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SHORT COMMUNICATION

Convergence of processing channels in the extrastriate cortex of monkeys

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Abstract

The first (V-I) and second (V-II) visual areas of primates contain three types of anatomical segregations of neurons as parts of hypothesized "P-B" or "color", "P-I" or "form," and "M" or "motion" processing channels. These channels remain distinct in relays of P-B and P-I information to the inferior temporal lobe via V-II and dorsolateral visual cortex for object recognition, and "M" information to posterior parietal cortex via the middle temporal visual area (MT) for visual tracking and attention. The present anatomical experiments demonstrate another channel where "P-B" modules in V-I and "P-B" and "M" modules in V-II merge in the projections to the dorsomedial visual area (DM), which relays to MT and posterior parietal cortex. This integrative area may function in unifying our perception of the visual world, and may allow "color" as well as "motion" to play a role in visual tracking and attention.

Keywords: Parallel processing, Cortical connections, Columns

Introduction

Recent investigations have demonstrated the existence of three distinct processing channels in the visual system of primates (for review, see Maunsell & Newsome, 1987; DeYoe & Van Essen, 1988; Livingstone & Hubel, 1988; Zeki & Shipp, 1988). Two major processing streams (the magnocellular or M stream and the parvocellular or P stream) originate from separate classes of ganglion cells in the retina, remain segregated in the lateral geniculate nucleus, and project to separate layers in primary visual cortex (V-I) where the P stream splits into two separate channels (the parvocellular-blob or P-B stream and the parvocellular-interblob or P-I stream; terms from DeYoe & Van Essen, 1988). Neurons within the segregated channels are thought to project largely or exclusively to modules of neurons in other visual areas that share similar response properties. These channels have been associated with the functions of color and form perception for the P stream, and motion perception for the M stream, in part because lesions to cortical end stations of these pathways produce deficits in object recognition or visual attention (see Ungerleider & Mishkin, 1982; Mishkin et al., 1983).

Although recent discoveries clearly indicate that structural and functional differentiation and segregation are major features of visual processing channels, the unity of visual perception suggests that the merging of information across channels is also important. The visual stream of higher primates contains as many as 20 or more visual areas, and we are only beginning to understand the complexities of the interconnections between these areas (DeYoe & Van Essen, 1988; Zeki & Shipp, 1988; Kaas, 1989). Higher-order fields may combine information from these major streams in various ways and perhaps produce additional streams where other characteristics emerge.

The dorsomedial visual area (Allman & Kaas, 1975), DM, is a field that has been described as early in the multistage processing hierarchy of visual areas of owl monkeys (see Kaas, 1989). Like V-II and MT, DM receives inputs directly from V-I (Lin et al., 1982). MT receives inputs from modules in the M stream of V-I and V-II (e.g. DeYoe & Van Essen, 1985; Shipp & Zeki, 1989*a,b*; Krubitzer & Kaas, 1990), and projects to visual attention and tracking centers in posterior parietal cortex (e.g. Van Essen et al., 1981; Wall et al., 1982; Maunsell & Van Essen, 1983; Weller et al., 1984; Ungerleider & Desimone, 1986; Krubitzer & Kaas, 1990). Because the major outputs of DM are to MT and posterior parietal cortex (Wagor et al., 1975), DM provides an alternate pathway to posterior parietal cortex. We now provide evidence that DM receives information from the "P-B" stream in V-I, and from both the P-B stream and M stream in V-II. Thus, information from the two major channels merges in an early station in the hierarchy of visual areas.

Methods

Patterns of connections were revealed by placing single injections of wheatgerm agglutinin conjugated to horseradish peroxidase (WGA-HRP) in area DM in the brains of four owl

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monkeys (*Aotus trivirgatus*). In companion experiments in the opposite hemisphere of three of these owl monkeys, we used microelectrode mapping methods to reaffirm previous evidence that DM consists of a systematic representation of the contralateral visual hemifield within a densely myelinated block of cortex along the dorsomedial rostral border of V-II (Allman & Kaas, 1975). Owl monkeys were used because monkey visual cortex has been extensively studied in this New World monkey (see Kaas, 1988), and visual areas are more accessible in the less-fissured brains of New World than Old World monkeys. Although nocturnal, owl monkeys have color vision (Jacobs, 1977).

