

Transient and sustained responses in four extrastriate visual areas of the owl monkey*

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Summary. Single neuron responses to stationary flashed bars were recorded from four extrastriate visual areas in the owl monkey: the middle temporal area (MT), the dorsal lateral area (DL), the dorsal medial area (DM), and the medial area (M). Data were collected at the optimum bar size and orientation for each cell. Each post-stimulus histogram was normalized to its maximum bin height. A cumulative histogram was produced for each area by adding together all the corresponding cell histograms. The cumulative histograms reveal a short latency, transient component and a longer latency, sustained component to the response for each of the areas. In all four areas there was a strong response, but the sustained component was much larger in DL and DM than in MT or M. The transient response in DL had a much longer latency than in the other areas. The dichotomy between areas which are slow-sustained responding and areas which are fast-transient responding is similar to the differences found between the magnocellular and parvocellular pathways.

Key words: Extrastriate visual areas – Transient responses – Sustained responses – Owl monkey

Introduction

In the last two decades, studies of the organization of the visual system have revealed a set of parallel ascending systems (see Ungerleider and Mishkin

1982; Stone 1983; Maunsell 1986; Maunsell and Newsome 1987; Allman and McGuiness 1987). These parallel pathways begin at least as early as the retinal ganglion cells and are preserved across several levels into the visual system. In the macaque, two types of retinal ganglion cells, P- α and P- β , are present which differ in size and morphology; the larger P- α cells project preferentially to the magnocellular layers of the lateral geniculate nucleus (LGN), while the smaller P- β cells project to the parvocellular layers of the LGN (Perry et al. 1984). In both the owl monkey (Sherman et al. 1976) and the macaque (Dreher et al. 1976), the cells of the parvocellular layers have slower conducting retinal inputs and produce more sustained responses than the cells of the magnocellular layers. Additionally, in the owl monkey the parvocellular layer cells have slower conducting axons projecting to striate cortex than do the magnocellular neurons (Sherman et al. 1976). There is evidence from the macaque that the parvocellular and magnocellular LGN cells project onto different layers (4C β and 4C α , respectively) of striate cortex (Hubel and Wiesel 1972), and the cells in these layers project in turn to different layers within striate cortex (Lund and Boothe 1975; Fitzpatrick et al. 1985).

Maunsell (1986) hypothesized that the information carried by these two pathways may be kept separate further into the visual system, and predicted that the response properties of cells at higher levels of the hierarchy in extrastriate visual cortex would continue to reflect this segregation. He focused on the response latency, and the transient or sustained nature of the response. If striate cells outside of layer 4C, the thalamic recipient zone, were divided into a group showing the most transient responses, and a group showing the most sustained responses, there was a clear difference in the latency of the combined responses of the two groups. Those cells with the most sustained responses had a longer latency as a

