by visual, auditory and somatosensory cortices (see e.g., Caplan, 1987; Ellis and Young, 1988; 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 (Kaas, 1987). 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. Polymodal cortex remains a small strip in between the different modalities, occupying if anything, a smaller proportion of the neocortex in animals with larger brains (see next section).

A particularly striking example of how cortical areas have actually evolved comes from recent work in several different rodent species (Olavarria and Montero, 1984; Thomas and Espinoza, 1987; Sereno et al., 1991; Rodman et al., 1992). Rats are nocturnal animals, and like many other nocturnal animals (notably excepting nocturnal primates) have a reduced dependence on vision. They can be compared to other rodents like squirrels. Squirrels live during the day, have a much

better-developed cone retina and color vision, and rely much more extensively on vision than rats do for avoiding predators, finding food and mates, and navigating through their environment. Figure 6 illustrates the main cortical fields in a rat and a ground squirrel at the same magnification.

Figure 6

RAT
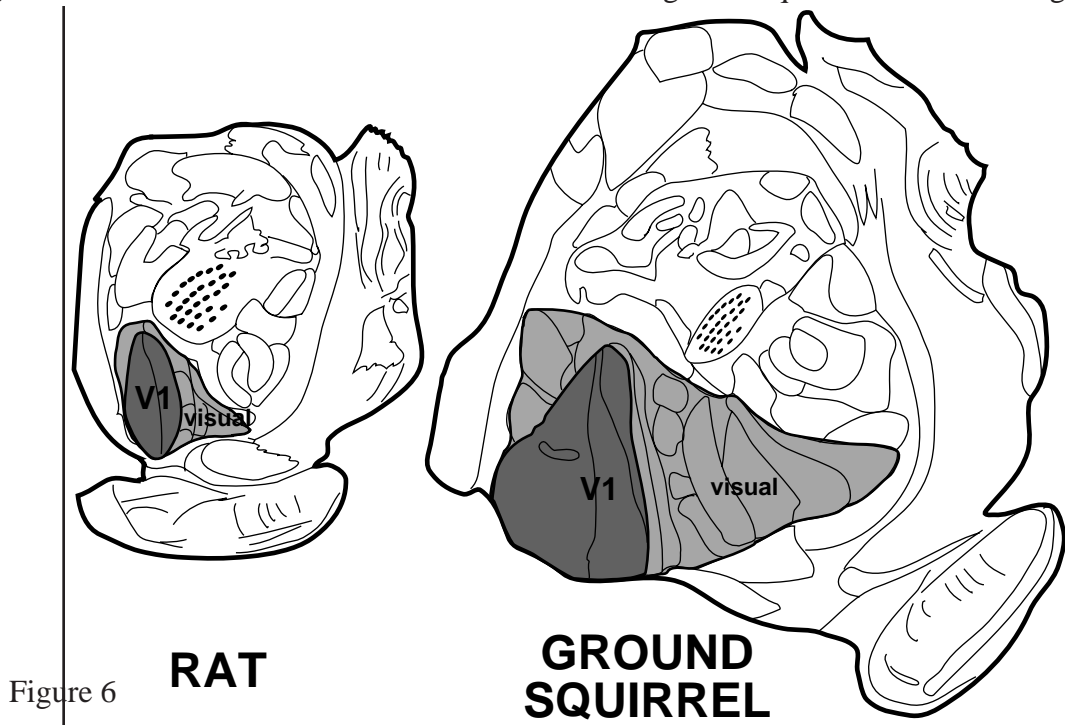
GROUND SQUIRREL

The ground squirrel cortex is considerably larger than that of the rat, but there are striking differences among the subfields. Some areas are quite similar in size. Auditory and somatosensory cortical areas, for example, cover about the same total area in absolute terms in the two animals (which have similar body sizes). The barrel fields, which represent the whiskers, for examples are actually smaller in squirrels (see above). Visual cortex, by contrast, is enormously expanded in the ground squirrel compared to the rat. Primary visual cortex is much larger than in the rat (about 4 times as large), but extrastriate cortex has expanded even more; it is over 8 times as big in ground squirrels as it is in rats. Areas of overlap between modalities are present in both species; for example, combined somatosensory and visual responses are elicited in a small region between the anterior lateral corner of primary visual cortex and the face (vibrissae) representation in S-I cortex. But any differences between the extent of the polymodal areas in rat and squirrel are dwarfed by the striking differences involving visual cortex proper.

I would argue that the differences we see between rats and squirrels are a better paradigm for how cortical areas evolve than the notion of a *scala natura* in which more advanced animals have increasing amounts of central, 'uncommitted' cortex. We now turn directly to evidence about the location and function of polymodal cortex in non-human primates.

Anatomical Evidence for Polymodal Cortex

Pandya and his colleagues have over the years conducted many studies of the anatomical organization of unimodal and presumed polymodal cortical areas in macaque monkeys (review:

Pandya and Yeterian, 1985). They have defined several regions—in parts of the superior temporal sulcus, cingulate cortex, prefrontal cortex, and parahippocampal cortex—where input from different modalities overlap. Many of these studies compared the results of single tracer injections in one animal to single injections in another animal. Given the difficulty of locating subtle, variable architectonic boundaries, it has been difficult to evaluate conclusions about the regions of overlap between modalities. Recently, however, they carried out more definitive experiments in which three distinguishable retrograde tracers were injected into single hemispheres—one in parietal visual cortex, another in inferotemporal visual cortex, and third in superior temporal gyrus auditory cortex (Barnes and Pandya, 1992). The results demonstrated unequivocally that there are small regions of overlap of two or more tracers in parts of the upper bank of the superior temporal sulcus. But, they also showed a remarkable degree of segregation and interdigitation; virtually all but a small handful of the cells labeled by these injections were situated within the same modality as the injection (inferotemporal injections labeled cells on the ventral bank of the sulcus and in inferotemporal cortex; superior temporal injections labeled cells in superior temporal auditory areas). There was even a clear segregation between the origin of the feedback connections to parietal visual and inferotemporal visual cortices.

