Velocity Sensitivity and Direction Selectivity of Neurons in Areas V1 and V2 of the Monkey: Influence of Eccentricity

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SUMMARY AND CONCLUSIONS

1. One hundred and forty two neurons in V1 and V2 were quantitatively tested using a multihistogram technique in paralyzed and anesthetized macaque monkeys.

2. V1 neurons with receptive fields within 2° from the fixation point (central V1 sample) and V1 neurons with eccentric receptive fields (15–25° eccentricity, peripheral V1 sample) were compared to assess changes in velocity sensitivity and direction selectivity with eccentricity. The central V1 sample was compared with V2 neurons with receptive fields in the same part of the visual field (central V2 sample) to compare the involvement of both areas in the analysis of motion.

3. Velocity sensitivity of V1 neurons shifts to faster velocities with increasing eccentricity. V1 and V2 neurons subserving central vision have similar preference for slow movements.

4. All neurons could be classified into three categories according to their velocity-response curves: velocity low pass, velocity broad band, and velocity tuned. Most cells in parts of V1 and V2 subserving central vision are velocity low pass. As eccentricity increases in V1, velocity low-pass cells give way to velocity broadband cells.

5. There is a significant correlation between velocity upper cutoff and receptive field width among V1 neurons. The change in upper cutoff velocity with eccentricity depends both on temporal and spatial factors.

6. Direction selectivity depends on stimulus velocity in most V1 cells. Neurons in the central V1 sample retain their direction selectivity at lower speeds than do neurons in the peripheral V1 sample.

7. The proportion of direction-selective cells is low in both V1 and V2. In V1, direction selectivity decreases with eccentricity.

8. In V1, both velocity upper cutoff and direction selectivity correlate more with laminar position than with receptive field type.

9. The similarity between V1 of the monkey and area 17 of the cat, and the dissimilarity between V2 of the monkey and area 18 of the cat, are discussed.

INTRODUCTION

There is little information on the influence of stimulus velocity on the response of cells in areas V1 and V2 of the macaque monkey. Dow (4), using velocities of up to 10°/s, was able to show that over 30% of cells in V1 subserving central vision only respond to low velocities (2°/s or less). Wurtz (46) showed that some V1 cells with somewhat more peripheral receptive fields (RFs) (3–10° eccentricity) respond to very fast movements (90°/s). Subsequent work from the same group (20) demonstrated that, in fact, cells responding to saccadic velocities are rare in this part of V1 unless the optimally oriented slit moves along its axis of optimal orientation. In all these studies only a limited range of velocities was explored and no velocity-response (VR) curves were obtained. VR curves have been shown to provide important information on the properties of area 17, 18, and 19 neurons in the cat (9, 33). In all three areas the range of velocities to which cells are the most sensitive
shifts to faster velocities with increasing eccentricity. In addition, VR curves have revealed that neurons in area 18 respond to faster velocities and are more frequently tuned for velocity than are neurons in areas 17 or area 19. These differences between areas 17, 18, and 19, suggesting that in the cat area 18 is more involved in motion perception, are the most clear-cut for those regions of these areas subserving central vision. Hence we set out to compare the VR curves of three groups of monkey neurons: V1 neurons with central and peripheral RFs and V2 neurons with central RFs.

In addition to speed, direction of movement is an important spatiotemporal stimulus parameter. Several experimenters have commented on direction selectivity of V1 monkey cells (4, 17, 36, 46), but few systematic studies have been carried out. The major study to date is that of Schiller et al. (39) using edges moving at only one velocity. Although direction selectivity for edges depends very much on the contrast sign of the edge, recent work (47) in the cat shows that direction selectivity for bars is almost totally independent of contrast sign. Further, in monkey, as in cat (34), direction selectivity depends on stimulus velocity. Therefore the second objective of this study was to measure direction selectivity for light bars over a range of speeds in the three populations of cells mentioned above. Comparison of the spatiotemporal properties of the neurons in central and peripheral V1 will reveal the influence of eccentricity on the processing of moving images in that area. Comparison of the V1 and V2 samples with central RFs will reveal the degree of involvement of these two areas in the analysis of motion.

METHODS

The methods used in this study are similar to those of Orban and Kennedy (32) and Kennedy et al. (23) for qualitative testing and of Orban et al. (33, 34) for quantitative testing. The major difference is that the stimuli used for handplotting and for quantitative testing were projected onto the same screen and could be either under manual or computer control. This allowed us to quickly check quantitatively the different tests used in handplotting for classifying neurons according to RF organization.

General procedure

Seven monkeys (Macaca irus) weighing between 1.5 and 5 kg were used for this study. The animals were anesthetized with short-acting anesthetics (ketamine 15 mg/kg im followed by Alfaxalone-Alfadolone iv) for initial surgical procedures and subsequently with a 70:30 mixture of nitrous oxide and oxygen supplemented with Nembutal at 1 mg · kg⁻¹ · h⁻¹. Monkeys were placed in a stereotaxic apparatus by means of a painless headholding device cemented to the skull. Eye movements were reduced to a very low level by general paralysis with Flaxedil (10 mg · kg⁻¹ · h⁻¹). Artificial respiration was adjusted to keep the end-tidal CO₂ at 4.5–5%. Rectal temperature was monitored and kept at 38°C. Pupils were dilated and substituted by artificial pupils of 3 mm diam. Corneas were prevented from drying by plano contact lenses, and refractive errors were corrected by appropriate spectacle lenses selected by retinoscopy. A small craniotomy (4 mm φ) was made in the skull posterior to the lunate sulcus. Single units, either on the dorsal surface of the operculum or in the banks of the lunate and calcarine sulci, were recorded by means of glass-insulated tungsten electrodes (5) driven through the dura with a Narishige microdrive. The units were handplotted and quantitatively tested with moving and stationary flashed light slits projected on a tangent screen located at 1.14 m from the monkey. Four-day experimental sessions allowed us to make between one and four penetrations in the brain of each animal. Several small lesions (5 µA, 5 s) were made in each penetration. Penetrations were histologically reconstructed on frozen sections (60 µm thick) stained with cresyl violet. The sections were examined to determine whether the penetrations were in V1 or V2. The laminar position of neurons was determined only in those tracks in which all lesions could be unambiguously identified. Both the foveal pit and the retinal vessels emerging from the blind spot were plotted by means of a reversible ophthalmoscope every morning. So as to maintain clear optics over the full 4 days it was necessary to clean the eyes with hypertonic solution and to apply local antibiotics each morning before plotting the retinal landmarks.