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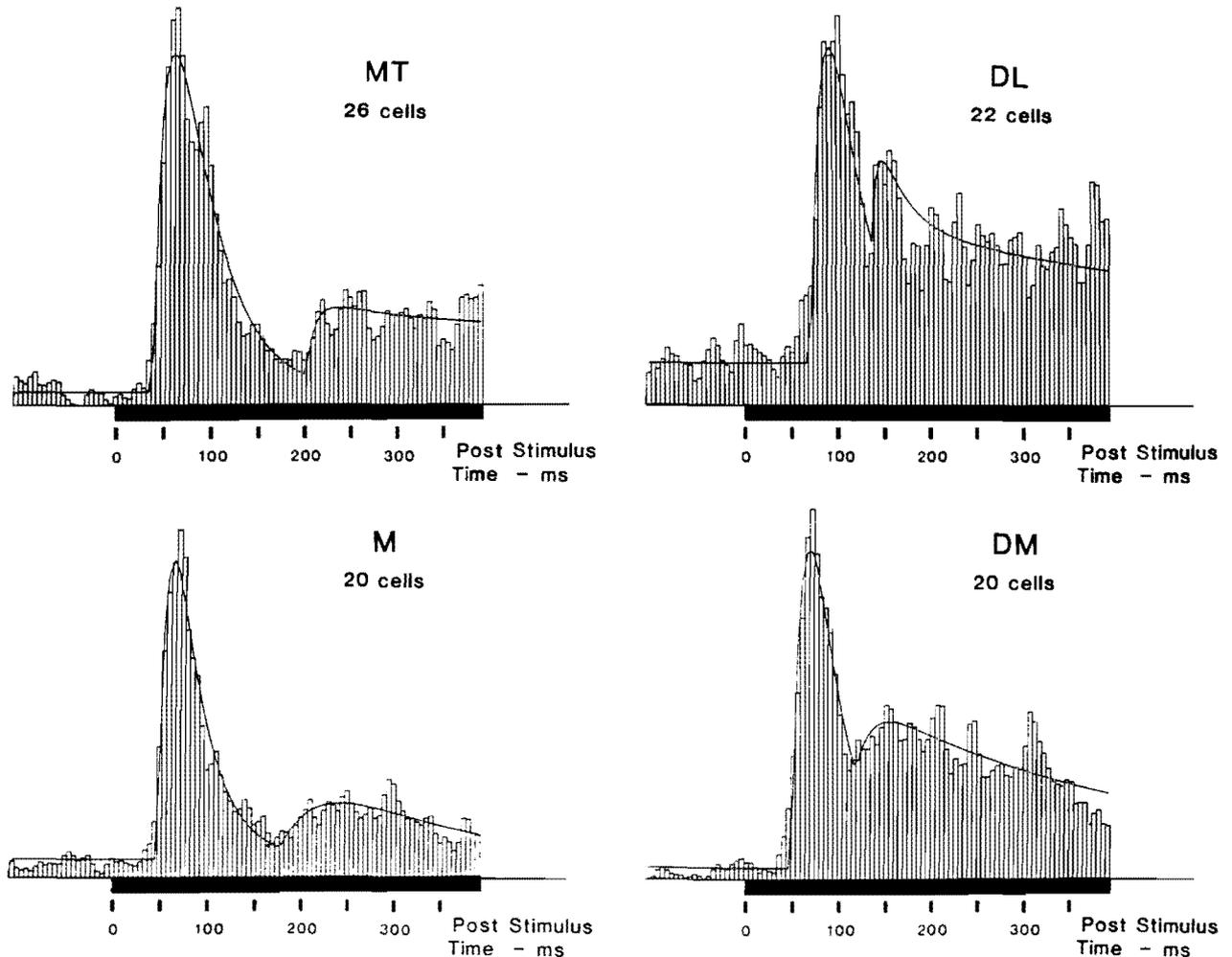


Fig. 1. Each panel displays the averaged peristimulus histogram for the response to a flashed oriented bar. The different panels correspond to the four cortical areas recorded from. The histogram bins are 5 ms wide. Time since stimulus onset is represented on the horizontal axis: with responses before 0 ms being spontaneous activity. The vertical axis is normalized to the peak response for each panel. Superimposed on each histogram is the best fitting curve obtained by using a random search algorithm (Curry 1975). The form of the curve is described in the text and the parameters for the curves are listed in Table 1. The number of cells recorded from each area is listed above each histogram

group than those with more transient responses. In the V4 complex Maunsell (1986) found that the grouped response latency was longer, and the response profile much more sustained than for the responses of cells in the middle temporal visual area (MT).

We analyzed the responses of groups of cells in four extrastriate regions of the owl monkey to determine whether a similar distinction in response profile exists in a different species of monkey, and to extend the distinction to other extrastriate cortical areas. The areas included MT, as well as the dorso-lateral (DL), the dorsomedial (DM) and the medial (M) areas. DL probably is homologous to the V4 complex, DM to V3, and M to the parieto-occipital area (PO) in macaque monkeys (Baker et al. 1981; Allman and McGuinness 1987).