Injections of 0.1–0.3 μl of WGA-HRP were placed in DM of anesthetized monkeys (20–25 mg/kg ketamine hydrochloride supplemented with acepromazine) using sterile surgical procedures (see Krubitzer & Kaas, 1990 for details). Survival periods were 2–3 days. At that time, microelectrode recordings were obtained after the monkeys were anesthetized with urethane (250 mg/100 g). Using a hand-held projector to produce bars of light on a translucent hemisphere, receptive fields were delimited for neurons at 20–30 recording sites. After recording for several hours, the animals were given a lethal dose of anesthetic, and the brain was perfused with fixative. The cortex was immediately separated from the rest of the brain and manually flattened. The cortices were submerged in 30% sucrose in phosphate buffer for approximately 15 h and then cut parallel to the cortical surface so that surface-view patterns of areas, modules, and connections could be directly appreciated in sections processed for HRP (Mesulam, 1978), myelin (Gallyas, 1979), or cytochrome oxidase, CO (Wong-Riley, 1979). Sections reacted for HRP were superimposed upon sections stained for myelin or for CO by carefully aligning blood vessels and tissue artifacts across sections, and the connections of DM relative to modules in V-I, V-II, and MT were determined. The myelin patterns indicated that each injection was completely confined to DM.

Results

The recordings and the histological preparations allowed us to identify a number of visual areas. Consistent with previous descriptions, the recordings identified DM as a complete or nearly complete representation of the contralateral visual hemifield. The representation of the zero horizontal meridian divided DM into a medial half devoted to the lower quadrant and a lateral half devoted to the upper quadrant. Part of the horizontal meridian splits to form the caudal border of DM immediately adjacent to the rostral border of V-II. The zero vertical meridian was represented along the rostral border of DM. DM was coextensive with a darkly myelinated rectangle of cortex lateral to the medial visual area, M, and medial to the dorsolateral visual area, DL (see Kaas, 1989 for visual areas).

Histologically distinct modules in V-I, V-II, and MT were readily apparent in all cases. As previously reported (Krubitzer & Kaas, 1989), the CO and myelin preparations produced complementary patterns in that the CO-dense blobs in V-I, and CO-dense bands in V-II, were myelin poor. Although adjacent CO bands in V-II were often of equal thickness, alternating thick and thin CO bands could be distinguished in portions of V-II. A mottled appearance of CO dark and light regions, similar to that described by Tootell et al. (1985), was apparent in MT. Structural differences in V-I and V-II have been related to functionally distinct neural groups associated with the M stream or P stream. Recordings in macaque monkeys suggest that CO blobs in V-I, as part of the P stream, contain more neurons that respond to color than interblob regions, and alternating CO-dense bands in V-II contain neurons that appear to be more selective for stimulus orientation and movement, as part of the M stream, or color, as part of the P stream (see Livingstone & Hubel, 1988; DeYoe & Van Essen, 1988; Zeki & Shipp, 1988). By relating connection patterns of DM to these structural modules in V-I and V-II, we could infer the types of functional inputs that are likely to be relayed to DM from V-I and V-II.

