Neurons in the Ventral Intraparietal Area of Awake Macaque Monkey Closely Resemble Neurons in the Dorsal Part of the Medial Superior Temporal Area in Their Responses to Optic Flow Patterns

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SUMMARY AND CONCLUSIONS

1. Neurons in the ventral intraparietal area (VIP) are known to respond to translating random dot patterns. Such responses can be explained on the basis of the input of the middle temporal area (MT) to this area. Anatomic evidence has shown that VIP receives input from the dorsal part of the medial superior temporal area (MSTd) also. Neurons in the latter area are thought to be involved in egomotion because they are sensitive to first-order optic flow components such as divergence and rotation. Because of their MT and MSTd input, neurons in VIP may be expected to show sensitivity to such first-order optic flow as well.

2. The question of whether VIP neurons are selective to translation and/or first-order optic flow was investigated quantitatively in two awake monkeys by recording the responses of 52 visually responsive units and by fitting their tuning curves. The responses after presentation of random dot patterns exhibiting either expansion, contraction, clockwise rotation, or counterclockwise rotation were compared with the responses to translation stimuli tested in eight directions.

3. Most VIP neurons showed clear direction-selective responses, particularly to expansion but sometimes also to a combination of components (spiral stimuli).

4. A typical feature of VIP neurons is that their responses to these optic flow components remain when different parts of the receptive field are stimulated separately ("scale invariance"). For the most responsive subfield the response was on average 93% of the whole field response. For all subfields the mean response was on average 64% of the whole field response.

5. To test whether the scale invariance arose from convergence of translation-sensitive subfields with radial or circular direction preferences ("mosaic hypothesis"), the direction selectivity for translating stimuli was tested over these subfields. Basically the direction selectivity for translation was unchanged in the various subfields, thereby excluding the direction mosaic hypothesis.

6. It is concluded that the receptive field characteristics of VIP neurons are very similar to those of MSTd neurons.

INTRODUCTION

When an observer moves through a scene or when an object moves relative to an observer, much information can be derived from the time-varying projection on the retina. This information can be used to extract the movement of the observer and the motion and shape of objects in the surround. Thus the information derived from optic flow fields has a dual functional role. 1) It informs an observer about self motion. 2) It informs an observer about the layout of the visual world.

In monkey extrastriate cortex, several areas are suspected to be important for the analysis of optic flow. Most attention has focused on the dorsal part of the medial superior temporal area (area MSTd) (Duffy and Wurtz 1991a,b; Graziano et al. 1994; Lagae et al. 1994; Orban et al. 1992; Saito et al. 1986; Tanaka and Saito 1989; Tanaka et al. 1986, 1989), which receives input from the middle temporal area (MT). MSTd is the first visual area with neurons tuned to first-order basic optic flow components such as those defined by Koenderink and van Doorn (1975), namely curl (rotation; clockwise or counterclockwise), div (divergence; expansion or contraction), and def (deformation; in horizontal or vertical direction). Originally it was thought that neurons in MSTd could selectively respond to only one of these components, or could perform a decomposition (Saito et al. 1986; Tanaka et al. 1989). However, more recent studies have shown that most neurons in area MSTd are sensitive to several components (Duffy and Wurtz 1991a; Lagae et al. 1994) or to linear combinations of these components (such as spiral stimuli that are based on a combination of divergence and rotation) (Graziano et al. 1990, 1994; Orban et al. 1992).

In contrast, neurons in MT are mainly responsive to translating stimuli in a direction-selective manner (Albright 1984; Maunsell and van Essen 1983b). MT neurons can also respond to more complex optic flow fields than translation, but only when these flow fields contain translation components presented over the receptive field (RF) (Lagae et al. 1994). In further contrast to MST, MT generally lacks “position invariance” for direction selectivity to first-order optic flow components.

Anatomic studies (Baizer et al. 1991; Boussaoud et al. 1990) have shown that MSTd projects into several areas of the parietal cortex, including area 7a, the superior temporal polysensory area within the superior temporal sulcus, and the ventral intraparietal area (VIP). Area 7a was found to contain neurons with “opponent vector” sensitivity, well suited to detect expanding or contracting flow fields (Steinmetz et al. 1987). A similar RF organization was found in the superior temporal polysensory area (Bruce et al. 1986; Hikosaka et al. 1988). In contrast, relatively little is known about the third projection area, VIP. VIP receives input both from MT (Blatt et al. 1990; Maunsell and van Essen 1983a; Ungerleider and Desimone 1986) and from MSTd (Baizer et al. 1991; Boussaoud et al. 1990).

