Distributed Hierarchical Processing in the Primate Cerebral Cortex

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In recent years, many new cortical areas have been identified in the macaque monkey. The number of identified connections between areas has increased even more dramatically. We report here on (1) a summary of the layout of cortical areas associated with vision and with other modalities, (2) a computerized database for storing and representing large amounts of information on connectivity patterns, and (3) the application of these data to the analysis of hierarchical organization of the cerebral cortex. Our analysis concentrates on the visual system, which includes 25 neocortical areas that are predominantly or exclusively visual in function, plus an additional 7 areas that we regard as visual-association areas on the basis of their extensive visual inputs. A total of 305 connections among these 32 visual and visual-association areas have been reported. This represents 31% of the possible number of pathways if each area were connected with all others. The actual degree of connectivity is likely to be closer to 40%. The great majority of pathways involve reciprocal connections between areas. There are also extensive connections with cortical areas outside the visual system proper, including the somatosensory cortex, as well as neocortical, transitional, and archicortical regions in the temporal and frontal lobes. In the somatosensory/motor system, there are 62 identified pathways linking 13 cortical areas, suggesting an overall connectivity of about 40%. Based on the laminar patterns of connections between areas, we propose a hierarchy of visual areas and of somatosensory/motor areas that is more comprehensive than those suggested in other recent studies. The current version of the visual hierarchy includes 10 levels of cortical processing. Altogether, it contains 14 levels if one includes the retina and lateral geniculate nucleus at the bottom as well as the entorhinal cortex and hippocampus at the top. Within this hierarchy, there are multiple, intertwined processing streams, which, at a low level, are related to the compartmental organization of areas V1 and V2 and, at a high level, are related to the distinction between processing centers in the temporal and parietal lobes. However, there are some pathways and relationships (about 10% of the total) whose descriptions do not fit cleanly into this hierarchical scheme for one reason or another. In most instances, though, it is unclear whether these represent genuine exceptions to a strict hierarchy rather than inaccuracies or uncertainties in the reported assignment.

During the past decade, there has been an explosion of information about the organization and connectivity of sensory and motor areas in the mammalian cerebral cortex. Many laboratories have concentrated their efforts on the visual cortex of macaque monkeys, whose superb visual capacities in many ways rival those of humans. In this article, we survey recent progress in charting the layout of different cortical areas in the macaque and in analyzing the hierarchical relationships among these areas, particularly in the visual system.

The original notion of hierarchical processing in the visual cortex was put forward by Hubel and Wiesel (1962, 1965) to account for a progressive increase in the complexity of physiological receptive field properties in the cat visual cortex. In particular, they suggested that a serial, feedforward scheme could account for the generation of simple cells from LGN inputs, and complex cells, in turn, from simple cells. Likewise, the properties of hypercomplex cells and even "higher-order hypercomplex cells" were attributed to inputs from their immediate predecessors. However, the pure form of this hypothesis is difficult to reconcile with the finding of highly reciprocal connectivity and parallel channels discovered in more recent studies of the visual pathway (cf. Rockland and Pandya, 1979; Stone et al., 1979; Lennie, 1980; Lennie et al., 1990; Shapley, 1990). On the other hand, there is no a priori reason to restrict the notion of hierarchical processing to a strictly serial sequence. In general, any scheme in which there are well-defined levels of processing can be considered hierarchical.

The notion that anatomical criteria could be used to delineate a hierarchy of cortical areas first received detailed scrutiny about a decade ago (Rockland and Pandya, 1979; Friedman, 1983; Maunsell and Van Essen, 1983). Since this hypothesis was last reviewed systematically (Van Essen, 1985), the number of identified visual areas and identified connections has increased greatly. In addition, 2 recent studies (Andersen et al., 1990; Boussaoud et al., 1990) have proposed hierarchical relationships for parietal, temporal, and frontal areas that are largely, but not completely, consistent with one another and with our previous schemes. Here, we provide a critical examination of the degree to which the entire ensemble of available data fits into an overall hierarchical scheme. We also review the evidence that the principle of hierarchical

organization applies to other functional modalities and to other species besides macaques.

A related theme in our analysis concerns the nature of concurrent processing streams in the visual cortex. These streams are linked at the input side to specific subcortical inputs from the magnocellular (M) and parvocellular (P) layers of the LGN (cf. Blasdel and Lund, 1983; Hubel and Livingstone, 1987) and, at the output side, to functionally distinct regions of the parietal and temporal lobes (Ungerleider and Mishkin, 1982; Desimone and Ungerleider, 1989). Our analysis will emphasize that, on the one hand, there is considerable segregation of information flow throughout the visual pathway; on the other hand, there is also substantial intermixing and cross talk between streams at successive stages of processing. It is likely that these complexities in the anatomical circuitry reflect the multiplicity of computational strategies needed for efficient visual function (DeYoe and Van Essen, 1988).

Subdivisions and Interconnections of the Visual Cortex

A Cortical Map

Our primary format for illustrating the location of different visual areas involves the use of 2-D cortical maps that are generated from contours of layer 4 in a series of regularly spaced histological sections (Van Essen and Zeki, 1978; Van Essen and Maunsell, 1980). Previous summary maps showing the distribution of areas (Van Essen and Maunsell, 1983; Van Essen, 1985) were based on section drawings from a hemisphere published by Brodmann (1905). That map was not especially accurate, however, because of the large and somewhat nonuniform spacing between sections, and no scale was provided. We have therefore generated a complete map from a hemisphere used in a previous study from this laboratory, in which information about the pattern of interhemispheric connections and about cortical myeloarchitecture was available for identifying certain visual areas (Van Essen et al., 1986). Figure 1 shows the overall layout of the map, including the section contours upon which the map was based (thin lines; 2-mm spacing between sections), the location of cortex within sulci (shading), and the position of the fundus of each sulcus (dashed lines). As in previous cortical maps, it was necessary to introduce a few cuts, or discontinuities, to prevent serious distortions in the representation, and these are indicated by heavy solid lines along the perimeter. In addition to the obvious cut that surrounds area V1 (the elliptical region on the left), there are 2 smaller discontinuities, one along the ventrolateral side of the frontal lobe (upper right), and the other at the temporal pole (lower right). The remainder of the perimeter of the map represents intrinsic borders between the cortex and various noncortical structures (e.g., the dentate gyrus, amygdalar nuclei, and corpus callosum). This map also differs from its predecessors in that it contains the entirety of the cerebral cortex, including archicortical, paleocortical, and transitional regions, as well as the standard 6-layered neocortex.

Visual Areas

Our current understanding of the layout of different visually related areas is indicated by the color-coded scheme in Figure 2. Altogether, there are 32 separate neocortical areas that are implicated in visual processing, based on the occurrence of visually responsive neurons and/or the presence of major inputs from known visual areas. Each of these visual areas is shaded with a different color. The overall extent of the visual cortex corresponds closely to the visually responsive regions identified in the 2-deoxyglucose study of Macko and Mishkin (1985). However, not all of these areas are exclusively visual in function. Nonvisual contributions include inputs from other sensory modalities (especially auditory and somatosensory), visuomotor activity (i.e., related to eye movements), and attentional or cognitive influences (cf. Andersen, 1987; Maunsell and Newsome, 1987; Goldman-Rakic, 1988; Desimone and Ungerleider, 1989). We have drawn a distinction between 25 areas that appear to be predominantly or exclusively visual and another 7 neocortical areas that are less intimately linked to vision and will be considered visual-association areas. This is unlikely to reflect a strict dichotomy, though, and there may well be a continuum in the degree to which various areas are selectively involved in visual processing.

There are 9 visual areas in the occipital lobe, which are shaded in purple, blue, and reddish hues in Figure 2. The 10 visual areas of the parietal lobe (1 of which is associational) are in shades of yellow, orange, or light brown; the 11 areas of the temporal lobe are in various shades of green; and the 2 visual-association areas of the frontal lobe are in dark shades of brown. The criteria used in identifying these areas are discussed in detail below.

On the remainder of the cortical map, various functional or regional domains are delimited in black and white by heavy outlines. These include somatosensory, auditory, motor, olfactory, gustatory, subicular, hippocampal, entorhinal, retrosplenial, and cingulate regions, plus medial, dorsal, lateral, and orbital regions of the prefrontal cortex. Most of these regions have been further subdivided into specific cortical areas, indicated by fine lines, on the basis of cortical architecture and/or connectivity. Many of these areas are denoted by the same type of numbering scheme promulgated by Brodmann (1905). However, in many instances, we have used areal identifications from more recent studies that differ substantially from Brodmann's original scheme. (This can be seen by comparing Fig. 2 of the present study with Fig. 9 of Van Essen and Maunsell, 1980).

The demarcation of areal boundaries on the cortical map involved several stages. As noted, a few visual areas were explicitly identified by architectonic criteria in the hemisphere from which the map was made, and the locations of several additional areas were constrained by the pattern of interhemispheric connections that had been determined in this hemisphere. For the remaining areas, it was necessary to transpose boundaries not only from a different brain,

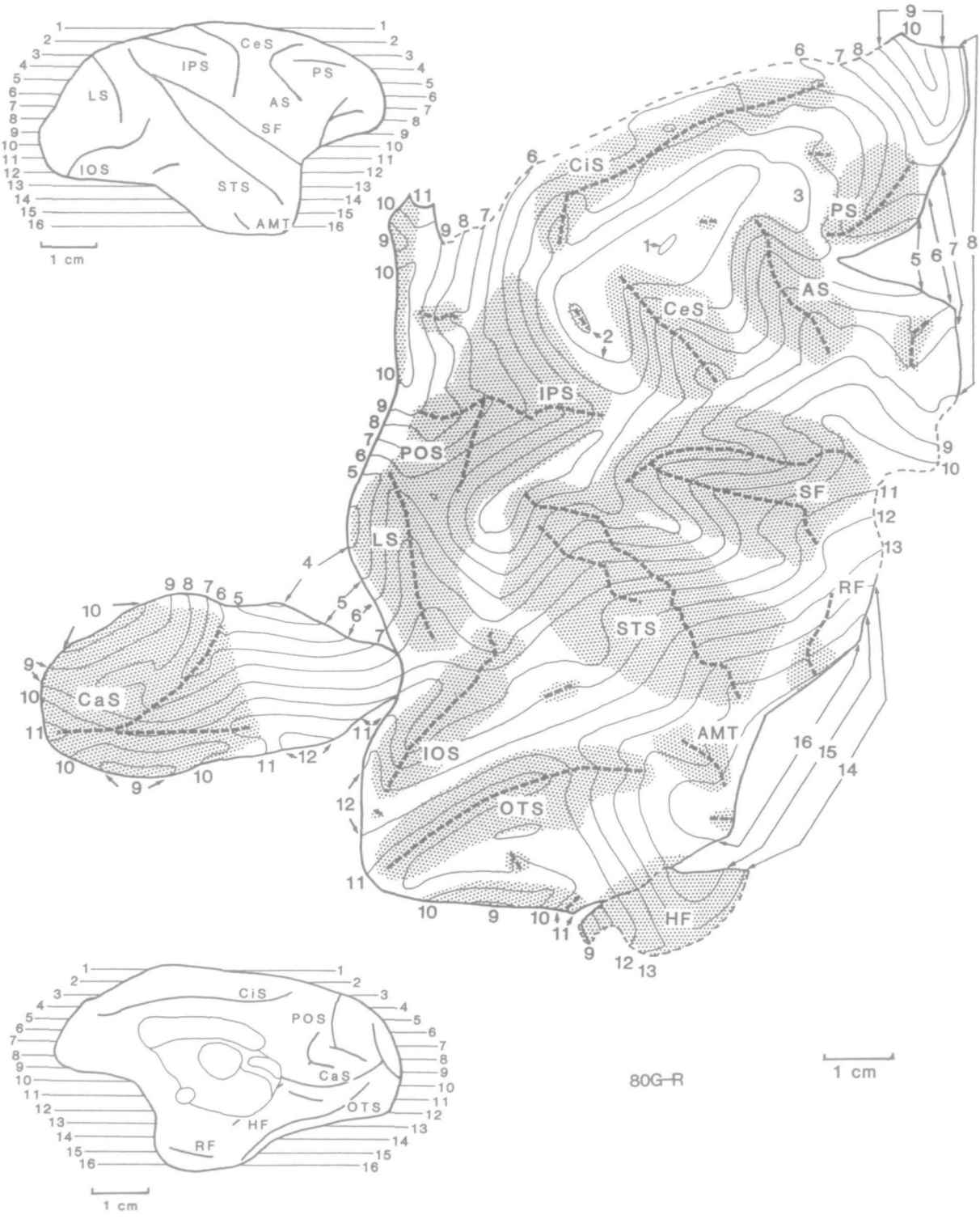

Figure 1. A 2-D map of cerebral cortex in macaque monkey, prepared by the method of Van Essen and Maunsell (1980). *Fine solid lines* represent the contours of layer 4 from a series of 16 horizontal sections taken at 2-mm intervals through the cortex. *Numbers* along the margins of the map correspond to the different section levels indicated in the lateral (*upper left*) and medial (*lower left*) views of the hemisphere. *Shading* indicates cortex lying within various sulci, and the fundus of each sulcus is indicated by *heavy dashed lines*. *Solid lines* along the perimeter of the map indicate regions where artificial cuts have been made to reduce distortions. *Dashed lines* along the perimeter represent the margins of the cortex, where it adjoins various noncortical structures: the corpus callosum/induseum griseum (*top*), olfactory tubercle and amygdalar nuclei (*right*), and dentate gyrus of the hippocampus (*bottom*). The scale on the map has been adjusted to correct for the estimated 16% shrinkage that occurs during histological processing (cf. Van Essen and Maunsell, 1980; Van Essen et al., 1986). *AMT*, anterior middle temporal sulcus; *AS*, arcuate sulcus; *CaS*, calcarine sulcus; *CeS*, central sulcus; *CiS*, cingulate sulcus; *HF*, hippocampal fissure; *IOS*, inferior occipital sulcus; *IPS*, intraparietal sulcus; *LS*, lunate sulcus; *OTS*, occipitotemporal sulcus; *POS*, parieto-occipital sulcus; *PS*, principal sulcus; *RF*, rhinal fissure; *SF*, sylvian fissure; *STS*, superior temporal sulcus.

