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Visual latencies in cytochrome oxidase bands of macaque area V2

(visual cortex/magnocellular/parvocellular/color)

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ABSTRACT **Cytochrome oxidase bands in area V2 of the primate visual cortex constitute separate relays for parallel channels relaying information from area V1 to other extrastriate cortical areas. We investigated whether information is transferred at the same speed in the different channels by measuring the latencies of neurons in different cytochrome oxidase bands identified by the presence or absence of retrogradely labeled cells from injections in area V4. Results show that neurons in the thick and pale bands respond 20 msec earlier than those in the thin bands. We also found that color-selective neurons respond later than neurons with no selectivity for color and that direction-selective neurons have shorter latencies than neurons with no selectivity for the direction of stimulus movement.**

Area V2 of the primate visual cortex can be subdivided into separate functional compartments. When the cortex of V2 is cut parallel to the surface and the sections are stained for the enzyme cytochrome oxidase, a succession of dark (cytochrome oxidase-rich) and pale bands can be observed (1–7). Although the distinction is often difficult to make, as evidenced by the published figures (6, 8–10), one can sometimes identify two types of cytochrome oxidase-rich bands, the thin and the thick bands.

The cytochrome oxidase bands in area V2 relay information circulating through parallel pathways between area V1 and other extrastriate areas. Thus, cells in the thin cytochrome oxidase bands are innervated by the cytochrome oxidase blobs in area V1 (2) and project to area V4 (4, 5, 8, 11). Neurons of the pale bands in area V2 receive afferents from the interblob regions in area V1 (2) and send projections to area V4 (4–6, 11). Finally, the thick cytochrome oxidase bands in area V2 are mostly driven by layer 4B neurons of area V1 (12, 13) and send projections to the middle temporal area (MT) (4–6).

This anatomical segregation of cortical pathways reflects at least partially the presence of separate channels in thalamocortical inputs. It is known that neurons of layer 4B in area V1 are activated by the magnocellular-layer neurons of the lateral geniculate nucleus (LGN) via layer 4Cα (14, 15). Because layer 4B constitutes the major drive to the thick cytochrome oxidase bands in area V2, it appears that these neurons are under the influence of the magnocellular pathway (M pathway). Because of its afferents from the thick cytochrome oxidase bands in area V2 and layer 4B in area V1, area MT is also considered to belong to the M pathway. This relationship has been confirmed by the finding that most MT neurons decrease firing considerably when the magnocellular layers of the LGN are reversibly inactivated (16).

The thin and pale cytochrome oxidase bands receive their afferents from the blob and interblob regions of area V1 that were initially thought to be under the influence of the parvocellular pathway (P pathway). However, it has recently been shown that the P and M pathways converge in the cytochrome oxidase blobs of V1 and that the interblobs receive their inputs from neurons of layer 4C activated by the M and P pathways (17–20). In keeping with this convergence of the M and P pathways, Maunsell and his collaborators (21) found that neurons in area V4 are under the influence of M and P layers of the LGN.

Thus, one can distinguish two pathways running through the visual cortical areas: an M pathway from area V1 to area MT through the thick cytochrome oxidase bands and a mixed P/M pathway circulating from area V1 to area V4 through the thin and pale cytochrome oxidase bands in V2. A third thalamocortical pathway involving neurons of the intercalated, koniocellular or S layers of the LGN has also been shown to terminate in the cytochrome oxidase blobs (22–24).

It has also been claimed that the cytochrome oxidase bands contain different functional types of neurons. Thus, color-selective neurons are most often found in thin and pale bands and are rare in thick bands (4, 7, 25). Unoriented cells are principally found in thin bands (7, 25, 26), and binocular cells are concentrated in the thick bands (4, 7, 25). It is less certain whether length-selective neurons are found mostly in the pale bands (7, 25, 26) or whether direction-selective cells are more frequent in thick bands (4, 25, 26).

