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)
F, '86			S, '87		
S, '87			S, '87		
			SP, '87		
	L, '80		AAES, '90		
	SGR, '88; CG, '89; AAES, '90		MVPG, '77; CG, '89; AAES, '90		
	SP, '84; CG, '89	E: AAES, '90	MVPG, '77; CG, '89		
	SP, '84		MVPG, '77; CG, '89		
BM, '81	L, '80; AAES, '90	A: HKK, '87	AAES, '90		
BM, '81	L, '80		AAES, '90	SG, '84	
	SP, '89a		SP, '89a		
SP, '89a	KA, '77		BM, '81; HKK, '87	SP, '89a	
B, '88	HKK, '87; BP, '89	E: KA, '77	B, '88		
SP, '89b	SP, '89b		SP, '89b	SP, '89b	
		E: *SP, '87*	B, '85		
		E: *SP, '87*	B, '85		
BM, '85	SP, '89a		SP, '89a	SG, '88	
		E: *SP, '87*	B, '85		
		E: *SP, '87*	B, '85		
BM, '85				SG, '88	
			F, '86		
					E: F, '86
					E: F, '86
	SP, '76		S, '87		
	SP, '76		S, '87		
SP, '89a				SP, '89a	
	GSS, '84; SG, '88		GSS, '84		
	GSS, '84		GSS, '84		

NMV, '86	Newsome, Maunsell, and Van Essen, 1986	SP, '89b	Seltzer and Pandya, 1989b
PBK, '86	Perkel, Bullier, and Kennedy, 1986	UD, '86a	Ungerleider and Desimone, 1986a
RP, '79	Rockland and Pandya, 1979	UD, '86b	Ungerleider and Desimone, 1986b
S, '87	Shiwa, 1987	*UGSM, '83*	*Ungerleider, Gattass, Sousa, and Mishkin, 1983*
SG, '84	Schwartz and Goldman-Rakic, 1984	VFDOK, '91	Van Essen, Felleman, DeYoe, Olavarria, and Knierim, 1991
SG, '88	Selemon and Goldman-Rakic, 1988		
SP, '76	Seltzer and Pandya, 1976	VNMB, '86	Van Essen, Newsome, Maunsell, and Bixby, 1986
SP, '80	Seltzer and Pandya, 1980	YI, '85	Yukie and Iwai, 1985
SP '84	Seltzer and Pandya, 1984	Z, '78a	Zeki, 1978a
SP '87	*Seltzer and Pandya, 1987*	Z, '78b	Zeki, 1978b
SP, '89a	Seltzer and Pandya, 1989a	Z, '80	Zeki, 1980

Table 6
Irregular and mismatched connectivity patterns

Irregular Terminations			Origin-Termination Mismatches			
From	To	Pattern	From	To	Origin	Termination
VP	V3A	F/C	V4	MT	S/B	C
MT	V3A	C/M	FST	MSTd	S/B	C
DP	PO	C/M?	STPp	46	S	C
LIP	PO	C/F	46	CIT	S/B	M
MT	PO	C/M	46	7a	B/S	M
V4	V4t	F/C	46	STPp	S	M
MT	V4	C/M				
DP	LIP	C/F				
LIP	DP	C/M				
MSTl	FST	C/F				
MSTl	VIP	C/M				
MSTd	FST	M/C				
FST	PIT	M/C				
FST	VIP	M/C				
FST	LIP	C/M?				
FST	FEF	F/M				
LIP	MSTd	C/F				
LIP	TF	F/C?				
FEF	46	F/C				
7a	STP	F/M?				
7a	FEF	C/M?				
7a	46	F/C				
AITv	TH	F/C				
46	TF	M/C				

architectonically defined FEF. The remaining 22 irregular patterns are all C/F or C/M mixtures and therefore involve an apparent conflict of only one step (lateral vs. ascending or lateral vs. descending). We suspect that this bias for C/F and C/M patterns is not a coincidence and that it may be important for understanding the significance of mixed or intermediate termination patterns (see below).

Step 2: Matching Origins and Terminations

The next step is to assess the consistency of retrograde and anterograde patterns for the 88 pathways in which both types of laminar information are available. In 39 of these cases, the retrograde pattern is bilaminar and hence is compatible with any anterograde pattern. There are 26 S→F and 8 I→M combinations, both of which are strongly consistent with an orderly hierarchical relationship. In addition, most of the 16 cases with mixed patterns on either the retrograde or the anterograde side also are fully consistent with this scheme (e.g., S/B→F, etc.). In a few cases, however, there are possible hierarchical inconsistencies, which are listed separately as "origin-termination mismatches" in Table 6. In 4 instances, the assignment for the origin is mixed (S/B). If further investigation reveals that these are B patterns, then there would be no conflict with the C or M terminations. If, on the other hand, any of them turn out to be S patterns, it would be an overt conflict with the criteria we have used. In the remaining 2 cases (area 46 to STPp and STPp to 46), the reported origin is an explicitly (S) pattern giving rise to an M or C termination pattern (Barbas and Mesulam, 1985; Selemon and Goldman-Rakic, 1988; Seltzer and Pandya, 1989a). It will be important to reexamine these pathways using combined retrograde and anterograde tracers and injections unequivocally restricted to a single visual area.

Step 3: Reciprocal Relationships

Analysis of reciprocal pathways provides the next test of the consistency of hierarchical relationships. From the data in column 11 of Table 5, there are 65 linkages in which the pattern is explicitly identifiable as ascending in one direction and descending in the other (49 designated as A-D, 16 designated as A-D?). There are only 5 linkages that are identifiably lateral in both directions (L/L), and all of these are questionable in one way or another. There are also 10 possible exceptions to this pattern, which are listed as "reciprocity mismatches" in Table 6 and also are indicated by "NC" or "NC?" (not consistent) in column 11 of Table 5.

In nearly all of the irregular cases (9 of 10), the comparison involves hierarchical assignments that are questionable on 1 or more counts, owing to the types of uncertainties described in the preceding 2 sections. Thus, while these putative counterexamples should be taken seriously, they should not all be regarded at present as unequivocal violations of our scheme. The strongest case for a genuine violation is the linkage between MSTd and 7a, which is reported to be descending from 7a to MSTd but lateral in the reverse direction (Andersen et al., 1990; Boussaoud et al., 1990).

Table 6
Continued

Reciprocity Mismatches

Pathway	Direction	Pathway	Direction	Hierarchical Mismatches
PO-LIP	A	LIP-PO	L/A?	FST-TF
DP-MSTd	A?	MSTd-DP	L	MSTd-PIT
FST-TF	L	TF-FST	A?	AITd-46
MSTd-7a	L	7a-MSTd	D	
CIT-FEF	A	FEF-CIT	A?	
CIT-46	A	46-CIT	A/D?	
7a-STP	A/D?	STP-7a	D?	
FEF-STPp	D?	FEF-STPp	D?	
STPp-46	A/L?	46-STPp	A/D?	
46-TH	L?	TH-46	D?	

Step 4: Global Hierarchical Constraints

We now address whether these pairwise relationships can be used to generate an overall hierarchy involving the entire collection of visual areas and pathways. To avoid logical inconsistencies, each area must be placed above all areas from which it receives ascending connections and/or sends descending connections. Likewise, it must be placed below all areas from which it receives descending connections and/or sends ascending connections. Finally, if an area has lateral connections, these must be with other areas at the same hierarchical level. All of the information needed to construct such a hierarchy is contained within Table 5, but it is not formatted optimally for the task. We therefore created an intermediate tabulation that greatly facilitated the process (Table 7).

Table 7 represents a "constraint chart" that indicates, for each visual area, all of the other areas with which it is connected and the hierarchical relationships that can be inferred solely on the basis of their direct linkages. For example, based only on what is known about it own connections, MT is unequivocally at a lower level than 7 areas (VIP, LIP, FST, MSTd, MSTl, FEF, and 46), level with 1 area (V4t), and higher than 4 areas (V1, V2, V3, and VP). In addition, MT is constrained to be level with or higher than areas V3A, V4, and PO, based on the mixed pattern of connectivity with those areas. Finally, MT has a known connection with area PIP that provides no constraints at all, making their hierarchical relationship indeterminate.

Once all of these pairwise relationships were tabulated, we began the task of generating an internally consistent hierarchy. This was done in a "bottom-up" fashion, by progressively adding areas to successive stages on the basis of information contained in the "higher than" and "level with" columns of Table 7. The sequence begins by identifying the area, namely V1, that has no entries in the "higher than" or "level with" categories and must therefore be at the lowest hierarchical level. The next level is populated by the area, namely V2, whose listing of "higher than" includes only the lowest area, V1. The process continues iteratively by adding at the next stage only areas whose listing of "higher than" includes those areas already entered in the emerging hierarchy. If more than 1 entry at a given level occurs, it is critical that they either be unconnected or be connected by lateral or indeterminate pathways. In cases where the constraint chart only partially restricts the positioning of areas (e.g., MT is level with *or* higher than V4), we chose the configuration that left all areas in the lowest possible state and minimized inconsistencies within the overall hierarchy. The resultant choices for these flexible cases are indicated by entering the linkage in the appropriate subcolumn within Table 7. This process continues iteratively until all hierarchical levels are established. Once the positioning of all areas is achieved, the wiring diagram can be added by inclusion of all linkages listed in the constraint table.

The hierarchical scheme that results from this analysis is shown in Figure 4. It includes all of the 32 visual cortical areas organized into 10 hierarchical levels. Each visual area is represented by a box colored in the same shade as on the cortical map (Fig. 2). In addition, we have included at the bottom the 2 subcortical levels (retina and LGN) that represent the primary source of visual inputs to the cortex. Finally, we have included at the top several uncolored entries that represent some of the linkages of the visual system to other sensory modalities and to "higher" associational cortex (see below).