Handplotting procedures

The initial handplotting stage involved determination of optimal orientation and length. The precision of these values could be checked, especially for orientation biased or nonoriented cells, by measuring a computer-controlled orientation tuning curve and by constructing poststimulus time histograms for moving slits of different lengths. A narrow light slit (typically 0.1° wide for central and 0.2° wide for peripheral RFs) of optimal length and orientation was then used to outline the minimum discharge field according to the procedures of Kato et al. (21). The eccentricity of the RF was estimated by measuring the distance from its center to the projected point of the foveal pit. In both V1 and V2, neurons were included in the group subserving
central vision when the eccentricity of the RF was <2°. The V1 neurons subserving peripheral vision had RFs with eccentricities between 15 and 25°. The dimension of the discharge field orthogonal to the optimal orientation is defined as the RF width. RF width together with the spatial disposition of the ON-OFF subregions are the main criteria used to classify the RFs into four families (A, B, C, S) (10, 23, 30, 32). Since the responses to stationary flashed slits are sometimes difficult to judge by ear (6), we frequently ran poststimulus time histograms (PSTHs) to slits flashed in different positions to confirm the spatial disposition of subregions obtained by handplotting. Cells with narrow RFs belonged to the S family when the subregions do not overlap and to the B family when they do overlap. Cells with wide RFs belong to the C family when the ON-OFF subregions overlap and to the A family when they do not overlap. Each family has an end-free member (A, B, C, S cells) and an end-stopped member (HA, HB, HC, and HS cells). As mentioned above, when the presence of end stopping was in doubt, PSTHs to moving slits of different lengths could be used to ascertain the end-stopped property. Since end stopping is a graded quality, cells with incomplete end stopping were included in the end-stopped category (21).

Quantitative testing
The influence of velocity was tested monocularly in the dominant eye with a narrow light slit of optimal orientation and length. For end-free cells, a 6° long slit was used, whereas for end-stopped cells shorter slits (0.3–2°) of optimal length were used. The luminance of the light slit was 40 cd/m² on a homogeneous background that had a luminance of 8 cd/m². The light slits were moved back and forth by a General Scanning galvanometer under computer control (MINC-11). In order to save computer memory space, slower speeds were tested with shorter movement amplitudes. The minimum amplitude of movement at the slowest speeds (0.2–2°/s) was 2°. Since the RF was plotted directly on the screen used for quantitative testing, the RF was always well centered in the middle of the movement traverse, so that only for exceptionally wide RFs did we have to increase the minimum amplitude to 5°. For velocities between 2 and 20°/s, the amplitude was proportional to the speed, so that movement duration remained equal to 1 s. For velocities over 50°/s, the amplitude of movement was kept fixed at 30°. Between movements in each direction the slit was stationary outside the RF for 5 s. Hence changes in movement duration had relatively little effect on stimulation frequency. The influence of velocity (range 0.2–800°/s) was tested by means of a multihistogram technique to offset response variability. The multihistograms produced a set of interleaved PSTHs, each corresponding to a forward or backward sweep at a given velocity. Included in the set were two PSTHs in which no stimulus was presented and which were used to evaluate spontaneous activity. Usually each PSTH represented the average of 10 stimulus presentations. The PSTHs were constructed with a 10-ms bin width and maximum firing rate, evaluated from the bin in the PSTH with the highest spike count, was used as response measure. The responses obtained at different velocities were compared with a significance level defined as the maximum firing in the blank PSTHs. VR curves were obtained by fitting a spline function through the data points plotting response as a function of slit velocity.

Figure 1 illustrates the characteristics used to describe the VR curves (33). The optimal velocity (V2) is the velocity corresponding to the maximum of the VR curve. The response strength (2α) is the height of the VR curve above the significance level at optimal velocity. The velocity upper cutoff (V3) is the higher velocity at which the response is half the maximum response. The width of velocity tuning (V3/V1) is the ratio of the two velocities corresponding to the intersection of the VR curve with the half-maximum response level. The response to slow movement (100b/2α) is the response to the slowest movement tested (0.2°/s) for cells with RFs narrower than 1.5 and 0.5°/s for cells with RFs wider than 1.5° expressed as a percentage of the maximum response. The VR curve in the preferred direction of motion was taken as characteristic of the neuron. If a cell completely lacked direction selectivity [mean direction index (MDI) < 20, see below] the average of the VR characteristics were taken for both directions of motion.

Using these characteristics, cells fall into one of four velocity types (33). Velocity tuned cells have an optimal velocity, and their response decreases on either side of the optimum. These cells have a width of velocity tuning of 50 or less and an upper cutoff velocity below 200°/s. Velocity broad-band cells have no optimum velocity but respond over a wide range of velocities (width of velocity tuning over 80). Velocity low-pass cells respond very well to low velocities and have an upper cutoff velocity below 20°/s. The response of velocity high-pass cells increases with velocity above a threshold of 2 to 14°/s and saturates at velocities of ~100°/s. Their median response level at 700°/s is 80% of maximum response (range 40–100%).