One interesting question concerning parallel pathways in monkey visual cortex is that of the timing of information transfer through extrastriate cortical areas. In other words, is the information processed more rapidly in one stream than in the other? It is known that the visual responses of P neurons of the LGN lag some 20 msec behind those of the M neurons (27, 28). More recently, it has been demonstrated that latencies to visual stimulation also differ by ≈20 msec for neurons of the P and M pathways at their input layers in area V1 (29). We wanted to determine whether this temporal difference was retained during the transfer of visual information in area V2 or whether it was lost because of the convergence of the M and P pathways at later stages of integration in areas V1 and V2.

We therefore recorded neurons in different cytochrome oxidase bands in area V2 and measured latencies to stimulation by a small spot of light flashed in the receptive field. It is often difficult to identify without ambiguity the thin and thick cytochrome oxidase bands on sections stained for cytochrome oxidase (4, 6–9). To overcome this difficulty we injected area V4 with retrograde tracers and used the distribution of labeled cells as landmarks because V4-projecting cells belong mostly to thin and pale cytochrome oxidase bands and rarely to the thick bands (4, 5, 8, 11).

MATERIALS AND METHODS

Recordings were made in cynomolgus monkeys (*Macaca cynomolgus*) anesthetized and paralyzed according to described methods (30). Anesthesia was maintained with 70% nitrous

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Abbreviations: LGN, lateral geniculate nucleus; M pathway, magnocellular pathway; P pathway, parvocellular pathway.

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oxide/30% oxygen supplemented with small regular injections of fentanyl (5 μg/kg·hr). Tungsten-in-glass microelectrodes (31) were used for the recording. Penetrations were angled to be normal to the surface of area V2 in the lunate sulcus. During the microelectrode penetrations, we first traversed area V1 and entered area V2 through the infragranular layers. After we hit the first V2 neurons, we advanced the recording electrode by 700 μm before recording to restrict the sample to supragranular layers. This procedure was checked by verifying that lesions placed during the recording track were located in supragranular layers. Because of the limited extent of the recording in area V2, the angle normal to the surface, and the large widths of the cytochrome oxidase bands (see Fig. 2), it is reasonable to expect that all units sampled in a given penetration belong to the same cytochrome oxidase band; this hypothesis was verified in one penetration with two lesions. Recording was made every 80 or 100 μm. At each site, single units and multiunit activities were separated with a window discriminator, and latencies were measured for ON and OFF responses.

Visual stimuli consisted of small (0.25°–2°) squares or bars of white light produced by an optic bench and placed inside or covering the receptive fields of recorded units. Light was ON for 3 sec and OFF for 3 sec. Latencies were corrected for the opening and closing delays of the shutter (5 and 7 msec). Opening and closing times were faster than 1 msec. The spot and background luminances were respectively 15 and 0.8 candela/m^2. We verified the effect of stimulus size on response latency in 39 neurons by stimulating with a small bar (usually 0.5° × 1°) and a square of light (1°–2° wide). We found that the latency did not differ significantly for these two stimuli (Wilcoxon ranked-pair test; 95% confidence). The usual stimulus was white, but we used red or green isoluminant stimuli to optimize the response of some color-selective units. We verified that the color of the stimulus did not influence the latency (Wilcoxon test on paired recordings in 37 units; see also ref. 32).

Orientation-selective units were defined as those for which a clear cut-off in the response to moving bars could be observed when the orientation of a moving bar was varied. Color selectivity was assessed by comparing qualitatively the responses to isoluminant red, green, blue, yellow, and white stimuli moved through the receptive field or flashed ON and OFF. In some cases, this was verified by a quantitative comparison. Direction-selective cells were those for which the response to stimulation by a moving bar moving in the nonoptimal direction was weak or absent.