As already noted, the coloring scheme for different areas provides information about the geographical location and the cortical processing stream in which they reside. In the upper part of the hierarchy, orange and yellow hues represent parietal areas, green hues represent temporal areas, and brown hues represent frontal areas. For the areas in the occipital lobe (lower part of Fig. 4), the primary distinction is between the M (magnocellular) stream (red and pink areas) and components of the P (parvocellular) stream (purple, blue, and violet). The P stream can be further split into the P-B (parvo-blob) and P-I (parvo-interblob) streams of V1 and V2 (see DeYoe and Van Essen, 1988). Connections of V1 and V2 that can be assigned explicitly to components of these streams are indicated appropriately in the figure; those that have not been specifically linked are represented by the lines emerging from the generically labeled boxes in V1

Table 7
Hierarchical constraints

Area	Lower than	Lower	or	Level	Level with
V1	V2, V3, V3A, PIP, V4, V4t, MT, PO, MSTl?				
V2	V3, VP, V3A, V4, V4t, MT, PO, MSTd, MSTl, FST, FEF				
V3	V3A, PIP, V4, V4t, MT, PO, MSTd, FST, LIP, VIP, FEF, TF				
VP	PIP, V4, PO, MT, VOT, MSTd, FST, LIP, VIP, FEF, TF	V3A			
V3A	V4, DP, MSTd, MSTl, FST, LIP, FEF	MT			
PIP	V4, PO, DP				
PO	MSTd, MSTl, 7a, FEF	DP		MT	
V4	VOT, DP, LIP, FST, PITd, PITv, CITd, CITv, FEF?, AITv, TF, TH, 46			MT, V4t	
V4t	MSTd?, MSTl?, FST, FEF				MT
MT	MSTd, MSTl, FST, LIP, VIP, FEF, 46				V4t
MIP					
MDP					
VOT	PITd, PITv				
DP	MSTl?, 7a, 46	MSTd LIP			
FST	STPp			MSTd	
VIP	FEF			MSTl, FST	MSTd
LIP	7a, FEF, 46	TF		MSTd, FST	PITv
MSTd	FEF, STPp, PIT?, TF	7a			VIP
MSTl	FEF, STPp			FST	
PIT	FEF, 46			FST	
PITd	CITv?, AITd?, AITv?				
PITv	CITd?, CITv?, AITd?, AITv?, TF?, TH				LIP
CIT	TH				STPp
CITd	AITd?, AITv?				
CITv	AITd?, AITv?, TF				
7a	AITd, TF, TH	46?		FEF	
FEF	AITd	46			
STP					
STPp	STPa, TF, TH				CIT
STPa	TF, TH, 46				
AITd					
AITv	TF, TH				
46	AITd			TH	
TF				FST, 46	
TH					

and V2. A similar strategy is used to represent connections between regions representing more than a single area in our partitioning scheme. For example, there are connections of PIT that cannot yet be assigned specifically to PITd or PITv. The connection between 7a and STP is also of this type, but we have shown this as a linkage with STPa in particular, in order to avoid the complications of an STP entry that would have to be placed between 2 levels. Areas MIP and MDP have been placed at the fifth hierarchical level, even though the connections known for both areas are ambiguous (bilaminar retrograde labeling)

Table 7
Continued

Level	or	Higher	Higher than	Indeterminant
			V1	VOT, PIP, VIP
			V1, V2	VP
			V2	V3
		VP	V1, V2, V3	PO
			V1, V3, VP	V2, MT, 7a
			V1, V2, V3, VP, PIP	V3A, V4t, MIP, MDP, VIP, LIP
			V1, V2, V3, VP, V3A, PIP	
V4			V1, V2, V3	PO
V4, PO		V3A	V1, V2, V3, VP	PIP
				PO, 7a
				PO, 7a
			VP, V4	V2
		PO	V3A, PIP, V4	FST, FEF
PIT, LIP, VIP, MSTl, TF			V2, V3, VP, V3A, V4, V4t, MT	DP, 7a, FEF
			V3, VP, MT	V2, PO, LIP, 7a
		DP	V3, VP, V3A, V4, MT	PO, VIP, MSTl
FST, LIP		DP	V2, V3, VP, V3A, V4t?, MT, PO	
VIP			V1?, V2, V3A, MT, PO, V4t?, DP?	LIP, 7a
			MSTd?	
			V4, VOT	
			V4, VOT	
				FEF, 46
			V4, PITv	
			V4, PITd, PITv	
		MSTd	PO, DP, LIP	PIP, VIP, FST, MSTl, STP, MIP, MDP
7a			V2, V3, VP, V3A, PO, V4?, V4t, MT, MSTd, MSTl, VIP, LIP	DP, CIT, FST, STPp
				7a
			MSTd, MSTl, FST	FEF, 46
			STPp	AITd
			7a, FEF, PITd?, PITv?, CITd?,CITv?, 46	STPa, TF, TH
			V4, PITd?, PITv?, CITd?, CITv?	
TF		7a?, FEF	V4, MT, DP, LIP, PIT, STPa	CIT, STPp
		LIP	V3, VP, V4, PITv, MSTd, CITv, AITv, 7a, STPp, STPa	AITd
46			V4, PITv, CIT, AITv, STPp, STPa, 7a	AITd

and would technically be consistent with placement at any lower level. This assignment is obviously provisional, pending additional connectivity information. However, it would be surprising if either MDP or MIP ultimately ended up at a lower level, because there is a strong tendency for areas positioned more anteriorly in the cortex (to the right on the cortical map) to be situated at higher levels of the hierarchy.

This hierarchy is consistent with all but 3 of the relationships listed in the constraint chart. One exception is the linkage between FST and TF, which constrains TF to be level with or lower than FST

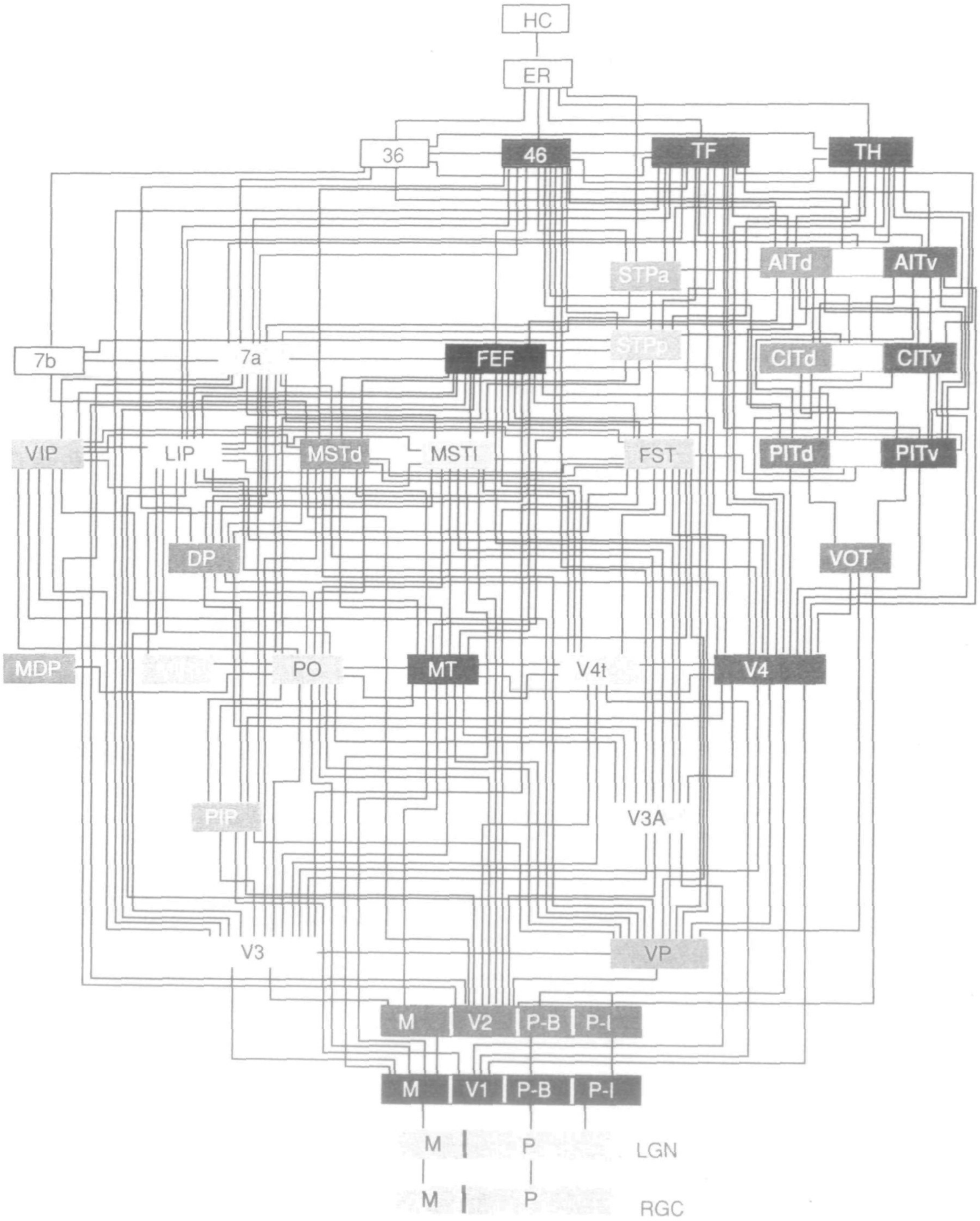

Figure 4. Hierarchy of visual areas. This hierarchy shows 32 visual cortical areas, shaded according to the same scheme as in Figure 2, 2 subcortical visual stages (the retinal ganglion cell layer and the LGN), plus several nonvisual areas (area 7b of somatosensory cortex, perirhinal area 36, the ER, and the hippocampal complex). These areas are connected by 187 linkages, most of which have been demonstrated to be reciprocal pathways.