Methods

Single neurons were recorded from four extrastriate visual areas of three chronically implanted owl monkeys. Procedures were identical to those described extensively in Baker et al. (1981). Under sterile conditions and deep ketamine anesthesia (25 mg/kg), a chamber was implanted in each owl monkey over an opening in the skull that exposed a region of extrastriate cortex. In preparation for each recording experiment, the animal was tranquilized with a small dose of trifluopromazine and anesthetized with ketamine-HCl. The animal's sedation was maintained throughout the experiment with small doses of ketamine-HCl (3 mg/kg/h). Both eyes were anesthetized with dibucaine HCl, fixed and brought into binocular alignment, and the pupils were dilated with Cyclogyl. Contact lenses were fitted to protect the corneas from drying and bring the eyes into focus on a tangent screen 28.5 cm from the animal. Visual stimuli were projected onto the tangent screen.

A map of the exposed cortex within the chamber was constructed by recording the position of visual receptive fields. This allowed later penetrations to be placed in visual areas



Table 1. Response latency

| Cortical area | Number of cells | Early component latencies (ms) | | Late component latencies (ms) | | Variance accounted for (%) |
|---------------|-----------------|--------------------------------|------|-------------------------------|------|----------------------------|
| | | Onset | Peak | Onset | Peak | |
| MT | 26 | 33 | 59 | 192 | 229 | 95 |
| M | 20 | 42 | 59 | 172 | 234 | 96 |
| DM | 20 | 42 | 64 | 111 | 146 | 94 |
| DL | 22 | 63 | 84 | 129 | 139 | 87 |

The latency values were obtained by fitting the curve described in the text to the averaged response to flashed oriented bars for each of the cortical areas. The onset latency is the poststimulus time delay to the start of the early component or late component of the response. The peak latency is the poststimulus time delay to the maximum response for each of the components. The last column, variance accounted for, is the percentage of the total variance in the data accounted for by the fitted curve. The number of neurons recorded from each of the areas is also listed

tentatively identified by comparison to the published visuotopic maps of Allman and Kaas (1976). Lesions were placed in selected penetrations so that electrode placements and the border of areas could be later confirmed by histological reconstruction of Nissl and myelin stained sections.

Following the preliminary mapping, single units were studied using hand-controlled visual stimuli to determine receptive field borders and some preferred stimulus properties such as stimulus length and width. Each cell was then studied with stimuli under computer control for quantitative assessment of the cell's response to oriented stationary bars flashed in the excitatory receptive field. An electronic shutter was used to produce precise and reproducible latency measurements. Bars of white light were flashed in a pseudorandom series of 6 bar orientations such that each orientation was presented 10 times. Information was stored on magnetic disk for later analysis. The oriented bar was presented for at least 1 s with a 6 s intertrial interval. The 3 s period preceding the stimulus presentation was used to determine the mean spontaneous firing rate.

The best orientation for each cell was chosen by comparing the response magnitudes at each of the six orientations presented. Response magnitude was defined as the difference between the mean impulse rate during the presentation and the mean spontaneous firing rate. The best response for each cell was combined with that for all other cells of the particular extrastriate area. The combination was accomplished in a manner similar to the technique employed by Allman et al. (1985) and Maunsell (1986). Briefly, a peristimulus (latency) histogram of 500 ms duration (116 ms immediately preceding stimulus onset time and 384 ms following stimulus onset) was constructed for each cell using the ten presentations of its best orientation. A bin width of 5 ms was used and each histogram was normalized by dividing all of its bin heights by the maximum bin height for that histogram. This effectively normalizes the maximum bin height in each of the histograms to a value of 1.0. The normalized histograms were averaged together for all of the cells in each of the four areas (see Fig. 1).