Previous physiological studies (summarized by Colby et al. 1993; Duhamel et al. 1991) have shown that VIP neurons are mostly direction selective and respond well to whole field translating motion of random dot patterns. On average, they prefer higher speeds and are more broadly tuned for...
velocity than MT neurons (Colby et al. 1993). So far, however, translating stimuli have mostly been used to study VIP. Also, there have been no systematic studies to explore how VIP neurons react to more complex optic flow patterns as tested by others in MSTd. The input from MT and MSTd suggests that neurons in this area might respond to first-order optic flow components. Moreover, one might expect VIP neurons to exhibit scale invariance, as found in MSTd. If so, it would be interesting to explore the mechanisms of such invariance, and to compare the results with those obtained in MSTd. For MSTd, one of the models suggested is the vector field hypothesis. It is based on the ideas of Koch et al. (1982) regarding dendritic processing and it states that sensitivity to first-order optic flow components is a distributed property and could rely on dendritic compartments receiving convergent MT input of neurons with a different direction selectivity (Saito et al. 1986). Alternatively, the direction mosaic hypothesis relies on a “patchwork of planar directional subfields arranged to yield large-field aggregate selectivity for planar, circular or radial motion” (Duffy and Wurtz 1991b).

The present study addresses the questions of how optic flow responses of MT and MSTd neurons are represented and transformed in VIP neurons of awake monkeys, and which RF structure underlies these responses.

METHODS

The responses of VIP neurons were recorded from two awake male monkeys (Macaca mulatta) both weighing ~6 kg.

Preparation

Surgery was performed under general anesthesia. Ketamine (50 mg mixed with 0.25 mg atropine sulfate; intramuscular injection) was used for the initial anesthesia. Halothane with a mixture of N2O and 32% O2 was applied during the rest of the surgery. During the first operation a skull cap was installed with the use of titanium bone screws and dental cement (Resin Kaltpolymerisat, Paladur). This cap, which contained four bolts embedded in the cement, allowed for rigid fixation of the monkey’s head during experiments. In a subsequent operation, a polished copper ring, plated with gold, was implanted on the monkey’s right eye for the recording of eye movements (Judge et al. 1980). The monkeys were then trained to perform accurately on a fixating task, with the use of water as a reward. After training was completed, a trephine hole of 16 mm diam was made during a third operation. A stainless steel chamber was mounted on the skull over the parietal cortex. A second chamber was placed on one of the animals to enable recording from the second hemisphere.

Stimuli

For quantitative tests, stimuli were generated by a graphics workstation (HP-9000/4335-TVRX-T1) at a 60-Hz frame rate. The awake monkey was sitting in front of a 2 x 2.5 m translucent screen, situated at a distance of 46.0 cm. The viewing area of the monkey was 117 x 113°. This viewing area was larger than the one used in most other studies on MSTd and VIP. Nevertheless, the viewing area still did not completely coincide with the complete physiological viewing range of the monkey. Thus it could be that a few of the most peripheral RFs were not stimulated over the entire RF. For the majority of neurons, however, the viewing area was adequate to allow stimulation over the full extent of the RF. All stimuli were calculated on-line and projected on the screen by a Barco graphics 400 video projector. Experiments were conducted under scotopic background conditions (0.05 cd/m²). The stimuli were green (phosphor p53) and had a luminance of 0.5 cd/m². The software allowed for stimulation with optic flow patterns (up to 2nd order) in any position within the viewing window. For translation stimuli, all dots moved in the same direction (8 directions used). For divergence stimuli, all dots moved toward the center (contraction) or away from it (expansion). For rotation stimuli, all dots moved clockwise or counterclockwise at the same distance from the center. The spiral stimuli were constructed with combinations (2 x 2) of the divergence and rotation stimuli, so that all dots moved around clockwise or counterclockwise, and at the same time moved away or toward the center.

The stimulus normally consisted of 40 dots, except for a few experiments in which the effects of masking was studied (masking parts of the stimulus area). To keep the ratio of stimulated over nonstimulated areas constant, the size of the dots depended on the size of the stimulated area when all 40 dots were shown. Some preliminary experiments (7 neurons) showed that dot size and density were relatively unimportant for the neurons in VIP. This relative unimportance of the dot size is similar to MSTd, where Tanaka and Saito (1989) showed that changes in these parameters were of little importance in determining the response levels. Because of these initial trials, an arbitrary dot size of 4.7° was chosen when the stimulus was projected on the complete screen (117 x 113°). With 40 dots, this results in a density factor (fraction of area covered with dots) of 0.21. Because there were relatively few dots, it was felt that such large dots were sometimes needed to activate the neurons optimally. For a smaller stimulus area, for example 12 x 11°, the diameter of the dots was 0.5°. At the lower end the size of the dots was limited by the pixel size (0.1° diam). In the summation test, when only a part of the stimulus was shown, the stimulus was not scaled down to the visible stimulus area. In this test, the stimuli over the subsections had the properties (speed, dot size, etc.) of the complete, unmasked stimulus.