Direction selectivity refers to a preferred direction (PD) on the optimal axis of movement. This selectivity was measured at a given velocity by the direction index that compares the responses (minus mean spontaneous activity) in the preferred (PD) and the nonpreferred (NPD) direction. The direction index is defined as follows

\[
\text{direction index} = \frac{(\text{response in PD} - \text{response in NPD})}{\text{response in PD}} \times 100
\]
FIG. 1. Characteristics of the velocity-response (VR) curves. The optimal velocity (V2) was 8°/s, the response strength (2a) was 96 spikes/s, the velocity upper cutoff (V3) was 49°/s, the response to slow movement (100b/2a) was 9°, and the tuning width (V3/V1) was 37. The cell was a HS cell of the peripheral V1 sample, recorded in layer IVC. This cell was exceptional in being both velocity tuned and direction selective.

where the response has to be significant (2 SD above the mean). Selectivity to the direction of movement is dependent on stimulus velocity in the cat (34). To characterize the direction selectivity of a neuron we define MDI. The MDI is the absolute value of the weighted average of the direction indexes at different velocities, using the responses in the preferred direction at each velocity as weighting factors.

Statistical testing was performed with nonparametric tests: *χ*² test, Mann-Whitney *U* test, and the Spearman rank correlation. Throughout this report the significance level was set at *P* < 0.05 (two tailed).

RESULTS

One hundred and sixty two neurons were studied qualitatively, and VR curves were obtained for 142 of them. As shown in Table 1 the V1 samples were larger than the V2 sample. The V1 samples of cells subserving central (0–2°) and peripheral vision (15–25°) will be referred to as “central V1” and “peripheral V1”. Cells in the V2 sample all subserved central vision (0–2°), and this sample will be referred to as “central V2”.

RF width and RF classification

Figure 2 shows the distribution of RF widths in our three experimental samples. The RF widths of the central V1 and V2 samples were quite similar, with median values of 0.35 and 0.45°, respectively. As shown by the comparison of the two V1 samples, RF width increases only slightly with eccentricity: median RF widths were 0.35 and 0.9° for central and peripheral samples, respectively. Comparison of the present data with those of a previous study on the baboon (23) shows that RF size increases much more steeply in V2 than it does in V1, confirming results of Gattass et al. (13) [see Fig. 13 in Gattass et al. (13)]. The RF width distributions of all three samples are multimodal (Fig. 2) with a first major mode followed by several smaller subsequent modes.

<table>
<thead>
<tr>
<th>TABLE 1. Data base</th>
<th>Studied (RF width)</th>
<th>Classified (RF)</th>
<th>VR Curve</th>
</tr>
</thead>
<tbody>
<tr>
<td>V1 central</td>
<td>70</td>
<td>67</td>
<td>59</td>
</tr>
<tr>
<td>V1 peripheral</td>
<td>56</td>
<td>54</td>
<td>55</td>
</tr>
<tr>
<td>V2 central</td>
<td>36</td>
<td>32</td>
<td>28</td>
</tr>
<tr>
<td>Total</td>
<td>162</td>
<td>142</td>
<td></td>
</tr>
</tbody>
</table>

RF, receptive fields; VR, velocity response.
FIG. 2. A–C: receptive field (RF) width distribution in the 3 experimental samples. Arrows indicate the medians of the distribution. Small and large RFs are indicated by different hatching. D: median RF width plotted as a function of eccentricity: open symbols, present results; filled symbols, data of Kennedy et al. (23); circles, V1; triangles, V2. Error bars indicate first and third quartiles.

The first major mode corresponds to cells with small RFs (S and B families), whereas the other modes correspond to the A and C families. The separation between narrow and wide RFs was set at 0.45° for central samples in V1 and V2 and 1.05° for the peripheral V1 sample. Cells were classified into nonoriented and oriented cells (Table 2). Nonoriented cells
TABLE 2. Proportion of RF types

<table>
<thead>
<tr>
<th>RF type</th>
<th>V1 Central</th>
<th>V1 Peripheral</th>
<th>V2 Central</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nonoriented</td>
<td>10</td>
<td>13</td>
<td>16</td>
</tr>
<tr>
<td>S family</td>
<td>45</td>
<td>35</td>
<td>40</td>
</tr>
<tr>
<td>B family</td>
<td>15</td>
<td>13</td>
<td>9</td>
</tr>
<tr>
<td>C family</td>
<td>21</td>
<td>33</td>
<td>16</td>
</tr>
<tr>
<td>A family</td>
<td>9</td>
<td>6</td>
<td>19</td>
</tr>
<tr>
<td>End stopped*</td>
<td>38</td>
<td>36</td>
<td>44</td>
</tr>
<tr>
<td>End free</td>
<td>62</td>
<td>64</td>
<td>56</td>
</tr>
</tbody>
</table>

Values are given as percentages. RF, receptive fields. *Calculated only for oriented cells.

could have small or large RFs. Oriented cells were further divided into the four families as outlined in METHODS. The proportion of end-stopped cells was only calculated for the oriented cells. End-stopped cells constituted a sizeable proportion (~40%) of each sample. Confirming a previous result (23) the proportions of different RF types were quite similar in the central V1 and V2 samples. Likewise there was no obvious change in proportions of different RF types with eccentricity within V1.

Velocity sensitivity range

A narrow slit of optimal length and orientation was used for quantitative testing. For neurons with a RF in the central visual field the median slit width was 0.15° (range 0.05–0.3°), and for neurons with RFs in the peripheral visual field the median was 0.3° (range 0.1–0.7°). Control experiments showed that changes in slit width by a factor of two or three had little influence on the VR curves. This is illustrated in Fig. 3 showing the VR curves of a HC cell taken from the peripheral V1 sample and tested with both a 0.1 and a 0.3° wide slit. The upper cutoff velocity was 38°/s with the 0.1° wide slit and 41°/s with the 0.3° wide slit, whereas the response to slow movement was 75% with the narrow slit and 85% with the wider slit. In none of the three neurons tested was there a systematic change in upper cutoff velocity, response to slow movement, or MDI when the width of the slit was changed.