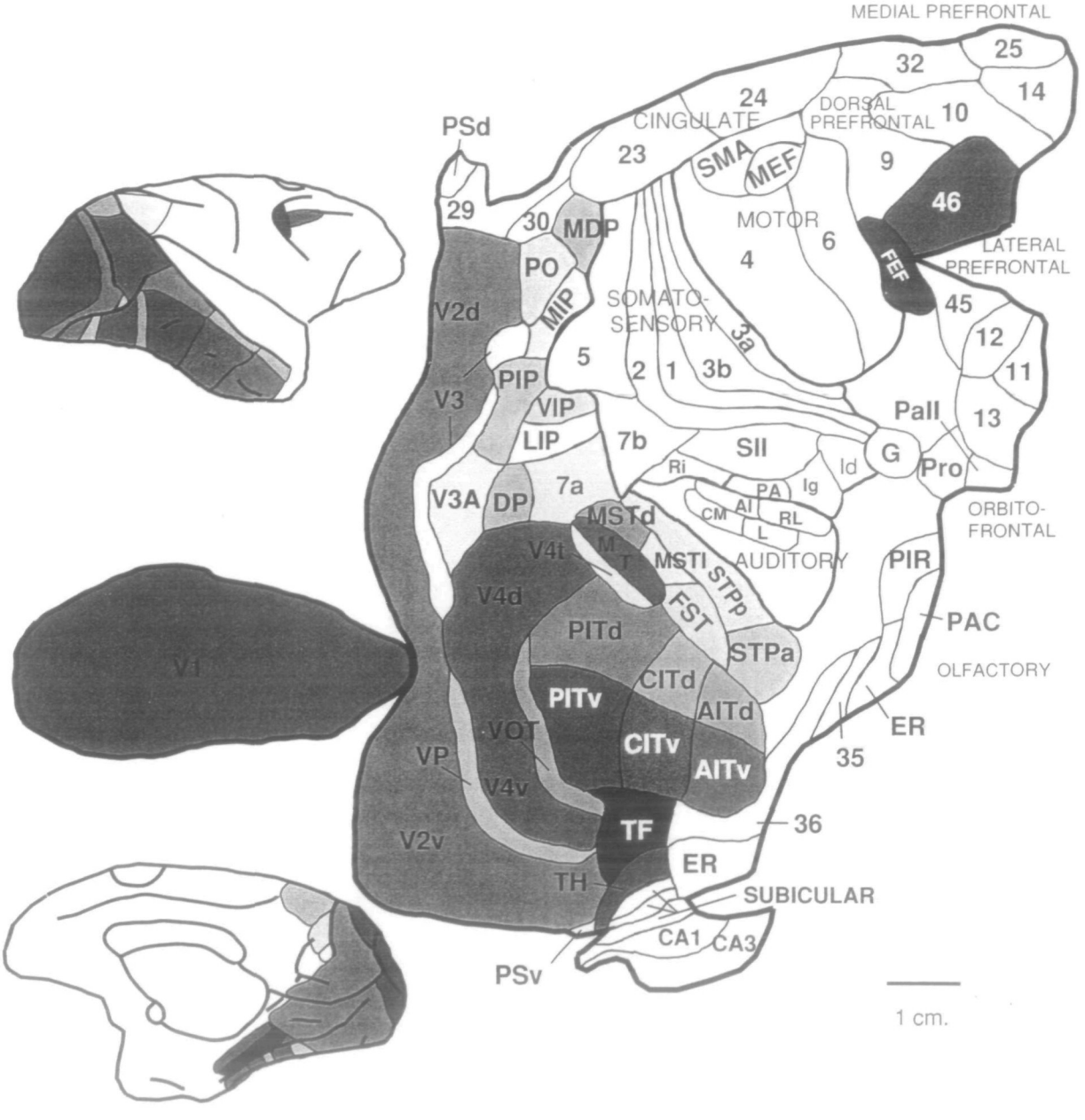

Figure 2. Map of cortical areas in the macaque. The locations of 32 visual areas are indicated with colors that indicate whether they are in the occipital lobe (*purple, blue,* and *reddish hues*), parietal lobe (*yellow, orange,* and *light brown hues*), temporal lobe (*green hues*), or frontal lobe (*brown hues*). The references used in placement of boundaries for the different visual areas are listed in Table 1. The scale applies only to the map; the brain drawings are smaller by 20% (cf. Fig. 1). The specific studies used in estimating the border of the various nonvisual areas are as follows: Somatosensory areas 3a, 3b, 1, 2, 5, 7b, *SII, Ri* (retroinsular), *Pa* (postauditory), *Ig* (insular granular), and *Id* (insular dysgranular) were based on Jones and Burton (1976), Jones et al. (1978), Robinson and Burton (1980), Friedman et al. (1986), Huerta et al. (1987), and Andersen et al. (1990). Note that, in this scheme, areas 1 and 2 intervene between SII and area 3b. In other primates, including the marmoset and the owl monkey, SII appears to directly adjoin area 3b, and it has been suggested that more detailed mapping will reveal the same arrangement in the macaque (Cusick et al., 1989; Krubitzer and Kaas, 1990). Auditory areas *A1* (primary auditory), *RL* (rostrolateral), *CM* (caudomedial), and *L* (lateral) were based on Merzenich and Brugge (1973). The postauditory area (*Pa*) is described as a somatosensory area by Robinson and Burton (1980) and as an auditory area by Friedman et al. (1986). We have included it as part of the auditory cortex in our analysis, but obviously this issue merits further investigation. Areas of the hippocampal complex (HC), including the entorhinal cortex (ER), areas *35* and *36*, prosubiculum, prosubiculum, subiculum, and fields CA1 and CA3, were based on Amaral et al. (1987), Insausti et al. (1987), and Saunders et al. (1988). Olfactory areas, including the piriform cortex (PIR) and periamygdaloid cortex (PAC), were based on Insausti et al. (1987). Orbitofrontal areas 11, 12, and 13, proisocortex (Pro), periallocortex (PaII), lateral prefrontal area 45, dorsal prefrontal areas 9 and 10, and medial prefrontal areas 14, 25, and 32 were based on Barbas and Pandya (1989) and Insausti et al. (1987). Motor areas *4* (primary motor) and *6* (premotor and arcuate premotor, or 6s and 6i), supplementary motor area (*SMA*), and medial eye field (*MEF*, or supplementary eye fields, SEF) were based on Brodmann (1905), Matelli et al. (1986), Insausti et al. (1987), Schlag and Schlag-Rey (1987), Hutchins et al. (1988), and Mann et al. (1988). Finally, cingulate and other limbic areas 23, 24, 29 (retrosplenial), 30 (PGm or 7m), and prostriate [PS, divided by an artificial cut into dorsal (d) and ventral (v) sectors] were based on Insausti et al. (1987) and Sanides (1970). A few regions in the posterior orbitofrontal, lateral prefrontal, and anterior sylvian cortices have not been closely studied and are left unspecified here.

but usually from a different type of representation as well, because the best available information on areal boundaries, in may cases, was on a drawing of a brain or on a series of brain sections cut at a different angle than the horizontal plane used for our map.[1]

Table 1 provides additional information pertaining to the identification and characterization of different visual areas. The areas are grouped according to their geographic location in different lobes (column 1). Columns 2 and 3 give the acronyms and full-length names, respectively, that we prefer for each area. Column 4 provides information about the degree of topographic organization, rated on a scale of 1–4 (see below). It also identifies the visual-association areas alluded to above. Column 5 provides a measure of the confidence with which different areas have been identified, as discussed below. Column 6 provides 1 or more references that have been particularly useful in determining the extent and the boundaries of each area. These citations do not necessarily reflect either the most recent study or the original study involved in its identification. They are designated by abbreviations based on the first letters of the authors' surnames plus the publication year. A key that links these abbreviations to the standard text citations is given in the table notes. This format, which we will use in other tables as well, provides a compact representation that allows more rapid recognition of specific references than is attainable with a simple numerical listing.

In general, 3 methodological approaches have been most useful in identifying different visual areas: (1) *Connectivity analysis* relies on finding a characteristic pattern of inputs and outputs for each cortical area. This approach has proven useful for nearly all visual areas and is considered in detail below. (2) *Architectonics* relies on a distinctive structure as seen in Nissl, myelin, or other staining techniques. It offers a reliable approach for only a minority of the areas listed in Table 1 and was used to map 3 of the areas (V1, V3, and MT) in the particular hemisphere illustrated in Figure 2. (3) *Topographic organization* relies on an orderly mapping of the visual field in each area, as revealed physiologically or anatomically. About half of the identified visual areas show a measurable degree of topographic organization. However, the precision and orderliness of the visual representation varies widely. As indicated in column 4 of Table 1, we have grouped areas into 4 categories: extremely precise and regular topography (category 1), intermediate resolution (category 2), coarse and irregular (category 3), and finally, little or no discernible topography (category 4). In addition, some visual areas (most notably V3 and VP) contain incomplete representations, including only the superior (S) or inferior (I) contralateral quadrant; nonetheless, several lines of evidence argue that these areas should be considered distinct from one another (cf. Burkhalter et al., 1986). Hence, topographic information, like architectonics, is a valuable tool, but can be inadequate or even misleading when applied in isolation from other approaches.

In addition to these 3 primary methodological approaches, the identification of some areas has been facilitated by information about physiological characteristics, as evidenced by distinctive receptive field properties of neurons, and by examining the behavioral consequences of restricted lesions or focal electrical stimulation. Ideally, each area should be independently identifiable using all 5 of the aforementioned approaches. In practice, however, the identification of most areas is based only on a subset of these approaches, often just 1 or 2 (cf. Van Essen, 1985).

Different cortical areas vary in the reliability with which they have been identified and the precision with which their borders have been mapped, as indicated by the 3 categories of confidence level in column 5 of Table 1. The first 2 categories include areas we consider to have been identified with a reasonably high degree of confidence. Category 1 refers to areas, such as V1 and V2, whose borders have been mapped with considerable precision (usually to within 1–2 mm). Category 2 refers to areas, such as V3A and V4, whose identity is widely accepted but whose borders are known only approximately. Category 3 includes areas whose identification is less secure and more open to debate. This is the largest of the 3 categories, and it signifies that the basic task of determining how the cortex is partitioned into specific areas is by no means complete.

Most regions of the visual cortex have more than 1 name that is in common use. Table 1 provides a partial listing of these alternative terminologies. In dealing with the nomenclature issue, we have drawn a distinction between (1) names that are simply different descriptors for what is clearly the same underlying visual area (e.g., areas 17 vs. V1, V3v vs. VP, and MT vs. V5; column 7), and (2) names that reflect substantially different schemes for partitioning the cortex (column 9). In some cases, the alternative scheme is a more coarse partitioning than the one we prefer (e.g., TEO vs. PITd and PITv). In other cases, the alternative scheme is even more fine grained (e.g., POa–i and POa–e vs. LIP). In still other cases, most notably in the inferotemporal cortex (IT), the relationship between different schemes is more complex and irregular.