Latencies were measured by using the same method as Maunsell and Gibson (33). Latencies were measured from poststimulus time histograms computed from >100 stimulus cycles in 90% of the cases (in the remaining cases, the number of presentations was 80–100 or the poststimulus time histogram had a very high signal-to-noise ratio). The method assumes a Poisson distribution of the number of spikes per bin during spontaneous activity, and a threshold value is calculated on the basis of this distribution. We computed the mean value of the number of spikes falling in the bins contained in the period 250 msec before light onset or offset. This technique was used to determine the mean of the Poisson distribution and the 99% confidence value. The latency was taken as the bin number for which this confidence value was crossed, provided that the count in the next bin stayed above this level and that the following bin did not fall below the 95% level. Because there is a compromise to be found between precision of the latency estimate and noisiness of the histogram, the latency measurements were repeated for bin widths of 1, 2, and 5 msec. The latency was taken from the histogram with the smallest bin width that gave an unambiguous estimate of the rise of the response, as judged by visual inspection. The influence of variable bin width and number of presentations was assessed by calculating all the latencies recorded in a large sample in areas V1 and V2 for a single bin width (5 msec) and for a fixed number of presentations (100). The latencies thus obtained correlated highly with the original values ($r = 0.95$), and the mean values calculated in this way in the different layers of areas V1 and V2 were within 3 msec of original values (29).

To achieve an unambiguous identification of thin and thick cytochrome oxidase bands in area V2, we injected fluorescent retrograde tracers in area V4 2 weeks before recording. The animals were anesthetized with alphadolone/alphaxolone (Saffan, Glaxovet, Harefield, U.K.; see ref. 34 for further details). Multiple small (0.1- to 0.2-μl) injections of fast blue or diamidino yellow were made in the region of area V4 located on the prelunate gyrus.

During recording, lesions were placed in each electrode track (7–10 μA for 7 sec, electrode negative) for histological reconstructions. At the end of the recording session and after a Nembutal overdose, animals were perfused with normal saline followed by 4% (vol/vol) paraformaldehyde or Zamboni fixative (35) in phosphate buffer. Two days before cutting, the brain was placed in a 30% (wt/vol) sucrose solution for cryoprotection. A cut was made in the fundus of the lunate sulcus, and the surface of area V2 was flattened mechanically while the brain was placed on a freezing microtome. Fifty-micrometer sections were cut. Alternate sections were stained for cytochrome oxidase (36) or just mounted and observed for the presence of fluorescent labeled cells (34).

RESULTS

Latencies from 213 responses [148 multiunit (94 ON, 54 OFF), 65 single unit recordings (49 ON, 16 OFF)] were obtained from neurons recorded in 105 sites in 12 penetrations from three hemispheres in two monkeys. Fig. 1 illustrates the responses of V2 neurons to small stimuli flashed in their receptive fields. Fig. 1*A* presents the response of multiunit activity recorded in a pale band. Responses of a single unit in a thick band is shown in Fig. 1*B*, and a multiunit response from a thin band is illustrated in Fig. 1*C*. Note the longer latency and the more sustained response of the thin-band neurons in Fig. 1*C*.

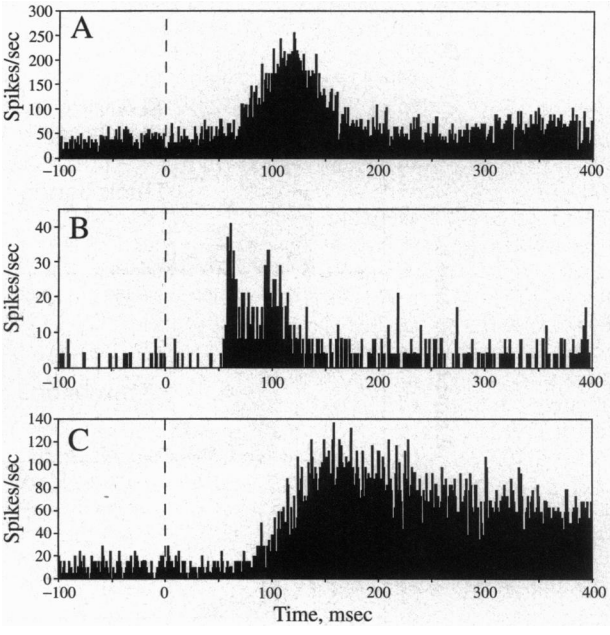

FIG. 1. Examples of responses of area V2 neurons to stimulation by a small flashing bar of light presented within the receptive field. (*A*) Multiunit recording in a pale band (ON response; case MM9 27401). (*B*) Single unit recording in a thick band. (ON response; case MM8 25C01.) (*C*) Multiunit response in a thin band (ON response; case MM8 22801). Bin width was 1 msec in all three cases.

