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Introduction.

The mammalian visual system contains numerous visual areas that collectively occupy a large fraction of cerebral cortex. For cortical cartographers interested in vision, a fundamental set of objectives is to identify in key species of interest the overall extent of visual cortex, the total number of visual areas, the identities of these areas, and their location in relation to one another and to various gyral and sulcal landmarks. Over the past three decades there has been much progress in this endeavor for a number of primate and non-primate species. However, this task remains far from complete. Numerous qualitatively different partitioning schemes abound, even for the most intensively studied species. Our fragmentary and rapidly evolving understanding is reminiscent of the situation faced by cartographers of the earth's surface many centuries ago, when maps were replete with uncertainties and divergent portrayals of most of the planet's surface.

The primary objective of this chapter is to summarize our current understanding of visual cortical organization in two primate species, the macaque monkey and human. The macaque is the most intensively studied nonhuman primate and has been charted using a wide variety of approaches. Human visual cortex, largely terra incognita until the past decade, is now accessible thanks to modern neuroimaging methods, especially functional magnetic resonance imaging (fMRI; see DeYoe chapter, this volume). A secondary objective, more methodological in nature, is to illustrate the utility of computerized surface-based atlases in elucidating visual cortical organization. In brief, surface-based atlases offer many advantages over conventional atlases (e.g., stereotaxic atlases and pictorial representations). These include the ability to (i) visualize the cortical surface in multiple configurations, including smoothed and flattened maps, (ii) view any number of partitioning schemes and open-ended amounts of complex data in a convenient and electronically-accessible format; (iii) represent various types of spatial uncertainty that are associated with real experimental data; (iv) compensate for individual variability and (v) make objective interspecies comparisons of cortical organization.

Visual areas in the macaque monkey.

Figure 1 shows the estimated extent of visual cortex in the macaque and its relationship to other sensory modalities and to motor cortex. This is displayed on a surface-based atlas of the right cerebral hemisphere that was generated from a high-resolution structural MR image volume (Van Essen et al., 2002; see legend to Fig. 1 for details). The top panels show lateral and medial views, respectively, of the fiducial (3-D) configuration; the lower left panel (Fig. 1C) is a flat map that shows the entire surface in a single view.

The dotted lines on the flat map represent the estimated boundary between regions dominated by different modalities, based on the analysis of Felleman and Van Essen (1991). These boundaries are not sharply defined, as there is considerable intermixing of function in transitional regions between modalities. The blending of colors on the maps in Figure 1 qualitatively reflects this functional overlap. Cortex that is predominantly or exclusively visual (blue shading) occupies about half (52%) of cortical surface area (as measured on the fiducial surface rather than on the flat map, which contains significant distortions). This greatly exceeds the amount devoted to other modalities: somatosensory (green, 10%), auditory (red, 3%), motor (magenta, 8%), and olfactory (brown, 1%). Unassigned cortex (gray, 25%) is mostly cognitive or emotional in function, but is not subdivided along these lines in the figure.

Figure 1 also shows latitude and longitude isocontours that are determined on a spherical map (Panel D) and projected to the flat map (Panel E). As with earth maps, spherical coordinates provide a concise and objective way to specify precise locations on the map (Drury et al, 1999; Fischl et al., 1999a,b; Van Essen et al., 2001a).

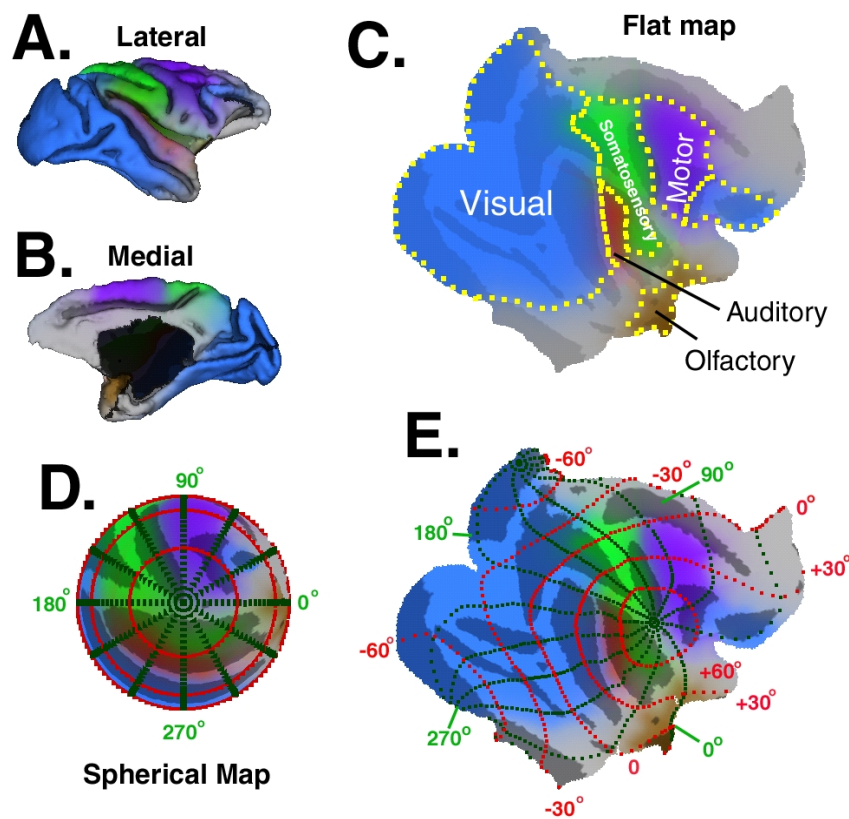


Figure 1. Visual cortex and other functional modalities mapped onto a surface-based atlas of macaque cerebral cortex. The atlas was generated from a high-resolution (0.5 mm^3 voxels) structural MRI volume generously provided by N. Logothetis (Case F99UA1, M. mulatta), using the SureFit segmentation method for surface reconstruction and Caret software for surface manipulation and flattening (Van Essen et al., 2001a). This atlas has many advantages over its predecessors, which include manually generated maps (Van Essen and Maunsell, 1980; Felleman and Van Essen, 1991) and surface-based atlases from a hemisphere that lacked corresponding structural MRI data (Van Essen et al., 2001a). A. Lateral view. B. Medial view. C. Flat map. Surface coloring represents different functional modalities, as identified on the flat map; darker shading represents cortex buried in sulci. D. Lateral view of the atlas spherical map, with latitude and longitude isocontours. By convention, the lateral pole is set at the ventral tip of the central sulcus. E. Latitude and longitude isocontours displayed on the flat map. Data for Figures 1-3 can be accessed via <http://brainmap.wustl.edu/sums/sums-cgi?specfile=Macaque.F99VA1.Cerebral.R.ATLAS.VanEssen.2002.spec>