Surface Area

Measurements of the surface area of different regions of the cortical map (Table 2) provide useful information about the absolute and relative amounts of cortical machinery devoted to different types of processing. The total extent of the cerebral cortex in this particular hemisphere, after correcting for shrinkage during histological processing, is 10,575 mm^2, of which 9940 mm^2 (94%) is neocortex. Besides the neocortex, there are 245 mm^2 of the hippocampus proper (fields CA1 and CA3, the subiculum and the prosubiculum), 120 mm^2 of paleocortex (pyriform and periamygdaloid cortex), and 270 mm^2 of transitional cortex [entorhinal cortex (ER), periallocortex, parasubiculum, presubiculum, and prostriate cortex]. The visual cor-

Table 1
Visual areas in the macaque monkey

Lobe	Area Acronym	Area Full Name	Topography[a]	Confidence[b]	References[c]
Occipital	V1	Visual area 1	1	1	VNM, '84; VNMB, '86
	V2	Visual area 2	2	1	GGS, '81; VNMB, '86
	V3	Visual area 3	2; I	1	VNMB, '86
	VP	Ventral posterior	2; S	1	NMV, '86
	V3A	Visual area V3A	3	2	VZ, '78; GSG, '88
	V4	Visual area 4	3	2	Z, '78; GSG, '88
	VOT	Ventral occipitotemporal	3; S	3	*FOV, '85*; VFDOK, '91
	V4t	V4 transitional	3; I	2	DU, '86; GSG, '88
	MT	Middle temporal	3	1	VMB, '81; DU, '86; MV, '87
Temporal	FST	Floor of superior temporal	4	2	DU, '86
	PITd	Posterior inferotemporal (dorsal)	3	3	VFDOK, '91
	PITv	Posterior inferotemporal (ventral)	3	3	VFDOK, '91
	CITd	Central inferotemporal (dorsal)	4	3	VFDOK, '91
	CITv	Central inferotemporal (ventral)	4	3	VFDOK, '91
	AITd	Anterior inferotemporal (dorsal)	4	3	VFDOK, '91
	AITv	Anterior inferotemporal (ventral)	4	3	VFDOK, '91
	STPp	Superior temporal polysensory (posterior)	4; A	3	BUD, '90
	STPa	Superior temporal polysensory (anterior)	4; A	3	BUD, '90
	TF	TF	4; A	3	VB, '47; SP, '76
	TH	TH	4; A	3	VB, '47; SP, '76
Parietal	MSTd	Medial superior temporal (dorsal)	4	2	KW, '88
	MSTl	Medial superior temporal (lateral)	4	2	KW, '88
	PO	Parieto-occipital	3	2	CGOG, '88
	PIP	Posterior intraparietal	3	2	*FBV, '87*; CGOG, '88
	LIP	Lateral intraparietal	3	3	AAC, '85; AAES, '90; BAS, '90
	VIP	Ventral intraparietal	3	3	BAS, '90; MV, '83; UD, '86
	MIP	Medial intraparietal	?	3	CGOG, '88
	MDP	Medial dorsal parietal	?	3	CGOG, '88
	DP	Dorsal prelunate	3	3	AAC, '85; MA, '86
	7a	7a	4; A	2	AAC, '85; AAES, '90
Frontal	FEF	Frontal eye field	3; A	2	BGBS, '85; SDGM, '89
	46	46	4; A	3	B, '88; BP, '89

The visual areas in the macaque monkey are grouped according to physical location (column 1) and identified according to acronym, full name, and alternative names. Alternative partitioning schemes for the same region are indicated in column 9, as well.

[a] Topography refers to degree of topographic organization and is rated according to a qualitative 4-point scale, going from extremely precise (rating 1) to completely nontopographic (rating 4). S and I refer to areas that contain an incomplete representation of superior and inferior quadrants, respectively, and A refers to areas that are associational.

[b] Confidence refers to the confidence with which each area has been identified and charted and is rated by a qualitative 3-point scale: confident identification and well-defined borders (rating 1), confident identification but only approximate border determination (rating 2), and significant uncertainties in both identification and border assignments (rating 3).

[c] Reference key (italic entries signify abstracts):

AAC, '85	Andersen, Asanuma, and Cowan, 1985	BP, '89	Barbas and Pandya, 1989
AAES, '90	Andersen, Asanuma, Essick, and Siegel, 1990	BRL, '87	Baylis, Rolls, and Leonard, 1987
B, '05	Brodmann, 1905	BUD, '90	Boussaoud, Ungerleider, and Desimone, 1990
B, '85	Brady, 1985	CGOG, '88	Colby, Gattass, Olson, and Gross, 1988
B, '88	Barbas, 1988	CG, '89	Cavada and Goldman-Rakic, 1989a
BAS, '90	Blatt, Andersen, and Stoner, 1990	DU, '86	Desimone and Ungerleider, 1986
BDG, '81	Bruce, Desimone, and Gross, 1981	F, '86	Fenstemaker, 1986
BGBS, '85	Bruce, Goldberg, Bushnell, and Stanton, 1985	*FBV, '87*	*Felleman, Burkhalter, and Van Essen, 1987*

tex (including the visual-association areas) occupies an estimated 5385 mm², or 55% of the neocortex. As noted previously, the visual cortex dwarfs the regions devoted to somatosensory, motor, and auditory processing, which occupy 11%, 8%, and 3% of neocortex, respectively. Finally, the remainder of the neocortex consists of areas in the cingulate region on the medial wall (450 mm²), in the prefrontal cortex (930 mm²), and in the insular region between the frontal and temporal lobes. To provide a physical perspective for these numbers, it is useful to note that the visual cortex as a whole has about the same surface area as a medium-sized cookie (about 8 cm diameter), while the entire cerebral cortex in one hemisphere corresponds to a large cookie (about 12 cm diameter).

Individual visual areas on the cortical map span a 50-fold range in size. V1 and V2 are by far the largest, with each occupying 1100–1200 mm², or 11–12% of the neocortex. V4 is about half their size (540 mm²). Ten areas are in the intermediate range of 100–200

Table 1
Continued

Alternative Name	References[c]	Alternative Scheme	References[c]
area 17			
V-II		area 18	B, '05
V3d	GSG, '88		
V3v	GSG, '88		
		V4pm/V4al	MB, '84
		V4/TEO border	GSG, '88
V5	SZ, '85	OAa	SP, '78
TEOd	IY, '88	TEO	F, '86; IY, '87
TEOv	IY, '88	TEO	F, '86; IY, '87
		TEd; TEp; TEa/TEm	SP, '78; BRL, '87; IY, '87; YNSI, '88
		TEv; TEp; TE3/TE2	SP, '78; BRL, '87; IY, '87; YNSI, '88
		TEd; TEa; TEm/TEa	SP, '78; BRL, '87; IY, '87; YNSI, '88
		TEv; TEa; TE1/TE2	SP, '78; BRL, '87; IY, '87; YNSI, '88
		STP; PGa/IPa/TPO 3, 4	BDG, '81; SP, '89
		STP; IPa/TPO 1, 2	BDG, '81; SP, '89
		TFm, TFl	AAES, '90
		TFl, TF2	B, '85
MSTc	BUD, '90	DSR area; DMZ	SYTKFI, '86; UD, '86
MSTp	BUD, '90		
		part of V3A	VZ, '78
		7ip; LIPd/LIPv; POa–e/POa–i	SP, '80, '86; CG, '89; BAS, '90
		VIP*; 7ip; POa–i; IPd	SP, '80; UD, '86; B, '88; CG, '89
DPL			V, '85
		IPG; PP; PG	VB, '47; BUD, '90
		8a; FDγ	W, '40; VB, '47
Principal sulcus	CG, '89	9	B, '05

FDV, '85	*Felleman, DeYoe, and Van Essen, 1985*	SP '89	Seltzer and Pandya, 1989b
GGS, '81	Gattass, Gross, and Sandell, 1981	SYTKFI, '86	Saito, Yukie, Tanaka, Kikosaka, Fukada, and Iwai, 1986
GSG, '88	Gattass, Sousa, and Gross, 1988		
IY, '87	Iwai and Yukie, 1987	SZ, '85	Shipp and Zeki, 1985
IY, '88	Iwai and Yukie, 1988	UD, '86	Ungerleider and Desimone, 1986b
KW, '88	Komatsu and Wurtz, 1988a	V, '85	Van Essen, 1985
MA, '86	May and Andersen, 1986	VB, '47	Von Bonin and Bailey, 1947
MB, '84	Maguire and Baizer, 1984	VFDOK, '91	Van Essen, Felleman, DeYoe, Olavarria, and Knierim, 1991
MV, '83	Maunsell and Van Essen, 1983		
MV, '87	Maunsell and Van Essen, 1987	VMB, '81	Van Essen, Maunsell, and Bixby, 1981
NMV, '86	Newsome, Maunsell, and Van Essen, 1986	VNM, '84	Van Essen, Newsome, and Maunsell, 1984
SDGM, '89	Stanton, Deng, Goldberg, and McMullen, 1989	VNMB, '86	Van Essen, Newsome, Maunsell, and Bixby, 1986
SP, '76	Seltzer and Pandya, 1976	VZ, '78	Van Essen and Zeki, 1978
SP, '78	Seltzer and Pandya, 1978	W, '40	Walker, 1940
SP, '80	Seltzer and Pandya, 1980	YNSI, '88	Yukie and Iwai, 1988
SP '86	Seltzer and Pandya, 1986	Z, '78	Zeki, 1978a,b

mm², and 18 areas are small (by macaque standards), ranging from 100 mm² down to a low value of 25 mm² for area MSTl.

There are several sources of uncertainty associated with these estimates of surface area. The cortical map itself (Fig. 2) has some areal distortions, whose magnitude is likely to be in the range of 10%–20% for most regions of the map, but is probably larger in some regions (cf. Van Essen and Maunsell, 1980). There are also inaccuracies in our transposition of areal boundaries defined in other studies onto the particular hemisphere used for this map (see above). These are hard to quantify, but they probably reflect errors of 50% or more for some areas. Finally, there is intrinsic variability in the size as well as the location of particular areas from one brain to the next. Areas with sharply defined borders such as V1 and MT show roughly 2-fold individual variability in surface area (Van Essen et al., 1981, 1984), and it seems likely that this range will be applicable to most, if not all, cortical

Table 2
Surface area of cortical subdivisions in the macaque

Subdivision	Cortical Area	Area (mm^2)	% of Visual Cortex	% of Neocortex	% of Cerebral Cortex
Visual Areas					
Occipital	V1	1120	20.8	11.5	
	V2	1190	22.1	12.2	
	V3	120	2.2	1.2	
	VP	95	1.8	1.0	
	V3A	110	2.0	1.1	
	V4	540	10.0	5.5	
	VOT	75	1.4	0.8	
	V4t	35	0.6	0.4	
	MT	55	1.0	0.6	
Total Occipital		3340 mm^2	62.0%	34.0%	
Temporal	FST	65	1.2	0.7	
	PITd	200	3.7	2.0	
	PITv	190	3.5	1.9	
	CITd	80	1.5	0.8	
	CITv	120	2.2	1.2	
	AITd	70	1.3	0.7	
	AITv	110	2.0	1.1	
	STPp	120	2.2	1.2	
	STPa	90	1.7	0.9	
	TF	100	1.9	1.0	
	TH	45	0.8	0.5	
Total Temporal		1190 mm^2	22.0%	12.0%	
Parietal	MSTd	35	0.6	0.4	
	MSTl	25	0.5	0.3	
	PO	75	1.4	0.8	
	PIP	85	1.6	0.9	
	LIP	55	1.0	0.6	
	VIP	40	0.7	0.4	
	MIP	55	1.0	0.6	
	MDP	50	0.9	0.5	
	DP	50	0.9	0.5	
	7a	115	2.1	1.2	
Total Parietal		585 mm^2	11.0%	6.0%	
Frontal	FEF	70	1.3	0.7	
	46	200	3.7	2.0	
Total Frontal		270 mm^2	5.0%	3.0%	
Total Visual Cortex		5385 mm^2	100.0%	55.0%	52.0%
Other Neocortex					
Somatosensory		1130		11.5	
Motor		770		7.9	
Auditory		330		3.4	
Gustatory		40		0.5	
Prefrontal (Areas 9, 10, 11, 12, 13, 14, 25, 32, 45)		920		9.4	
Cingulate (Areas 23, 24, 29, 30, PS)		520		5.3	
Perirhinal (35/36)		160		1.6	
Unspecified Neocortex		515		5.3	
Total Neocortex		9970 mm^2		100.0%	94.0%
Transitional Cortex					
Hippocampal Formation					
Subiculum		65			
CA1		70			
CA3		110			
Total Hippocampal Cortex		245 mm^2			2.3%
Transitional Areas					
Presubiculum		15			
Parasubiculum		20			
Entorhinal		160			

Table 2
Continued

Subdivision	Cortical Area	Area (mm²)	% of Visual Cortex	% of Neocortex	% of Cerebral Cortex
Pro		50			
Pall		25			
Total Transitional Cortex		270 mm²			2.6%
Paleocortex					
Pyriform		65			
Periamygdaloid		55			
Total Paleocortex		120 mm²			1.2%
Total Non-neocortex		635 mm²			6.1%
Total Cerebral Cortex		10575 mm²			100.0%

This table shows surface area estimates for different cortical areas, geographic regions, and modality-specific regions. Surface areas were calculated from the 2-D cortical map illustrated in Figure 2. Values are shown as absolute surface areas (mm², corrected for tissue shrinkage) and as percent of total visual cortex, total neocortex, and/or total cerebral cortex. Absolute values are shown to 2 significant digits or, for small areas, to the nearest 5 mm². A number of uncertainties apply to all of these estimates (see text), and the values for individual areas should, in general, be regarded as accurate only to within about a factor of 2.

areas. Thus, the values in Table 2 should be regarded as only rough approximations to the physical extent of any given area in any particular hemisphere.

Connectivity

Nearly all of the areas included in this scheme can be distinguished on the basis of their overall pattern of connectivity, and for many, this is the primary basis for identification. This can be seen from Table 3, which gives a concise summary of the corticocortical visual pathways identified as of mid-1990. Each entry in the 2-D matrix denotes the status of a pathway (present, absent, unknown, or questionable) from an area shown on the left to an area shown on the top. Specifically, a plus sign (+) signifies an identified pathway, a dot (·) signifies a pathway that has been tested for and found absent, "NR" (nonreciprocal) signifies a pathway that is reported to be absent in one direction even though the projection in the reverse direction has been demonstrated, and a question mark (?) signifies a pathway that has been reported but is questionable owing to individual variability in occurrence or conflicting reports from different laboratories. For each area, one can quickly ascertain all of its outputs by scanning the appropriate horizontal row and all of its inputs by scanning the appropriate vertical column. In some cases, a pathway has been identified that involves a coarse subdivision (e.g., PIT) but cannot yet be assigned to the finer subdivisions indicated by more recent evidence (e.g., PITd and PITv). Consequently, we have included entries for both coarser and finer subdivisions when appropriate in the table.