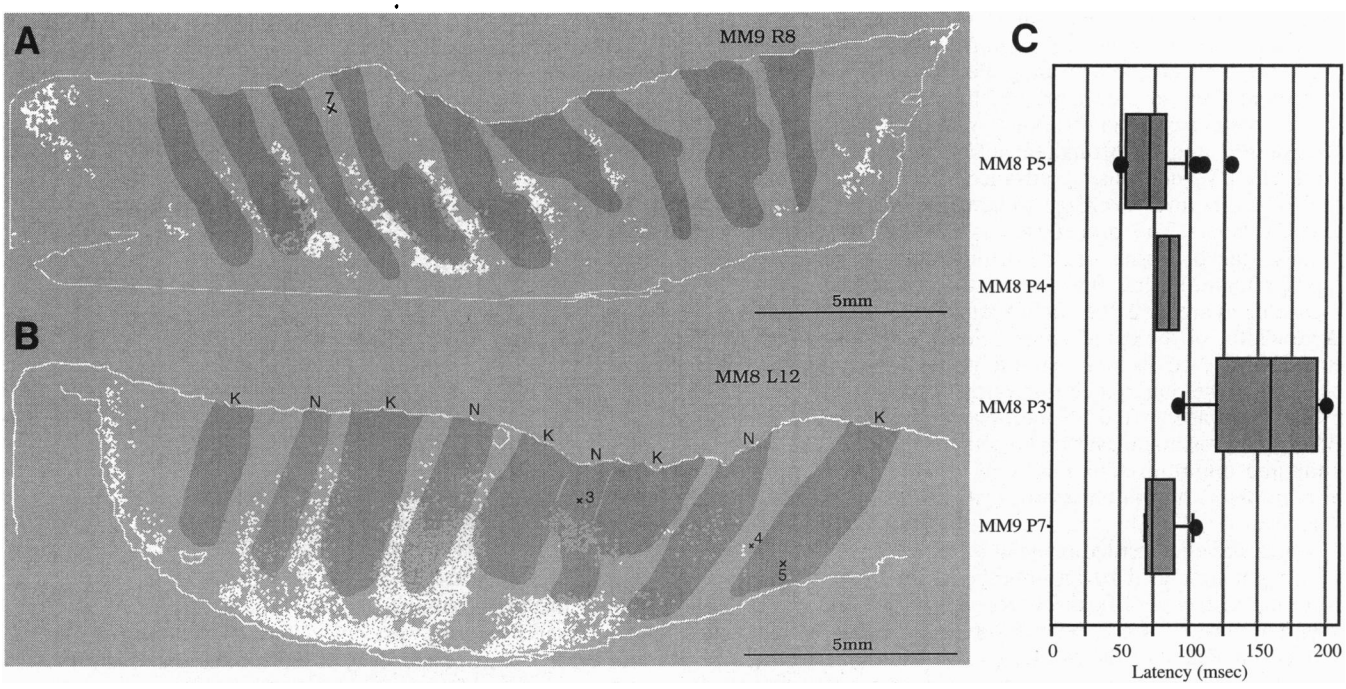

FIG. 2. (*A*) Section through flattened area V2 showing the cytochrome oxidase bands (dark) and the neurons labeled by an injection in area V4 (white dots). In that case labeled neurons were located mostly outside the cytochrome oxidase bands. (*B*) Section through flattened area V2 with labeling from an injection in area V4. In that case, the labeled cells were mostly found in pale and thick bands. K, thick bands; N, thin bands. (*C*) Box plot presentation of the latency distribution for neurons recorded in the penetrations identified by crosses and numbers in *A* and *B*. The box corresponds to the 25–75 percentiles, with the median identified by the vertical bar within the box. The small bars correspond to the 10 and 90 percentiles. Additional individual values are illustrated by dots. Latencies in the thin band (MM8 P3) are clearly longer than in the pale and thick bands.