The identification of distinct visual areas is generally based on finding reliable differences in one or more characteristics related to: (i) architecture, (ii) connectivity, (ii) visual topography, and/or (iv) functional characteristics (Felleman and Van Essen, 1991, Kaas, 1997). Using various combinations of these criteria, numerous partitioning schemes for visual cortex in the macaque monkey have been published over the past century. Figure 2 shows ten such schemes that were mapped to the atlas using a surface-based registration method (Van Essen et al., 1998, 2001; see Figure 2 legend for details). Panels A-C illustrate three schemes that encompass most or all of visual cortex. The Felleman and Van Essen (1991) and Ungerleider and Desimone (1986) schemes are based on anatomical and physiological data from many sources. The Lewis and Van Essen (2000) scheme is based on an architectonic analysis of multiple hemispheres, with the atlas map generated via surface-based registration of a particular individual map. Panel D shows several schemes that cover more restricted regions, including a connectivity-based analysis of occipital cortex (Lyon and Kaas, 2002) and architectonic analyses of temporal and parietal cortex (Seltzer and Pandya, 1978, 1980, 1986). Similarly, panel E shows two additional architectonic schemes covering temporal (Bayliss et al., 1987) and parietal (Preuss and Goldman-Rakic, 1991) regions, plus a visuotopic mapping analysis of dorsal occipital cortex (Galletti et al 1999). While far from an exhaustive compilation, Figure 2 includes most of the partitioning schemes in current use that have been reported in a format suitable for registration to the atlas.

Although there are many similarities, these partitioning schemes differ in many ways, for reasons that reflect various technical impediments faced by cortical cartographers. (i) *Subtle boundaries*. The distinctions between neighboring regions are often subtle, even when evaluated with the most sensitive anatomical and physiological techniques available. (ii) *Internal heterogeneity*. Many (perhaps most) visual areas are internally heterogeneous. This heterogeneity may be manifested by *modularity* (repetitive organization at a finer scale than the overall areal dimensions); *asymmetries* (differences between the representations of the upper (superior) and lower (inferior) visual fields; or internal *gradients* (gradual shifts in characteristics rather than discrete modularity). (iii) *Individual variability*. The overall size of well-defined visual areas such as V1 and MT can vary two-fold or more from one individual to the

next (Van Essen et al., 1984; Maunsell and Van Essen, 1987). This is compounded by substantial variability in the exact pattern of convolutions and in the location of areal boundaries relative to gyral and sulcal landmarks

A compelling case for areal identification entails finding region-specific characteristics that are robust, consistent across multiple approaches, and replicated by multiple laboratories. The diversity among partitioning schemes signifies that a consensus has been achieved for only a minority of the visual areas illustrated in Figure 2. Several well-defined areas (V1, V2, V4, and MT) are shown by individualized colors in Figure 2; others are included as part of a regional coloring pattern that includes six clusters discussed below.

The differences among partitioning schemes can be categorized along four lines: *Terminological equivalence*. Some differences are essentially terminological, in that different labels are assigned to what is fundamentally the same visual area. For example, area 17 is equivalent to area V1; MT (Fig. 2A-C) is equivalent to V5 (Shipp and Zeki, 1985);, and PO (Fig. 2A-C) is equivalent to V6 (Fig. 2F). *Lumping vs. Splitting*. Some regions are considered a single area by some investigators (the “lumpers”) but as two separate areas by other investigators (the “splitters”). This is an issue, for example, for subdivisions V3d/V3v, V4d/V4v, and LIPd/LIPv. In some cases it can be helpful to use the expression “zone” to describe a consistently identifiable region whose status as a distinct area is uncertain, ambiguous, or contentious (Lewis and Van Essen, 2000a). The term “subdivision” can then encompass both zones and well-defined cortical areas. *Boundary uncertainty*. Even when there is a consensus on the identity of an area and the main criteria for its identification, the location and extent of any particular area on the atlas map varies substantially across schemes, (cf. V2 and MT in Figure 2A-D). These differences may reflect (i) the choice of criteria or emphasis among different criteria available for delineating boundaries; (ii) variability in the size and location of areas in the individuals studied, (iii) inaccuracies in portraying areal boundaries on a summary diagram in the original publication; and (iv) inaccuracies or distortions arising when registering data to the atlas. *Genuine incompatibility*. In some regions, partitioning schemes differ more profoundly than can be explained by the factors just mentioned. For example, in inferotemporal cortex (blue) there is rather little correlation between the areal boundaries in panel A vs. E; hence the schemes are largely incompatible.

Occipital visual areas. V1 and V2 are both large, well-defined areas, with V1 occupying 13% and V2 occupying 10% of total cortical surface area (12.6 cm²) in the atlas right hemisphere. V1 and V2 have a mirror-symmetric visuotopic organization, with the vertical meridian represented along their common boundary, and with upper fields represented ventrally and lower fields dorsally in each area. In addition, both areas have a prominent internal modularity related to the processing streams described in other chapters (Hendry, Jones, Grinvald chapters, this volume). Interestingly, there are significant asymmetries between dorsal V2 (V2d) and ventral V2 (V2v): V2v is notably wider than V2d (Figure 2A-D), and the two subregions differ in the global pattern of thick, thin, and inter-stripes (Olavarria and Van Essen, 1997).

Area V3 was originally identified as a strip of cortex that adjoins V2 and has mirror-symmetric visuotopic organization (Zeki, 1969). Subsequent studies confirmed this visuotopic organization but revealed that the dorsal and ventral subdivisions are physically separated from one another by the interposition of area V4 (cf. Fig. 2A-C). More significantly, evidence for pronounced dorso-ventral asymmetries in connectivity (especially with V1), myeloarchitecture, and physiological properties prompted the classification of these dorsal and ventral subdivisions as distinct visual areas: VP (or V3v) and V3 (or V3d), each containing a partial representation of the visual field (cf. Burkhalter et al., 1986). In contrast, Lyon and Kaas (2002) reported relatively symmetric projections of V1 using more sensitive tracers, and they support Zeki's original proposal that V3d and V3v are subdivisions of a single area V3. A sensible interim strategy is to designate these subdivisions as “zones” V3d and V3v while awaiting additional data on the overall magnitude and nature of V3d/V3v asymmetries, along with insights regarding the asymmetries encountered in other regions and other species (see below). Independent of this terminological debate, it is noteworthy that V3d and V3v vary considerably in location and size among the various maps shown in Figure 2.