Additional information on the characteristics of these pathways is provided in a subsequent section (see Table 5). This will include specific references for every connection and documentation of the questionable or controversial nature of certain connections. Many of the recently identified pathways are reported only in abstracts, and it is important not to give them the same credence as pathways that are illustrated or otherwise well documented in full-length reports. On the other hand, our description would be out of date if we included only the latter category. The compromise that we have adopted is to use large symbols for pathways in Table 3 that are documented in full-length publications and small symbols for the remainder.

It is apparent that each visual area has many inputs and outputs. Moreover, the particular pattern of connections is distinctive for each area, in terms of the overall constellation of inputs and outputs. In most cases, this pattern provides a characteristic "fingerprint" that can uniquely distinguish one area from all others. This is particularly true for areas whose connections have been thoroughly studied, such as those in the occipital lobe. Many areas, particularly the recently defined ones, have yet to be studied in detail; hence, our description of the connectional pattern is surely far from complete. For example, areas MDP and MIP each have only 2 connections shown in Table 3, but neither of these areas has yet been studied by making direct tracer injections into them.

Our emphasis on connectional information in the identification of areas continues a recent trend away from the traditional primacy given to architectonically defined subdivisions. The justification for this is largely empirical. There are now numerous instances where the original architectonic subdivisions of the classical neuroanatomists conflict with areas defined by connections or topographic organization. In several of these cases, reexamination of cortical architecture has revealed previously unrecognized architectonic transitions that do coincide with the boundaries of visual areas identified on connectional grounds, as in the cases of V3 and MT (Van Essen et al., 1981, 1986) and FST (Boussaoud et al., 1990). It is likely that there will be additional examples of this type, in part because standard Nissl and myelin stains can now be supplemented with histochemical and immunocytochemical markers that reveal distinctive patterns for different areas (cf. Hendry et al., 1988; DeYoe et al., 1990). Also, newly developed procedures for flatten-

Table 3
Matrix of connections in visual cortex

	OCCIPITAL									TEMPORAL													PARIETAL									FRONTAL	
To:										PIT			CIT						STP														
From:	V1	V2	V3	VP	V3A	V4	VOT	V4t	MT	FST	PITd	PITv	CITd	CITv	AITd	AITv	STPp	STPa	TF	TH	MSTd	MSTl	PO	PIP	LIP	VIP	MIP	MDP	DP	7a	FEF	46
V1		+	+	.	+	+	.	NR	+	.	.		.	.		.	.	.	.	.	.	.	.	?	+	+	.	.	.	.	.	.	.
V2	+		+	+	+	+	+	+	+	+	.		.	.		.	.	.	.	.	.	.	+	+	+	+	.	+	.	.	.	.	?	.
V3	+	+			+	+	.	+	+	+	.		.	.		.	.	.	.	+	.	+	.	+	+	+	+	.	.		.	?	.
VP	.	+	+		+	+	+	.	+	+	.		.	.		.	.	.	.	+	.	+	.	+	+		+	.	.		.	?	.
V3A	+	+	+	+		+			+	+	.		.	.		.	.	.	.	.	.	+	+	+				.	.	+	.	?	.
V4	+	+	+	+	+			+	+	+	+		+	+		+	.	+	.		.	+	+	+	.	.	.	.	.	+	.	?	+
VOT	.	+	.	+		+					+		+																			
V4t	+		+	.		+			+	+												NR?	+	+								?	
MT	+	+	+	+	+	+		+		+	.		.	.		.	.	.	.	.	.	+	+	?	+	+	+	.	.	.	.	+	?
FST	.	NR?	+	NR?	+	+		+	+			+		.		.	.	.		+		+	+	.	.	+	+				+	+	.
PITd	.	.	.	.	.	+			.						+	+	+							.	.	.	.				.		
PIT										+												+									+	+
PITv	.	.	.	.	.	+			.					+		+							.	.	.	.					.		
CITd	.	.	.	.	.	+			.			+			+	+						.	.	.	.	.	.			.		
CIT																															+	+
CITv	.	.	.	.	.	+			.			+			+	+						.	.	.	.	.	.			.		
AITd	.	.	.	.	.	.			.	.		+		+								.	.	.	.	.	.	.		+	+	+
AITv	.	.	.	.	.	+			.	.		+		+				.	+	+		.	.	.	.	.	.	.					
STPp	.	.	.	.	.	.			.	+			+		.			+	+	+	+	+	.	.	.	.	.	.			+	+
STP																														+		
STPa	.	.	.	.	.	.			.						+	.	+		+	+			.	.	.	.	.	.				+
TF	.	.	+	+	.	+			.	+			+		+	+	+	+			+		.	.		.	.	.		+		+
TH	.	.	.	.	.	+			.				+	+	+	+	+	+			.	.	.	.	.	.	.	.		+		+
MSTd	.	+	+	+	+	.		+	+	+		+		.	.	.	+						+		+	+			+	+	+	
MSTl	NR	+	.	.	+	.		NR?	+	+	.	.	.	.		.	.	+					+	.		+			NR?	NR?	+	
PO	+					.			+	.	.		.	.		.	.	.	.	.	.	+	+		+	+			+	+	?	
PIP	+		+	+		+			+		.		.	.		.	.	.						+					+	+		
LIP	.		+	+	+	+			+	+	.		+	.		.	.	.		+	.	+	+	+			+			+	+	+	+
VIP	.		+						+	+	.		.	.		.	.	.				+	+	+		+				+	+	
MIP	.	.	.	.	.	.			.	.	.		.	.		.	.	.				.	.	+						+		
MDP	.	.	.	.	.	.			.	.	.		.	.		.	.	.				.	.	+						+		
DP	.	.	.	.	+	+			.	+	.		.	.		.	.	.		.	.	+	+	+	+	+				+		+
7a	.	.	.	.	.	.			.		.		.	.		.	+		+		+	+	?	+		+				+	+	+
FEF	.								?	+				+		+		+				+	+	+		+	+			+		+
46	.	.	.	.	.					.				+		+		+		+	+	+	.							+	+	+	

This table is a connectivity matrix for interconnections between visual cortical areas in the macaque. Each row shows whether the area listed on the left sends outputs to the areas listed along the top. Conversely, each column shows whether the area listed on the top receives inputs from the areas listed along the left. Large plus symbols (+) indicate a pathway that has been reported in 1 or more full-length manuscripts; small plus symbols indicate pathways identified only in abstracts or unpublished studies. Specific citations are listed in Table 5. Dots (·) indicate pathways explicitly tested and found to be absent. Blanks indicate pathways not carefully tested for. Question marks (?) denote pathways whose existence is uncertain owing to conflicting reports in the literature. "NR" and "NR?" indicate nonreciprocal pathways, i.e., connections absent in the indicated direction even though the reciprocal connection has been reported. Shaded boxes along the diagonal represent intrinsic circuitry that exists within each area; these are not included among the pathways tabulated in the following table.

ing the cortex prior to sectioning can facilitate the recognition of subtle architectonic transitions (Olavarria and Van Sluyters, 1985; Tootell and Silverman, 1985).

Specific Visual Areas

In order to put the current map into perspective, it is useful to comment on the layout of specific visual areas, with emphasis on recently identified areas and areas for which uncertainties in identification persist.

We will begin with the 9 areas of the occipital lobe. First, there is a triplet of large, well-studied areas, V1, V2, and V4, each of which contains a complete topographic representation. These are surrounded anteriorly by a collection of smaller areas, 3 of which have been mapped in some detail (MT, V3, and VP), and the remainder of which are less well characterized (V3A, V4t, and VOT). V3A was originally identified and mapped by Van Essen and Zeki (1978), but its borders have been revised (see area PIP below).

Desimone and Ungerleider (1986) identified area V4t (transitional V4) as a narrow strip between MT and the dorsal half of V4; it can be distinguished from both of these neighbors by its architecture, connectivity, and neuronal receptive field properties (cf. also Schein et al., 1982; Perkel et al., 1986; Gattass et al., 1988). In ventral occipital cortex, we have identified area VOT (the ventral occipitotemporal area) as a narrow cortical strip sandwiched between the ventral half of V4 and the inferotemporal cortex (Felleman et al., 1985; Van Essen et al., 1991). VOT lies just posterior to a callosal-recipient strip that delineates the border of inferotemporal cortex (Van Essen et al., 1982). V4t and VOT contain representations of the lower and upper parts of the visual field, respectively; we provisionally consider them to be separate areas with incomplete visual representations, much as has been argued for areas V3 and VP (Burkhalter et al., 1986).

In the parietal lobe, the visual cortex occupies most or all of Brodmann's area 7 (PG and PE of von Bonin and Bailey, 1947). This region includes 3 areas (PO, PIP, and DP) situated posteriorly, 5 areas (7a, LIP, VIP, MIP, and MDP) situated more anteriorly and arranged in a lateral-to-medial swath that adjoins the somatosensory cortex, and 2 areas (MSTd and MSTl) within the dorsal part of the superior temporal sulcus (STS). MST was originally identified as the region receiving direct inputs from MT and lying near the fundus of the STS (Maunsell and Van Essen, 1983). As initially defined, however, MST is not a homogeneous region. There is now evidence for splitting it into 3 distinct areas: a dorsal region (MSTd), a "lateral" region (MSTl) that is situated ventro-antero-lateral to MSTd, and a region situated even further ventro-antero-laterally in the floor of the superior temporal sulcus (FST), which lies within the temporal lobe but which we consider here because of its affinity with the MST complex. This partitioning is based on findings of (1) different receptive field properties in all 3 regions (Desimone and Ungerleider, 1986; Hikosaka et al., 1988; Komatsu and Wurtz, 1988a,b; Newsome et al., 1988), (2) different connections of all 3 areas (Ungerleider and Desimone, 1986b; Andersen et al., 1990; Boussaoud et al., 1990), and (3) differential effects on pursuit eye movements from selective stimulation of MSTd versus MSTl (Komatsu and Wurtz, 1989).

Area PIP (posterior intraparietal) lies in a region once considered to be part of V3A (Van Essen and Zeki, 1978), but the 2 areas can now be distinguished by their topographic organization and by their connections with other visual areas (Felleman et al., 1987; Colby et al., 1988). Area PO (parieto-occipital) is a topographically organized area situated medial and dorsal to PIP (Colby et al., 1988). Areas MIP (medial intraparietal) and MDP (medial dorsal parietal) have been identified on the basis of their connections with area PO (Colby et al., 1988). Area DP, which occupies the dorsal aspect of the prelunate gyrus, is a major source of visual inputs to area 7a (Andersen et al., 1990). DP has been distinguished from adjoining areas (V4, V3A, and 7a) primarily on the basis of differential connections, but also on the basis of visual topography and receptive field size and responsiveness (Maguire and Baizer, 1984; May and Andersen, 1986; Andersen et al., 1990). Area 7a, as described by Andersen et al. (1985), occupies the posterior part of the inferior parietal lobule and extends only a short distance into the intraparietal sulcus. Area VIP (ventral intraparietal) occupies the fundus of the intraparietal sulcus (Maunsell and Van Essen, 1983). LIP (lateral intraparietal) lies in the lateral bank of the intraparietal sulcus, in between VIP and area 7a (Andersen et al., 1985). However, there is considerable uncertainty about the border between these areas. On the basis of projection patterns from MT, Maunsell and Van Essen (1983) suggested that VIP was restricted to the fundus of the intraparietal sulcus. Ungerleider and Desimone (1986b) found that MT projections sometimes extend substantially farther up the lateral bank of the sulcus into a heavily myelinated zone that they termed VIP*. This region lies within area LIP as described by Andersen et al. (1985) and may correspond to area LIPv of Blatt et al. (1990) and to the posterior portion of area POa–i of Seltzer and Pandya (1980). Overall, it remains unclear whether this heavily myelinated strip should be considered part of VIP or LIP or as a distinct area unto itself.

The numerous visually related areas of the temporal lobe can be subdivided into 3 broad groups (not counting area FST, which has already been discussed with the parietal areas). The first group lies within the classical inferotemporal cortex (IT), which extends from the lower (posterior) bank of the STS to the lateral bank of the occipitotemporal sulcus. The second group lies within the polysensory strip occupying the upper (anterior) bank of the STS. The third group lies more medially, including the parahippocampal gyrus, and has traditionally been regarded as part of the limbic cortex.