(Boussaoud et al., 1990). Another is the connection between MSTd and PIT, which constrains PIT to be higher than MSTd. The third is the connection between AITd and 46, which constrains 46 to be level with or lower than AITd. All attempts to reposition these areas led to an even larger number of inconsistencies. Hence, we regard the current version as a "best fit" to the available data. It is notable that all 3 of these inconsistencies involve relationships that were already questionable from an earlier stage of the analysis.

The sheer complexity of Figure 4 makes it difficult in many places to trace the lines representing specific pathways. In order to permit inspection and updating of these connections in a flexible manner, we created the hierarchy on a graphics drawing program (CANVAS) that runs on Macintosh computers. Each area and all of its connections are represented in a different "layer" that can be independently switched on or off, thereby allowing easy visualization of any desired subset of the overall hierarchy.

The current hierarchy is more extensive than, but otherwise largely consistent with, recently published hierarchical schemes that have been based on similar anatomical criteria (Van Essen, 1985; Andersen et al., 1990; Boussaoud et al., 1990). However, there are a few significant differences that merit explicit mention. Our new version differs from the Van Essen (1985) scheme in having area 7a moved 1 step higher and area DP 1 step lower. The differences with the Andersen et al. (1990) scheme are slightly greater: (1) We have DP 1 step lower and PO 2 steps lower than in theirs; (2) we have MSTd/l level with LIP, rather than above it; (3) instead of a single area IT sitting above 7a, we have multiple subdivisions of IT, and AITd/v above and CITd/v level with 7a; and (4) instead of a single STP, we have STPp and STPa, with only the former being level with 7a. The differences with the Boussaoud et al. (1990) scheme include (1) our positioning of areas V3A and DP each at 1 stage lower than in theirs, (2) our positioning of 7a at 1 stage higher than their PP/IPG, and (3) our positioning of TF several stages higher than in theirs. In most instances, these differences can be traced to the way in which different investigators have interpreted the various irregularities and conflicts that we have already discussed in connection with Table 6.

Significance of Hierarchical Irregularities

The red lines in Figure 4 indicate the 33 linkages having one or another of the hierarchical irregularities discussed in connection with Table 6. Their presence raises the issue of whether the cortex is inherently only a "quasi-hierarchical" structure that contains a significant number (perhaps 10%) of bona fide irregularities and exceptions to any set of criteria that can be devised. Alternatively, the visual cortex might contain an essentially perfect anatomical hierarchy that has been imperfectly studied using inherently "noisy" methods of anatomical analysis. Either interpretation is an interesting one, in our opinion, but we doubt that it is possible to obtain a clear-cut answer on the basis of currently available data.

The anatomical data on which our analysis is based are often fuzzy and replete with uncertainties of one or another type. Thus, it would have defied the odds if every single one of the 305 pathways had fit precisely into an orderly hierarchy. It is very likely that at least a few of the laminar and hierarchical assignments cited in our analysis will change when additional experimental data become available. If one suspects that the underlying biology is extremely orderly, one would predict that the apparent discrepancies listed in Table 6 will largely disappear upon careful reexamination, thereby improving the overall fit to the hierarchy. This might be accompanied by changes in some of the specific hierarchical assignments. If, on the other hand, one suspects that a hierarchical relationship merely reflects a strong statistical bias, the prediction would be that an increasing number of unambiguous inconsistencies with our scheme will be found. This is a matter of speculation at the moment, and we do not take a strong stand on either side, except to emphasize that the issue is amenable to experimental validation or refutation. To distinguish incisively among different alternatives, however, it is crucial that reports of anatomical connectivity be as precise and quantitative as possible with regard to basic questions of (1) the confidence with which sources and targets have been identified in relation to areal boundaries and (2) the exact laminar distribution of anterograde and retrograde tracers.

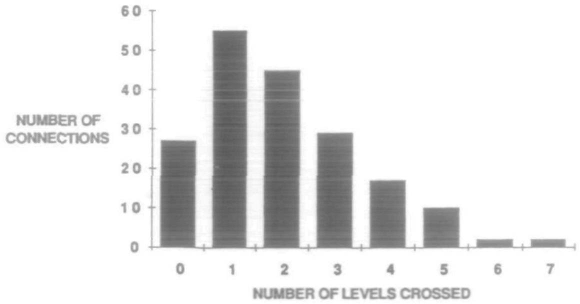

Figure 5. Histogram of number of hierarchical levels traversed by different pathways. Most pathways traverse only 1 or 2 levels, but a few ascend or descend as many as 6 or 7 levels.

As a reminder, we note that about 10% of the pathways shown in Figure 4 are distinctive in terms of being sparse, occasional, or controversial in nature, and a somewhat larger percentage is based on information currently available only in abstracts. We found that resolution limits made it impractical to flag these special cases by distinctive colors in the figure, but they can nonetheless be readily tracked down with reference to Tables 3 and 5.

Number of Levels Traversed

While some pathways link areas at the same or immediately adjacent hierarchical levels, the majority of pathways traverse more than 1 level. For example, V1, at the first cortical level, projects to areas at the next 4 levels, from the second (V2) to the fifth (MT). The extreme limit is represented by the projections from areas V3 and VP (level 3) to parahippocampal areas TF and TH (level 10), thereby traversing 7 hierarchical levels. Moreover, because V3 receives direct inputs from V1, it is, in principle, possible for signals to span the entire visual hierarchy with only 1 relay. The route from V1 to MT to area 46 provides another example of this type.

A systematic analysis of this issue is shown in Figure 5a, which is a histogram of the number of levels separating all pairs of visual areas known to be interconnected. The mean value is 1.8 levels. Signals that traversed the hierarchy at approximately this rate

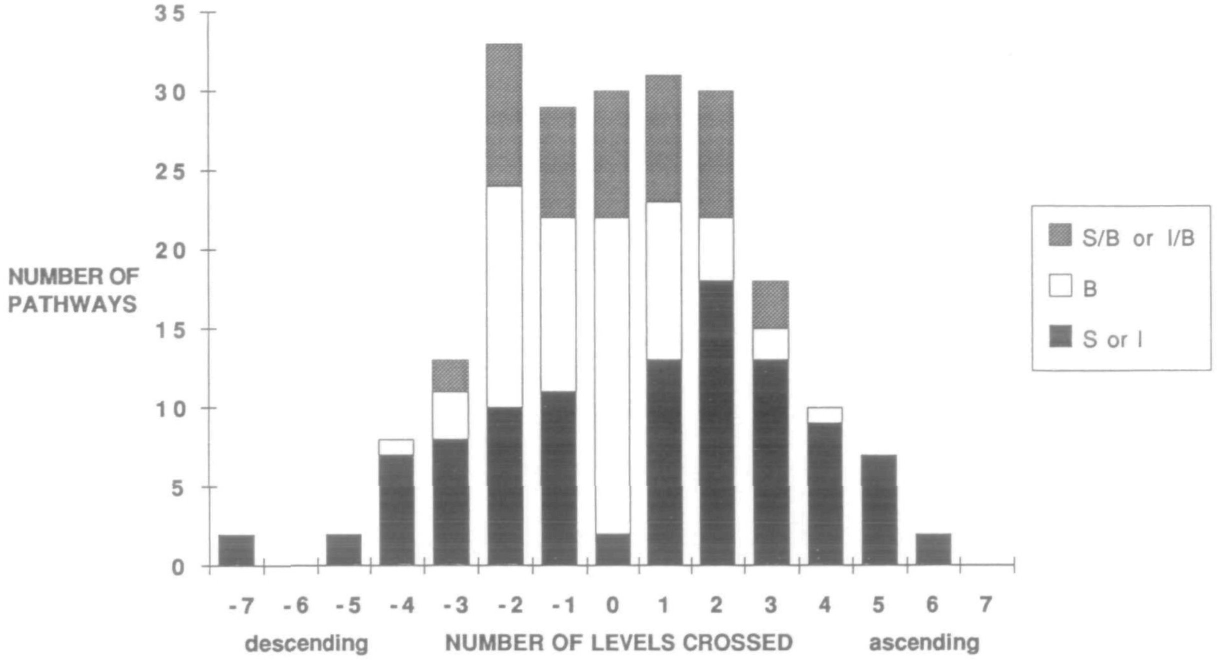

Figure 6. Relationship of laminar patterns for cells of origin to number of levels traversed. The great majority of bilaminar patterns (*open regions*) arise from pathways traversing no more than 2 levels, whereas unilaminar patterns are encountered over the entire range and are especially predominant for pathways traversing 3 or more levels.

would pass through 5 or 6 stages between start and finish.

Given that ascending pathways and descending pathways can both be associated with a retrograde labeling pattern that can be either bilaminar or unilaminar (supragranular for ascending, infragranular for descending), we wondered whether there was anything systematic about the occurrence of one or the other pattern. Figure 6 shows that there is an interesting difference along these lines. Descending and ascending pathways are indicated, respectively, by negative and positive values for the number of levels crossed. Pathways originating from unilaminar patterns are indicated by solid bars, those of bilaminar origin are indicated by open bars, and the mixed assignments (S/B and I/B) are indicated by shading. There is considerable overlap between bilaminar and unilaminar populations. Nonetheless, it is apparent that the more specific unilaminar projections, on average, traverse more hierarchical levels than do the bilaminar projections: 2.68 levels for I patterns, 2.76 levels for S patterns, and 1.71 levels for B patterns, excluding all of the lateral pathways. These differences (S vs. B; I vs. B) are highly significant ($p < 0.005$, Student's *t* test). Stated differently, a majority (60%) of the pathways traversing only 1 level are of bilaminar origin, whereas a majority (66%) of those traversing 2 or more levels are of unilaminar origin.