V4 is a moderately-sized area whose lower-field (V4d) and upper-field (V4v) representations are contiguous with one another, in contrast to the physical separation of V3d and V3v. The visuotopic organization of dorsal V4 appears to be more complex and variable across individuals than that of ventral V4 (Maquire and Baizer, 1984; Gattas et al., 1988; Van Essen et al., 1990; Boussaud et al., 1991). Because analogous but more pronounced dorso-ventral asymmetries have been reported for the corresponding region of human cortex (see below), Tootell and Hadjikhani (2001) have suggested that macaque V4d and V4v might themselves constitute distinct visual areas.

Five additional areas adjoin or closely approach V2 along its dorso-medial and ventro-medial boundaries. The dorso-medial cluster (magenta in Fig. 2) includes areas V3A, PIP, and PO, each of which includes an upper-field as well as lower-field representation (Colby et al., 1988; Felleman and Van Essen, 1991; Lyon and Kaas, 2002). Area

PO as charted by Colby et al. (1988) corresponds to area V6 of Galletti et al. (1999). The ventro-medial cluster (brown in Fig. 2) includes areas TF and TH (near the bottom of the flat map) both of which receive visual inputs (see Felleman and Van Essen, 1991). The posterior portion of TF, identified as VTF by Boussaoud et al. (1991), is visually responsive but has at best a crude visuotopic organization.

Dorsal temporal and posterior parietal cortex. The “dorsal stream” of visual areas (Ungerleider and Pasternak, this volume) includes cortex in and near the intraparietal sulcus, plus the dorsal part of the superior temporal sulcus. Area MT, the most extensively studied area in the dorsal stream, contains a complete visuotopic map, but with a bias of lower versus upper visual fields (Maunsell and Van Essen, 1987). Though MT is well-defined by several criteria (including a high incidence of direction-selective cells), its precise location and extent on different summary maps varies significantly (cf. Fig. 2A-D; see also Desimone and Ungerleider, 1986). Adjoining MT on its lateral side is a narrow strip that has been identified as V4t (Ungerleider and Desimone, 1986, Felleman and Van Essen, 1991) or MTc (Lyon and Kaas 2002). Within V4t, architectonically distinct zones V4tp and V4tp have been described (Lewis and Van Essen, 2000a)

A major target of MT is the MST complex (orange in Fig. 2), which lies dorsal and medial to MT and is implicated in higher-order motion analysis. MST is heterogeneous both anatomically and physiologically, but it remains unclear whether there are two subdivisions (MSTd and MSTl; of Komatsu and Wurtz 1988a,b and Felleman and Van Essen, 1991; MSTc and MSTp of Boussaoud et al., 1990) or three (MSTdp, MSTm, and MSTl of Lewis and Van Essen, 2000) and whether these constitute distinct areas or zones within a larger MST complex. Area FST lies ventral to the MST complex and medial to MT, but its position differs markedly in different partitioning schemes (Fig. 2A versus 2B,C).

Posterior parietal visual cortex (yellow in Fig. 2) includes several elongated areas in and near the intraparietal sulcus, plus additional areas in more posterior regions that are represented in some schemes. The most fine-grained scheme (Lewis and Van Essen, 2000a; Figure 2C) is based on immunohistochemical as well as cyto and myelo-architecture and includes seven distinct areas (7a, LIPd, LIPv, VIP, MIP, MDP, and DP) plus additional architectonic zones. In the region previously described as area LIP (Blatt et al., 1990), subdivisions LIPd and LIPv differ from one another in architecture, connectivity, and physiological characteristics and are thus likely to constitute separate visual areas (cf. Lewis and Van Essen, 2000a,b). Area VIP, along the fundus of the intraparietal sulcus, contains lateral (VIPl) and medial (VIPm) architectonic zones, but these are not considered distinct areas on the basis of current evidence (Lewis and Van Essen, 2000a,b). Areas LIPd, LIPv, and VIP of Lewis and Van Essen (2000a) largely correspond with POa-e, POa-i, and IPd of Seltzer & Pandya (1980, 1986) except that they are more restricted antero-posteriorly. The relationships with other schemes are somewhat confusing because of “cross-talk” in the terminology: area VIP* of Ungerleider and Desimone corresponds to LIPv of Lewis and Van Essen; areas LIP and VIP of Felleman and Van Essen correspond to LIPd and LIPv/VIPl, respectively, of Lewis and Van Essen.

A second group of areas, near the posterior end of the intraparietal sulcus, includes areas MDP, MIP, and DP, plus zone LOP (Fig. 2C). Area MDP corresponds to V6A of Galletti et al. (1999). Zone LOP may correspond to the cIPS subdivision identified physiologically by Taira et al., (2000) based on surface orientation selectivity.

Ventral temporal areas. Cortex ventral to area MT and anterior to V4 is generally considered part of the ventral processing stream (cf. Ungerleider and Pasternak, this volume). This region includes a cluster of inferotemporal areas (blue in Figure 2) that are implicated mainly in pattern recognition and form analysis (Desimone and Ungerleider, 1989; Tanaka, 1997). Another cluster of ventral-STS areas (dark green in Fig. 2) includes polysensory regions and regions involved in both form and motion processing (Perrett et al., 1997s; Cusick, 1997). The five schemes in Figure 2 subdivide ventral temporal cortex along both antero-posterior and dorso-ventral axes, but the number of identified subdivisions ranges from four to ten and the location of areal boundaries varies widely as well.

The simplest scheme (Ungerleider and Desimone, 1986, Fig. 2B) includes a visuotopically organized area TEO that contains a lower-field and an upper-field representation (see also Boussaoud et al., (1991), plus three areas (TEc, TEr, and TEm) that lack clear visuotopic organization. The Felleman and Van Essen (1991) scheme, based mainly on topographic and connectional data, includes three areas (VOT, PITd, and PITv) in the region corresponding to TEO of Ungerleider and Desimone. VOT contains only an upper-field representation, whereas PITd and PITv are reported to each contain a crude topography with lower-field and upper-field inputs (Van Essen et al., 1990). Areas CITd and CITv of Felleman and Van Essen (1991) together correspond approximately to TEc of Ungerleider and Desimone (1986) but are distinguished from one another by differential connections. More anteriorly on the atlas map, there is reasonable correspondence between AITd and TEr in the two schemes but poor correspondence between AITv and TEm.