In the present scheme, IT has been subdivided into 6 distinct areas. These can be grouped into 3 pairs, each containing separate dorsal and ventral subdivisions (Felleman et al., 1986; Van Essen et al., 1991; cf. also Fenstemaker et al., 1984; Fenstemaker, 1986). In particular, we distinguish among dorsal and ventral subdivisions of posterior inferotemporal cortex (PITd and PITv), central inferotemporal cortex (CITd and CITv), and anterior inferotemporal cortex (AITd and AITv). The dorsal areas lie largely within the lower bank of the STS, extending a short distance onto the middle temporal gyrus. The ventral areas occupy most of the middle and inferior temporal gyri and extend into the lateral bank of the occipitotemporal sulcus. The distinction between posterior and central pairs is based on topographic organization (present to a crude degree in PITd and PITv but not CITd and CITv) and on the laminar organization of projections back to V4 (Van Essen et al., 1991). Anterior inferotemporal cortex (AIT) differs from CIT in having much weaker connections with V4. The distinction between dorsal and ventral subdivisions (PITd vs. PITv and CITd vs. CITv) is based, in part, on the large sepa-

ration of foci resulting from single V4 injections. In addition, the dorsal subdivisions are reported to have strong connections with nuclei in the amygdalar complex, whereas the ventral subdivisions are more strongly connected with the subicular/hippocampal complex (Fenstemaker, 1986; Iwai et al., 1987; Yukie et al., 1988; but see Suzuki and Amaral, 1990). However, a potential qualification to this latter distinction is that the border between dorsal and ventral subdivisions suggested by Iwai et al. (1987) is more ventral than that illustrated in Figure 2, theirs being approximately in line with the anterior middle temporal sulcus.

Several previous studies have subdivided IT mainly along the anteroposterior axis (Turner et al., 1980; Iwai, 1981; Iwai and Yukie, 1987), the dorsoventral axis (Brodmann, 1905; Horel et al., 1987; Iwai et al., 1987; Yukie et al., 1988), or a mixture of both (Seltzer and Pandya, 1978). Our scheme is, in effect, a combination of the Iwai and Yukie (1987) anteroposterior partitioning with their subsequent dorsoventral partitioning (Yukie et al., 1988).

Immediately dorsal to IT is a long strip of polysensory cortex on the dorsal (anterior) bank of the STS. This strip was identified as the superior temporal polysensory area (STP) by Bruce et al. (1981), because they encountered many auditory and somatosensory responses along with a high incidence of visual responsiveness. Based on connectional differences described in several studies (Seltzer and Pandya, 1989a,b; Boussaoud et al., 1990), we have drawn a distinction between a posterior region, STPp, and an anterior region, STPa. Although it is based to a substantial degree on their connectional data, our scheme differs from that of Seltzer and Pandya (1978). They partitioned this region into 3 longitudinal strips, areas TPO, PGa, and IPa. More recently (Seltzer and Pandya, 1989b), they further subdivided the widest of these strips, area TPO, into 4 subregions along the anteroposterior dimension (TPO1–4). We have refrained from using their finer-grained scheme pending clarification of how robust and consistent the connectional differences are between different subregions.

In the parahippocampal gyrus, areas TF and TH are associated with vision by virtue of their connections with more than a half dozen different visual areas. Both of these areas are also strongly connected with the entorhinal cortex, area 36, and the cingulate cortex (Van Hoesen and Pandya, 1975; Brady, 1985; Insausti et al., 1987), but they apparently lack strong connections with the somatosensory cortex (Friedman et al., 1986; Cavada and Goldman-Rakic, 1989a; Andersen et al., 1990).

Finally, in the frontal cortex, 2 regions have been implicated in visual, visuomotor, or visually guided memory functions. FEF (the frontal eye field) is an area that plays an important role in saccadic eye movements and has extensive connections with visual areas in the occipital and parietal lobes (Bruce and Goldberg, 1984; Bruce et al., 1985). It overlaps partially with architectonic area 8a of Walker (1940), but the 2 are not coextensive (Stanton et al., 1989). Immediately anterior to FEF is area 46 (Walker, 1940; Barbas and Pandya, 1989), which fills most of the principal sulcus and extends onto its dorsal and ventral lips. Based on the heterogeneous pattern of connectivity with parietal and temporal areas, there are probably distinct subdivisions within area 46 (Goldman-Rakic, 1988; Barbas and Pandya, 1989; Cavada and Goldman-Rakic, 1989b; Seltzer and Pandya, 1989a), but a coherent scheme for subdividing it has yet to emerge.

The collection of visual areas just described is by no means a closed system. There are additional linkages to cortical areas associated with motor function, higher cognitive functions, and other sensory modalities. For example, some visual areas have strong connections with the entorhinal complex, a group of areas that serve as a major gateway to and from the hippocampal formation. There are also pathways that link the visual cortex to the cingulate cortex and to various subdivisions of the prefrontal cortex. Some of these will be discussed later in relation to the notion of hierarchical processing and information flow. Finally, all visual areas also have extensive connections with multiple subcortical nuclei, which will be discussed below.

Reciprocity and Distributed Connectivity

Up to this point, we have used the information in Table 3 to distinguish different areas on the basis of their specific connections. This tabulation also provides a useful framework for discussing other important principles concerning the numbers and patterns of connections among different areas.

The first principle is that of reciprocity of corticocortical connections. More than a decade ago, it was noted that pathways within the visual cortex tend to be bidirectional, such that if area *A* projects to area *B*, then area *B* is likely to project in turn to area *A* (Tigges et al., 1973; Rockland and Pandya, 1979). The degree to which this relationship holds is reflected in the symmetry of Table 3 about the diagonal axis (shaded boxes). If connections were invariably reciprocal, each entry would have a counterpart at the mirror-symmetric position on the opposite side of the diagonal.

Altogether, there are 305 identified pathways entered in Table 3, including 53 pathways reported only in abstracts and 13 pathways explicitly listed as questionable on the basis of conflicting reports (cf. Table 5). The majority of these pathways (242) are demonstrably bidirectional, forming 121 pairs of reciprocally interconnected areas (Table 4). Of the remaining "singlet" pathways, nearly all (58 of 63) are cases in which there has not been a clear-cut test for the reverse direction. However, there are a few examples of apparently unidirectional corticocortical pathways. In particular, there is a reported lack of reciprocity in the projections from V4t to V1 (Perkel et al., 1986; Ungerleider and Desimone, 1986b; Van Essen et al., 1986), from V2 to FST, and from V4t and DP to MSTl (Boussaoud et al., 1990). An intermediate example is the linkage between V1 and V4, which reportedly is robust and consistent from V4 to V1 (Perkel et al.,

1986), but relatively weak and occasional from V1 to V4 (Van Essen et al., 1986), in a way that may depend on eccentricity (Zeki, 1978a, 1980). Thus, the reciprocity of connections may, in some cases, vary among individuals or from one location to another within an area. However, in evaluating such possibilities, it is important to bear in mind that different tracer substances and different injection protocols can vary enormously in their sensitivity and thus in their ability to reveal relatively weak or diffuse projections. Pathways that appear absent or sparse using one pathway-tracing approach (e.g., from V1 to PO; Van Essen et al., 1986) may appear much more robust when using larger injections of a more sensitive tracer (Colby et al., 1988). For this reason, we have avoided attempting to systematically report the magnitude or density of these connections, even though such information would be extremely useful to have.

Table 4 provides several additional types of information about the overall population statistics for the connections between cortical areas. In particular, it is possible to estimate the average number of corticocortical connections made by each visual area, the range among different areas, and what fraction of the total number of possible connections are actually made. Analyses of this type become increasingly meaningful now that the number of identified pathways has outstripped the ability and/or desire of most investigators to keep track of them all individually. There are several ways of evaluating the data, however, owing to the fact that the charting of visual pathways is still far from complete. A lower bound on the overall degree of connectivity can be set from the overall number of 305 identified pathways linking 32 visually related neocortical areas. Because each pathway is an input to one area and an output from another, this works out to an average of about 19 connections per area (nearly 10 inputs and 10 outputs per area). A better estimate can be obtained by considering only those areas that have been extensively studied using both anterograde and retrograde tracer injections. For the 5 best-studied areas, V1, V2, V3, V4, and MT, the average number of connections per area is 27. The average number of areas with which there is any linkage (i.e., a connection in at least 1 direction) is 15 for this group. Interestingly, there is more than 2-fold variability in connectivity even among these well-studied areas. At the low end, V1 has "only" 16 connections that link it to 9 areas (3 robust, reciprocal pairs plus various minor, occasional, or unidirectional pathways). At the high end, V4 has 39 identified connections with 21 areas, signifying that it is linked to about ⅔ of all known visual areas. Moreover, the majority of these are robust pathways, suggesting that V4 may play a pivotal role in many different aspects of cortical processing.

In a fully interconnected network involving N areas, there would be a total of $N(N-1)$ connections. For $N=32$ areas, this number would be 992 pathways (446 pairs). By expressing the 305 reported pathways as a fraction of this theoretical limit, we conclude that nearly ⅓ of all possible connections have been empirically demonstrated. If each area has an average of 27 connections, as found for well-studied areas, the connectivity level would exceed 40% of the theoretical limit (432/992). If we take into account the fact that only about 680 of the 992 possible pathways have been explicitly tested, the 305 identified pathways represent a connectivity level of approximately 45%. Finally, if we assume that each area is connected with 15 other areas on average and that nearly all of these linkages will turn out to be reciprocal, then the estimated connectivity level approaches 50%. Of course, some of the pathways whose existence is reported to be questionable or only occasional in occurrence may, upon more careful scrutiny, turn out to be absent altogether, but we doubt that this will occur very frequently. Thus, no matter how the estimates are generated, there is no escaping the notion that the visual cortex is a highly distributed information-processing system. To keep this conclusion in perspective, however, we reemphasize that different pathways vary enormously in strength. Quantitative data on this issue are scarce, but we estimate that there may be a range of 2 orders of magnitude or more in the percentages of cells that project from a given target area. The fraction of pathways that are "robust," in the sense of showing heavy labeling when analyzed with conventional tracers, may be only 30%–50% of the total number of identified connections.

Table 4
Connectivity patterns among visual areas

Reciprocity	
Total number of pathways	305
Reciprocal pathways	121
Singlet pathways	63
Critically tested	5
Not critically tested	58
Connectivity	
Total number of pathways	305
Total number of areas	32
Average number of pathways per area	19
Highest number of pathways per area	39
Average number of pathways per well-studied area	27
Average number of linkages per well-studied area	15
Maximum possible connectivity among 32 areas	992
Observed pathways	305/992 = 31%

Hierarchical Relationships in the Visual Cortex

The possibility that the visual cortex might operate by a strictly serial processing scheme can be ruled out just from knowing the multiplicity of connections per area and the near ubiquity of reciprocal connections. On the other hand, it seems highly unlikely that the visual cortex is a network that altogether lacks any distinction between processing levels. Many studies, both electrophysiological and lesion based, indicate that some visual areas, such as those in the temporal and parietal lobes, are involved in a higher level of information processing than that mediated by occipital areas such as V1 and V2 (cf. Ungerleider and Mishkin, 1982; Van Essen, 1985; Maunsell and New-

some, 1987; Goldman-Rakic, 1988). Between these 2 extremes (a strictly serial scheme on the one hand and a completely nonordered network on the other), there are many intermediate possibilities. One hypothesis is that cortical areas are hierarchically organized in some very well-defined sense, with each area occupying a specific position in relationship to all other areas, but with more than 1 area allowed to occupy a given hierarchical level. Another possibility is that a hierarchy exists only in a loose sense, for instance, at the level of the different cerebral lobes, but not in any precisely definable manner for individual cortical areas.

To illustrate the importance of such distinctions, consider for a moment an analogy with various groupings characteristic of human societies, including social, political, and business organizations (e.g., the U.S. government). Except in a complete anarchy, there is generally some form of hierarchical organization, in which there are leaders and followers, chairpersons and committee members, or various other measures of rank. Some organizations have an utterly rigid hierarchy, in which every individual knows precisely his or her place within a pecking order. Others are less well defined, and there may be basic uncertainties as to who ranks above whom in various interactions. Still others may be inherently fluid and context dependent, in that one person ranks above another in one particular circumstance but below the other in another circumstance (e.g., on different committees). Distinguishing among such possibilities can be pivotal for understanding the operation of any complex system, whether it be in the domain of the cerebral cortex or of human society. It is worth noting in general terms that information flow in a hierarchical system (1) can go in both directions (upwards and downwards), (2) can skip over intermediate levels to go directly from a low to a high level, and (3) can travel in parallel through multiple, functionally distinct channels.

Current ideas about hierarchical organization in the primate visual system were spurred by notions of forward and feedback pathways suggested by connectivity patterns. In particular, Rockland and Pandya (1979) noted that projections in one direction tend to originate from superficial layers and terminate in layer 4, whereas those directed in the opposite direction tend to arise from deep as well as superficial layers and to terminate outside layer 4. They suggested that these 2 directions might correspond to forward and feedback directions of information flow. Subsequently, this notion was used as a basis for proposing an explicit, anatomically based hierarchy of visual cortical areas (Maunsell and Van Essen, 1983). In addition to ascending (forward) and descending (feedback) pathways, a few pathways were hypothesized to represent lateral information flow between areas at the same level. This designation was assigned to pathways terminating in a columnar pattern, involving all cellular layers to a comparable extent. The original version of the cortical hierarchy in the macaque visual pathway spanned 6 levels and was based on 36 distinct pathways among 13 identified cortical areas. Subsequently, this was extended to 7 hierarchical levels, based on 92 pathways among 17 cortical areas (Van Essen, 1985).

The number of identified pathways for which useful laminar information is available has more than tripled in the past 5 years. Given this huge increase in recently available information, our aim here is to assess whether the same or similar principles of organization allow for the incorporation of many more cortical areas and pathways into a single, internally consistent hierarchy. Our analysis indicates that the hierarchy can indeed be expanded to include all of the visually related areas for which connectional data exist. However, this has entailed a significant modification in the criteria used for distinguishing forward and feedback pathways. There are also a number of apparent inconsistencies. Some of these may represent bona fide exceptions to the general rule, but we suspect that the majority reflect inaccurate assignments stemming from technical considerations that will be discussed below.