In the anterograde direction, it is instructive to consider the subset of pathways that show mixed, or borderline, termination patterns (C/M and C/F patterns in Tables 5, 6). On average, these pathways traverse less than 1 level (~0.8), which is less than half what would be expected if they were picked randomly from the overall pool. Thus, it appears that, in both retrograde and anterograde directions, differences in laminar patterns are statistically correlated with the number of levels separating any given pair of areas, as well as the sign (ascending, descending, or lateral) of the relationship.

A related set of questions arises when considering connectivity patterns and hierarchical relationships among adjacent visual areas, that is, ones that share a common boundary in the intact cortex. In terms of connectivity, the great majority of areas that adjoin one another are directly and reciprocally interconnected. There are only a few clear-cut exceptions, such as the reported lack of a connection between ventral area V2 and adjoining areas TF and TH. Thus, while many pathways connect areas that are widely separated within the cortex, it is rare to see adjoining areas that fail to communicate directly with one another.

In terms of hierarchical relationships, the majority of adjoining areas are either at the same level or are separated by only 1 level. However, there are numerous examples of neighboring areas separated by 2 or 3 levels (e.g., V2/V4, VP/V4, and PIP/VIP). The maximum hierarchical jump between neighbors is the 8 steps between V2 and TF/TH, but very few others are separated by more than 1 level.

Finally, the tendency for areas more anterior in the cortex (to the right on the map in Fig. 2) to be at a higher level, or at least the same level, is quite striking. This geographical relationship was pointed out by Rockland and Pandya (1979), at a time when only a handful of well-defined areas were known, and our point here is simply that the trend persists even at the much finer grain of analysis now available. However, there are a few specific counterexamples, such as the fact that TF and TH are posterior to, but at a higher level than, AITd and AITv, and likewise for 7a versus MT, MSTd, MSTl, and FST. With the exception of MDP and MIP (see above), these geographical considerations played absolutely no role in the formulation of the cortical hierarchy, so we regard the "anterior signifies upwards" trend to be genuine and perhaps of significance with regard to the way in which the number of visual areas has increased during evolution.

Hierarchical Relationships in Other Regions and in Other Species

The visual cortex has extensive connections with a variety of nonvisual areas, both cortical and subcortical. It is naturally of interest to know the levels at which communication takes place between different functional modalities and whether these other systems are themselves hierarchically organized.

Four nonvisual areas, chosen because they can be directly linked to the visual hierarchy in an orderly fashion, are shown by the noncolored boxes in Figure 4. One of these is somatosensory area 7b, which is connected to areas MSTd and MSTp (Andersen et al., 1990) in a way that places it at the eighth hierarchical level. This allows us to link the visual hierarchy with a somatosensory hierarchy that will be discussed below.

The 3 remaining entries shown in Figure 4 [area 36, the entorhinal cortex (ER), and the hippocampal complex (HC)] are all associated with the limbic system. Area 36 (TG, or temporal polar cortex) is a strip of polysensory neocortex that adjoins entorhinal cortex, area TF, and AITv. It can be placed at the same level as TF because it receives lateral projections from TF and area 46 as well as ascending projections from 7a and perhaps also AIT (Van Hoesen and Pandya, 1975; Goldman-Rakic et al., 1984; Seltzer and Pandya, 1984). The analysis is less straightforward for entorhinal cortex, a complex of several small areas (Amaral et al., 1987) all having a transitional architecture that lacks the cell-dense layer 4 characteristic of most neocortical areas. Entorhinal cortex receives neocortical inputs preferentially from the superficial layers of areas STPp, STPa, TF, TH, 46, and 36 (Amaral et al., 1983; Insausti et al., 1987). This suggests that entorhinal cortex is at a higher level than all of the neocortical areas with which it is connected. The fact that the inputs from these neocortical areas terminate in superficial layers of ER (Van Hoesen and Pandya, 1975) appears, at first glance, to argue against this assignment. However, we presume that the superficial terminations may be related to the absence of a standard granular layer 4 in ER. This interpretation fits well with the fact that the projections from the olfactory bulb, which clearly represent ascending sensory inputs, also terminate in superficial layers in both the pyriform cortex and the olfactory portion of entorhinal cortex (Turner et al., 1978; see also Swanson et al., 1987).

At the top of the hierarchy, we have placed the hippocampal complex, an archicortical region that includes the dentate gyrus, fields CA1 and CA3, and the subiculum, parasubiculum, and presubiculum. The architecture and connectivity of the hippocampal complex is radically different from the neocortical areas discussed above (cf. Swanson et al., 1987). Hence, it should not be surprising that a modified set of criteria would be necessary for making any hierarchical assignments. Our assignment is based on the fact that the projection from entorhinal cortex arises predominantly from superficial layers, at least in the rat (cf. Swanson et al., 1987), and terminates strongly in the dentate gyrus (Van Hoesen and Pandya, 1975), which, despite its different topology, is a granular layer analogous to neocortical layer 4. Also, the reciprocal projection from CA1 terminates mainly in deep layers of entorhinal cortex (Saunders and Rosene, 1988), and hence is complementary to the neocortical inputs that terminate mainly in superficial layers. Thus, the hippocampal complex is arguably at a higher level than neocortical and transitional cortical areas. We reiterate, however, that this illustration is deceptive in one sense, because the hippocampus and entorhinal complex are by no means the only high-level targets of visual information flow (see below).

Somatosensory and Motor Cortex

The notion that forward and feedback connections can be used to delineate hierarchical relationships is nearly as old for the somatosensory cortex as it is for the visual cortex. The first hierarchical scheme proposed for the somatosensory cortex involved 4 stages of processing among 5 somatosensory areas (Friedman, 1983). More recent studies have extended this hierarchical analysis to include more areas and connections, including several motor areas (Friedman et al., 1986; Neal et al., 1987). As in the visual system, the number of areas and pathways has become so large that it is difficult to analyze all of the critical relationships without having an organized database for the relevant circuitry. Because of our interest in understanding the detailed hierarchical relationships among different modalities, we have extended our analysis to include the 62 known connections among 13 areas of the somatosensory and motor cortices. The laminar information pertaining to these pathways is contained in Table 8, whose format is identical to that of Table 5.

As in the visual system, reciprocity of connections between areas appears to be a general rule, but there are several possible exceptions, including pathways from 7b to 1, SII to 4, and granular insular (Ig) to dysgranular insular (Id) that apparently lack connections in the reverse direction. The great majority of pathways fit cleanly into ascending, descending, and lateral connections according to the same criteria used for the visual cortex. However, by this point, it should not be surprising to find that there are a few irregularities that must be addressed. For example, the projection from SII to 7b appears to terminate in a mixed C/F (columnar/forward) pattern (Friedman et al., 1986), and there are conflicting reports on the ter-

Table 8
Connectivity table for sensorimotor areas

1	2	3	4	5	6	7	8	9	10	11	12
	Outputs					Inputs				Hierarchical relationship	Levels crossed
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)		
3a	1				1	3a		M	D		1
3a	2	S	F	A	2	3a		M?	D?	A-D?	2
3a	SII	S		A	SII	3a		M	D	A-D	5
3b	1		F	A	1	3b		M	D	A-D	1
3b	2	S	F	A	2	3b		M(S)	D	A-D	2
3b	SII	S	F	A	SII	3b		M	D	A-D	5
1	2	S/B	F	A	2	1		M(S)	D?	A-D?	1
1	5			u	5	1		M	D		2
1	SII	S	F	S	SII	1		M	D	A-D	4
1	7b		F	S	7b	1				NR	5
2	5		F	A	5	2	S		A	NC	1
2	7b		F	A	7b	2	S(3, 4)		A?	NC?	4
2	SII	S		A	SII	2		M	D	A-D	3
2	4		F	A	4	2	I/S?		?		5
2	SMA		F	A	SMA	2					6
5	Ri				Ri	5	I	M	D		1
5	7b	S	F	A	7b	5	I	M	D	A-D	3
5	4	B	F		4	5	S?			NC	4
5	SMA		F	A	SMA	5		(M)	D?	A-D?	5
5	SII				SII	5			u		2
5	6	B			6	5					5
Ri	7b	S	F	A	7b	Ri		M	D	A-D	2
Ri	SII	S	F	A	SII	Ri		M	D	A-D	1
Ri	Ig	S	F	A	Ig	Ri		M	D	A-D	3
SII	7b	S	C/F	A	7b	SII	S	M/F	?	NC	1
SII	Ig	S	F	A	Ig	SII		M(1)	D	A-D	2
SII	Id	B	F	A	Id	SII	B	M	D	A-D	3
SII	4		F?(3)	A?	4	SII			u	NR?	2
SII	6		F?(3)	A?	6	SII					3
7b	Ig		F	A	Ig	7b	I		D	A-D	1
7b	6	B	F	A	6	7b		M		A-D	2
7b	4	B/I		D?	4	7b					1
Ig	Id				Id	Ig		M/C		NR	1
4	SMA	S/B	F(3)/C?	A/L?	SMA	4	B/S	M/C?	D/L?	A-D?	1
4	6	S/B	F(3)/C?	A/L?	6	4	B	M/C?	D/L?	A-D?	1
6	SMA		C?	L?	SMA	6		C?	L?	L-L?	0
Id	35		F?	A?	35	Id	I		D	A-D?	1
Id	36				36	Id	B				1

This table shows connections among somatosensory and motor areas in the macaque. Format and symbols are identical to those used in Table 5.