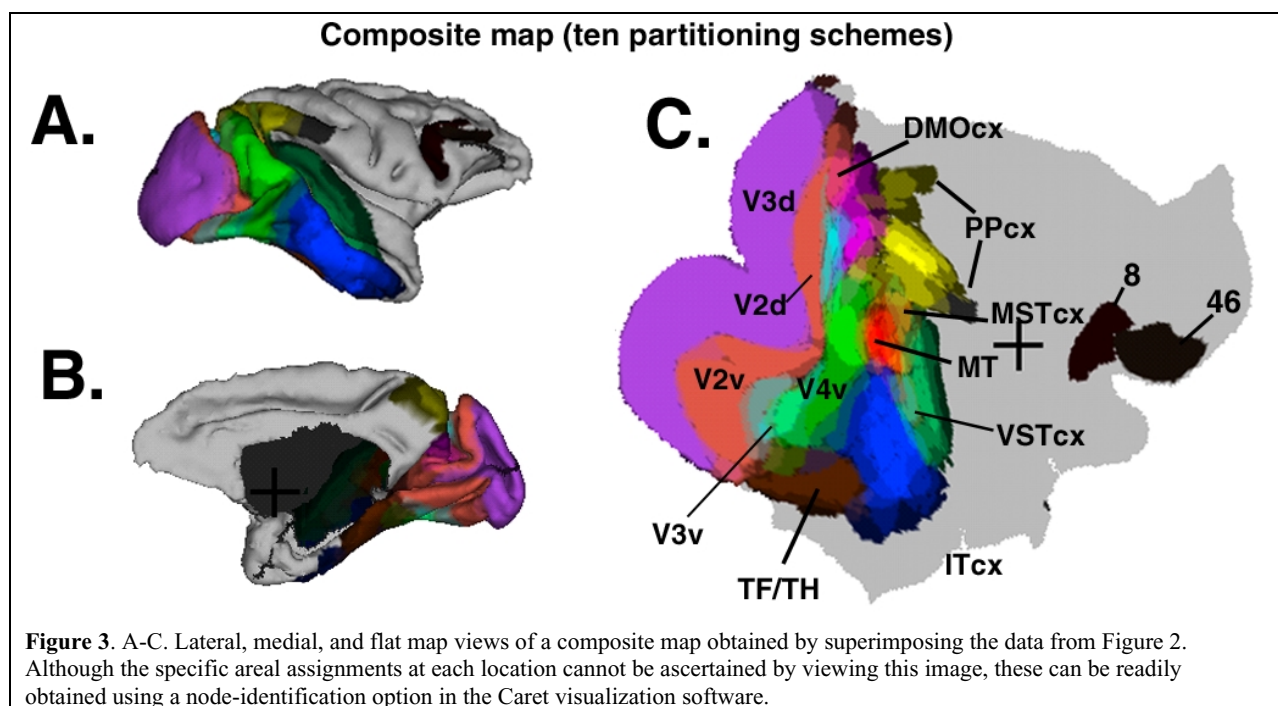
The Seltzer and Pandya (1978) architectonic scheme (Fig. 2E) includes five inferotemporal areas (TEa, TEm, TE1, TE2, TE3), plus four additional areas in the superior temporal sulcus (TAa, TPO, PGa, and IPa). The Bayliss et al.

(1987) scheme (Fig. 2D) uses the same criteria and terminology as Seltzer and Pandya, but the areal boundaries differ significantly on the atlas map. The Lewis and Van Essen scheme, like that of Cusick (1997), identifies three subdivisions within TPO (TPOc, TPOi, TPOr). In inferotemporal cortex the Lewis and Van Essen (2000a) scheme does not discriminate among TE1, TE2, and TE3 but does identify dorso-ventral subdivisions TE1-3d and TE1-3v. The latter correspond approximately to subdivisions TEad and TEav of Yukie et al. (1990) and Saleem and Tanaka (1996).

Frontal areas. Felleman and Van Essen classified areas 8 (FEF) and 46 as part of visual cortex. Areas 8 and 46 have both been partitioned into multiple subdivisions, including eight zones (8A, 8Am, 8Ar, 46d, 46v, 46dr, 46vr, and 46r) by Preuss and Goldman-Rakic (1991b), and zones 8Ac, 46p, and 46v by Lewis and Van Essen (2000a).

It remains unclear which of the aforementioned schemes for inferotemporal and parietal cortex best reflect the underlying neurobiological reality. Indeed, alternative possibilities worth bearing in mind are that much of inferotemporal and frontal cortex might contain gradual gradients of properties rather than sharply defined areas, or else irregular clustering whose arrangement varies markedly from one individual to the next.

Figure 3 shows a composite map, in which all of ten schemes represented in the preceding panels are superimposed and displayed in lateral (Fig. 3A), medial (Fig. 3B) and flat map (Fig. 3C) views. Besides the individually colored areas, the composite map includes the six clusters discussed in preceding sections: the dorso-medial occipital complex (DMOcx), posterior parietal complex (PPcx), MST complex (MSTcx), ventral superior temporal complex (VSTcx), inferotemporal complex (ITcx), and the TF/TH cluster.