Criteria

Our revised criteria for identifying hierarchical relationships are illustrated schematically in Figure 3. This scheme is similar to previously published ones (Van Essen and Maunsell, 1983, their Fig. 2; Maunsell and Van Essen, 1983, their Figs. 6, 13), but it has been expanded to include all major types of laminar patterns identified to date. The different patterns are arranged to show the laminar distributions of cells of origin and axonal terminations that we consider to be indicative of ascending (A, upper row), lateral (L, central row), and descending (D, bottom row) pathways.

For the axonal terminations of any given pathway, we distinguish 3 characteristic patterns as revealed by anterograde tracer injections (Fig. 3, center column). In one pattern (F), terminations are densest in layer 4, though they may also be prominent in layer 3 and other layers, as well. In another pattern (M), terminations preferentially avoid layer 4, usually forming a multitier pattern including both superficial and deep layers. Occasionally, patterns are encountered that involve primarily superficial layers (e.g., layers 1 and 2 in the projection from V4 to V1; predominantly layer 3 in the projection from AITd to FEF). Even though these are not strictly multilaminar, we have grouped them in the same category because they appear to represent descending pathways. In the third pattern (C), terminations extend in a columnar fashion continuously and with relatively uniform density across layer 4, often extending the entire thickness of the cortex.

For the cells of origin of each pathway, we distinguish 3 characteristic patterns as revealed by retrograde labeling experiments (Fig. 3, left and right columns). In one pattern (S), a large majority of cells (>70%) lie in supragranular layers. In another pattern (I), a large majority (>70%) lie in infragranular layers. In the third pattern (B), there is a strongly mixed

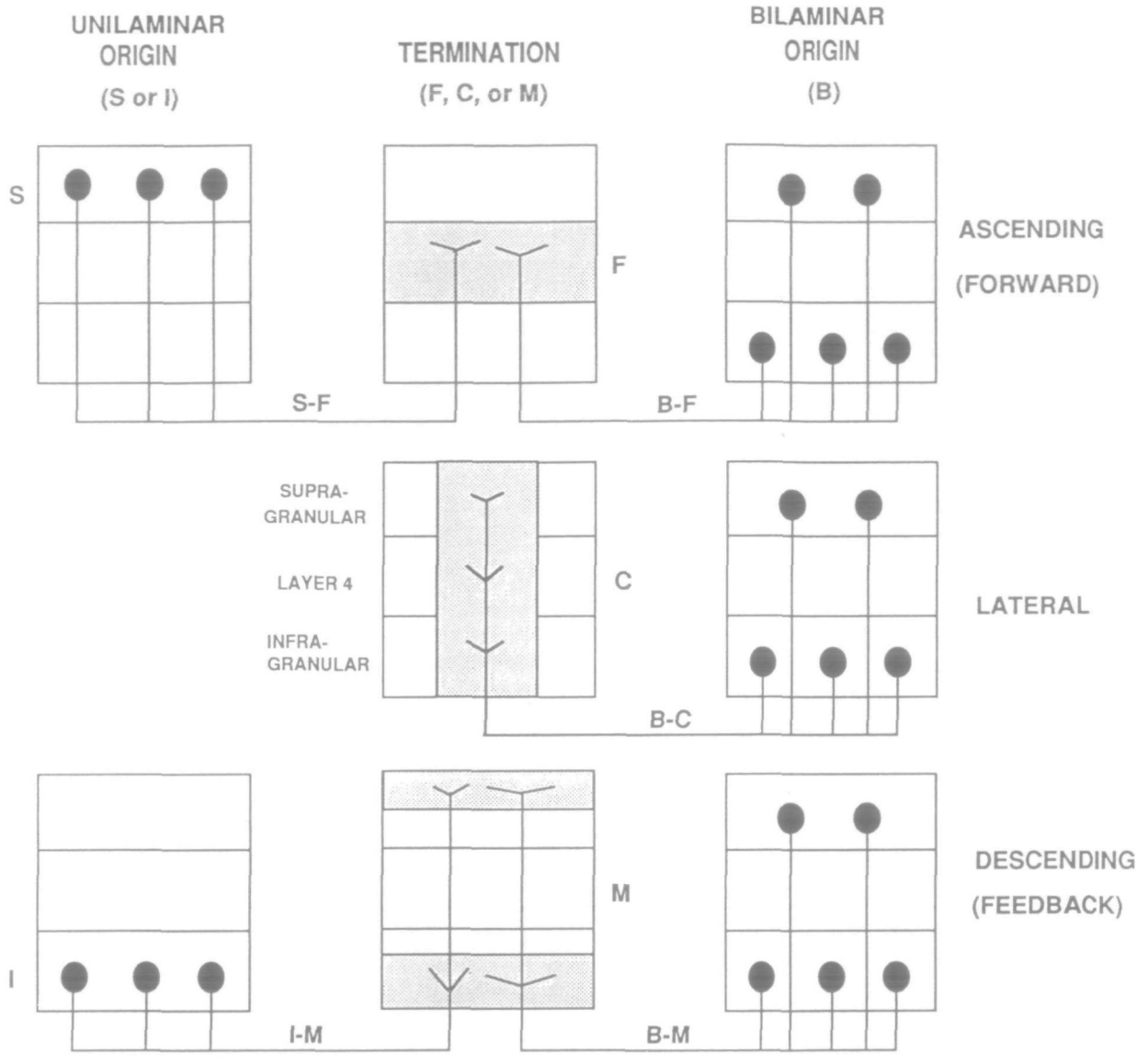

Figure 3. Laminar patterns of cortical connectivity used for making hierarchical assignments. Three characteristic patterns of termination are indicated in the *central column*. These include preferential termination in layer 4 (the *F* pattern), columnar (*C*) pattern involving approximately equal density of termination in all layers, and a multilaminar (*M*) pattern that preferentially avoids layer 4. There are also 3 characteristic patterns for the cells of origin of different pathways. Bilaminar (*B*) patterns, shown on the *right*, include approximately equal numbers of cells from superficial and deep layers (no more than a 70%–30% split) and are found to occur with all 3 types of termination pattern. Unilaminar patterns include predominantly superficial-layer inputs (*S* pattern), which correlate with F-type terminations, and predominantly infragranular-layer inputs (*I* pattern), which correlate with M-type terminations. Within this general framework, a number of variations on a theme can be encountered. Some pathways terminate primarily in superficial layers, but we group them with the M pattern because they avoid layer 4. Other pathways are quasi columnar, but do not include all layers; we classify them as a C pattern if the labeling in layer 4 is neither heavier nor sparser than in adjoining layers.

(bilaminar) distribution, with roughly similar proportions (30%–70%) of the labeled cells in each compartment.

Ascending projections were originally proposed always to originate predominantly from superficial layers (S pattern; Rockland and Pandya, 1979; Maunsell and Van Essen, 1983). However, a few pathways, such as that from DP to 7a (Andersen et al., 1990), are now known to originate in a bilaminar (B) pattern and yet terminate mainly in layer 4 (F pattern). Such B–F combinations invalidate one of the initial assumptions about feedforward pathways, but they do not necessarily invalidate the notion of hierarchical organization. The key issue is whether a consistent hierarchical scheme can be identified using a modified set of criteria. The modification that we propose is to treat any bilaminar retrograde pattern as ambiguous if it is the only type of laminar information available. Conversely, it is compatible with any of the 3 hierarchical relationships (A, L, or D) that may be indicated from other data on a given pathway. A similar suggestion has been made by Andersen et al. (1990) and Boussaoud et al. (1990).

A Database for Analyzing Hierarchical Relationships

Our goal in this section is to apply the scheme illustrated in Figure 3 as objectively and rigorously as

possible to the analysis of hierarchical relationships in the visual cortex, while taking into account the uncertainties and qualifications that are associated with some of the experimental data. In principle, the task is no different than for the hierarchical schemes that we and others have proposed previously. However, in practice, we found the analysis to be much more difficult, owing to the sheer amount and complexity of anatomical data now available. It became essential to establish a computerized database in order to handle the data efficiently and examine all relationships critically. We used the EXCEL database package, which runs on both Macintosh and PC-compatible computers.

The format we used for the database is illustrated in Table 5. The first 12 columns on the left provide information about the laminar patterns of connections and the hierarchical relationships that can be inferred from them. The 6 columns on the right provide specific citations, listed separately for the origins and terminations of each pathway.

Each row across the table deals with both pairs of a reciprocal linkage (e.g., from V1 to V2 in columns 1–5 and from V2 back to V1 in columns 6–10). The connections of V1 are listed first, because its outputs (left) are all of the ascending type and its inputs (right) are all descending. Those of V2 are listed next, because its outputs are all ascending, except for the linkage with V1 that has already been accounted for. The sequence continues by selecting areas in an order (V3, VP, etc.) chosen so that the output pathways remaining to be listed (columns 1–5) are all ascending, lateral, or indeterminate, the descending pathways having already been listed.

The complete hierarchical analysis involved 4 major stages, and it is useful to outline the overall sequence briefly before discussing each stage in detail. For each pathway under consideration, the first step is to use the available laminar information to make assignments according to the categories we have proposed for retrograde labeling (S, B, or I designations in columns 3 and 8) and anterograde labeling (F, C, or M designations in columns 4 and 9). One or 2 key references for each of these assignments are listed in the appropriate column (13, 14, 16, or 17) on the right. For pathways that have been identified in several studies, we have selected those references that provide the best information on laminar patterns, rather than necessarily the first study or the most recent study. As in Table 1, the references are designated by abbreviations that are matched to the standard citation format in the table notes. With a little experience, one can quickly recognize the specific study associated with any given finding contained in the table. In order to facilitate making distinctions between pathways that are identified on the basis of abstract versus those documented by full reports, all of the abstracts in the reference key are italicized.

The second step in the analysis is to make assignments of the direction of information flow (ascending, lateral, or descending) based on the laminar information available for each pathway. Using the criteria illustrated in Figure 3, the entries in column 3 and 4 are used to make the assignments of A, L, or D shown in column 5, while the entries in columns 8 and 9 are used for the assignments shown in column 10. Columns 5 and 10 also contain many "u" entries, which stand for a pathway whose existence is documented but whose hierarchical assignment is undefined, either because there is no laminar information whatsoever or because the only information is the nonspecific B (bilaminar) cell-of-origin pattern. The third step is to examine all reciprocal pairs, in order to see whether there is complementarity of the 2 patterns indicated in columns 5 and 10. If one pathway is ascending, the reciprocal path should be descending (an A–D pair), and if one is lateral, its counterpart should also be lateral (an L–L pair). The results are indicated in column 11. The fourth and final step is to determine whether an internally consistent global hierarchy can be assembled by using the relationships inferred from the entire collection of pairwise comparisons. Before we reached this step, there were numerous complexities and subtleties that required careful attention and merit explicit discussion.

Table 5 also contains additional information pertaining to the existence, special nature, or controversial nature of certain pathways, which is indicated in columns 15 and 18 for the 2 directions. Each of these "special" references is preceded by an "E" if the existence of the pathway has been demonstrated but there is no laminar information for either the origin or termination, by an "S" if the pathway is notably sparse, by an "R" if it occurs only rarely, and by an "A" if the pathway has been reported to be altogether absent. However, for simplicity, we filled in this last entry (absent pathways) only for cases of particular interest, for example, when other studies have reported the presence of that pathway or of the pathway in the reciprocal direction. There are a total of 38 entries in the sparse, rare, or absent groups, amounting to slightly more than 10% of the total number of pathways.

The most critical stage of the entire analysis was the entry and validation of experimental data on laminar patterns (Table 5, columns 3, 4, 8, and 9). This is based on information from a total of 52 studies, listed in the table notes. For many studies, the relevant information was already available in an appropriate format, and data entry was straightforward. However, in numerous cases, it was difficult to decide on the appropriate assignment, for reasons that can be grouped into 2 broad categories: (1) *Areal uncertainties:* Many pathways have been reported using a different partitioning scheme than ours for identification of areas (cf. Table 1), and others have been demonstrated by illustrating the connections as they relate to geographical landmarks, without explicit assignment of both tracer injection sites and target sites to specific areas. The ease and reliability with which such data could be related to our partitioning scheme varied widely and depended to a large extent on how much detailed information was given about the pathways under consideration. To facilitate this process,

we often made recourse to comparisons with a scale model of the macaque brain, which was available in our laboratory and was painted according to the scheme illustrated in Figure 3. (2) *Laminar uncertainties:* As with the areal assignments, the determination of laminar patterns associated with each pathway was often difficult, depending on the nature and extent of published information available. Obviously, the easiest cases were those in which the laminar patterns had been analyzed and tabulated using criteria similar to or identical to ours (e.g., Andersen et al., 1990; Boussaoud et al., 1990). However, in many publications, the critical patterns are often illustrated or described only in sketchy or fragmentary fashion.

Altogether, we made numerous judgment calls, many of which are explicitly indicated by question marks (e.g., S?) or mixed assignments (e.g., C/M?) in the relevant columns of Table 5. Because this was an interactive process, frequently requiring discussion and reassessment of the data, it was important to be able to access the published information quickly and repeatedly. For this reason, our computerized database included, in addition to the relevant publications, a listing of their specific page numbers and figure numbers that are particularly informative about laminar patterns. This information is not included in Table 5, simply for reasons of clarity and space.