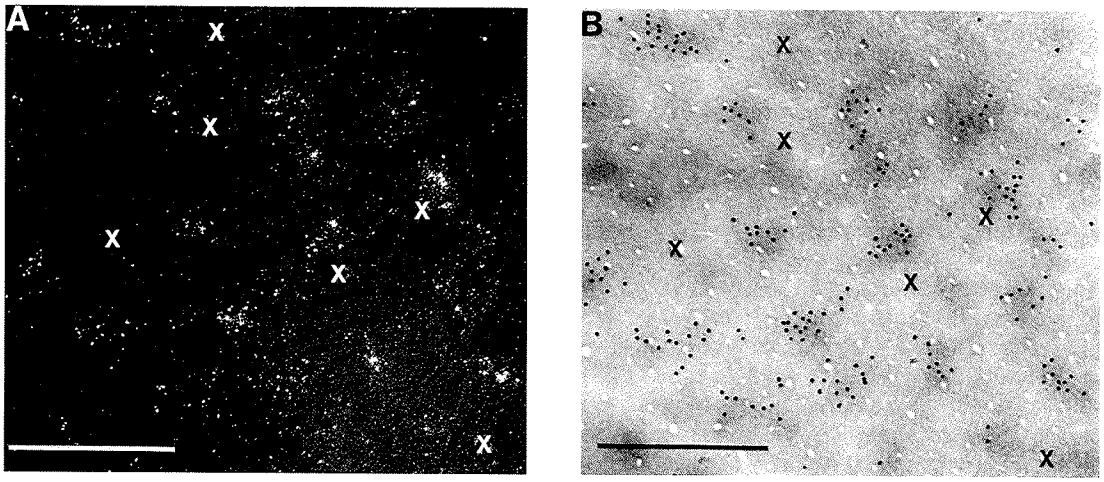

Fig. 1. A: A dark-field photomicrograph of labeled cell bodies in V-I after injections in the dorsomedial visual area (DM) of owl monkeys. Note that the cells are generally in clusters. B: A light-field photomicrograph of an adjacent brain section showing the CO blobs. Small black dots mark the locations of labeled cells from the section in A. Some of the blood vessels used to align the two sections are marked with Xs. Note that the labeled cells overlap the CO blobs. Scale bar = 1 mm.