One striking feature of the monkey cortex is that most of the cells in V1 and V2 are very sensitive to low velocities. This is illustrated for one neuron in Fig. 4. It is clear from the PSTHs that the cell only responded to the three or four lowest velocities tested. This results in a low upper cutoff velocity (1.4°/s) and maximal response to slow movement (100%) measured on the VR curve. Figure 5 shows the distribution of these two VR curve characteristics among the overall neuronal population for the three experimental samples. The neurons of the two central samples have a similar

FIG. 3. VR curves of cell 14.09 (peripheral V1 sample) obtained with moving slits 0.1° wide (crosses and stippled line) and 0.3° wide (dots and full lines). The thin horizontal lines indicate the corresponding significance levels. This HC cell was classified as a VBB cell. See text for abbreviations.
FIG. 4. PSTHs representing average responses to slits moving in the preferred direction at different speeds (A) and the VR curve derived from these histograms (B). The data are from cell 13.09 (central V1 sample), a direction selective (MDI 81) HS cell recorded in layer IVB and classified as VLP. In A velocities are indicated on the left of the PSTHs. In B the thin horizontal line indicates the significance level. See text for abbreviations.

FIG. 5. Distribution of velocity upper cutoff, response to slow movement, and response strength in the overall population of the 3 experimental samples. See Table 1 for sample sizes and text for abbreviations.
preference for slow movements: the median upper cutoff velocity is 9°/s for V1 and V2, respectively, whereas the median response to slow movement was 82 and 90%, respectively. With increasing eccentricity, the sensitivity gradually shifts to higher velocities. For the central V1 sample the median upper cutoff velocity was 9°/s (range 0.9–90°/s) compared with 49°/s (range 4.4–166°/s) for the peripheral V1 sample. The median response to slow movement decreased from 82% in the central V1 sample to 68% in the peripheral V1 sample. This shift in sensitivity to faster movements is accompanied by an increase in average response strength from 70 spikes/s for central V1 to 94 spikes/s for peripheral V1. All three changes with eccentricity within V1 were statistically significant (Fig. 5). While the central V1 and V2 sample did not differ significantly in upper cutoff velocity or in response to slow movement, their response strengths were statistically different. In V2 it is known (23, 37) that a large proportion of cells respond optimally only when stimulated binocularly, so that the lower response level that we have found in V2 may quite simply reflect less than adequate stimulation.

Velocity types

Almost every cell in areas 17, 18, and 19 of the cat can be classified into one of four velocity types: velocity low-pass (VLP), velocity tuned (VT), velocity high-pass (VHP), and velocity broad-band (VBB) (33) (see METHODS for definition). Recent studies have shown that with low-contrast levels, such as used in the present study, VHP cells are found only in small numbers (6 out of 192 cells) in area 17 of the cat (G. A. Orban, B. Gulyas, R. Vogels, J. Duysens, and M. Maes, unpublished observations). None of the cells studied in the present experiments fit the definition of the VHP category, suggesting that there may be a species difference. All cells could be fit into the three other types: VLP, VT, and VBB cells, of which examples are given in Fig. 6. As shown in the same figure, VT cells, which are thought to be involved in velocity judgments (31), were only present in small proportions (~10%) in all three samples. While VLP and VBB cells have only a range of optimal speeds with no clear peak in the VR curve, VT cells do have a genuine preferred velocity. These preferred velocities ranged from 1.5° to 39°/s in the central V1 sample (median 1.8°/s), from 0.9 to 2.3°/s in the central V2 sample (median 2.2°/s), and from 7.5 to 37°/s in the peripheral V1 sample (median 21°/s). In both central samples, the VLP cells clearly dominated, representing 71% of both samples. With increasing eccentricity in V1 the proportion of VLP cells decreased, whereas the proportion of VBB cells increased. This change in proportion was statistically significant (P < 0.0001; χ² = 32.02).

Association between RF and velocity types

In the cat, there is a clear association between RF and velocity types in area 17 and to a lesser extent in area 18. In area 17 subserving central vision almost every S or B family cell belongs to the VLP category, whereas A and C family cells are about equally divided between VLP and VBB cells. In area 17, subserving peripheral vision, a similar but weaker trend was observed. In none of the three monkey samples (Table 3) was there such a clear association between narrow field cells (S and B families) and VLP cells. In all three samples there is only a weak tendency for narrow field cells to be more often VLP, and this tendency was clearest in the peripheral V1 sample where it just reached significance (P < 0.05, χ² = 4.38). In both the central V1 and V2 samples there was a small tendency for end-stopped cells to be more often VLP. This tendency was significant for the central V1 sample (P < 0.025; χ² = 5.13).

Laminar distribution of velocity types

Table 4 gives the laminar distribution of velocity types and velocity characteristics for the central V1 sample. The cells in laminae IVB and VI had different velocity characteristics from those in the other layers. And indeed it has been shown (24, 25, 29) that both these laminae project to middle temporal area (MT). Given the importance of MT in movement analysis (26, 50), we have compared in Table 4 the velocity characteristics of those layers which provide an input to MT (laminae IVB and VI) with those of all the other cortical layers. Cells located in layers IVB and VI respond to faster velocities than those located in other layers as indicated by a significantly higher upper cutoff velocity. This is also reflected by the much larger proportion of VLP cells outside layers IVB and VI. Both small and large RFs were found in the different layers, and in particular there was no significant difference
FIG. 6. A–C: representative examples of the 3 velocity types: VLP (A), VT (B), and VBB (C). D–F: proportion of the 3 velocity types in the 3 experimental samples. See text for abbreviations.

In RF width between laminae IVB and VI and the other layers. It is interesting to note that most small field cells (S and B families) that were not VLP were found in layers IVB and VI (see Fig. 7A), whereas all cells with wide RFs located in the superficial layers (II, III, and IVA) were VLP. In other words, cells in layers IVB and VI respond to faster velocities than those in layers II and III whatever their RF type or size. It seems, therefore, that in monkey area V1, there is a better correlation between velocity characteristics and laminar position than between velocity characteristics and RF type.
TABLE 3. Association between velocity types and RF organization