Step 1: Individual Laminar Patterns

Columns 3 and 8 of Table 5 contain data on cells of origin for 217 pathways, 177 of which fell clearly in the S, B, or I categories illustrated in Figure 3. The 40 irregularities (25 S/B, 14 I/B, and 1 S? patterns) are of several types: (1) borderline patterns (e.g., results showing labeling of roughly ⅓ infragranular and ⅔ supragranular neurons but without sufficient quantitation to decide unambiguously between S vs. B patterns), (2) heterogeneous results within a single hemisphere (e.g., some S clusters and some B clusters from a single injection), (3) heterogeneity across different hemispheres used in the same study, and (4) discrepant outcomes reported by different studies. Overall, it is difficult to ascertain how many of these instances represent genuine biological variability within a well-defined pathway and how many represent technical complications and uncertainties. With respect to determining hierarchical relationships, however, the presence of a mixed result (S/B or I/B) in a single pathway does not represent an inherent conflict, because a bilaminar pattern is consistent with all possibilities, ascending, descending, or lateral. Such a conflict would arise if a mixed S/I pattern were encountered for a particular pathway, but we are not aware of any examples of this type. In cases where there is a mixed pattern of origin (S/B or I/B) and no data on termination patterns, a question mark (A? or D?) is used to indicate uncertainty about the hierarchical assignment.

With regard to patterns of termination, columns 4 and 9 of Table 5 contain data on 156 pathways, 132 of which fit cleanly into the F, C, or M categories of Figure 3. The 24 exceptions are listed individually in Table 6 because, unlike the various irregularities in patterns of cell origin, they represent a potentially serious challenge to our simple scheme for hierarchical relationships. For example, a genuinely mixed F/C pathway would suggest that one area is simultaneously level with and higher than another area. This would be logically inconsistent with a static hierarchy based on our particular anatomical criteria. Although it is obviously critical to know whether these mixed patterns are genuine or artifactual, in most cases, there is insufficient information to resolve the issue unambiguously. Perhaps the clearest example of laminar heterogeneity is the projection from MT to V4, which has been shown in 2 studies to include some patches having a columnar pattern and other patches having a multilayer pattern (Maunsell and Van Essen, 1983; Ungerleider and Desimone, 1986b). It is unlikely that this heterogeneity is an artifact resulting from mistaken assignments of the borders of V4 or MT. Interestingly, however, there is independent evidence for a form of compartmental organization within V4, based on its pattern of connectivity with different subregions of V2 (DeYoe et al., 1988; Zeki and Shipp, 1989; Van Essen et al., 1991). It is unclear whether these 2 types of heterogeneity bear any systematic relationship to one another. Other examples of mixed, or variable, laminar patterns (MST to PO; MSTd and MSTl to FST; LIP to PO and MSTd) represent situations in which both the target area and the injected area are small and lack sharply defined borders. Hence, it is possible that the heterogeneity sometimes resulted from imperfect border assignments in which the injection site or the target region might inadvertently have included 2 areas at different hierarchical levels.

In some instances, the descriptions involve relatively sparse connections in which it is difficult to discern laminar patterns precisely (e.g., DP to PO; Andersen et al., 1990). In other cases, the reported distribution is borderline or intermediate between a clear-cut F or C pattern. For example, the projection from MT to V3A is a borderline pattern in which the text describes a columnar (C) pattern (Ungerleider and Desimone, 1986b), but in the accompanying illustration (their Fig. 2), the labeling appears slightly denser in superficial and deep layers than in layer 4 and hence could arguably correspond to a multilayer (M) pattern (see Seltzer and Pandya, 1989a, for other examples of this type).

Interestingly, there are only 2 cases of F/M termination patterns, that is, involving a direct conflict between ascending and descending directions. In one case (area 7a to STP; Andersen et al., 1990), there is independent evidence that the target region includes 2 separate areas (STPp and STPa) at different hierarchical levels, but the projections are not described in sufficient detail to ascertain whether the F pattern is in STPa and the M pattern in STPp, as we would predict. In the other case (FST to FEF; Boussaoud et al., 1990), the projection was to 2 separate foci in the arcuate sulcus having different termination patterns, but it is unclear whether both foci were within the

Table 5
Connectivity table for visual areas

1	2	3	4	5	6	7	8	9	10	11	12
	Outputs					Inputs				Hierarchical	
From	To	Origin (S, B, I)	Termination (F, C, M)	Direction (A, L, D)	From	To	Origin (S, B, I)	Termination (F, C, M)	Direction (A, L, D)	relationship	Levels crossed
V1	V2	S	F	A	V2	V1	B	M	D	A-D	1
	V3	S	F	A	V3		B	M	D	A-D	2
	V3A		F	A	V3A		I		D	A-D	3
	PIP		F	A	PIP				u		3
	V4	S		A	V4		B	M(s)	D?	A-D?	4
	V4t				V4t		I		D	NR	4
	MT	S	F	A	MT		I	M	D	A-D	4
	PO	S		A	PO				u		4
	MSTl	S		A	MSTl					NR	6
V2	V3	S	F	A	V3	V2		M	D	A-D	1
	VP	S	F	A	VP		B	M	D	A-D	1
	V3A	S	F	A	V3A			M	D	A-D	2
	PIP			u	PIP						2
	V4	S	F	A	V4		B	M	D	A-D	3
	VOT			u	VOT				u		4
	V4t	S	F	A	V4t						3
	MT	S	F	A	MT		B	M	D	A-D	3
	PO	S		A	PO						3
	MSTd	S	F	A	MSTd			M	D	A-D	5
	MSTl	S		A	MSTl			M	D	A-D	5
	FST	S		A?	FST					NR?	5
	VIP			u	VIP						5
	FEF	S		A	FEF						6
V3	VP				VP	V3	B		u		0
	V3A		F	A	V3A		I	M	D	A-D	1
	PIP		F	A	PIP		B		u		1
	V4	S	F	A	V4		I	M	D	A-D	2
	V4t	S	F	A	V4t		B		u		2
	MT	S	F	A	MT		B	M	D	A-D	2
	PO	S		A	PO						2
	MSTd	S	F	A	MSTd		I		D	A-D	4
	FST	S		A	FST			M	D	A-D	4
	LIP		F	A	LIP		I		D	A-D	4
	VIP		F	A	VIP		I		D	A-D	4
	FEF	S		A	FEF						5
	TF		F	A	TF		I		D	A-D	7
VP	V3A		F/C	A/L?	V3A	VP	B		u		1
	PIP		F	A	PIP		B		u		1
	V4	B	F	A	V4		I		D	A-D	2
	VOT		F	A	VOT			M	D	A-D	3
	MT	S	F	A	MT		I	M	D	A-D	2
	PO	S		A	PO						2
	MSTd	S	F	A	MSTd		I		D	A-D	4
	FST	S	F	A	FST					NR?	4
	LIP				LIP			M	D		4
	VIP		F	A	VIP						4
	FEF	S		A	FEF						5
	TF		F	A	TF		I		D	A-D	7
V3A	V4	B	F	A	V4	V3A		M	D	A-D	1
	MT	B	F	A	MT		I	C/M	D/L?		1
	PO	B		u	PO						1
	DP	S/B		A?	DP			M	D	A-D?	2
	MSTd	S/B		A?	MSTd			M	D	A-D?	3
	MSTl	S/B		A?	MSTl			M	D	A-D?	3
	FST	S		A	FST			M	D	A-D	3

Table 5
Continued

13	14	15	16	17	18
Output References*			Input References*		
Origin	Termination	Special (E, R, S, A)	Origin	Termination	Special (E, R, S, A)
LH, '84	RP, '79		VNMB, '86	RP, '79	
BFNV, '86	C, '69		PBK, '86	*FV, '84*	
	Z, '80		PBK, '86		R: VNMB, '86
	Z, '80	E: VNMB, '86			E: PBK, '86
YI, '85		E: Z, '78a	PBK, '86	YI, '85	R: VNMB, '86
		A: UD, '86a; VNMB, '86	PBK, '86		
MV, '83	UD, '86a		PBK, '86	MV, '83	
CGOG, '88					E: VNMB, '86
BUD, '90		A: VNMB, '86			A: PBK, '86
FV, '84	*UGSM, '83*			*FV, '84*	
BV, '83	NMV, '86		NMV, '86	*BV, '83*	
BV, un	Z, '78b			*FV, un*	
		E: NMV, '86			
DV, '85	*UGSM, '83*		RP, '79	*FV, '83*	
		E: NMV, '86			E: NMV, '86
FDKOV, '88	UD, '86a				
DV, '85	UD, '86a		RP, '79	MV, '83	
CGOG, '88					
BUD, '90	UD, '86a			BUD, '90	
BUD, '90				BUD, '90	
BUD, '90		S: NMV, '86; R: BUD, '90			A: BUD, '90
		E: NMV, '86			
B, '88		A: HKK, '87			
			FV, '84		
	FV, '84		*FV, '84*	*FV, un*	
	FBV, '87		*FBV, '87*		
FV, '83	*FV, '84*		*FV, '84*	*FV, '83*	
FDKOV, '88	*FV, '84*		*FV, '84*		
MV, '83	*FV, '84*		*FV, '84*	MV, '83	
CGOG, '88					
BUD, '90	*FV, '84*	R: BUD, '90	*FV, '84*		R: BUD, '90
BUD, '90	*FV, '84*			BUD, '90	R: BUD, '90
			FV, '84		
	FV, '84		*FV, '84*		
B, '88		A: HKK, '87			
	FV, '84		*FV, '84*		
	BV, '83		*BV, '83*		
	BV, '83		*BV, '83*		
FV, '84	*BV, '83*		*BV, '83*		
	BV, '83			*FV, '84*	
UD, '86b	*BV, '83*		*BV, '83*	MV, '83	
CGOG, '88					A: *BV, '83*
BUD, '90	*BV, '83*		*BV, '83*		R: BUD, '90
BUD, '90	*BV, '83*	R: BUD, '90			A: BUD, '90
				AAES, '90	
	BV, '83				
B, '88		A: HKK, '87			
	BV, '83		*BV, '83*		
FV, '84	*FV, un*			*FV, '84*	
UD, '86b	*FV, un*		*FV, un*	UD, '86b	A: MV, '83
CGOG, '88					
AAES, '90				AAES, '90	
BUD, '90				BUD, '90	
BUD, '90				BUD, '90	
BUD, '90				BUD, '90	

Table 5
Continued

1	2	3	4	5	6	7	8	9	10	11	12
	Outputs					Inputs				Hierarchical relationship	
From	To	Origin (S, B, I)	Termination (F, C, M)	Direction (A, L, D)	From	To	Origin (S, B, I)	Termination (F, C, M)	Direction (A, L, D)		Levels crossed
V3A (cont'd)	LIP				LIP	V3A (cont'd)	I	M	D		3
	FEF	S		A	FEF						4
PIP	V4	B		u	V4	PIP		M	D		1
	MT			u	MT				u		1
	PO	S		A	PO						1
	DP	S/B		A?	DP			M	D	A-D?	2
	7a	B		u	7a						4
PO	V4t				V4t	PO	B		u		0
	MT	B		u	MT		B	C/M	L/D?		0
	MIP				MIP		B		u		0
	MDP				MDP		B		u		0
	DP	S/B?		A?	DP			C/M?	L/D?		1
	MSTd	S		A	MSTd		B	M	D	A-D	2
	MSTl	S		A	MSTl			M	D	A-D	2
	LIP	S		A	LIP		B	C/F	L/A?	NC	2
	VIP			u	VIP		B		u		2
	7a	S/B		A?	7a		B	M(I)	D?	A-D?	3
	FEF	S		A	FEF				u		3
V4	V4t	B	F/C	L/A?	V4t	V4	B		u		0
	MT	S/B	C	L/A?	MT		B	C/M	L/D?	L-L?	0
	VOT				VOT		B	M	D		1
	DP	B		u	DP			M	D		1
	LIP		F	A	LIP		B	M	D	A-D	2
	FST	S		A	FST			M	D	A-D	2
	PITd	S	F	A	PITd		B	M	D	A-D	2
	PITv	S	F	A	PITv		B	M	D	A-D	2
	CITd	S	F	A	CITd		I		D	A-D	3
	CITv	S	F	A	CITv		I		D	A-D	3
	AITv	S		A	AITv				u		4
	FEF	S		A?	FEF						3
	TF		F	A	TF		I	M	D	A-D	5
	TH		F	A	TH		I		D	A-D	5
	46	S		A	46						5
V4t	MT	B		u	MT	V4t	B	C	L		0
	MSTd				MSTd		B	M	D?	NR?	2
	MSTl	S		A?	MSTl					NR?	2
	FST	S		A	FST		B	M	D	A-D	2
	FEF	S		A	FEF						3
MT	MSTd	S/B	F	A	MSTd	MT	B/I	M	D	A-D	2
	MSTl	S/B	F	A	MSTl		B/I	M	D	A-D	2
	FST	S/B	F	A	FST		I	M	D	A-D	2
	LIP			u	LIP			M	D		2
	VIP		F	A	VIP		B		u		2
	FEF	S	F	A	FEF			M?	D?	A-D?	3
	46	S		A	46						5
MIP	7a	B		u	7a	MIP					3
MDP	7a	B		u	7a	MDP					3
VOT	PITd		F	A	PITd	VOT					1
	PITv		F	A	PITv						1