[a] Reference key:

AAES, '90	Andersen, Asanuma, Essick, and Seigel, 1990	FMOM, '86	Friedman, Murray, O'Neill, and Mishkin, 1986
F, '83	Friedman, 1983	GLKR, '84	Godschalk, Lemon, Kuypers, and Ronday, 1984
FJB, '80	Friedman, Jones, and Burton, 1980	J, '84	Jürgens, 1984 (squirrel monkey)

Table 8
Continued

13 Output References*	14	15	16 Input References*	17	18
Origin	Termination	Special (E, R, S, A)	Origin	Termination	Special (E, R, S, A)
				PK, '86	
PK, '86	JCH, '78			PK, '86	
FMOM, '86				FMOM, '86	
	JCH, '78			VP, '78; PK, '86	
PK, '86	JCH, '78			PK, '86	
FMOM, '86	FJB, '80			FMOM, '86	
PK, '86	PK, '86			PK, '86	
		E: PK, '86		PK, '86	
FMOM, '86	FJB, '80			FMOM, '86	
	PK, '86				A: FMOM, '86
	PK, '86		PK, '86		
	PK, '86		PK, '86		A: FMOM, '86
FMOM, '86				FMOM, '86	
	JCH, '78		PK, '86		
	JCH, '78				
			NPP, '87	FMOM, '86	
NPP, '87	NPP, '87		NPP, '87	NPP, '87; AAES, '90	
GLKR, '84	JCH, '78; K, '78; PK, '86		PK, '86		
	JCH, '78			J, '84(SqM)	
					A: JCH, '78; E: PK, '86
GLKR, '84					
NPP, '87				NPP, '87	
FMOM, '86	F, '83; FMOM, '86			F, '83; FMOM, '86	
FMOM, '86	FMOM, '86			FMOM, '86	
NPP, '87	FMOM, '86		FMOM, '86	FMOM, '86; NPP, '87	
FMOM, '86	F, '83; FMOM, '86			FMOM, '86	
FMOM, '86	F, '83; FMOM, '86		FMOM, '86	FMOM, '86	
	FMOM, '86	A: FJB, '80			E: FJB, '80
	FMOM, '86				
	NPP, '87		NPP, '87		
GLKR, '84	FMOM, '86; AAES, '90			K, '78	
GLKR, '84					
		A: FMOM, '86		FMOM, '86	
PS, '85	JCH, '78; MCGR, '86; PS, '85		MS, '79; GLKR, '84	J, '84(SqM); PS, '85	
GLKR, '84; PS, '85	PS, '85 MCGR, '86		GLKR, '84; MCGR, '86	PS, '85 MCGR, '86	
	K, '78; MCGR, '86			J, '84(SqM)	
	FMOM, '86		FMOM, '86		
			FMOM, '86		

JCH, '78	Jones, Coulter, and Hendry, 1978	NPP, '87	Neal, Pearson, and Powell, 1987
K, '78	Künzle, 1978	PK, '86	Pons and Kaas, 1986
MCGR, '86	Matelli, Camarda, Glickstein, and Rizzolatti, 1986	PS, '85	Primrose and Strick, 1985
MS, '79	Muakkassa and Strick, 1979	VP, '78	Vogt and Pandya, 1978

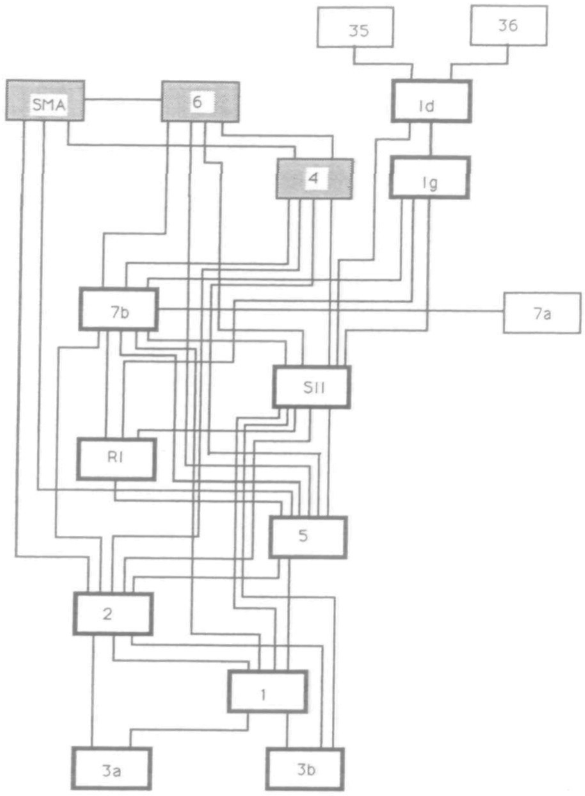

Figure 7. A proposed hierarchy for somatosensory and motor areas, based on 62 linkages among 10 somatosensory and 3 motor areas. Hierarchical assignments are based on the laminar information contained in Table 7. Also included in the hierarchy are connections with visual area *7a* (cf. Fig. 4) and with higher associational areas *35* and *36*. Counting the highest level, there are 10 levels in the hierarchy, and possibly an eleventh, depending on uncertainties with regard to interconnections among motor areas (see text).

mination pattern in the reverse direction, with Neal et al. (1987) and Andersen et al. (1990) reporting a descending projection from 7b to SII and Friedman et al. (1986) reporting an ascending projection. There are also apparent inconsistencies in the linkages between areas 2 and 5, 2 and 7b, and 5 and 4, in that both directions appear to be of the ascending pattern (Jones et al., 1978; Pons and Kaas, 1986). However, some of these assignments are based on our interpretation of 1 or 2 schematic illustrations, and it is important that these questionable cases receive further scrutiny. In the motor cortex, a critical issue is whether the projections among areas 4 and 6 and SMA (supplementary motor area) are all of the columnar (C) pattern or whether there are ascending projections from 4 to SMA and descending projections from 6 to 4. The patterns illustrated in the literature (Jones et al., 1978; Künzle, 1978; Matelli et al., 1986) are difficult to interpret unambiguously, but Primrose and Strick (1985) reported in an abstract that the premotor areas (SMA and 6) appear to be at a higher level than area 4 on the basis of both anterograde and retrograde labeling patterns. The ascending anterograde patterns they described terminated preferentially in layer 3 rather than layer 4, but this seems a reasonable assignment given that the motor cortex lacks the granular layer 4 characteristic of most other neocortical regions.

Figure 7 shows the somatosensory-motor hierarchy that results from the systematic application of the pairwise hierarchical assignments contained in Table 8. Somatosensory areas are outlined with heavy lines, motor areas are shaded, and other areas (visual and associational) are outlined with fine lines. In brief, this hierarchy starts with areas 3a and 3b at the bottom and extends in successive stages through areas 1, 2, 5, retroinsular (Ri), SII, 7b, Ig, and Id. The motor areas included are areas 4, 6, and SMA, with area 4 placed at a lower level than the other 2. The other nonsomatosensory areas shown (with thin outlines) are area 7a of the visual cortex and associational areas 35 and 36 of the perirhinal cortex, which are included in order to indicate the relationship to areas shown in the visual hierarchy (Fig. 4).

Remarkably, the 9 levels of the somatosensory–motor hierarchy are nearly as many as the 10 levels of the visual hierarchy, even though there are fewer than half the number of areas involved. This scheme is based on a larger number of connections than in the schemes proposed by Friedman et al. (1986, their Fig. 16) and Neal et al. (1987), but it is similar to theirs in most respects. The major difference with the Friedman et al. (1986) scheme is that we have placed each area at an explicit level of the hierarchy, rather than relying as they did on a large number of arrows to reflect pairwise hierarchical relationships. It was only after doing this that we appreciated that there are so many levels in the somatosensory–motor hierarchy. Also, we have placed area 7b above SII, rather than below as in their scheme, pending resolution of the conflicting observations mentioned above. The differences with the Neal et al. (1987) scheme involve the relative placement of areas 5, Ri, SII, 7b, and Ig, which we have repositioned on the basis of the additional evidence included in our analysis.

As already noted, the pathways between the somatosensory and visual systems allow the different modalities to be linked into a unified sensorimotor hierarchy. The configuration of this unified hierarchy can be inferred from examination of Figures 4 and 7 together, but it can also be visualized directly, in a manner that we have illustrated elsewhere (Van Essen et al., 1991). For the most part, each level in the visual system can be matched to a corresponding level in the somatosensory–motor system, and vice versa. This is not invariably the case, however, because area 36 is 3 levels above areas 7a and 7b in Figure 7 but only 2 levels above them in Figure 4. This suggests that one of the intervening somatosensory–motor levels lacks a corresponding visual level, assuming that these hierarchical assignments are indeed all correct.

Auditory Cortex

In the auditory system, Galaburda and Pandya (1983) analyzed connections among 12 cytoarchitectonic areas that they identified within the superior temporal gyrus and supratemporal plane of the lateral sulcus. These areas were grouped into 4 rostrocaudally aligned triplets of "root," "core," and "belt" areas. Their analysis showed the same basic types of laminar patterns found in the visual and somatosensory systems, including S, B, and I patterns for cells of origin. With anterograde labeling, they found that the feedback-type pattern was generally strongest in layer 1, but otherwise conformed to the F, C, and M description that we have used. They reported that rostral-to-caudal projections tended to be of the descending pattern, and that caudal-to-rostral projections tended to be ascending in some cases but columnar in others. In the mediolateral direction, their description suggests that each of the belt areas is at a higher level than the corresponding core area. However, the relationship described for the root areas is incompatible with an internally consistent hierarchy: The root areas show a descending projection to both belt and core areas, but the reciprocal projection from belt and core to the root areas are described as columnar. Clearly, this issue merits further investigation, in order to ascertain whether these constitute unequivocal conflicts with an orderly hierarchy of auditory areas. One small piece of evidence in further support of an auditory hierarchy comes from a single tracer injection in the postauditory area (Pa), which demonstrated descending projections to A1 and ascending connections to a different auditory area (Friedman et al., 1986).