<table>
<thead>
<tr>
<th>RF characteristic</th>
<th>VLP</th>
<th>VBB</th>
<th>VT</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>V1 central</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small RF (36)</td>
<td>78</td>
<td>14</td>
<td>8</td>
</tr>
<tr>
<td>Large RF (16)</td>
<td>69</td>
<td>25</td>
<td>6</td>
</tr>
<tr>
<td><strong>V1 peripheral</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small RF (25)</td>
<td>32</td>
<td>60*</td>
<td>8*</td>
</tr>
<tr>
<td>Large RF (21)</td>
<td>5</td>
<td>90*</td>
<td>5</td>
</tr>
<tr>
<td><strong>V2 central</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small RF (12)</td>
<td>68</td>
<td>24</td>
<td>8</td>
</tr>
<tr>
<td>Large RF (10)</td>
<td>60</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td><strong>V2 central</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>End stopped (22)</td>
<td>90*</td>
<td>5</td>
<td>5*</td>
</tr>
<tr>
<td>End free (30)</td>
<td>63*</td>
<td>27</td>
<td>10</td>
</tr>
<tr>
<td><strong>V1 peripheral</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>End stopped (16)</td>
<td>19</td>
<td>68</td>
<td>13</td>
</tr>
<tr>
<td>End free (30)</td>
<td>20</td>
<td>77</td>
<td>3</td>
</tr>
<tr>
<td><strong>V2 central</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>End stopped (10)</td>
<td>70</td>
<td>20</td>
<td>10</td>
</tr>
<tr>
<td>End free (12)</td>
<td>58</td>
<td>25</td>
<td>17</td>
</tr>
</tbody>
</table>

VLP, velocity low-pass; VBB, velocity broad-band; VT, velocity tuned; RF, receptive field. Nos. in parentheses are no. of cells. * Significantly different on χ² test.

Spatial and temporal factors determining velocity upper cutoff

A correlation between RF width and velocity upper cutoff has been shown at different levels of the visual system of the cat: retina (2), lateral geniculate nucleus (LGN) (12), and cortical areas (33). In the monkey there is a correlation between RF width and velocity upper cutoff, if one considers the overall V1 sample (P = 0.68). This correlation is, however, much weaker when one considers (Fig. 7) the two eccentricity samples separately (P = 0.42 and 0.43 in the central and peripheral sample, respectively). Indeed a whole range of velocity upper cutoffs corresponds to a given RF width. For example, in the central V1 sample (Fig. 7A), the velocity upper cutoff values range from 3 to 90°/s at a RF width of 0.5°. This suggests that factors other than RF width contribute to the determination of the velocity upper cutoff. In the cat, Duysens et al. (8) have shown that for many area 17 cells, with RFs close to the fixation point, the velocity upper cutoff is determined by the duration threshold as well as by the RF width. The duration threshold is the minimum stimulus duration that will elicit a response from the cell. When velocity upper cutoff (in degrees per second) is plotted against RF width (Fig. 7), then a slope of +1 designates a constant stimulus duration, which seems a reasonable assumption since the RF width is determined with a moving light slit. Thus cells having a similar duration requirement will be located on a diagonal with a slope of +1, and these isoduration lines have been plotted in Fig. 7. Comparison of the duration requirements in the central and peripheral samples reveals that cells in the central sample required longer durations than those in the peripheral sample. The average duration requirement was 30 ms in the central sample and 18 ms in the peripheral one. The ratio of those two values is lower than the change in velocity upper cutoff with eccentricity (a factor of 5.5). The change in velocity upper cutoff is also larger than the change in RF width (a factor of 2.6). Therefore it seems that neither the change in temporal nor in spatial properties of the RFs can, on its own, account for the change in velocity upper cutoff with eccentricity. However, by considering both factors together it is possible to ex-

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TABLE 4. Laminar distribution of velocity sensitivity and direction selectivity in the central V1 sample

<table>
<thead>
<tr>
<th>Layers</th>
<th>n</th>
<th>VLP, %</th>
<th>Median Velocity* Upper Cutoff (Q1–Q3)</th>
<th>NDS, %</th>
<th>Median MD1† (Q1–Q3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>IVB and VI</td>
<td>16</td>
<td>44</td>
<td>14.2°/s (8.8–30)</td>
<td>38%</td>
<td>63 (37–80)</td>
</tr>
<tr>
<td>Others</td>
<td>25</td>
<td>84</td>
<td>8.5°/s (5.6–13.7)</td>
<td>72%</td>
<td>18 (6–53)</td>
</tr>
</tbody>
</table>

VLP, velocity low-pass; NDS, nondirection sensitive; MDI, mean direction index. Q1, Q3, 1st and 3rd quartiles. * Significantly different (P < 0.03). † Significantly different (P < 0.003).
plain the observed change. Multiplying the factors of the temporal and spatial changes yields a value (4.4) close to the observed change in velocity upper cutoff.

Figure 7 shows that, overall, neurons with peripheral RFs have larger RFs and respond to faster velocities than neurons with central RFs. Indeed, in the central sample, the vast majority (46/58) of cells have RF widths below 0.65° and velocity upper cutoffs below 20°/s, whereas in the peripheral sample only a minority (6/54) have both these characteristics. The change in proportion of cells with these characteristics with increasing eccentricity is extremely significant ($\chi^2 = 61.85$, $P < 0.001$). In fact consideration of both characteristics (RF width and upper cutoff) distinguished more clearly between central and peripheral samples than either characteristic taken on its own.

Changes in direction selectivity with stimulus speed

In areas 17 and 18 of the cat, the direction selectivity of many cells depends on slit velocity (28, 34). The same was true in area 17 of the macaque. For each cell, the direction selectivity at a given velocity is characterized by its direction index (DI), whereas its overall direction selectivity is measured by the MDI. The VR curve shown in Fig. 8A is that of a VLP C cell recorded in the upper part of layer IVC at the V1/V2 border and belonging to the central V1 sample. The cell was clearly direction selective (MDI 81) but at the lowest velocity (0.2°/s) the cell had little direction selectivity, the DI being 57. With increasing velocity, direction selectivity gradually increased reaching DIs over 90 for speeds between 2 and 10°/s. This increase in direction selectivity was not due to an increase of the response in the
FIG. 8. Loss of direction selectivity at low speeds. A and B: VR curves in preferred (dots, full lines) and nonpreferred (crosses, stippled lines) directions of a cell of the central V1 sample (A) and peripheral V1 sample (B). C and D: the DI of cells with MDI > 40 plotted as a function of stimulus velocity for the central V1 sample (C) and peripheral V1 sample (D). The median (dots) and first and third quartiles are indicated. Arrows indicate the speed at which on average V1 cells lose direction selectivity (DI = 50). Number of cells responsive at each velocity are indicated above the graphs. See text for abbreviations.