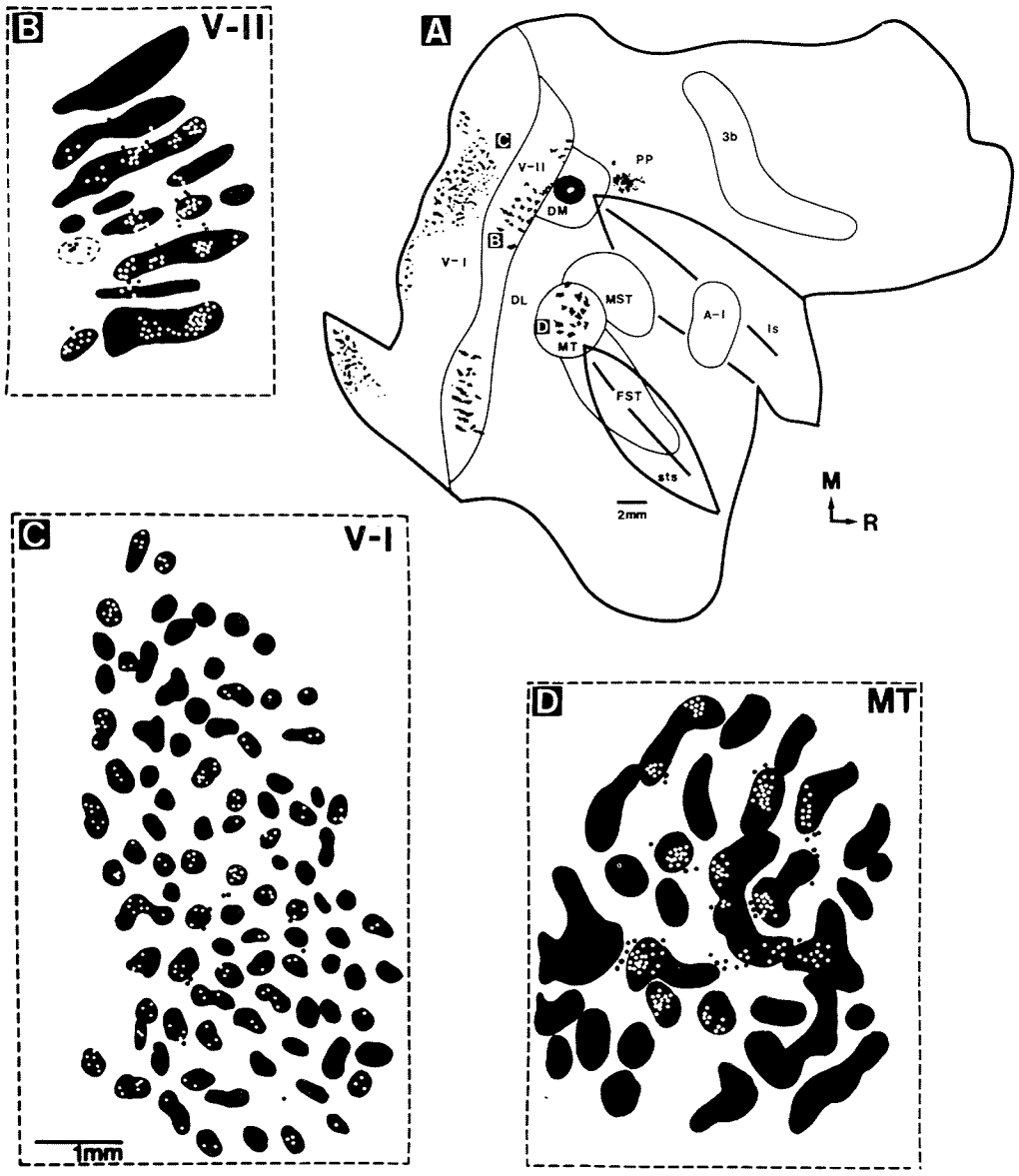

Fig. 2. Labeled cells and axon terminals in V-I, V-II, and MT after an injection of WGA-HRP in the dorsal medial visual area, DM. A: Owl monkey cortex that has been flattened and cut parallel to the surface. The superior temporal sulcus (sts) and the lateral sulcus (ls) have been opened, area V-I has been unfolded from the calcarine sulcus and cut to allow flattening. Somatosensory, auditory, and visual cortical areas were readily apparent in brain sections for stained myelin or reacted for cytochrome oxidase (CO). In DM, the white hole indicates the injection site and the dark-filled circle is the uptake zone of WGA-HRP relative to myeloarchitectonic boundaries. The areal distribution of anterograde and retrograde label from this injection is also shown for V-I, V-II, MT, and PP. Other connections of DM were noted, as described by Wagor et al. (1975), but they are not illustrated here. The blocked figures illustrate the relation of transported tracer to CO staining in V-I (C), V-II (B), and MT (D). CO-dense regions are solid black and small white and black dots denote anterograde and retrograde label. In all three areas, label is almost exclusively in CO-dense regions. V-I: primary visual area; V-II: second visual area; MT: middle temporal visual area; DM: dorsal medial visual area; DL: dorsal lateral visual area: MST: middle superior temporal area; FST: fundal superior temporal visual area; PP: posterior parietal cortex; 3b: primary somatosensory area; A-I: primary auditory area; M: medial; and R: rostral. B and D are of the same scale as C.

Connections of DM were concentrated in specific subunits of V-I, V-II, and MT. Restricted injections of WGA-HRP in DM produced a light scattering of labeled cell bodies and axon terminals across a wide expanse of V-I (Figs. 1 and 2) that varied somewhat in location according to the injection site in DM. Injections centered in DM, as in Fig. 2, labeled neurons over a mediolateral expanse of V-I that included representations of parts of both the upper and lower visual quadrants, in agreement with the electrophysiological evidence that DM represents both the upper and lower visual quadrants. The label in V-I was

in clusters of up to 15 neurons that overlapped the CO-dense blobs in layer III (Fig. 1A and 1B). Labeled neurons rarely were located in the CO interblob regions (Fig. 1B). Furthermore, the labeled neurons were largely in the superficial part of layer III, external to the neurons in layer IIIC (4B) that project to MT. Thus, the projections from V-I to DM originate in modules that have been related to color processing in the P-B stream.