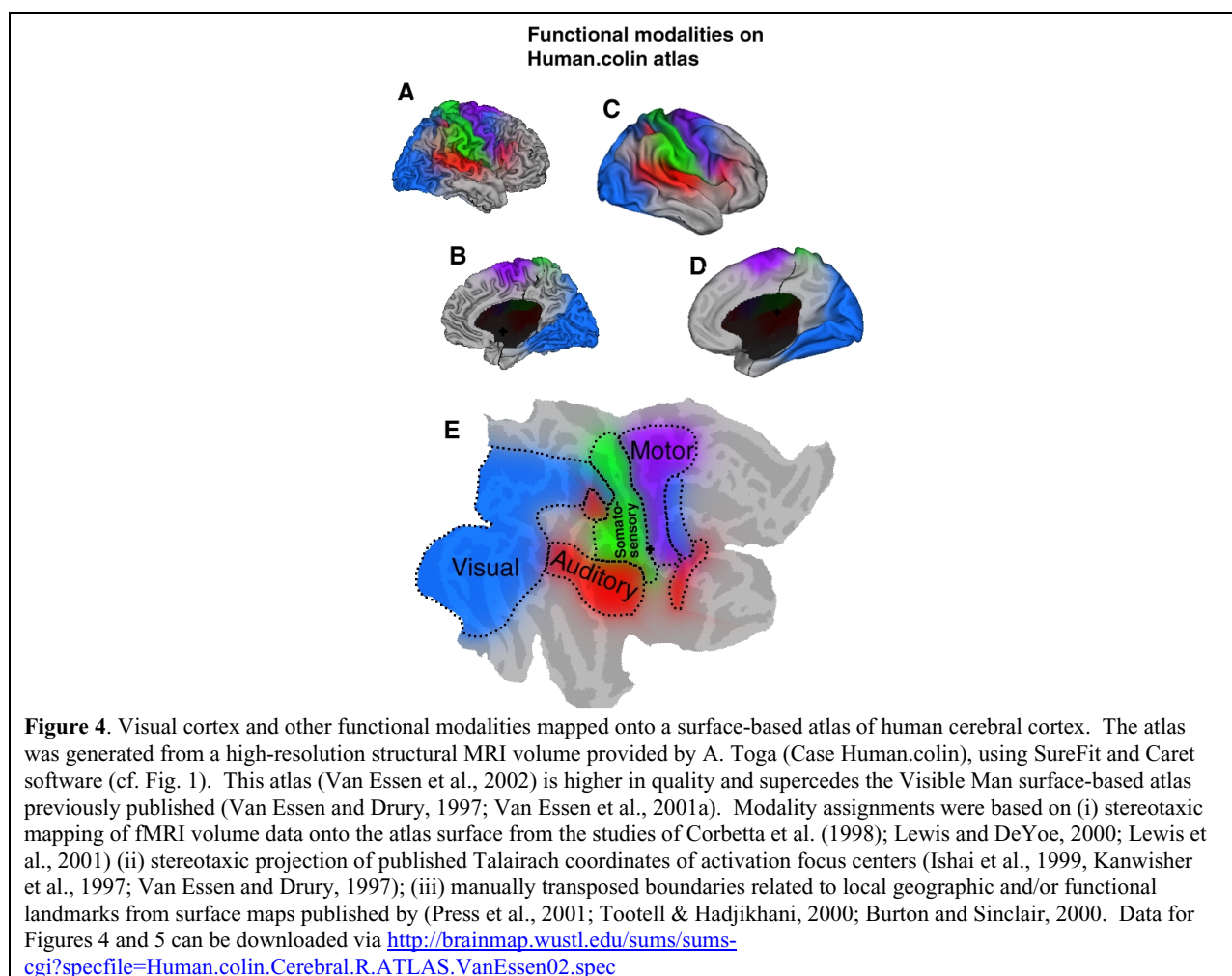
How many visual subdivisions? It is naturally of interest to have a current estimate of the total number of cortical areas and subdivisions associated with visual processing. Given the diversity among partitioning schemes, it is impractical to arrive at a definitive single number. Altogether, there is substantial evidence for more than 40 anatomically and/or functionally distinct subdivisions of visually responsive cortex, but for some the evidence does not warrant identification as separate areas. A conservative "lumper" can argue that the number of convincing visual areas is only about two dozen. A more generous "splitter" can make a credible case for at least three dozen distinct areas. The number of areas that show clear visuotopic organization is also difficult to determine precisely, but is in the range of 10 – 12, depending on designation of zones vs. areas.

Coping with multiple schemes, areal uncertainties, and individual variability. Several general observations emerge from the preceding discussion. First, a multiplicity of competing partitioning schemes will likely persist for years to come, because many of the issues remain inherently difficult to resolve with currently available techniques. Second, it is increasingly important to have objective methods for quantifying and visualizing the uncertainties associated with charting areal boundaries and the variability associated with individual differences in cortical organization. This leads to the notion of probabilistic surface-based maps of cortical organization. The composite map in Figure 3 constitutes one step in this direction, as it includes many different schemes in a common coordinate

system. Another important aspect of a probabilistic approach is to incorporate information about individual variability, by registering maps of many individuals onto the atlas (Van Essen et al., 2001a).

Another important issue involves the options for accessing and extracting information from surface-based atlases. The fundamental challenge is that existing atlases already contain far more information than can be easily gleaned from static pictorial images such as those shown in the present chapter. Moreover, the amount of information represented on such atlases is likely to grow exponentially over the next decade. An attractive alternative is to use computerized visualization software to access atlas data more efficiently and flexibly. For the atlases illustrated here, this can be done by downloading specific data sets (using hyperlinks included in the figure legends) and viewing the maps using the freely available Caret software (Van Essen et al. 2001b; <http://brainmap.wustl.edu/caret>). Existing visualization options in Caret include: zooming in on regions of interest; rapid toggling between different partitioning schemes; overlaying one scheme directly over another; listing areal identities for multiple partitioning schemes when clicking on locations of interest; specifying location by latitude and longitude (cf. Fig. 1E); encoding uncertainty limits for each boundary; and encoding variability by combining maps from different individuals.

Human visual cortex. The analysis of human visual cortex has benefited greatly from the advent of structural and functional MRI methods that can be routinely carried out on normal subjects. In the top half of Figure 4, the extent of visual cortex and other functional modalities is charted on the right hemisphere of a surface-based atlas (the "Human.Colin" atlas) that was generated from high-resolution structural MRI of a particular individual (Van Essen et al., 2002; Holmes et al., 1998). The surface displays include lateral and medial views of the fiducial surface (Fig. 4A, B) and the inflated surface (Fig. 4C, D), plus a flat map (Fig. 4E). The assignment of different functional modalities was estimated mainly from functional neuroimaging data that were mapped onto the atlas using a combination of methods applied to a number of published data sets (see Figure 4 legend). Based on these provisional assignments, cortex that is predominantly visual in function occupies about 27% of the total extent of cerebral cortex (950 cm^2) in the atlas right hemisphere. By comparison, about 8% of cortex is predominantly auditory, 7% somatosensory, and 7% motor. The remaining half (51%) includes major domains associated with cognition, emotion, and language.