PD, but to a decrease of the response in the NPD. Figure 8B shows a similar observation for a cell of the peripheral V1 sample. This S cell was moderately direction selective (MDI 58). At low speeds (0.2 to 1°/s) the cell was completely nondirection selective, and only for
speeds between 10 and 50°/s did the cell reach DIs above 80. For this cell, the increase in DI with increasing speed was the result of a decrease in response in the NPD as well as of an increase in response in the preferred direction.

In order to determine how general the loss of direction selectivity at low speed was, we calculated for each slit velocity tested, the median DI of the population of cells with some degree of direction selectivity (MDI > 40). The MDI characterizes the direction selectivity of an individual neuron over the range of velocities tested, whereas the median DI defines the direction selectivity of a population of neurons at a given velocity. So as to avoid spuriously high DIs due to very small responses, we only included a cell in the calculus of the median DI at a given velocity, if its response in the preferred direction was at least a third of its maximum response. The median DI of both V1 samples are plotted as a function of slit velocity in Fig. 8, C and D. Only velocities for which at least seven neurons were responding at a third of their maximum or more, were included in these figures. Taking a DI of 50 as lower limit for direction selectivity, cells in the central V1 sample on average lost their direction selectivity at 0.21°/s compared with 0.79°/s for cells from the peripheral sample. In the central V1 sample, 22 out of 26 cells with MDI > 40, did show some increase in DI (at least 20 points) with velocity: this was due either to the sole increase of response in the PD (3 cells) or to the sole decrease in response in the NPD (8 cells), or to both changes (11 cells). In the peripheral V1 sample 12 out of 16 cells with MDI > 40 did show an increase in DI with velocity: this change was due either to the sole increase in response in the PD (4 cells), or to the decrease in response in the NPD (2 cells), or to both changes (6 cells). Comparing both samples reveals that in the central sample the decrease of response in the NPD more frequently contributed to changes in DI with velocity than it did in the peripheral sample. This suggests that the relative importance of facilitation in the PD over inhibition in the NPD increases with eccentricity.

Other factors affecting direction selectivity

Since in many cells direction selectivity varies with slit velocity, it is crucial to use a measure averaged over different speeds to characterize overall direction selectivity. The MDI does exactly that. Figure 9 shows the distribution of MDIs in the three samples. A MDI of 0 corresponds to no direction selectivity at all and a MDI of 100 to a complete direction selectivity. The direction selectivity of cells in all three samples is small, being the lowest in the peripheral V1 sample. Indeed the median MDI is 35 and 32 for the central V1 and V2 samples, compared with 23 for the peripheral V1 sample. Following the definition of Orban et al. (34) we can define cells with a MDI > 66 as direction selective (DS), cells with a MDI < 50 as nondirection selective (NDS), and the remaining cells as direction asymmetric (DA). The distribution of these types in the three samples are indicated in Table 5. This confirms that, generally, the direction selectivity is small in all three samples and that the central V1 sample is the most direction selective and the peripheral V1 sample the least direction selective. The decrease in di-

FIG. 9. Distribution of MDI in the 3 experimental samples. See Table 1 for sample sizes and text for abbreviations.
TABLE 5. Proportion of DS cells in the different samples

<table>
<thead>
<tr>
<th>Sample</th>
<th>DS</th>
<th>DA</th>
<th>NDS</th>
</tr>
</thead>
<tbody>
<tr>
<td>V1 central (59)</td>
<td>27</td>
<td>14</td>
<td>59</td>
</tr>
<tr>
<td>V1 peripheral (55)</td>
<td>5</td>
<td>15</td>
<td>80*</td>
</tr>
<tr>
<td>V2 central (28)</td>
<td>11</td>
<td>14</td>
<td>75</td>
</tr>
</tbody>
</table>

Values for direction-selective (DS), direction-asymmetric (DA), and nondirection selective (NDS) cells are given as percentages. Nos. in parenthesis are no. of cells. * The change in proportion of NDS cells with eccentricity is statistically significant ($P < 0.025; \chi^2 = 5.72$).

Direction selectivity with the eccentricity within V1 was statistically significant.

Contrary to the cat, direction selectivity showed little correlation with velocity or RF types. In the cat, VT cells are significantly more direction selective than other types. In the present study, 70% of the VLP and the VBB cells were nondirection selective, compared with 58% of the VT cells. In the cat S cells were more direction selective than other RF types. In the present study, the A-family cells were the most direction selective followed in decreasing order by the S family, C family, and B family. However, this trend was not significant. All nonoriented cells were nondirectional selective. There was only a weak association between end stopping and direction selectivity; end free cells were somewhat more frequently not direction selective than end-stopped cells.

Direction selectivity was clearly correlated with laminar position in a similar fashion to velocity sensitivity (Table 4). Cells in layers IVB and VI cells were much more direction selective than those located outside these lamina, as revealed by the higher MDI values of cells in these layers compared with other cells as well as the lower proportion of NDS cells in these layers compared with other layers. It is noteworthy that except for the differences in velocity upper cutoff and MDI these layers did not differ significantly in the other neuronal parameters studied (RF width, response to slow movement, and response strength).

DISCUSSION

Our results show that those regions of V1 and V2 subserving foveal vision have an equally strong preference for slow movements and that, within V1, the preference shifts to faster movements with increasing eccentricity. This change in upper cutoff velocity is due to both changes in temporal and spatial RF properties. Our results further show that the number of direction selective cells is equally low in V1 and V2 subserving central vision and that within V1 direction selectivity decreases with eccentricity. In addition cells in V1 subserving central vision retain their direction selectivity at lower speeds than those in V1 subserving peripheral vision. Both velocity sensitivity and direction selectivity correlate well with laminar position and little with RF type.