After injections in DM, label in V-II was in clumps that joined to form bands that crossed the rostrocaudal extent of the field at various mediolateral levels. V-II is a "split" representation, with a medial representation of the lower visual quadrant and a lateral representation of the upper visual quadrant (Allman & Kaas, 1974). Thus, injections centered in DM produced bands of label in both medial and lateral portions of V-II (Fig. 2). Labeled neurons and axon terminals were in every CO-dense band and avoided the CO-poor interbands in V-II. Since CO-dense bands for the M stream and P stream alternate (see Livingstone & Hubel, 1988; DeYoe & Van Essen, 1988 for review), DM receives inputs from both the M stream and the part of the P stream specialized for color information. Notably, the interbands in V-II which receive inputs from the CO interblobs in V-I do not appear to contribute significantly to DM.

Dense interconnections were also apparent between DM and MT. Labeled neurons and axons in MT were in dense patches that were aligned with the CO-dense regions (Fig. 2), and these labeled clumps in MT often formed bands across the field. Very few labeled neurons were in the CO-light regions. Thus, as for V-I and V-II, connections with MT were with histologically distinct subunits. Although there is no known relationship of these CO-dense regions to functionally distinct neural groupings in MT, the results suggest that the connections of DM with MT may be with a subset of functionally distinct neurons. Other ipsilateral cortical connections of DM, as previously described (Wagor et al., 1975), included posterior parietal cortex (Fig. 2A), area M (Allman & Kaas, 1976) and DL_R (Cusick & Kaas, 1988*a*).

Discussion

The results are important for several reasons. First, the existence of CO-dense subregions in MT with connections specific to DM suggest that MT, like V-I and V-II, contains subsets of functionally distinct units that can be identified histologically and connectionally. Such modules may be characteristic of most or all visual cortical areas. Second, although we do not know if inputs from the parvocellular stream in V-I and the magnocellular and parvocellular streams in V-II terminate on the same neurons in DM, restricted locations in DM receive inputs from both the P-B and M pathways. Thus, neurons in DM potentially use information from both channels. The results may account for the electrophysiological observations that neurons in DM of owl monkeys and the probable homologue of DM, dorsal V3 of macaque monkeys (see Krubitzer & Kaas, 1990), have response properties reflecting inputs from both M and P streams. In DM of owl monkeys, responses of many neurons with longer latencies and sustained activity to a flashed bar of light suggested to Petersen et al. (1988) that DM includes P channel as well as M channel inputs. Felleman and Van Essen (1987) provide evidence for both P-channel and M-channel inputs to dorsal V3 of macaque monkeys by finding 20% of the neurons to be color selective. Such electrophysiological results are no longer puzzling if DM and dorsal V3 have inputs from the P as well as the M stream. However, dorsal V3 reportedly differs from DM by having inputs from neurons in the M stream rather than the P stream in V-I (Burkhalter et al., 1986). Third, DM may provide both P-B and M information to MT and posterior parietal cortex (PP), so that both channels can influence visual attention and tracking.

Although the segregation of functional units within visual areas appears to be a general feature of the visual system, subsystems clearly interact. In this report, we provide evidence for the merging of P-B and M streams in DM. In DM and other visual areas, the merging of inputs from different combinations of separate modules in other visual areas could endow each area with different roles in visual processing. Other interactions between streams may depend on "feedback" connections, which appear to more broadly distribute across processing streams than feedforward connections (Krubitzer & Kaas, 1989). Finally, it is important to note that even in area 17, intrinsic connections provide a substrate for interactions between M and P streams (Casagrande et al., 1989). In fact, it is possible that M stream rather than P stream inputs to blobs are relayed to DM.