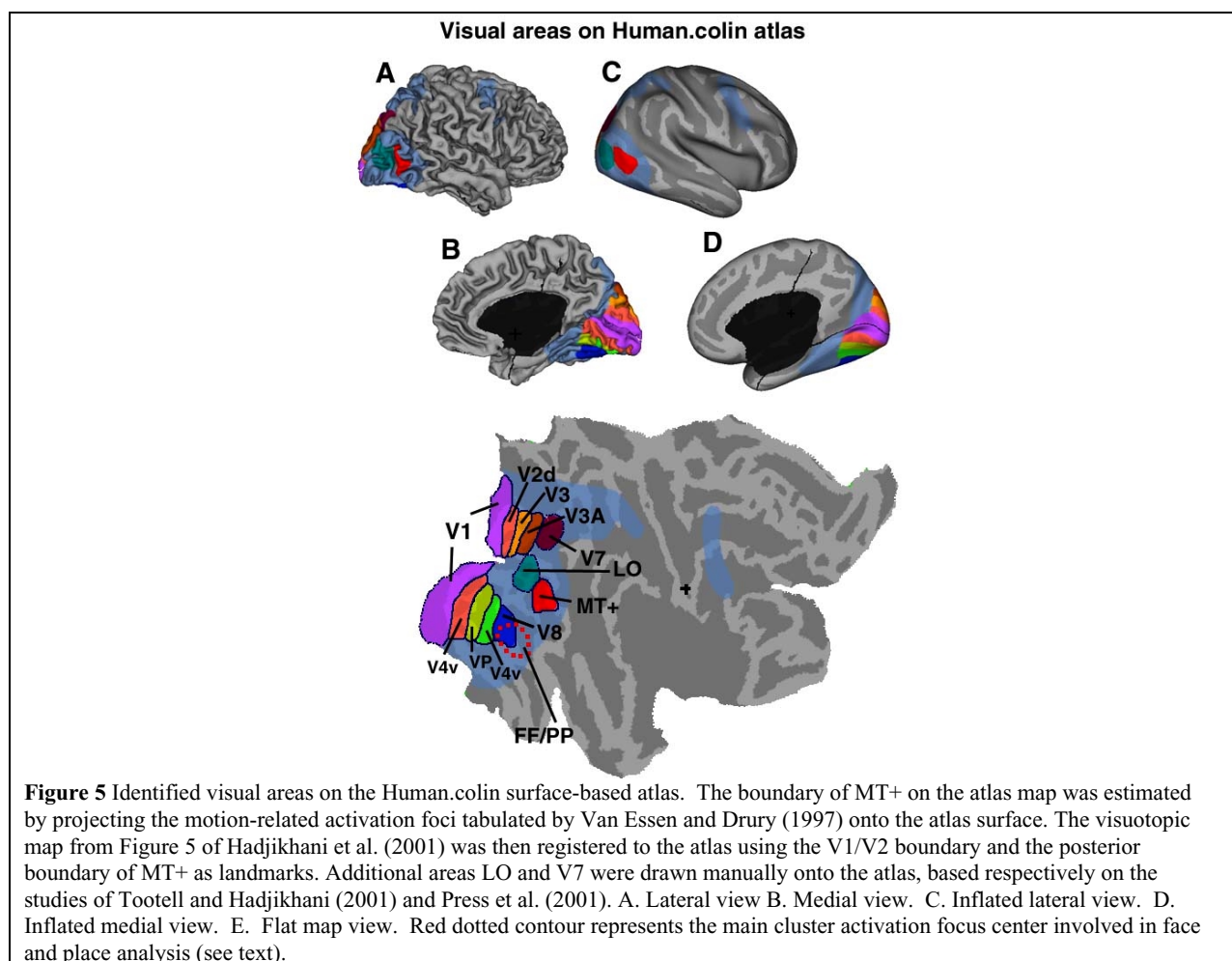


Human area V1 (area 17) has a well-defined architectonic boundary that runs near the margins of the calcarine sulcus but with considerable individual variability (Rademacher et al., 1997). The estimated surface area of V1 on the atlas map (charted using the most likely boundary in the Rademacher et al. study) is 21 cm², or 2.2% of cerebral cortex. This is about one-sixth of its fractional occupancy on the macaque atlas.

Neuroimaging studies have revealed numerous visuotopically organized extrastriate areas in human occipital cortex, in an arrangement that shows many similarities to the pattern found in the macaque. Corresponding areas that have fundamentally similar visuotopic organization in the two species include V1, V2, V3 (V3d), VP (V3v), V3A, and V4v (Sereno et al., 1995; DeYoe et al., 1996; Hadjikhani et al., 1998). In addition, tests for motion-related activation have consistently demonstrated a prominent focus in or near the posterior inferotemporal sulcus. This focus is generally presumed to correspond to macaque MT plus part of the MST complex and has therefore been identified as human MT+ (Tootell et al., 1995) or as V5 (Watson et al., 1993).

Figure 5 includes many visuotopic areas that were mapped onto the human atlas using surface-based registration of an individual case from Hadjikhani et al. (1998). For technical reasons these maps do not include the representation of the fovea or far periphery, so the extent of the extrastriate areas is likely to be modestly underestimated. Interestingly, the sizes of V3d, V3v and V3A relative to V1 and V2 are all substantially greater in humans than in the macaque, suggesting a marked evolutionary divergence in the relative sizes of nearby cortical areas. In the region adjoining V3, Smith et al. (1998) and Press et al. (2001) found evidence for two representations, V3A and V3B, instead of a single V3A, with V3B being located more posterior (lower on the flat map). Area V7 (Press et al., 2001; Tootell and Hadjikhani, 2001) is a visuotopically organized area that lies anterior to V3A; its location and extent is displayed on the atlas using dotted boundaries to signify greater uncertainty.

Human area V4v lies antero-lateral to VP/V3v and contains a mirror-symmetric upper-field representation. Interestingly, cortex lateral and dorsal to V4, identified as LO (Van Oostende et al., 1997) or the LOC/LOP complex (Tootell and Hadjikhani 2001), evidently lacks a complementary lower-field representation equivalent to that described for macaque V4d. Instead, the LO region represents both upper and lower fields, but with an irregular and



inconsistent map of polar angle and an apparent discontinuity in the transition between central and peripheral eccentricities. Area V8 lies anterior to V4v and contains a complete visuotopic map with a foveal representation near its anterior margin to the right on the flat map (Hadjikhani et al., 1998, but see Wade et al., 2002).

Tests using a variety of stimuli and behavioral paradigms besides those just discussed have revealed several additional regions of functional specialization. Ventral occipito-temporal cortex contains a region preferentially activated by object versus non-object stimuli. Based on published stereotaxic (Talairach) coordinates, foci involved in analysis of faces, houses, and chairs are concentrated in a region (red dotted outline in Fig. 5E) that partially overlaps V8 on the atlas map but extends more anteriorly (Kanwisher et al., 1997; Ishai et al., 1999; Haxby et al., 1999). This region has been proposed to include a fusiform face area (FF) and a parahippocampal place area (PP) (Kanwisher et al., 1997; Epstein and Kanwisher, 1998) and is accordingly identified as FF/PP in Figure 5E. Other studies suggest that these may not constitute distinct areas but a functional gradient within a larger subdivision (Haxby et al., 2001).