Fig. 2 *A* and *B* illustrates the relationship between cytochrome oxidase bands and the labeling observed in area V2 after injections in area V4 in two different monkeys. In Fig. 2*A* (case MM9) labeling was restricted to the pale bands. In Fig. 2*B* (case MM8) another example is shown, in which the labeling extends over the thin (labeled N in Fig. 2) and pale bands and largely avoids the thick bands (labeled K). These two examples correspond to the two types of labeling observed earlier by Zeki and Shipp (8) in area V2 after injections of retrograde tracers in area V4. The set of sections from the third hemisphere (not illustrated) was of the type illustrated in Fig. 2*B*.

Crosses and numbers on the histological sections in Fig. 2 *A* and *B* refer to the locations of electrophysiological penetra-

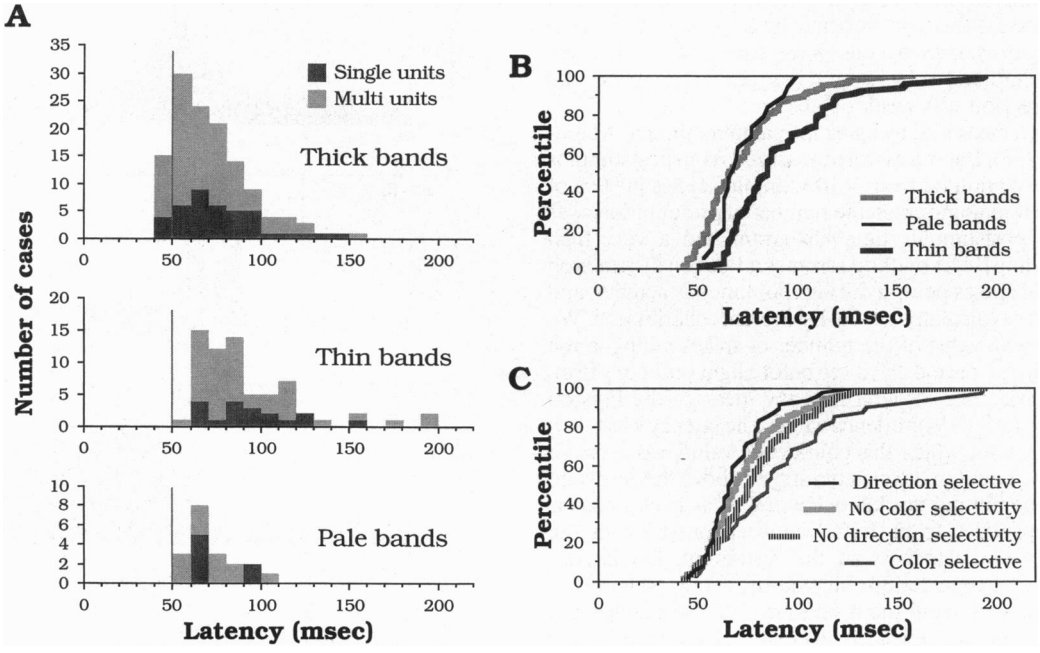

FIG. 3. (*A*) Frequency distribution histogram of multi- and single unit recordings in thin, thick, and pale bands. (*B*) Cumulative distribution of latencies of single and multiunit recordings in different bands. (*C*) Cumulative distribution of latencies of neurons with different receptive field properties. Color-selective units have longer latencies than non-color-selective units, and direction-selective units have shorter latencies than units with no direction selectivity.

Table 1. Latencies in cytochrome oxidase bands

Single or multiunit	C-O band	Mean latency, msec	SEM, msec	N	Median, msec
Multi	Thick	69.9	2.3	87	63
Multi	Thin	92	4.6	49	81
Multi	Pale	71.4	3.9	12	69.5
Single	Thick	76.2	3.6	40	71.5
Single	Thin	93.5	5.8	18	90
Single	Pale	72.9	5.5	7	65

C-O, cytochrome oxidase.

tions in pale bands in *A* and in thin, thick, and pale bands in *B*. Latency distributions of neurons recorded in these penetrations are shown as box plots in Fig. 2*C*. Latencies of the neurons recorded in the thin band (case MM8 P3) are clearly longer than those recorded in the thick (case MM8 P5) and pale bands (cases MM8 P4 and MM9 P7).