It is also important to have more information on the linkage between auditory and visual systems. It is known that there are auditory projections to the polysensory, but predominantly visual-association area STP (Galaburda and Pandya, 1983; Seltzer and Pandya, 1989b), but there is insufficient information about the laminar patterns to ascertain specific hierarchical relationships.

Other Cortical Regions

The remaining regions of the neocortex yet to be incorporated into our analysis include much of the frontal lobe (orbitofrontal, lateral prefrontal, dorsal prefrontal, and medial prefrontal), as well as cingulate, retrosplenial, and insular regions. Many of these regions have strong interconnections with areas near the top of the visual hierarchy, including areas 46 and 7a, and with somatosensory areas, as well (Selemon and Goldman-Rakic, 1988; Barbas and Pandya, 1989; Cavada and Goldman-Rakic, 1989b). However, there is not a great deal of information about the specific laminar patterns for pathways to and from precisely defined areas in these regions. One striking finding is that large paired injections centered in areas 7a and 46 led to interdigitating columnar patterns of terminations in some regions (e.g., cingulate cortex and orbitofrontal cortex), even though the same injections contributed to complementary (ascending and descending) patterns in other regions, such as the STS (Selemon and Goldman-Rakic, 1988). If this observation is confirmed using small tracer injections clearly confined to single cortical areas, it would indicate a clear breakdown in hierarchical relationships. Thus, there is a strong possibility that substantial portions of frontal and cingulate cortex lie outside the hierarchical framework proposed here for sensory and motor areas. In this regard, it is of interest that the incidence of irregularities in the current visual hierarchy (red lines in Fig. 4) seems to increase at progressively higher levels, suggesting a gradual rather than abrupt breakdown. However, this trend may instead simply represent the greater uncertainty and ambiguity about many of the high-level assignments.

The olfactory system is the last of the sensory modalities for which laminar information about some of the major connections is available. In the macaque, there are several paleocortical and transitional cortical areas associated with olfaction (pyriform cortex, periamygdaloid cortex, and the olfactory portion of the entorhinal cortex). Each of these regions receives direct inputs from the olfactory bulb that, as already noted, terminate preferentially in superficial layers of cortex (Turner et al., 1978). The reciprocal projection from ER terminates in the deeper layers of the pyriform cortex, at least in the rat (cf. Haberly, 1985). Thus, using a different set of criteria for forward and feedback directions, it should be possible to determine whether an orderly anatomical hierarchy can be identified in the olfactory system.

Subcortical Projections

All visual areas that have been appropriately examined have extensive connections with a variety of subcortical structures. Indeed, it would not be surprising if the sheer number of corticosubcortical pathways exceeds that of the corticocortical pathways analyzed in this article. These include linkages with nuclei in the forebrain (amygdala, claustrum, caudate nucleus), thalamus (pulvinar, reticular nucleus), midbrain (superior colliculus), brain stem (pons), hypothalamus, and basal forebrain, to name just some of the prominent structures (cf. Tigges and Tigges, 1985; Yeterian and Pandya, 1985; Andersen, 1987; Iwai and Yukie, 1987; Kaas and Huerta, 1988). In many cases, the connections are strongly reciprocal in nature, just as is characteristic of corticocortical pathways.

The pulvinar complex is physically the largest visually related nucleus and the most interesting to consider with respect to possible hierarchical relationships. The projections from cortex to different pulvinar subdivisions originate predominantly from layer 5, and the reciprocal projections from the pulvinar terminate most heavily in layers 4 and 3 of the extrastriate cortex (Lund et al., 1975; Benevento and Rezak, 1976; Ogren and Hendrickson, 1977). This would be consistent with the pulvinar lying near the bottom of the hierarchy and providing ascending projections to the extrastriate cortex. Interestingly, however, the pulvinar projection to V1 terminates mainly in superficial layers, even though the reciprocal pathway originates from layer 5, just as for extrastriate areas (Rezak and Benevento, 1979). Thus, there is no clear basis for placing the pulvinar in a specific hierarchical relationship relative to V1. The claustrum, on the other hand, projects to layer 4 of V1 and receives inputs

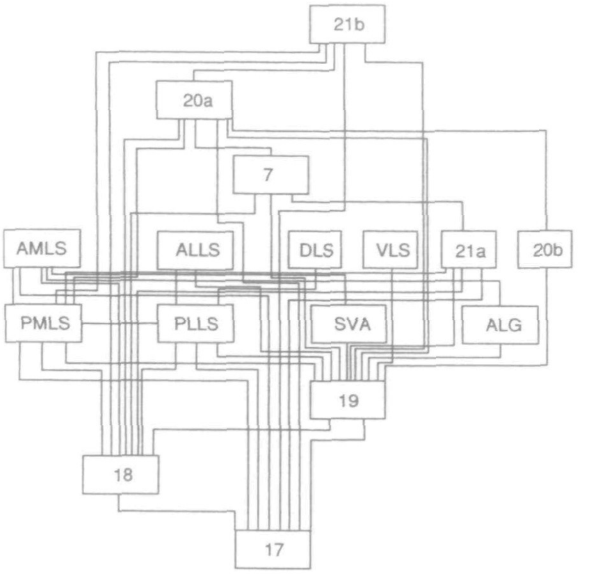

Figure 8. Hierarchy of visual cortical areas in cat, based on connections and laminar patterns reported by Symonds and Rosenquist (1984a,b). Sixteen cortical areas have been arranged into 8 hierarchical levels. Interestingly, the fourth and fifth levels each contain many areas, whereas all other levels contain only single entries. *ALG*, anterolateral gyrus area; *ALLS*, anterolateral lateral suprasylvian; *AMLS*, anteromedial lateral suprasylvian; *DLS*, dorsolateral suprasylvian; *PLLS*, posterolateral lateral suprasylvian; *PMLS*, posteromedial lateral suprasylvian; *SVA*, splenial visual area; *VLS*, ventrolateral suprasylvian.

from layer 6, at least in the cat (LeVay and Sherk, 1981) and thus is arguably at a lower level than any of the cortical areas.

The amygdala receives inputs from mainly superficial layers of areas in the inferotemporal complex and STP, whereas its inputs from TF and TH are mainly from infragranular layers (Aggleton et al., 1980). This is consistent with the amygdala being at a well-defined level just below TF and TH. Information on the anterograde terminations from the amygdala to specific cortical areas would be particularly useful for testing this possibility more precisely, by ascertaining whether there is an ascending (F) pattern to TF and TH and a descending (M) pattern to the other targets.

Other Species

Although the macaque has been the most thoroughly studied, there is also a considerable body of information about laminar connectivity patterns in other species. Among other primates, the owl monkey, squirrel monkey, and bushbaby all show striking similarities with the macaque in the layout and internal organization of the visual cortex, and there are clear homologies among V1, V2, MT (cf. Kaas, 1988), and perhaps many more areas (Sereno and Allman, 1991). In these species, pathways between visual areas are in general reciprocal, with asymmetries in laminar patterns similar to that in the macaque (Tigges et al., 1973, 1981; Weller and Kaas, 1987; Kaas, 1988). Thus, it seems likely that similar principles of hierarchical organization apply throughout the primate order, but this hypothesis clearly merits closer scrutiny.

Among nonprimates, the cat and the rat have been most closely studied. In the cat, 18 visual areas have been identified (Rosenquist, 1985), and connections between areas are generally reciprocal (Symonds and Rosenquist, 1984a; Sherk, 1986), just as in primates. The laminar distributions for individual pathways generally fit to 1 of the 3 categories we have used, namely, S, B, or I for cells of origin and F, M, or C for terminations (Gilbert and Kelly, 1975; Bullier et al., 1984; Symonds and Rosenquist, 1984a,b; Sherk, 1986). Laminar patterns for pathway terminations have not been studied as extensively as for the cells of origin, but the illustrations provided in Symonds and Rosenquist (1984a) suggest that the anterograde and retrograde labeling patterns are typically consistent with our scheme for ascending and descending pathways (Fig. 3). Moreover, when hierarchical assignments can be made independently for each direction of a reciprocal pair, the patterns are in general complementary. On the other hand, it has been explicitly suggested that connectivity patterns in the cat are not consistent with an anatomical hierarchy (Symonds and Rosenquist, 1984b; Rosenquist, 1985). This argument is based mainly on the occurrence of a bilaminar origin for pathways that would otherwise be constrained to be ascending, as in the specific case of area 19 projecting to area 21a. However, we have already discussed the need in the primate cortex to treat bilaminar retrograde labeling patterns as completely ambiguous with regard to hierarchical assignments.

By applying our revised criteria to connectivity patterns described in Symonds and Rosenquist (1984a,b) for visual cortex in the cat, we have constructed an orderly hierarchy that involves 62 connections among 16 areas organized into 8 levels (Fig. 8). In particular, areas 17, 18, and 19 are located at the first, second, and third stages, respectively. Thus, each occupies a different level despite the fact that they all receive major, direct inputs from the LGN (cf. Stone et al., 1979). This serves to reinforce a point already made in relation to the macaque, namely, that major pathways often traverse more than 1 hierarchical level. They are followed by 2 levels, each containing numerous entries (areas PLLS, PMLS, SVA, and ALG at the fourth level and areas AMLS, ALLS, DLS, VLS, 21a, and 20b at the fifth level). Finally, the top 3 levels revert to the pattern of containing only single entries (area 7 at the sixth level, area 20a at the seventh level, and area 21b at the eight level). There are a few apparent inconsistencies with this scheme, however. Specifically, using retrograde tracers, the connections between PMLS and PLLS are reported to have an infragranular labeling pattern in both directions, and the projection from VLS to area 19 has a predominantly supragranular origin, even though it is constrained to be higher by its other connections. These laminar assignments were based on relatively small numbers of retrogradely labeled cells, however. With anterograde tracers, the projections from area 21a and area 19 appear not to terminate in a feedback pattern in area 18 despite their being constrained to be at a higher level. Overall, we infer that the cat may have a similar pattern of hierarchical organization as in the macaque, as well as a similar incidence of irregularities whose biological significance remains to be determined. As in the macaque, however, this scheme is provisional in many respects and is likely to be subject to various revisions. Other recent reports have used different partitioning schemes for distinguishing visual areas, especially in the suprasylvian sulcus (e.g., Sherk, 1986), and much remains to be determined about the connectivity of many of these areas.