In the parietal lobe, visually-related activations have been reported in a large swath of cortex in and near the intraparietal sulcus, dorsal and anterior to the known visuotopic areas. Paradigms effective in activating this region include shifting visual attention, target-directed eye movements, visual motion, and spatial analyses (Haxby et al., 1994; Corbetta et al., 1998; Lewis and DeYoe, 2000; Lewis et al., 2001). This region presumably includes a number of functionally distinct areas or subdivisions that have not been clearly discriminated using existing paradigms and analysis methods.

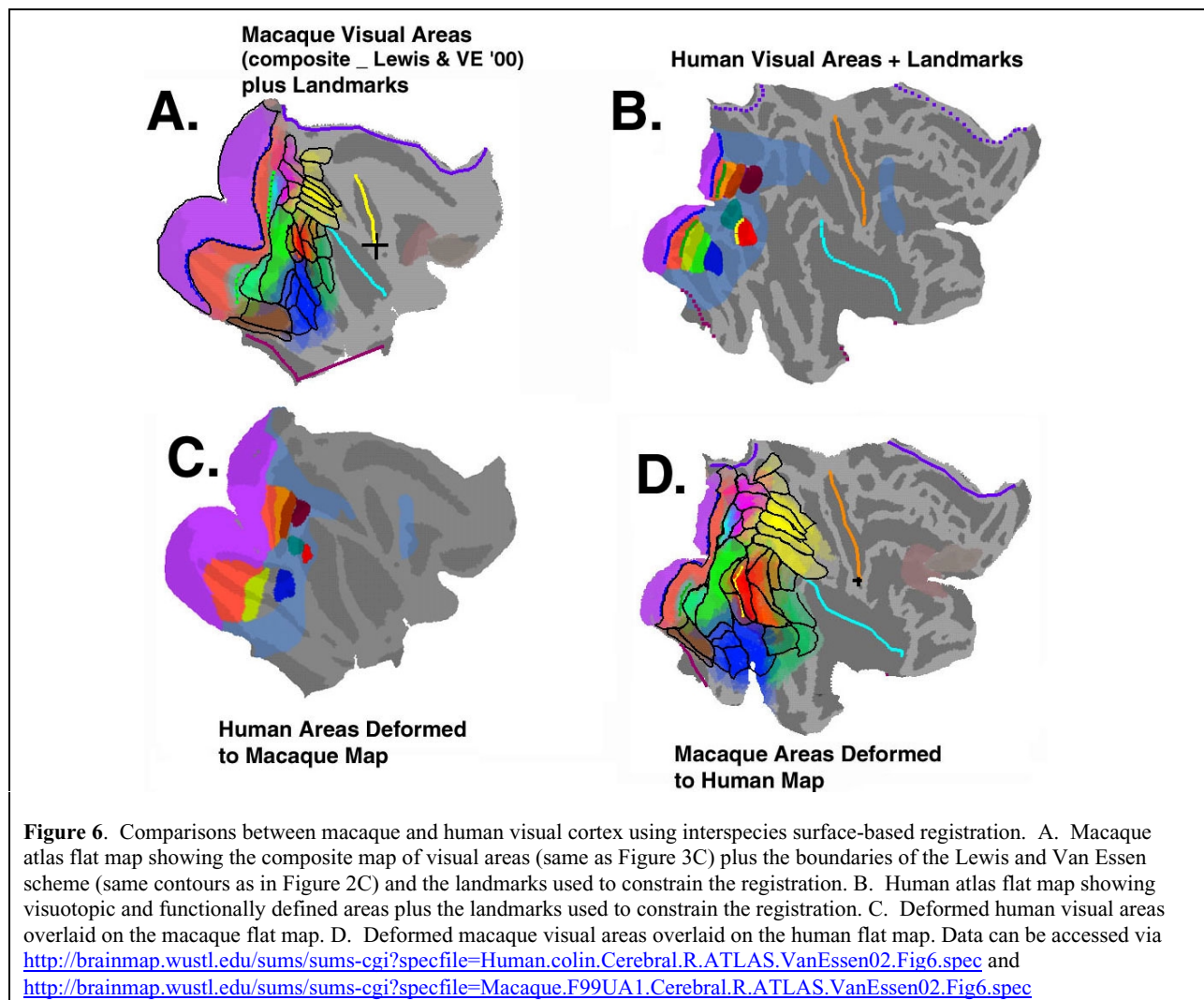
Macaque-Human interspecies comparisons.

While there are many striking similarities in visual cortical organization between macaque and human, there are numerous differences as well. Some of the differences are in relative size and in the geographic location of areas, but others presumably reflect fundamental differences in the existence of areas or in their topological relationships to one another. A useful general strategy for examining these relationships and candidate homologies is to use surface-based registration between species (Van Essen et al., 1998, 2001a). While neither proving nor disproving any particular homology, interspecies registration of surfaces provides a good testbed for exploring any particular set of proposed homologies implies for the relationships among areas in intervening regions.

In Figure 6, the macaque and human maps were registered to one another using explicit landmarks that are likely to reflect genuine homologies. These landmarks (colored contours in Fig. 6) include the fundus of the central sulcus (near the boundary between somatosensory and motor cortex); the fundus of the Sylvian fissure (near the boundary between somatosensory and auditory cortex); the boundaries of V1, V2, and MT+; and the boundaries of neocortex along the medial wall (Fig. 6A, B). To avoid confounds associated with artificial cuts on the flat maps, the landmarks were first projected to macaque and human spherical maps (not shown); the registration was applied to the spherical maps; and the deformed visual areas were then projected back to the flat maps. This is shown in Figure 6D for the human visual areas deformed to the shape of the macaque flat map (and superimposed on the macaque sulcal map). In Figure 6D, the corresponding relationships are shown with the macaque visual areas deformed to the shape of the human flat map (and superimposed on the human sulcal map). The macaque map (before and after deformation) includes the composite of all ten partitioning schemes painted onto the map, plus the Lewis and Van Essen partitioning scheme (black contours). The human map includes the same visuotopic areas delineated in Figure 5.

The deformation between species necessarily involves highly nonlinear distortions, mainly because V1 and V2 are much smaller (relative to overall cortical size) in humans vs. macaques, and also because the location of MT (relative to foveal V2 and to the Sylvian fissure) is more posterior and ventral in the human versus the macaque map. Consequently, in Figure 6D, there is considerably more expansion of parietal areas than inferotemporal areas on the deformed macaque map.