Comparison with previous work on macaque visual cortex

Our results are in good agreement with those of previous workers with respect to RF width and RF types. The range of RF widths in the present V1 central sample (0.15 to 0.6°) corresponds closely to the distribution of field size (0.2 to 0.5°) in the Dow et al. (5) study in the awake monkey. The change in RF width with eccentricity in V1 fits well with the changes reported by Hubel and Wiesel (19). Finally the steeper slope of the RF width-eccentricity relationship in V2 compared with V1 agrees with the results of Gattass et al. (13). The present study confirms the presence of S cells in the part of V2 neighboring V1 as reported by Kennedy et al. (23). The larger proportion of nonoriented cells in the V2 sample of the present study compared with the proportion reported by Kennedy et al. (23) could be explained by the fact that nonoriented cells in V2 are clustered in the thin cytochrome stripes running orthogonally to the V1/V2 border (15) and could have been missed in our previous study.

While no systematic study on velocity sensitivity in V1 of the monkey is available, our results are in agreement with the fragmented observations made by previous workers. The large number of velocity low-pass cells in the part of V1 subserving central vision extends the earlier observation of Dow (4) that many cells in the foveal region respond optimally at low velocities. The larger proportion of velocity broad-band cells in layers below IVA compared with the more superficial layers goes along with the observation of Judge et al. (20) that cells in the infragranular layers respond
more often to saccadic velocities at least when tested with axial movement (optimally oriented long slant moving along the axis of optimal orientation). If cells in the infragranular layers only require stimulus durations of the order of 4 ms (as is the case of some cells shown in Fig. 7A), one could understand that they respond to axial movement at fast speeds: for a RF length of 4° and speed of 900°/s, the duration of activation would be 4.4 ms.

The relatively low proportion of direction-selective cells in our V1 sample is in agreement with the study of Schiller et al. (39) on V1 cells with RFs within 2–5° from the fixation point. Thirty-five percent of the cells recorded by these authors correspond to our direction-selective cells, since their response in the preferred direction was at least three times or more that in the nonpreferred direction. This is in good agreement with our finding of 27% direction-selective cells in the central V1 sample. Furthermore, our observation that more cells are direction selective in layers IVB and VI than in the other layers is in agreement with Dow’s report that his class IV cells, of which direction selectivity was a defining characteristic, peak in layer IVB and occur only in very low proportions in the layers above IVB.

Few quantitative studies have been made of velocity and direction preference of other visual cortical areas. A notable exception is the MT. Maunsell and Van Essen (26) reported that the majority of cells (89/109) were tuned for velocity and that most cells were strongly direction selective. Overall, MT cells in their study responded to faster movements than do V1 neurons in the present study. However, the observation that among area V1 cells those that have a preference for the fastest movements reside in layers IVB and VI, which are known project to MT, raises the question whether these area V1 cells are fast enough to account for the speeds observed in MT. As far as the results obtained with slightly different procedures can be compared, it seems that the velocity upper cutoff are in fact compatible. The largest upper cutoff velocities observed in this study were 90 and 166°/s in the central and peripheral V1 samples, respectively. Taking into account that the contrast was higher in the Maunsell and Van Essen study (26) than in the present one, these values are in keeping with those (64 and 256°/s) derived from similar samples in MT [see Fig. 8 of Maunsell and Van Essen (26)]. It would thus seem that V1 could relay responses to fast enough movements to account for the range of velocities over which MT operates. This is not to say that the V1 signals do not need to be further processed within MT to produce the velocity tuning characteristic of that area. This will probably involve facilitatory spatiotemporal interactions in the preferred direction as recently proposed by Duy sens et al. (7) for velocity tuned cells in the cat.

Comparison with the cat

The results obtained in V1 of the monkey show similarities to those obtained in area 17 of the cat (30, 33, 34, and G. A. Orban, B. Gulyas, R. Vogels, J. Duy ens, and M. Maes unpublished observations). Despite a two- to threefold difference in RF width, the velocity characteristics and direction selectivity are similar as illustrated in Fig. 10. The contrast log [Δ L/L (log difference in luminance over luminance)] used in the present study (0.6) was between the two values used in the cat studies (1.82 and 0.4), although closer to the lower value. In many instances the velocity-response characteristics measured in the monkey are intermediate to those obtained in the two cat studies. The four basic similarities between V1 of the monkey and area 17 of the cat are 1) the overall preference for slow movements indicated by a low upper cutoff velocity and a large response to slow movement, 2) a shift in sensitivity toward faster speeds with increasing eccentricity, 3) few velocity tuned cells, and 4) few direction-selective cells. The three minor points of difference are 1) a somewhat lower upper cutoff velocity in the monkey compared with that in the cat, 2) the complete absence of velocity high-pass cells in the monkey, and 3) a somewhat lower proportion of direction-selective cells in the monkey compared with the cat, especially in the part of V1 subserving peripheral vision.

However, behind this apparent similarity between monkey V1 and cat area 17, there is an important difference. In the cat the velocity types and direction selectivity are more or less evenly distributed throughout cortical layers. Velocity types and direction selectivity correlate clearly with the RF classification into A, B, C, and S families. In the monkey V1, however, there is relatively little correlation between RF organization and velocity types
or direction selectivity. However, velocity types and direction selectivity are segregated according to laminar position. This correlation with laminar position, which is not found in the cat, could be related to the clearer definition of layers and a better laminar segregation of cells projecting to different extrastriate areas (22, 24, 42) in monkey V1. The difference in importance of lamination in cat and monkey might be due to the difference in anatomical position of V1 in these two species. While in monkey the LGN projects almost exclusively