Each of the four averaged histograms was fitted to a curve with the following three components:

$$F(t) = (\text{early response}) + (\text{late response}) + (\text{spontaneous level}).$$

The early response and late response components are modeled by identical functions (with different parameter values) and both

equal zero for poststimulus times less than the value of their corresponding response latency parameter. For times greater than this latency, each component is the product of an exponentially rising term, $1 - \exp(-(t-T)/d1)$, multiplied by an exponentially falling term, $A \cdot \exp(-(t-T)/d2)$, where:

t = poststimulus time

T = response latency or delay

$d1$ = response decay time for the exponential rise

$d2$ = response decay time for the exponential fall

A = the amplitude of the response

The spontaneous level is a constant and does not vary with time. A random search algorithm (Curry 1975) was used to fit the curve to each of the four averaged histograms. Initial estimates for the parameter values in each of the curves were provided to the algorithm and it calculated an error value equal to the mean square difference between the data and the curve. The error value was then minimized through an iterative process.

Results

The fitting of the curves to the summed responses revealed several differences among the four areas. For all the areas, the curves demonstrate a rapid, sharply-peaked ("short latency, transient") process plus a slower, longer-lasting ("long latency, sustained") process. MT, DM and M have similar latencies, while DL has a much slower response latency to stimulus onset. The onset latency of the early component of the fitted curve provides estimates for the response latencies: MT = 33 ms; M = 42 ms; DM = 42 ms; DL = 63 ms. The differential contributions of the processes are reflected in the relative magnitude of the early and late components. If the main contribution is from the early source, reflected by a large peak in the first term relative to the second term peak, most of the activity will take place in the early part of the stimulus presentation, and there will be little, if any, sustained activity. If, on the other hand, the greater contribution is from the slower process, the activity will have a slower build-up, and the spikes will be distributed throughout the stimulus presentation.

When the above curve is fitted to each of the four areas, three different combinations of responses are seen. For MT and M, the rapid process is predominant [the amplitude of the second peak (pk2) is about 1/4 (0.24) of the amplitude of the first peak (pk1) in MT; $pk2/pk1 = 0.28$ in M]. DL, on the other hand, appears to have a greater input from the slower process ($pk2/pk1 = 0.48$). The results from areas MT and DL agree qualitatively with the results from similar studies in the homologous areas in macaques (Maunsell 1986). The above results also indicate that the responses of cells in both MT and M must be predominantly transient, and a visual inspection of

the individual cells confirm this result. In DL, the response is much more sustained and the early and late components are much less distinct than in the other areas.

For the population response of the DM cells, an obvious question is whether the intermediate response profile represents a population of cells that have bimodal response characteristics, or whether the response profile represents the combination of two different types of cells that reflect the slow and fast processes independently. To address this question, for each cell we counted the number of spikes from 42 ms to 111 ms (spikes in first component) and from 111 ms to 400 ms (spikes in second component). The ratio of these two components in the population response was 0.47 (first component spike count divided by second component spike count). When the 20 cells were looked at individually, only a small number of cells had a similar ratio (5 cells between 0.40 and 0.8). Six cells had ratios below 0.4; these cells represent a later, more sustained population. The remaining 9 cells had ratios above 0.8 and represent an early transient population. When this analysis is applied to the other areas, MT and M have a preponderance of transient cells (68% and 75%, respectively) with only a small number falling in the sustained category (8% and 4%). The opposite is true for area DL (57% sustained, 14% transient).

Discussion and conclusions

The number of cortical visual areas and the complexity of their interconnections presents a daunting problem to those seeking to understand vision. A basic dichotomy exists between several of these areas with some areas being slow-sustained responding and others fast-transient responding. These differences are similar to those found between the magnocellular and parvocellular pathways.

MT is characterized by a short latency transient response and anatomical data suggest that it is part of the magnocellular pathway (see Maunsell 1986). This pathway has been traced to extend from the P- α retinal ganglion cells through the magnocellular layers of the LGN and on to layer 4C α of striate cortex. The pathway continues in striate cortex from 4C α to layer 4B and then projects to area MT. MT is the best characterized of the extrastriate areas, and attention has been directed to MT because of its strong specialization for the analysis of visual motion information. Greater than 80% of cells in MT are tuned for direction and velocity of motion (Baker et al. 1981; Zeki 1980). Animals with damage to small parts of MT have difficulty in using visual motion

information to properly initiate pursuit eye movements to smoothly moving targets (Newsome et al. 1985), or in determining the direction of motion in random dot displays (Newsome and Pare 1986; Andersen and Siegel 1987).