The frequency distributions of latencies for the whole sample of area V2 neurons are presented in Fig. 3*A* and Table 1. Fig. 3*B* illustrates the cumulative distributions of the latencies of all units recorded in the different cytochrome oxidase bands. ON and OFF latencies were not significantly different and were pooled in Fig. 3 *A* and *B*; single unit and multiunit recordings were pooled in Fig. 3*B*. The responses of neurons of the thick cytochrome oxidase bands start after 40 msec, whereas responses of neurons in the thin bands do not start before 60 msec (Fig. 3 *A* and *B*). The 22-ms latency difference between thin and thick bands is highly significant ($P < 0.0001$ in Mann–Whitney *U* test), and the population differences remain significant when the population is split between single unit and multiunit recordings ($P = 0.008$ for single unit and $P < 0.0001$ for multiunit). The latency difference between thin and thick bands is still significant when only ON responses of single units are considered ($P = 0.015$). The latencies also differ significantly between neurons of pale and thin bands ($P = 0.04$ for single unit, $P < 0.02$ for multiunit). No statistically significant differences were seen between latencies in thick and pale bands.

As mentioned in the introduction, the various cytochrome oxidase bands contain different proportions of cells with specific receptive field properties. We also observed this tendency (Table 2) because most color-coded cells in our sample were recorded in the thin bands ($P < 0.0001$ in χ^2 test between thin and thick bands), and most of the direction-selective units were found in thick bands ($P < 0.0001$ in a χ^2 test between thin and thick bands). The proportion of orientation-selective neurons was higher in the thick band than in the thin band, but the difference was not statistically significant ($P = 0.08$). The latencies of units with different receptive field selectivities are presented in Table 3 and Fig. 3*C*. Color-selective neurons have the longest latencies, in keeping with the concentration of color-selective units in thin bands ($P = 0.04$ in Mann–Whitney *U* test between color and noncolor selective single units, $P = 0.01$ for multiunits). Also, shorter latencies were associated with direction-selective neurons ($P = 0.02$ in Mann–Whitney *U* test between direction- and non-direction-selective multiunits; not significantly different for single units), as expected from their presence in thick bands.

Table 2. Proportion of sites with specific receptive field properties in cytochrome oxidase bands

C-O band	N	Color selective, %	Orientation selective, %	Direction selective, %
Thick	56	7.3	60.9	60.4
Thin	39	56.8	40.6	3

Proportions do not add up to 100% because classes are not exclusive. Proportions for pale bands are not included because of small sample size. C-O, cytochrome oxidase.

Table 3. Latencies of units with specific receptive-field properties

RF selectivity	Mean latency, msec	SEM, msec	N	Median, msec
Color selective	93.3	5.7	41	85
Non-color selective	74.6	1.7	164	69
Orientation selective	78.1	2.4	94	74
Non-orientation selective	79.1	3.5	74	74.5
Direction selective	70.1	2.5	49	66
Non-direction selective	80	2.2	125	76

RF, receptive field.

No significant difference was seen between the latencies of orientation-selective neurons and cells with no orientation selectivity.

DISCUSSION

Our results show that neurons of the thin cytochrome oxidase bands have longer latencies than cells of the thick and pale bands. We feel confident that fast-responding neurons must be rare in thin bands because of the long latencies measured in many cases of multiunit recordings (Figs. 1*C* and 3*A*). Should there be a sizeable number of fast-responding neurons in thin bands, they would have given rise to short latencies in the multiunit recordings. The presence of long latencies in thin cytochrome oxidase bands also fits with the observation of long latencies for color-selective cells (Table 3), which tend to be concentrated in thin bands.