Results reported here for owl monkeys may pertain to primates in general. Somewhat different schemes for subdividing visual cortex into areas have been proposed for New World owl monkeys (see Allman & Kaas, 1974; Kaas, 1989), and Old World macaque monkeys (see Maunsell & Newsome, 1987; DeYoe & Van Essen, 1988; Zeki & Shipp, 1988; Desimone & Ungerleider, 1986), and little is known about the organization of extrastriate cortex in prosimian primates (see Weller & Kaas, 1982), anthropoid apes, and humans. Although DM has not been clearly identified in primates other than owl monkeys (however, see Krubitzer & Kaas, 1990), an important feature of DM is the direct input from V-I. Cortex in the same relative position of DM receives inputs from V-I in many and perhaps all primates. In ongoing unpublished studies using WGA-HRP injections in V-I and flattening cortex as in the present study, we have demonstrated projections from V-I to the expected location of DM in New World marmosets and squirrel monkeys, Old World talapoin monkeys (see Kaas & Krubitzer, 1990), and prosimian galagos (also see Cusick & Kaas, 1988*b*). Similar projections have been repeatedly described for macaque monkeys (see Burkhalter et al., 1986 for review). It would seem parsimonious to assume that the V-I projections in all of these primates are to DM. However, the projections in macaque monkeys have been attributed to a "dorsal V3" and sometimes to adjacent cortex, V3a. Unlike DM, dorsal V3 has been described as representing only the lower visual quadrant and receiving input from the M rather than the P channel in V-I (see Burkhalter et al., 1986 for review). Further experiments may be needed to resolve this issue. If the projection zone of V-I is indeed DM in all of these primates, then the projections should originate in the CO blobs, and parts of V-I representing the upper visual quadrant as well as the lower visual quadrant should contribute to the projection. Presently, these features have been demonstrated only for the V-I projections in owl monkeys.

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References

ALLMAN J.M. & KAAS, J.H. (1974). The organization of the second visual area (VII) in the owl monkey: a second transformation of the visual hemifield. *Brain Research* **76**, 247–265.

ALLMAN, J.M. & KAAS, J.H. (1975). The dorsomedial cortical visual area: a third tier area in the occipital lobe of the owl monkeys (*Aotus trivirgatus*). *Brain Research* **100**, 473–487.

ALLMAN, J.M. & KAAS, J.H. (1976). Representation of the visual field on the medial wall of occipital-parietal cortex in the owl monkey. *Science* **191**, 572–576.

BURKHALTER, A., FELLEMAN, D.J., NEWSOME, W.T. & VAN ESSEN, D.C. (1986). Anatomical and physiological asymmetries related to visual area V3 and VP in macaque extrastriate cortex. *Vision Research* **26**, 63–80.

CASAGRANDE, V.A., BECK, P.D. & LACHICA, E.A. (1989). Intrinsic connections of cytochrome oxidase (CO) blob and nonblob regions in area 17 of a nocturnal primate. *Society Neuroscience Abstracts* **15**, 1398.

CUSICK, C.G. & KAAS, J.H. (1988*a*). Cortical connections of area 18 and dorsolateral visual cortex in squirrel monkeys. *Visual Neuroscience* **1**, 211–237.

CUSICK, C.G. & KAAS, J.H. (1988*b*). Surface view patterns of intrinsic and extrinsic cortical connections of area 17 in a prosimian primate. *Brain Research* **458**, 383–388.

DEYOE, E.A. & VAN ESSEN, D.C. (1985). Segregation of efferent connections and receptive-field properties in visual area V2 of the macaque. *Nature* **317**, 58–61.

DEYOE, E.A. & VAN ESSEN, D.C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neuroscience* **11**, 219–226.

FELLEMAN, D.J. & VAN ESSEN, D.C. (1987). Receptive-field properties of neurons in area V3 of macaque extrastriate cortex. *Journal of Neurophysiology* **57**, 889–920.

GALLYAS, F. (1979). Silver staining of myelin by means of physical development. *Neurology Research* **1**, 203–209.

JACOBS, G.H. (1977). Visual capacities of the owl monkey (*Aotus trivirgatus*), I: Spectral sensitivity and color vision. *Vision Research* **17**, 811–820.

KAAS, J.H. (1989). Why does the brain have so many visual areas? *Journal of Cognitive Neuroscience* **1**, 121–135.

KAAS, J.H. & KRUBITZER, L.A. (1990). The organization of visual cortex in Old World monkeys: studies on the miniature species, *Miopithecus talapoin. Investigative Ophthalmology and Visual Science* (Suppl.) **31**, 398.

KRUBITZER, L.A. & KAAS, J.H. (1989). Cortical integration of parallel pathways in the visual system of primates. *Brain Research* **478**, 161–165.