In the rat, a recent study by Coogan and Burkhalter (1990) has revealed consistent asymmetries in anterograde labeling patterns between visual areas, in a manner strongly analogous to the hierarchical relations we have described for primates. These findings differ from an earlier report by Miller and Vogt (1984); the difference may be attributed to the greater sensitivity and resolution of the tracer used by Coogan and Burkhalter (1990). The available evidence suggests that there are at least 3 hierarchical levels involving 5 visual areas in the rat. There are several additional visual areas in the rat (Olavarria and Montero, 1984, 1989) whose connectivities have yet to be explored in detail, so it may be that further analysis will reveal evidence for additional hierarchical stages.

In summary, a strategy based on laminar connectivity patterns, particularly in the anterograde direction, provides a rational and objective basis for systematically assessing hierarchical relationships throughout the mammalian neocortex. With appropriate refinements in the criteria for distinguishing forward and feedback connections, we have shown that this hierarchy encompasses the full extent of primate visual and somatosensory-motor cortex. However, much remains to be done in order to resolve the modest number of apparent discrepancies and to ascertain just how generally this hypothesis applies across systems and species.

Intertwined Processing Streams in the Visual Cortex

One of the striking features of the visual hierarchy is the extensive degree of parallel processing, as manifested by the presence of many areas at each level in the middle portion of the hierarchy (6 areas at level 5, 7 areas at level 7, and 5 areas at level 8 in Fig. 4). This contrasts sharply with the presence of only 1 or 2 areas at most levels in the somatosensory-motor hierarchy (Fig. 4 vs. Fig. 7).

The notion of parallel processing streams in the visual system has received considerable attention during the past decade and is the topic of several recent reviews (e.g., Livingstone and Hubel, 1987b; Maunsell and Newsome, 1987; DeYoe and Van Essen, 1988; Lennie et al., 1990). However, the highly distributed connectivity that we have analyzed in the present study raises questions that merit additional discussion. The central issue we wish to address in the remainder of this article is the relationship between the low-level M and P streams that originate in the retina and the high-level streams associated with areas in the temporal and parietal lobes (Ungerleider and Mishkin, 1982; Desimone and Ungerleider, 1989).

If one considers only the most robust anatomical pathways, there is striking evidence for segregated streams over many hierarchical stages (Livingstone and Hubel, 1984a,b, 1987a; DeYoe and Van Essen, 1988; Zeki and Shipp, 1989; Van Essen et al., 1991). This is reflected in the color coding of areas in Figure 4. In brief, the M stream, indicated in shades of red, includes the M layers of the LGN, layer 4B (and also layer $4C\alpha$) of V1, the cytochrome oxidase (CO)-enriched thick stripes of V2, and areas V3, MT, MST, and probably also areas V4t and V3A. The M stream provides a notably heavy input into areas of the parietal lobe, which are indicated in orange. The P stream originates from P neurons in the retina and LGN (purple), which then splits into 2 distinct streams that are relayed through layers $4C\beta$ and 4A of V1. They are represented in the superficial layers of V1 by the so-called blob and interblob regions revealed by CO histochemistry. The blobs and interblobs project, respectively, to the thin stripes and interstripes of V2; these 2 compartments, in turn, have segregated projections to V4. Both the P-B (blob-associated) stream, shown in shades of violet and the P-I (interblob-associated) stream shown in shades of blue project heavily (by way of V4) to areas in inferotemporal cortex, which are indicated in shades of green.

Superimposed on this skeletal framework are numerous additional pathways, many of which suggest extensive cross talk at different stages of processing, beginning even within V1. Some of this cross talk appears to be mediated by intrinsic circuitry within a single area. Malpeli et al. (1981) used reversible inactivation of specific LGN layers to show that about ⅓ of the cells in V1 can be activated independently through either the M or the P pathway. Anatomical substrates that might underlie this cross talk include dendritic arbors that traverse more than 1 geniculate afferent termination zone in layer 4C, robust projections from P-dominated layer $4C\beta$ to M-dominated layer $4C\alpha$, and projections from the M-dominated layer 4B to the P-dominated superficial layers of V1 (Fitzpatrick et al., 1985; Lund, 1987, 1988). In V1, the intrinsic connections of blobs and interblobs are highly specific to regions of the same type (Livingstone and Hubel, 1984b), but in V2, there appears to be a greater degree of cross talk in the intrinsic connections of different stripes (Livingstone and Hubel, 1984a; Rockland, 1985).

A second form of cross talk occurs in the ascending connections between areas. At intermediate levels of the hierarchy, areas MT, V3, V3A, and V4t all are dominated by M inputs (from the thick stripes of V2 in all cases, plus layer 4B of V1 for MT and V3). However, several of these areas receive substantial input from other stripe compartments of V2. In particular, projections to MT occasionally arise from thin stripes as well as thick stripes (DeYoe and Van Essen, 1985; Shipp and Zeki, 1989). Also, the projections to V3, V3A, and V4t arise from more than 1 stripe compartment in V2 (Felleman et al., 1988). Area V4 is dominated by P inputs in terms of the direct projections from V2 thin stripes and interstripes, yet it also receives major projections from each of the aforementioned M-dominated areas V3, MT, V3A, and V4t.

A comparable degree of cross talk persists in the ascending projections leading to the parietal and inferotemporal lobes. V4 projects most strongly to inferotemporal areas, but it also has substantial projections to parietal cortex, directly to VIP and LIP and indirectly through DP, MST, MSTl, and MT. Likewise, MT projects heavily to the parietal cortex (directly to VIP and indirectly via MSTd and MSTl), but it also has indirect connections with inferotemporal areas via FST and V4. There are also direct connections between parietal and inferotemporal areas (LIP-PITv and 7a-AITd), as well as indirect linkages by way of FST, STP, and frontal lobe areas.

A third mode for interaction between streams is by way of feedback pathways. For example, there is evidence that feedback from areas V4 and MT may include multiple stripe compartments in V2, suggesting greater cross talk in the descending than in the ascending direction (Zeki and Shipp, 1988, 1989; Shipp and Zeki, 1989). On the other hand, we have seen cases in which the feedback from V3 and V4 to V2 is more restricted than the reciprocal ascending pathway (D. J. Felleman and D. C. Van Essen, unpublished observations). The overall issue of cross talk in feedback pathways clearly deserves further investigation.

Taken as a whole, this anatomical description does not support a rigid segregation of pathways all the way from the magnocellular/parvocellular dichotomy at the low end to the parietal/temporal dichotomy at the high end. It remains to be seen to what degree the divergence and convergence that we have discussed at the level of areas and compartments as a whole persists when one examines the inputs and outputs of single cells.

Single Neuron Connectivity

Thus far, we have concentrated on the connections of entire areas or of layers and compartments within areas, without addressing the issue of heterogeneity among the individual neurons that make up a layer or an area. Presumably, any given neuron, for example, in V4, projects to far fewer areas than the total of 39 areas with which V4 is reported to be linked. In the extreme, any single neuron might project, at most, to 1 other cortical target area. Most of what we know about this issue comes from a relatively small number of double-retrograde-labeling studies in cats and monkeys, in which tracers are injected into topographically corresponding portions of 2 different areas (cf. Kennedy and Bullier, 1985; Bullier and Kennedy, 1987). In general, this approach reveals a significant number of doubly labeled cells, signifying that individual neurons can indeed have collaterals projecting to more than 1 area. Although the percentage of doubly labeled cells is relatively modest (e.g., less than 10% of the labeled cells in the study by Perkel et al., 1986), the interpretation of this number must take into account the likelihood that many, if not most, singly labeled neurons had collaterals that went to different areas that had not received a tracer injection. The average number of target areas per cortically projecting neuron could plausibly be well under or well over 2. In the cat, there is evidence that this number is greater for descending pathways than for ascending pathways, and that some cells can even contribute simultaneously to both directions, by making both an ascending and a descending connection (Bullier et al., 1984; Bullier and Kennedy, 1987).

Functional Implications

We have concentrated in this study primarily on an anatomical analysis that suggests 5 key principles of primate cortical organization: (1) a large number of visual areas, (2) highly distributed connectivity among areas, (3) reciprocity of connections, (4) hierarchical organization, and (5) distinct, yet intertwined, processing streams. We now comment on what these principles might signify for understanding the functions of different visual areas.

Distributed Hierarchical Processing

The hierarchical scheme for visual cortex that we have presented is grounded explicitly on anatomical criteria. Whether each level of the hierarchy represents a distinct stage of information processing is a separate issue that must be addressed mainly by physiological and behavioral approaches. One type of physiological evidence in support of the hierarchy comes from comparisons of receptive field size, as conventionally plotted using moving bars or edges (the "classical" receptive field). In V1, receptive fields are typically very small, and they increase progressively at successive stages of the hierarchy, ultimately approaching the entire visual field in extent in some of the inferotemporal and parietal areas (cf. Van Essen, 1985, for references). Ideally, one would like to know whether these increases occur in stepwise fashion at each hierarchical stage. However, such information is not readily attainable, given that several factors contribute to differences in receptive field size, including a strong dependence on eccentricity, plus effects of anesthesia and of interanimal variability.