The latency and response profile of area M is strikingly similar to that of MT. Connectional studies have not revealed a direct striate input to area M in the owl monkey (Lin et al. 1982), but the short response latency suggests that there is a striate projection to area M. There is evidence in the squirrel monkey of a striate projection on the medial wall of the hemisphere at the parieto-occipital junction that in location and organization is very similar to area M (Martinez-Millan and Hollander 1975; Allman and Kaas 1976). The visuotopic organization of area M most closely approximates the actual spatial representation of the visual hemifield of any area studied (Allman and Kaas 1976). The parieto-occipital area (PO) in the macaque is located in the same position, receives a striate input and has a similar visuotopic organization and thus probably is homologous to area M (Covey et al. 1982; Colby et al. 1983). It has been suggested on the basis of lesion experiments that the parietal cortex is a late stage in a "where it is" pathway (Ungerleider and Mishkin. 1982). Other results have emphasized the closely related contribution of parietal cortex to visual spatial attention (Posner et al. 1984; Bushnell et al. 1981). The connections that area M makes with the other areas of visual cortex are typical of the feedback type of projection, i.e., predominantly to layers 1 and 6 (Graham et al. 1979). If one considers spatial attention to be a function that modulates many other processes, then the multiple "downward" projections of area M fit well with this hypothesis. Area PO appears to connect to the dorsomedial lateral pulvinar (Pdm) and to parietal area 7a (Andersen 1987). There is strong evidence that Pdm participates in visual spatial attention on the basis of single unit recording (Petersen et al. 1985) and specific behavioral changes induced by local injection of GABAergic drugs (Petersen et al. 1987). Recent studies in humans using positron emission tomography have localized a region in the parieto-occipital junction in a set of conditions that are consistent with a spatial attention hypothesis (Fox et al. 1987).

DL emphasizes sustained activity that occurs at a longer latency. DL has been hypothesized, because of several similarities, to be homologous to all or part of the V4 complex in the macaque (Baker et al. 1981; Allman and McGuinness 1987). The neurons in DL have been shown to be selective for the size and shape of visual stimuli (Petersen et al. 1980), and similar results have been obtained in recordings from

neurons in V4 of the macaque (Desimone and Schein 1987). Both regions have very strong magnifications of the representation of the central visual field. Similar to the V4 complex, DL receives a major input from V2 (Weller and Kaas 1985), and contributes a major projection to inferotemporal cortex (Weller and Kaas 1987). On the basis of selective responses to size and shape, great emphasis on the central visual field, and projections to IT, DL appears to be specialized for functions related to the perception of visual form or pattern. Recent studies in IT by Optican and Richmond (1987) have shown that the spike train of the responses of these cells to sets of visual patterns contain more information than that measured simply by firing rate. While the early transient response in our population appears to our analysis to be quite stereotypic, the more prolonged sustained component may contain more complexity than we are measuring with our method. It is possible that the longer time course component which is largest in DL, reflects a greater use of extended temporal coding than in areas MT and M, which seem to be processing more transient events, such as visual motion and spatial attention shifts.

DM, like MT, is a distinctively myelinated zone that receives input from striate and extrastriate visual areas (Allman and Kaas 1975; Lin et al. 1982), and like MT has an early transient response. Unlike MT or M, DM has a relatively large sustained discharge as well. Based on the myelination pattern, striate input, and the position of DM with respect to other areas, it is probable that DM is homologous to area V3 in the macaque monkey (see Allman and McGuinness 1987).

Finally, in areas MT, DM, and M there is a second, distinct component of more sustained activity revealed in the grouped poststimulus histograms. This second component may reflect an additional input apart from that conveyed by the main ascending projections presumably responsible for the first component of activity. One possible source of this additional input might be found in the extensive array of other intracortical connections to these areas (Weller and Kaas 1981).

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