Table 5
Continued

13	14	15	16	17	18
Output References[a]			Input References[a]		
Origin	Termination	Special (E, R, S, A)	Origin	Termination	Special (E, R, S, A)
B, '88		A: HKK, '87	AAES, '90	*BSA, '87*	
FBV, '87				*FV, '84*	
CGOG, '88		E: UD, '86b			E: UD, '86b
AAES, '90				AAES, '90	
AAES, '90					
			CGOG, '88		
UD, '86b			CGOG, '88	UD, '86b	A: MV, '83
			CGOG, '88		
			CGOG, '88		
AAES, '90				AAES, '90	
BUD, '90			CGOG, '88	BUD, '90	
BUD, '90				BUD, '90	
BSA, '87			CGOG, '88	AAES, '90	
		E: SP, '80	CGOG, '88		
CG, '89; AAES, '90			*BSA, '87*	AAES, '90	
B, '88		A: HKK, '87			S: CGOG, '88
FDKOV, '88	*FV, '83*		*FV, '83*		
MV, '83; UD, '86a	*FV, '83*		*FV, '83*	MV, '83; UD, '86a	
			FKV, '86	*FV, '84*	
AAES, '90				AAES, '90	
	BSA, '87		*FV, '83*	*BSA, '87*	
BUD, '90			VFDOK, '91	BUD, '90	
DFG, '80	*FKV, '86*		VFDOK, '91	RP, '79	
DFG, '80	*FKV, '86*		VFDOK, '91	RP, '79	
DFG, '80	*FKV, '86*		VFDOK, '91		
DFG, '80	*FKV, '86*		VFDOK, '91		
F, '86					E: F, '86
BM, '81		A: HKK, '87			
	FKV, '86		*FKV, '86*	RP, '79	
	FKV, '86		*FKV, '86*		
BM, '81		S: B, '88			
UD, '86b			*FDKOV, '88*	UD, '86b	
			FDKOV, '88	BUD, '90	R: BUD, '90
BUD, '90		R: BUD, '90			
BUD, '90			*FDKOV, '88*	BUD, '90	
B, '88		A: HKK, '87			
BUD, '90	MV, '83		MV, '83; UD, '86b	BUD, '90	
BUD, '90	MV, '83		MV, '83; UD, '86b	BUD, '90	
BUD, '90	UD, '86b		UD, '86b	BUD, '90	
BSA, '87				*BSA, '87*	
	MV, '83		UD, '86b		
B, '88	UD, '86b			HKK, '87	A: UD, '86b
B, '88		A: UD, '86b; S: B, '88			A: UD, '86b
AAES, '90					
AAES, '90					
	FV, un				
	FV, un				

Table 5
Continued

1	2	3	4	5	6	7	8	9	10	11	12
	Outputs					Inputs				Hierarchical	
From	To	Origin (S, B, I)	Termination (F, C, M)	Direction (A, L, D)	From	To	Origin (S, B, I)	Termination (F, C, M)	Direction (A, L, D)	relationship	Levels crossed
DP	FST			u	FST	DP					1
	LIP		C/F	L/A?	LIP		B	C/M	L/D?	L-L?	1
	MSTd	S/B		A?	MSTd		B	C	L	NC?	1
	MSTl	S		A?	MSTl					NR?	1
	7a	B	F	A	7a		B	M	D		2
	FEF				FEF				u		2
	46		F	A	46				u		4
FST	MSTd	S/B	C	L/A?	MSTd	FST	B	M/C	L/D?	L-L?	0
	MSTl	B	C	L	MSTl		B	C/F	L/A?	L-L?	0
	PIT		M/C	D/L?	PIT		B		u		0
	LIP	B	C/M?	L/D?	LIP		B		u		0
	VIP		M/C	D/L?	VIP		B		u		0
	FEF	S	F/M	A/D?	FEF		I		D		1
	7a	B		u	7a						1
	STPp		F	A	STPp		I		D	A-D	1
	TF		C	L	TF		B/S		A?	NC?	3
VIP	MSTd	B		u	MSTd	VIP		C	L		0
	MSTl	B		u	MSTl			C/M	L/D?		0
	LIP			u	LIP				u		0
	FEF	B		u	FEF			M	D		1
	7a	B		u	7a						1
LIP	MSTd	B	C/F	L/A?	MSTd	LIP	B	C	L?	L-L?	0
	MSTl	B		u	MSTl						0
	PITv		C?	L?	PITv						0
	7a	B		u	7a			M	D		1
	FEF	S	F	A	FEF			M	D	A-D	1
	TF		F/C?	A/L?	TF						3
	46	S	F	A	46						3
MSTd	7a	B	C	L	7a	MSTd	B	M	D	NC	1
	PIT	S?		A?	PIT		B		u		0
	TF				TF		I		D		3
	FEF	S	F	A	FEF		I		D	A-D	1
	STPp		F	A	STPp		I/B		D	A-D	1
MSTl	7a				7a	MSTl	B		u	NR?	1
	FEF	S	F	A	FEF		I		D	A-D	1
	STPp		F	A	STPp		I/B		D?	A-D?	1
PIT	FEF	S		A	FEF	PIT					1
	46	S		A	46						3
PITd	CITv	S/B		A?	CITv	PITd					1
	AITd	S/B		A?	AITd						2
	AITv	S/B		A?	AITv						2
PITv	CITd				CITd	PITv	I/B		D?		1
	CITv	S/B		A?	CITv		I/B		D?	A-D?	1
	AITd				AITd		I/B		D?		2
	AITv	S/B		A?	AITv		I/B		D?	A-D?	2
	TF				TF		I/B		D?		3
	TH				TH		I		D		3
CIT	STPp				STPp	CIT		C	L		0
	TH				TH		I		D		2
	FEF	S		A	FEF		S/B		A?	NC?	0
	46	S		A	46		S/B	M	A/D?	NC?	2
CITd	AITd	S/B		A?	AITd	CITd					1
	AITv	S/B		A?	AITv						1

Table 5
Continued

13	14	15	16	17	18
Output References[a]			Input References[a]		
Origin	Termination	Special (E, R, S, A)	Origin	Termination	Special (E, R, S, A)
		E: AAES, '90			
	AAES, '90		AAES, '90	AAES, '90	
BUD, '90		E: AAES, '90	AAES, '90	BUD, '90	
BUD, '90		R: BUD, '90			A: BUD, '90
CG, '89; AAES, '90	AAES, '90		AAES, '90	CG, '89; AAES, '90	
					E: AAES, '90
	AAES, '90				E: AAES, '90
BUD, '90	BUD, '90		BUD, '90	BUD, '90	
BUD, '90	BUD, '90		BUD, '90	BUD, '90	
	BUD, '90		BUD, '90		
BUD, '90	BUD, '90		BUD, '90		
	BUD, '90		BUD, '90		
HKK, '87 AAES, '90	BUD, '90		BUD, '90		
	BUD, '90		BUD, '90		
	BUD, '90		BUD, '90		
BUD, '90				BUD, '90	
BUD, '90				BUD, '90	
		E: *BSA, '87*			E: *BSA, '87*
HKK, '87 AAES, '90				HKK, '87	
BUD, '90	*BSA, '87*	E: AAES, '90	*BSA, '87*	BUD, '90	
BUD, '90		R: BUD, '90			
	AAES, '90				
AAES, '90				AAES, '90	
B, '88	AAES, '90			KA, '77; HKK, '87	
	AAES, '90				
B, '88	AAES, '90				
AAES, '90	BUD, '90		BUD, '90	AAES, '90	
BUD, '90		S: BUD, '90	BUD, '90		
			BUD, '90		R: BUD, '90
BM, '81	BUD, '90		BUD, '90		
	BUD, '90		BUD, '90		
		A: BUD, '90	BUD, '90		R: BUD, '90
BM, '81	BUD, '90		BUD, '90		
	BUD, '90		BUD, '90		
BM, '81 B, '88 S, '87 F, '86 S, '87					
			S, '87		
S, '87			S, '87		
			S, '87		
S, '87			S, '87		
			S, '87		
			S, '87		
			SP, '84		
			SP, '87		
BM, '81		S: BM, '81	SP, '89a		
B, '88			SP, '89a	GSS, '84	
F, '86 S, '87					

Table 5
Continued

1	2	3	4	5	6	7	8	9	10	11	12
	Outputs					Inputs				Hierarchical	
From	To	Origin (S, B, I)	Termination (F, C, M)	Direction (A, L, D)	From	To	Origin (S, B, I)	Termination (F, C, M)	Direction (A, L, D)	relationship	Levels crossed
CITv	AITd	S/B		A?	AITd	CITv	I/B		D?	A-D?	1
	AITv	S/B		A?	AITv		I/B		D?	A-D?	1
	TF				TF		I		D		2
7a	AITd		F	A	AITd	7a	B		u		1
	STP		F/M?	A/D?	STP		B/I		u	NC?	1
	TF		F	A	TF		I/B		D?	A-D?	2
	TH		F	A	TH		I		D	A-D	2
	FEF	B	C/M?	L/D?	FEF		B		u		0
	46	B	F/C	A/L?	46		B/S	M	D?		2
FEF	AITd	S		A	AITd	FEF		M(s)	D?	A-D?	1
	STPp	B	M(s)	D?	STPp		B	M(s)	D?	NC	0
	46	B	F/C	A/L?	46		B		u		2
STPp	STPa	S	F	A	STPa	STPp	I	M	D	A-D	1
	TF			u	TF		I		D		2
	TH			u	TH		I		D		2
	46	S	C	A/L?	46		S	M	A/D?	NC	2
STPa	TF			u	TF	STPa	I		D		1
	TH			u	TH		I		D		1
	46	S		A	46			M	D	A-D	1
AITd	STPa				STPa	AITd	B		u		0
	TF				TF				u		1
	TH				TH				u		1
AITv	TF		F	A	TF	AITv	I		D	A-D	1
	TH		F/C	A/L?	TH		I		D	A-D?	1
46	AITd	S		A	AITd	46		M(s)	D?	A-D?	1
	TF		M/C	D/L?	TF		B		u		0
	TH		C	L?	TH		I/B		D?	NC?	0

This table shows connections among visual cortical areas listed in Table 1. Each row deals with pairs of a reciprocal linkage with the outputs listed in columns 1–5 and the inputs listed in columns 6–10. For each pathway, the laminar origin (S, supragranular; B, bilaminar; I, infragranular), laminar pattern of termination (F, layer 4 predominant; C, columnar; M, multilayer avoiding layer 4), and pathway direction (A, ascending; L, lateral; D, descending) is listed when known. The symbol "u" indicates the pathway has been demonstrated but the laminar features are unknown. Columns 11 and 12 refer to the hierarchical relationships between the pairs of areas. A-D indicates an ascending-descending pair where the laminar patterns of connections in both directions are consistent with a hierarchical pairing extending across layers of a hierarchy. Level indicates the number of hierarchical levels the pathway traverses (in either direction) in the hierarchy illustrated in Figure 4. Columns 13–15 and 16–18 provide references to each of the illustrated input and output pathways, respectively. Columns 15 and 18 provide pathway information: E, the existence of a pathway without laminar information; R, rare pathway; S, sparse pathway; A, absent pathway. Only those pathways whose absence provides some controversy are listed in this column.

• Reference key (italic signifies abstracts or unpublished observations):

AAES, '90	Andersen, Asanuma, Essick, and Siegel, 1990
B, '85	Brady, 1985
B, '86	Barbas, 1986
B, '88	Barbas, 1988
BFNV, '86	Burkhalter, Felleman, Newsome, and Van Essen, 1986
BM, '81	Barbas and Mesulam, 1981
BM, '85	Barbas and Mesulam, 1985
BP, '89	Barbas and Pandya, 1989
BSA, '87	*Blatt, Stoner, and Anderson, 1987*
BUD, '90	Boussaoud, Ungerleider, and Desimone, 1990
BV, '83	*Burkhalter and Van Essen, 1983*
BV, un	*A. Burkhalter and D. C. Van Essen, unpublished observations*
C, '69	Cragg, 1969
CGOG, '88	Colby, Gattass, Olson, and Gross, 1988
CG, '89	Cavada and Goldman-Rakic, 1989a
DFG, '80	Desimone, Fleming, and Gross, 1980
DV, '85	DeYoe and Van Essen, 1985
F, '86	Fenstemaker, 1986
FBV, '87	*Felleman, Burkhalter, and Van Essen, 1987*
FDKOV, '88	*Felleman, DeYoe, Knierim, Olavarria, and Van Essen, 1988*
FKV, '86	*Felleman, Knierim, and Van Essen, 1986*
FV, '83	*Felleman and Van Essen, 1983*
FV, '84	*Felleman and Van Essen, 1984*
FV, un	*D. J. Felleman and D. C. Van Essen, unpublished observations*
GSS, '84	Goldman-Rakic, Selemon, and Schwartz, 1984
HKK, '87	Huerta, Krubitzer, and Kaas, 1987
KA, '77	Künzle and Akert, 1977
L, '80	Leichnitz, 1980
LH, '84	Livingstone and Hubel, 1984a
MV, '83	Maunsell and Van Essen, 1983
MVPG, '77	Mesulam, Van Hoesen, Pandya, and Geschwind, 1977