Several potential homologies can be evaluated by comparing individual areas and clusters of areas in the deformed macaque visual areas in Figure 6D to the human map in Fig. 6B (or, equivalently, comparing the deformed human areas in Fig. 6D to the macaque map in Fig. 6A). One particular issue of interest is the relationship between macaque areas V4 and TEO/VOT on the one hand and human areas V4v, LO, and V8 on the other hand. Deformed macaque V4v overlaps extensively with human V4v, and deformed macaque V4d overlaps with human LO, consistent with the proposed homologies for these areas. In contrast, deformed macaque V4 differs greatly in size and location compared to human V8. As emphasized by Tootell and Hadjikhani (2001) these and other differences argue strongly against a homology between macaque V4 and human V8, as proposed by Zeki et al. (1998).



Based on its location just anterior to V4v, human V8 is a candidate for homology with area TEO in the Ungerleider & Desimone scheme and with VOT in the Felleman/Lewis/Van Essen schemes. However, the visuotopic organization of human V8 is not in accord with that reported for either TEO or VOT, making a homology implausible on those grounds. For human V7, its location just anterior to V3A makes areas DP and zone LOP the most plausible candidates for homologues in the macaque, but a visuotopic map consistent with that in V7 has not been reported in this region.

Parietal visual cortex in the deformed macaque map overlaps extensively with human parietal visual cortex, but is shifted somewhat more lateral (lower on this part of the map). Candidate homologies have been suggested between macaque LIP and human parietal areas involved in attention and eye movements (e.g., Corbetta et al., 1998; Sereno et al., 2001). These and other candidate homologies can be used as additional constraints to test for mappings that bring the overall parietal regions into closer register and may suggest additional homologies.

Deformed macaque inferotemporal and ventral superior temporal areas (blue and green in Fig. 4D) lie well anterior (to the right on the flat map) to the known visually responsive regions of human occipito-temporal cortex. One possible explanation for this discrepancy is that human visual cortex extends farther anterior in the temporal lobe than previously recognized. Alternatively, the homologues of the macaque inferotemporal complex may lie within currently designated human visual cortex, anterior to V8 and/or flanking it. If so, this would signify an even more pronounced over-emphasis on parietal visual areas and under-emphasis on inferotemporal visual areas in humans compared to macaques.

Other species. Although the focus of this chapter has been on the macaque and human, there is an enormous amount to be gained by obtaining a better understanding of visual cortex in other primate and non-primate species. There has been substantial progress in elucidating visual cortical organization in other nonhuman primates, most notably the owl monkey but also several other species as well (see Kaas et al., 1997; Rosa, 1997). In brief, these reveal similar patterns, especially for occipital visual areas, but many indications of significant differences.

Rodents, particularly the mouse, are likely to become increasingly important as model systems for studying many aspects of cortical organization. Studies of rat and mouse have revealed a primary visual area surrounded by a modest number of extrastriate visual areas (Wagor et al., 1980; Coogan and Burkhalter, 1990). However, the magnitude of differences in the overall number and layout of visual areas from species in different orders remains to be determined. A mouse surface-based atlas, akin to those for the macaque and human illustrated here, has recently been generated (Van Essen et al., 2002) and should aid in charting the detailed organization of mouse visual cortex.

Concluding remarks.

Progress in elucidating visual cortical organization is likely to accelerate markedly in the next few years, particularly with the use of fMRI and other imaging methods that can be applied to monkeys (Logothetis et al., 1999; Vanduffel et al. 2001) and to rodents as well as to humans. Because these data are represented digitally from the outset, registering such data to surface-based atlases should be easier and more accurate than for many of the data sets illustrated in this chapter. As the richness and complexity of such atlases and associated databases grow, the ways in which neuroscientists routinely access the data will likely evolve to be progressively more web-based, analogous to how molecular biologists use search engines and large databases to access an increasingly large fraction of the information they use in their research.

Abbreviations

Cortical Areas:			
DP	dorsal prelunate area	7al	lateral area 7a
FST	floor of superior temporal area	DMOcx	Dorso-medial occipital complex
IPa	area IPa from Cusick et al., (1995)	IPd	
LIPd	lateral intraparietal (dorsal)	ITcx	Inferotemporal complex
LIPv	lateral intraparietal (ventral)	MSTcx	Medial Superior temporal complex
MDP	medial dorsal parietal area	MTc	caudal to Middle Temporal
MIP	medial intraparietal area	OAA	
MST	medial superior temporal area	PGa	
MT	middle temporal area	POa-e	external division of area POa
PIP	posterior intraparietal area	POa-i	internal division of area POa
PO	parietal-occipital area	PPcx	Posterior parietal complex
TAA	area TAA from Cusick et al., (1995)	TE1	subdivision 1 of TE
TEad	antero-dorsal division of TE	TE1-3d	dorsal subdivision of TE1-3
TEav	antero-ventral division of TE	TE1-3v	ventral subdivision of TE1-3
TF	temporal area F	TE2	subdivision 2 of TE
TH	temporal area H	TE3	subdivision 3 of TE
Tpt	temporo-parietal area	TEa/m	subdivisions a and m of TE
TPOc	temporal parietal occipital (caudal)	TEm	medial division of TE
TPOi	temporal parietal occipital (intermediate)	TPO	temporo-parietal-occipital area
TPOr	temporal parietal occipital (rostral)	V2d	dorsal division of V2
VIP	ventral intraparietal	V2v	ventral division of V2
VIP*	heavily myelinated subdivision of VIP	V3d	dorsal division of V3
V1	visual area 1	V3v	ventral diivision of V3
V2	visual area 2	V6	visual area 6
V3	visual area 3	V6A	Visual area 6A
V3A	visual area V3A	VSTcx	Ventral superior temporal complex
V4	visual area 4		
V4t	V4 transitional area		
VOT	ventral occipitotemporal area		
VP	ventral posterior area		
7a	visual area 7a		
46	visual area 46		
LOP	lateral occipital parietal		
MST	medial superior temporal area		
MSTd	dorsal subdivision of MST		
MSTl	lateral subdivision of MST		
MSTda	dorso-anterior subdivision of MST		
MSTdp	dorso-posterior subdivision of MST		
MSTm	medial subdivision of MST		
VIPl	lateral subdivision of VIP		
VIPm	medial subdivision of VIP		
V4ta	V4 transitional area (anterior)		
V4tp	V4 transitional area (posterior)		

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