Another important physiological measure concerns the occurrence of emergent receptive field properties at progressively higher levels of the hierarchy. For example, area V1 clearly represents a more advanced stage of processing than the LGN by virtue of the emergence or sharpening of selectivity for stimulus orientation, spatial frequency, length, direction, and binocular disparity (cf. Hubel and Wiesel, 1968; Schiller et al., 1976a–c; Poggio and Fischer, 1977; DeValois et al., 1982). Until recently, however, there were few examples of this type to distinguish different extrastriate areas from one another or even from V1. That situation is now changing, and a few of the more notable examples are worth explicit mention: (1) Many cells in V2, but not in V1, are responsive to patterns that elicit percepts of subjective contours in human observers (Peterhans and von der Heydt, 1989; von der Heydt and Peterhans, 1989). (2) Some cells in MT, but not in V1, are selective for the motion of a complex pattern rather than the individual oriented components (Movshon et al., 1986). (3) Some cells in the inferotemporal cortex are selective for faces or other complex patterns (Desimone et al., 1984; Baylis et al., 1987; Perrett et al., 1987; Saito et al., 1987). These and other examples support the notion that higher stages of the cortical hierarchy represent more advanced levels of processing. Much more evidence is needed to test the generality of this hypothesis, however.

The physiological properties discussed thus far (increases in classical receptive field size and more advanced receptive field selectivities) may largely reflect the contributions of ascending pathways and of circuitry intrinsic to each area. The massive descending pathways that are so prominent anatomically may subserve a different set of functions. One likely possibility is that descending connections contribute to a set of modulatory surround influences, in which stimuli well outside the classical receptive field can dramatically influence the responses to stimuli within the receptive field. Such modulatory effects have now been demonstrated in the analysis of motion (Allman et al., 1985; Saito et al., 1986), color (Zeki, 1983), form (Desimone and Schein, 1987), and texture (Van Essen et al., 1989). Another perspective is that descending pathways may contribute to the modulation of response properties by visual attention in area V4 (Moran and Desimone, 1985) and more generally, for dynamic control of the routing of information through each visual area (Anderson and Van Essen, 1987; Van Essen and Anderson, 1990). However, there is no strong basis at present for assigning any of these interactions to a strictly corticocortical system as distinct from pathways involving the pulvinar or other subcortical structures. Finally, descending pathways may play a critical role in memory processes (including their formation, consolidation, and/or readout) at higher cortical levels, particularly in the temporal lobe.

These examples illustrate how the existence of feedback pathways can remain consistent with the notion of hierarchical processing in the broad sense, even though they rule out a strictly serial scheme. The physiological properties of any given cortical neuron will, in general, reflect many descending as well as ascending influences. Nevertheless, the cell may represent a well-defined hierarchical position in terms of the types of information it represents explicitly and the way in which that information is used.

Functionality of Processing Streams

Why should the visual system contain processing streams that, in some respects, remain distinct through many successive stages of the hierarchy, yet show significant anatomical cross talk at many (perhaps all) stages? To address this question, it is useful to consider the way in which visual information is encoded at each hierarchical stage and how this information may be used for perception and visually guided behavior.

Physiological distinctions between processing streams are evident from the outset, in that M and P channels differ markedly in how they represent information along spatial, temporal, and spectral dimensions (cf. Shapley and Perry, 1986; Lennie et al., 1990). At any given eccentricity, P cells, on average, have smaller receptive fields and higher spatial resolution, whereas M cells have higher temporal resolution, higher contrast sensitivity, and a lower absolute threshold. P cells tend to give sustained responses, whereas M cells respond only transiently. P cells also have spectrally opponent receptive fields, whereas M cells carry only a nonlinear representation of spectral contrast. These differences suggest an overall strategy in which the M and P channels handle distinct, but partially overlapping, portions of an information space that includes the dimensions of space, time, and spectral composition (Van Essen and Anderson, 1990).

In the visual cortex, each processing stream maintains a distinct profile of receptive field characteristics (for reviews, see DeYoe and Van Essen, 1988; Livingstone and Hubel, 1988). Most notably, the P-B stream contains a high incidence of cells that are wavelength selective, suggesting that it is particularly involved in color perception. The M stream contains a high incidence of cells selective for direction of motion and for binocular disparity, suggesting that it is heavily involved in the analysis of motion and depth. The P-I stream contains a high incidence of orientation-selective cells, suggesting that it is involved in pattern and form recognition. However, selectivity for these low-level stimulus parameters is, in general, distributed across more than 1 processing stream. For example, wavelength selectivity is common among neurons in the P-I stream as well as the P-B stream; orientation selectivity and disparity selectivity are common in both the P-I stream and the M stream. This physiological description is consistent with the anatomical picture of streams that are distinct, yet closely interlinked by cross talk at many levels.

Two types of reasoning support the notion that such cross talk and intermixing of information may reflect sensible design principles for the visual system. They can best be illustrated in relation to a specific example, such as the way in which we analyze an object that is moving across the visual field. First, consider what sources of information are useful for signaling object motion. If the object is moving rapidly, it will elicit responses mainly in M cells, because of their sensitivity to transient changes. However, if the object is moving very slowly, or if it is defined mainly by a high spatial frequency pattern, the evoked activity may be carried mainly by P cells. Hence, in order to have a motion-analyzing system that operates efficiently over a wide range of velocities, it would make sense to draw information primarily from the M channel, with the P channel playing an important, but subsidiary, role. There is now direct physiological evidence in support of this hypothesis (Maunsell et al., 1990).

Once motion information has been extracted, there are several distinct ways in which it can be used. The most obvious is for computing the trajectory in which the object is headed. In addition, velocity information contributes to our perception of depth (by way of motion parallax), shape (by way of structure from motion), and texture (by way of dynamic reflectance changes, as in a rippling surface). Consequently, it may be important for this information to be distributed both to parietal areas and to inferotemporal areas in order to mediate different aspects of perception.

For both form and distance perception, a stronger case can be made for a major role of both channels. The cues for shape and for depth arise from a wide range of spatial frequencies; moreover, form and distance perception are robust for static images, where the P channel presumably dominates, and for moving or transient images, where the M channel presumably dominates. For the P channel to be inoperative in these processes would imply that the high-resolution information conveyed by 90% of LGN neurons is irrelevant to processes that are demonstrably capable of hyperacuity levels of performance. For the M channel to be inoperative in either process would pose a puzzle as to how we do so well at perceiving depth and form at low contrast and also under scotopic conditions, where M cells are much more sensitive than P cells (Purpura et al., 1988). The effects of selectively lesioning the M and P layers of the LGN on specific behavioral tasks provide support for the notion that M and P channels each contribute to multiple aspects of perception (Schiller and Logothetis, 1990; Schiller et al. 1990; Merigan et al., 1991).

In a more general sense, there appears to be a complex, but orderly, relationship between low-level sensory cues (e.g., orientation, velocity, disparity, and spectral composition), high-level aspects of perception (e.g., perception of shape, surface qualities, and spatial relationships), and the processing streams that generate one from the other (DeYoe and Van Essen, 1988). The mapping is not 1:1, because many low-level cues are represented in more than 1 stream, both in the retina and at cortical levels, and because the attributes that we perceive about objects in the world can often be derived from more than 1 sensory cue. The determination of which particular computational strategies are associated with specific pathways, areas, compartments, and processing substreams remains a largely unresolved challenge for the future.

In the somatosensory cortex, there is physiological evidence for parallel channels that are manifested at the first hierarchical level by the partitioning of area 3b into modules dominated, respectively, by rapidly adapting and slowly adapting afferents (Sur et al., 1981) and by the preferential activation of area 3a by muscle spindle afferents (cf. Merzenich et al., 1978; Kaas et al., 1981). This functional segregation may persist at higher levels in terms of the preferential activation of area 1 by transient cutaneous stimulation and area 2 by sustained or deep pressure stimulation (Merzenich et al., 1978; E. Gardner, personal communication). At a still higher level, it has been suggested on the basis of lesion studies as well as connectional data that there may be a ventrally directed pathway, particularly involving SII, Ig, and Id, that is primarily involved in tactile object recognition, and a dorsally directed pathway, particularly involving areas 5 and 7b, that is primarily involved in somatomotor guidance, spatial perception of the body, and other somesthetic spatial functions (Friedman et al., 1986). Clearly, these observations suggest interesting analogies with the different processing streams in vision. Comparisons across these systems may help to clarify the nature of the tasks they must perform and the computational strategies that provide efficient and general solutions within the framework of the stereotyped architecture of the mammalian neocortex.

Notes

1. An accurate physical model of the macaque brain was a valuable adjunct in transferring areal boundaries on to the cortical map. Two such enamel-painted, plaster-coated, styrofoam models were available, one at 3 times life size and the other at a scale of 9-fold. They were based on the outlines of cortical layer 4 in a series of horizontal sections of the right hemisphere of a different brain than that used to generate the cortical map in this figure. Boundaries of individual cortical areas identified in the studies indicated in the text and in Table 1 were marked onto the brain model, mainly on the basis of the relationship to various geographical landmarks. Once the physical model had been marked, the various areal boundaries were transposed to outlines of the sections on which the model was based. The next step was to transpose boundaries to sections of the brain from which the cortical map was made. Although both the model and the map were based on quasi-horizontal sections, they were not precisely coplanar, and there were also modest individual differences in the exact size and configuration of various gyri and sulci. Nonetheless, we were able to determine an orderly mapping from one set of sections to the other and to use this mapping to transpose areal boundaries from one hemisphere to the other. The last step was a straightforward transposition from individual sections to the corresponding contours of the cortical map. The manually generated map, complete with areal boundaries, was optically scanned and used as a template for creating the color map with the CANVAS program on a Macintosh II computer. Boundaries for each area and for major cortical regions were traced over this template to create separate objects that could be independently colored, as in Figure 2, and also analyzed for surface area (see Table 2).

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