To compare latencies across cytochrome oxidase bands we had to use a common standard stimulus and not the optimal stimulus for each neuron. One may wonder whether using the optimal stimulus would have led to different conclusions. Although we did not systematically test the influence of all stimulus parameters on latency, our comparisons between the optimal color and a white stimulus for color-selective cells did not lead to a significant latency difference (*Materials and Methods*; see also ref. 32). We also compared the latencies to small bars and small squares and found again no significant difference between the two populations. The effect of stimulus orientation on latency (37) cannot influence our results because we stimulated neurons at the optimal orientation.

The latency difference seen between multiunit recordings in thin and thick cytochrome oxidase bands is 22 msec (Table 1). This value is similar to that seen between neurons in layers 4 Cβ and 4Cα in area V1 (29) and between parvo- and magnocellular layer neurons of the LGN (27, 28). The simplest explanation for the conservation of the latency difference in the two areas is that the timing of the responses is maintained for the M and P pathways in areas V1 and V2. The presence of long latencies in thin cytochrome oxidase bands in area V2 is surprising, given the convergence of M and P pathways in the blobs of V1 that project to thin bands (see introduction) and the interconnections between neurons of different bands in area V2 (13, 38). Despite this convergence, most color-coded cells of the thin cytochrome oxidase bands retain long latencies to visual stimulation. This result is reminiscent of that reported by Maunsell (39), who showed that V4 neurons have long latencies consistent with a P pathway channel input, although convergence of M and P pathway channels has been demonstrated physiologically in many neurons of area V4 (21).

Fig. 4 summarizes the latencies to visual stimulation of neurons belonging to the different channels of information transfer between areas V1 and V2. Our results and those of others (29, 33, 39) show that the M pathway through layers 4Cα and 4B in area V1, thick cytochrome oxidase bands in area V2 and area MT is made up mostly of fast-responding neurons with transient responses (top of Fig. 4). This conclusion is in

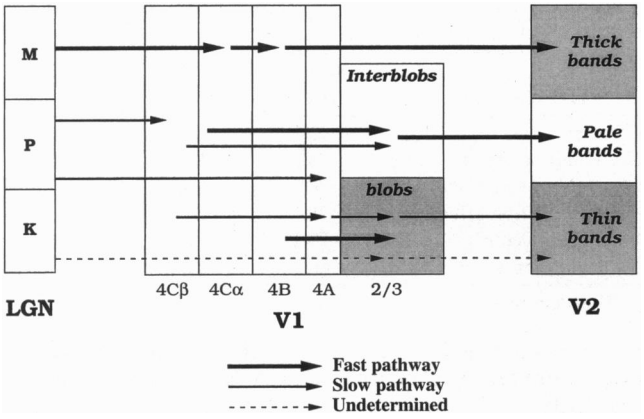

FIG. 4. Summary figure of the connectivity and processing speed between anatomical subunits in areas V1 and V2. M, P, and K in LGN, magno-, parvo-, and koniocellular layers. The dashed line through the koniocellular layers, the cytochrome oxidase blobs, and thin bands correspond to a third pathway of unknown visual latencies. Fast pathways (thick line) link together populations responding early to visual stimulation. Slow pathways (thin line) correspond to a network of neurons responding late to visual stimulation. The connectivity data are based on refs. 17 and 18.

keeping with the participation of this pathway in processing of high temporal frequencies (40, 41).

The pathway through the interblobs in area V1 and the pale cytochrome oxidase bands in area V2 also appears to rapidly transfer visual information (middle pathway in Fig. 4). The presence of fast-responding units in pale bands is in keeping with the presence of a mixing of P and M pathway inputs in the interblob regions of area V1 (18, 20) that project to the pale bands.

Finally, the pathway that appears to carry color information through layers 4C β in area V1, thin bands in area V2, and area V4 is slower by 20 msec than the M and interblob/pale band pathways. This latency difference in the neuronal responses of color versus non-color-selective units may be related to the observations that evoked potentials and reaction times are slower when evoked by chromatic isoluminant stimuli than by luminance stimuli (42–45).

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