FIG. 10. Comparison of changes in neuronal properties with eccentricity in cat and monkey. The values obtained in the monkey (full lines) are compared with those obtained at 2 different contrast levels in the cat (dotted lines) monkey contrast level: 0.6, cat high-contrast level: 1.82, and cat low-contrast level: 0.4. The high-contrast cat data are from Orban (30) and the low-contrast cat data from R. Vogels, G. A. Orban, B. Gulyas, and J. Duysens (unpublished observations). A: RF width-ecentricity relationship. B: velocity upper cutoff eccentricity relationship. C: response to slow movement-ecentricity relationship. D: response strength-ecentricity relationship. E: percentage of VT cells as a function of eccentricity. F: MDI-ecentricity relationship. In A, filled circles and crosses correspond to monkey and cat data, respectively, and in B-F filled circles correspond to monkey; open circles to low-contrast cat, and triangles to high-contrast cat. In A the cat sample sizes were n = 235 and n = 40 for the central and peripheral samples, respectively. In B-F the high-contrast cat sample sizes were n = 153 and n = 36 for the central and peripheral samples, and for the low-contrast conditions n = 66 and n = 48, respectively.
to V1 (1, 48, 49), this is not the case in the cat (for review see Ref. 30). This means that the role of information distribution to other visual cortical areas is going to be all the more emphasized in V1 of the monkey than it is in V1 of the cat.

While area 17 of the macaque has striking similarities with area 17 of the cat, V2 of the monkey and area 18 of the cat appear very different as shown by the comparison of the present study with the data of Orban et al. (33, 34). While most cells of area 18 of the cat are direction selective and many cat area 18 cells are velocity tuned, especially in the part subserving central vision, these two properties are almost entirely absent in V2 of the macaque subserving foveal vision. This agrees with the difference between V2 of the monkey and area 18 of the cat revealed by the study of other RF properties (18, 23). The preference of V2 cells with foveal RFs for slow movements suggests that, in monkey, V2 is involved in the analysis of stationary objects, a hypothesis that is in keeping with its exquisite tuning for static disparity (18, 37, 38). While area 18 of the cat has little in common with V2 of the macaque with respect to velocity sensitivity and direction selectivity, it shares some similarities with MT of the monkey: notably, the high proportion of velocity tuned and direction-selective cells as well as the heavy myelination of afferent fibers (16, 26, 33, 34, 43). However, area 18 of the cat operates directly on the geniculate input, whereas signals to MT have to relay through V1.

Functional significance

According to Skavenski et al. (40), in the monkey retinal images drift over the retina during fixation of a target at an average speed of 0.1°/s. Hence cells responding well to the lowest speed tested in our study are very likely to be activated during the fixation of stationary objects. Therefore, velocity low-pass cells, dominating in V1 and V2 subserving central vision, are likely to be involved in the analysis of stationary objects during fixation. Our observation, that with increasing eccentricity, cells in V1 respond less to slow movements, suggests that cells in V1 subserving peripheral vision will be less active during fixation of stationary objects than cells in V1 subserving central vision. This may explain why peripheral vision is less sensitive to stationary objects than central vision during fixation. Since on average cells in V1 subserving peripheral vision have a response to slow movement of only 68% (Fig. 5), these cells will respond better to a moving object than to a stationary object drifting over the retina during fixation. This is consistent with a better detection of moving objects than of stationary objects in peripheral vision but need not imply a superiority of peripheral vision in the processing of movements as claimed by Exner (11). Indeed recent psychophysical experiments (35, 41) have disproved the latter claim.

One of the major changes in velocity sensitivity with increasing eccentricity is the increase in velocity upper cutoff. Neurons subserving peripheral vision are responsive to faster movements than those subserving central vision. A similar trend was present in all three cortical areas (17, 18, 19) of the cat for which velocity sensitivity was studied quantitatively (9, 33). This seems therefore to be a basic property of the visual field representation at the cortical level and in this respect is similar to the increase in RF dimensions with eccentricity. This property of neuronal visual field representations fits well with the distribution of velocity vectors over the visual field for an observer moving through the environment. As shown by Gibson (14), the optical flow field generated by such a movement consists of very small velocity vectors (low speeds) in the center of the visual field and increasingly larger velocity vectors (fast speeds) as distance from the fixation point increases.

The low upper cutoff velocity of V1 cells subserving foveal vision, which are the cells with high spatial resolution (3), may explain why in human vision, acuity falls off sharply once velocity increases above 2–3°/s (45). Since velocity low-pass cells respond about equally well to speeds of the order of magnitude of slow drifts during fixation (0.1°/s) as to slightly faster speeds (1–2°/s), it is no wonder that grating acuity is equally sharp for a stationary grating as for a slowly drifting grating.

The observation that V1 cells lose their direction selectivity at low speeds is in agreement with human psychophysical experiments (35) showing that discrimination of opposite directions of motion fails at low speeds and that this lower speed limit increases with increasing eccentricity. Using slits of slightly lower con-
than those used in the present experiment Orban et al. (35) found that subjects failed to discriminate opposite directions of motion at 1 to 2°/s at 0° eccentricity and at 4 to 6°/s at 20° eccentricity. The change with eccentricity by a factor of four is close to the change observed in the present experiments, since cells in the central V1 sample lost their direction selectivity at 0.21°/s and cells in the peripheral V1 sample at 0.79°/s. This suggests that discrimination deteriorates simply because of the loss in direction selectivity of the neurons in V1. In addition, our results suggest that the lower speed at which direction selectivity fails is related more to RF width than to magnification factor. Indeed, the factor of four by which the lower speed limit for direction selectivity changes is clearly smaller than the factor by which cortical magnification drops with increasing eccentricity (>10 between eccentricity 1 and 20°, Van Essen et al. [44]), but is relatively similar to change in RF width with eccentricity (a factor of 3).

These close correlations between physiological properties and psychophysical results clearly demonstrate that quantitative study of visual cortical cell properties can reveal the neuronal mechanisms that underly higher mental functions such as visual perception.

ACKNOWLEDGMENTS

We are grateful to Noelle Boyer, Guido Vanparrijs, and Gerrit Meulemans for technical assistance as well as to Michèle Rouvière and Yolande Celis for the expert typing.

This study was supported by Ministère de la Recherche et Technologie Grant No. 83.C.0907. G. A. Orban was partially supported by Institut National de la Santé et de la Recherche Médicale. (C.A.09401).

Received 2 October 1985; accepted in final form 14 March 1986.

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