KRUBITZER, L.A. & KAAS, J.H. (1990). Cortical connections of MT in four species of primates: areal, modular, and retinotopic patterns. *Visual Neuroscience* **5**, 165–204.

LIN, C.S., WELLER, R.E. & KAAS, J.H. (1982). Cortical connections of striate cortex in the owl monkey. *Journal of Comparative Neurology* **211**, 165–176.

LIVINGSTONE, M. & HUBEL, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science* **240**, 740–749.

MAUNSELL, J.H.R. & VAN ESSEN D.C. (1983). The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *Journal of Neuroscience* **3**, 2563–2586.

MAUNSELL, J.H.R. & NEWSOME, W.T. (1987). Visual processing in monkey extrastriate cortex. *Annual Review of Neuroscience* **10**, 363–401.

MESULUM, M.M. (1978). Tetramethylbenzidine for horseradish peroxidase neurohistochemistry: a non-carcinogenic blue reaction product with superior sensitivity for visualizing neural afferents and efferents. *Journal of Histochemistry and Cytochemistry* **26**, 106–117.

MISHKIN, M., UNGERLEIDER, L.G. & MACKO, K.A. (1983). Object vision and spatial vision: two cortical pathways. *Trends in Neuroscience* **6**, 414–417.

PETERSEN, S.E., MIEZIN, F.M. & ALLMAN, J.M. (1988). Transient and sustained responses in four extrastriate visual areas of the owl monkey. *Experimental Brain Research* **70**, 55–60.

SHIPP, S. & ZEKI, S. (1989*a*). The organization of connections between areas VI and V5 of macaque monkey visual cortex. *European Journal of Neuroscience* **1**, 309–332.

SHIPP, S. & ZEKI, S. (1989*b*). The organization of connections between areas V2 and V5 of macaque monkey visual cortex. *European Journal of Neuroscience* **1**, 333–354.

TOOTELL, R.B.H., HAMILTON, S.L. & SILVERMAN, M.S. (1985). Topography of cytochrome oxidase activity in owl monkey cortex. *Journal of Neuroscience* **5**, 2786–2800.

UNGERLEIDER, L.G. & DESIMONE, R. (1986). Cortical connections of visual area MT in the macaque. *Journal of Comparative Neurology* **348**, 190–222.

UNGERLEIDER, L.G. & MISHKIN, M. (1982). Two cortical visual systems. In *Analysis of Visual Behavior*, ed. INGLE, J.D., GOODALE, M.A. & MANSFIELD, R.J.W., pp. 549–586. Cambridge, Massachusetts: MIT Press.

VAN ESSEN, D.C., MAUNSELL, J.H.R. & BIXBY, J.L. (1981). The middle temporal visual area in the macaque: myeloarchitecture, connections, functional properties, and topographic organization. *Journal of Comparative Neurology* **199**, 293–326.

WAGOR, E., LIN, C.S. & KAAS, J.H. (1975). Some cortical projections of the dorsomedial visual area (DM) of association cortex in the owl monkey, *Aotus trivirgatus. Journal of Comparative Neurology* **163**, 227–250.

WALL, J.T., SYMONDS, L.L. & KAAS, J.H. (1982). Cortical and subcortical projections of the middle temporal area (MT) and adjacent cortex in galagos. *Journal of Comparative Neurology* **211**, 193–214.

WELLER, R.E. & KAAS, J.H. (1982). The organization of the visual system in Galago: comparisons with monkeys. In *The Lesser Bush Baby (Galago) as an Animal Model: Selected Topics*, ed. HAINES, P.E., pp. 107–135, Boca Raton, Florida: CAC Press.

WELLER, R.E., WALL, J.T. & KAAS, J.H. (1984). Cortical connections of the middle temporal visual area (MT) and the superior temporal cortex in owl monkeys. *Journal of Comparative Neurology* **228**, 81–104.

WONG-RILEY, M. (1979). Changes in the visual system of monocularly sutured or enucleated cats demonstrable with cytochrome oxidase histochemistry. *Brain Research* **171**, 11–28.

ZEKI, S. & SHIPP, S. (1988). The functional logic of cortical connections. *Nature* **355**, 311–317.