Physiological Evidence for Polymodal Cortex

Recently, Colby has provided striking evidence of overlap between visual and somatosensory information in a small region at the fundus of the intraparietal cortex—the ventral intraparietal area (VIP) (Colby et al., 1993). Recalling the discovery of motor cortex one hundred years earlier, these studies have revealed unexpectedly non-abstract functional properties of bimodal neurons in VIP, quite at odds with conventional neuropsychological notions of what is supposed to be going on in the highest levels of "association cortex".

VIP neurons are sensitive to the direction of visual motion, but especially visual motion towards the animals face. Neurons in different parts of VIP respond best to visual motion in different parts of the visual field. Like many visual areas, it seemed to show some degree of retinotopy. However, VIP neurons also respond vigorously to stimuli that touch the animal's face. As with the visual stimuli, different parts of VIP respond to different parts of the face. Interestingly, the overlapping maps in VIP seem to be arranged in face-centered coordinates, not retina-centered coordinates. A neuron that responds well to a touch to the mouth will respond to a visual stimulus that is heading toward the mouth, regardless of whether that visual stimulus appears in the upper or lower visual field on the retina.

The response properties in area LIP, situated just posterior to VIP, stand in sharp contrast to it (Colby et al., 1995). LIP neurons code the location of objects (especially, but not exclusively, intended targets of eye movements) in retina-centered coordinates

There are several interesting points here. First, the region of explicit somatosensory/visual overlap is quite restricted; VIP is only a few millimeters wide, situated exactly at the border between large expanses of somatosensory and visual cortex. Second, the information in VIP does *not* appear to be abstract or 'modality-free'; rather, it seems to be arranged as a quite concrete face-(skin-centered) bi-modal map. Third, the abrupt transition from a retinal-centered to a skin-
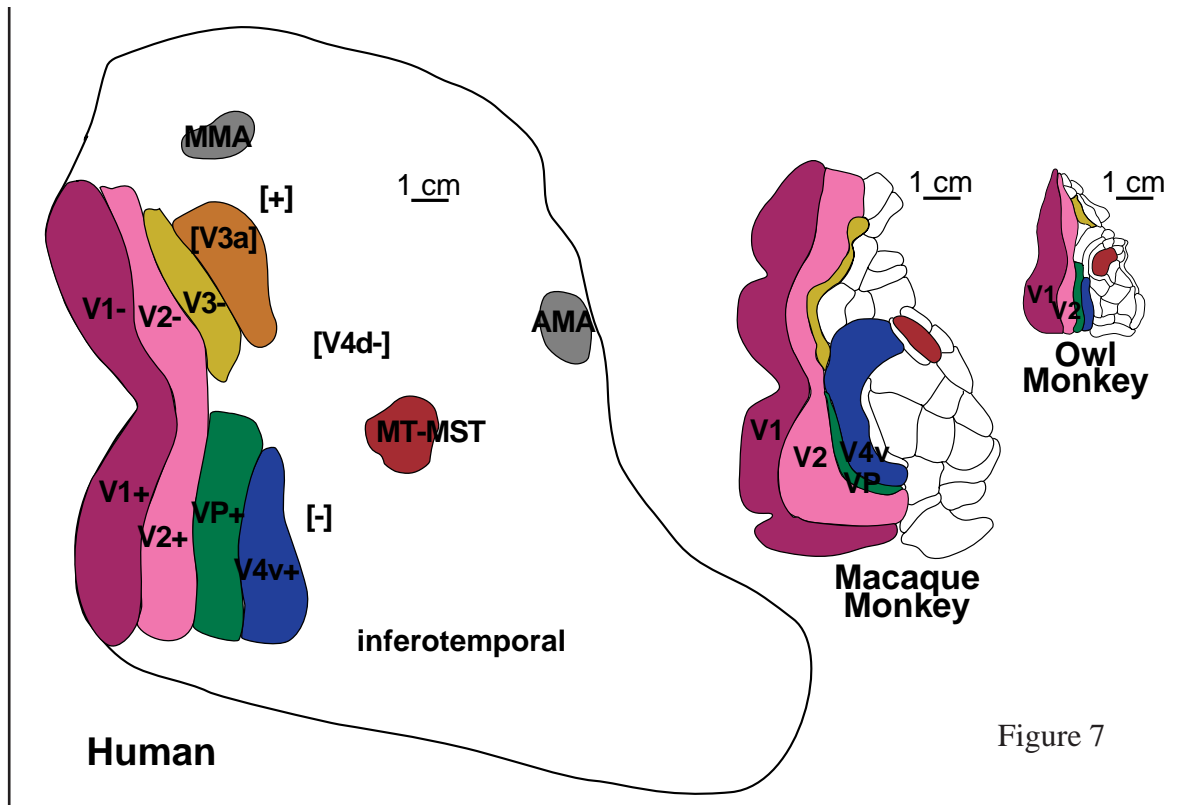
Figure 7

centered coordinate system again suggests a certain immiscibility between the modalities.

Human (and Ape) Cortex

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 ape and human visual cortical areas are organized quite similarly to those of other primates.

Location of V1, V2, V4, MT

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, 1991; Sereno et al., 1993a,b) (Fig 7). 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).

Relative size of cortical areas

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.

Before we turn to a model more closely based on the recent results about primate brains, we will first very briefly consider some of the main types of models of how language processing works in the brain.

Additional References (put at end)

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