The standard lifetime of each dot was 332 ms (except for some preliminary experiments in which it was 133 ms). For six neurons, we tested the influence of the dot lifetime qualitatively. On the basis of these tests a value of 20 frames (332 ms) was chosen for all the subsequent experiments. Shorter lifetimes resulted in a reduced response for some neurons. Longer lifetimes induced a stronger density cue and were therefore less desirable. In each stimulus, the mean dot speed was constant (66.7 or 100°/s). Although these speeds were relatively high, they were found to elicit strong responses in VIP. For translation, dot speed was the same everywhere. For the first-order flow fields, it varied from zero in the center to twice the mean dot speed at the border of the stimulus. Note that these speeds are fast relative to the speeds used to study other visual areas. Most studies in MSTd used an average speed of 40°/s (Duffy and Wurtz 1991a, 1995; Tanaka and Saito 1989). Colby et al. (1993) reported a distribution of preferred speeds ranging from 10 to 320°/s for VIP. They reported that the degree of speed tuning was on average twice as broad as reported for area MT. Optimum speeds reported for MT ranged from 2 to 256°/s (Maunsell and van Essen 1983b), from 5 to 150°/s (Rodman and Albright 1987), and from 2 to 90°/s (Lagae et al. 1994).

A red dot (0.64° diam) was used as a fixation point. The fixation dot could be made to move in a circle to test whether the neuron was involved in smooth pursuit.

Experimental paradigm

Before the experiment (18 h) the monkey was deprived of water. During the experiment the calibration of eye position was tested at regular intervals. For this purpose, the monkey had to make saccadic eye movements to nine different positions which it then had to fixate (with the use of a red fixation dot) for a duration of 3 s. After correct fixation the monkey was rewarded with water. During the quantitative trials, the monkey was rewarded for correct
fixation within an electronic window (4 × 4°). This window was kept relatively large to keep the monkey cooperating. Trials with poor fixation could be eliminated at a later stage. Saccade-related activity was evaluated by recording the neural activity during simultaneous eye movements in the rest periods. At the end of each session the monkey could drink at libitum.

After the isolation of a single unit, the responses of the neuron and the location of the RF were first tested qualitatively with a hand-held projector. With this projector, a light bar or a random dot pattern could be shown, and the neurons could be tested for their sensitivity to translation, rotation, and divergence. This generally allowed us to roughly determine both the optimal type of stimulation and the size and location of the RF. For quantitative testing, the stimuli were generated by the HP stimulus computer while the monkey fixated. Trials lasted mostly for 15 s. During these fixation periods, first the background activity was sampled for 1 s. Second, one to five stimuli were shown. The pause between subsequent stimulus presentations was 1.5 s. The different fixation periods were separated by 5-10 s.

If the response showed signs of adaptation, the fixation periods were shortened. Only one stimulus was then shown for each fixation period (lasting 3 s) and pauses of 10 s were used. During quantitative testing, the stimuli were first used to determine the location of the RF. The on-line construction of the optic flow patterns allowed for a flexible optimization of the stimuli for each neuron. By repeating the same stimulus at slightly different locations and with different sizes, a good determination of the optimal location and size of the RF could be made. After the definition of the RF, the responses to translation in eight different directions were tested. Subsequently the neurons were tested for rotation, divergence, and combinations of these two (spirals). All stimuli were shown in pseudorandom order during the fixation periods. All types of stimuli within an experiment were given with equal frequencies. The number of repetitions for each experiment ranged from 6 to 15, but occasionally up to 40 trials were sampled. The number of repetitions was based on the on-line buildup of the response histograms for every stimulus. All neurons were tested binocularly.

Recording

Recording sessions were usually conducted twice a week. Typically, about two neurons could be studied in detail during one session. During the experimental sessions the recording chamber was filled with 0.9% NaCl to prevent cortical pulsations and thus ensure stable recordings. Neurons were recorded with home-made glass-coated tungsten electrodes (0.6-1.5 MΩ at 1 kHz). When more than one unit was recorded simultaneously, the action potentials were discriminated routinely with the use of two level detectors. If there was still doubt about the spike separation, a custom-made spike analyzer was used as described elsewhere (Epping 1985). When multunit recordings were made, only the most reliably separated unit was chosen for further analysis.

With a gold-plated copper ring in the eye (see above), a signal related to the eye position was obtained with the use of the double magnetic induction method (modified search coil technique) (Bour et al. 1984). Eye movements were recorded at 100 Hz. In addition to the eye position signal, we recorded the time of occurrence of action potentials, the reward, the vertical retrace of the video signal, and the blue line of the video output. The vertical retrace corresponded to the exact onset of every frame in the stimulus. The blue line made it possible to align the onset and offset of the stimulus with the neuronal responses and the eye movements. In Fig. 1 the onset and offset of the stimulus are shown as vertical lines. All data (eye position signals, action potentials, video timing signals, reward timing) were collected by a special purpose hardware interface composed of several 12-bit analog-to-digital converters and timers (time resolution 10 μs).

Off-line analysis

All trials during which the fixation was insufficient were rejected. In most of the rejected trials, the monkey presumably fixated one of the moving dots or was not fixating at the onset of the random dot stimulus. The selected responses to the repeated stimuli were averaged and peristimulus time histograms were constructed. An example of an averaged response of a VIP neuron responding to expansion is shown in Fig. 1. There was a clear phasic on response followed by a tonic discharge. Latency was typically ~80-100 ms.

Several response characteristics were calculated from this histogram. The amplitude of the responses was evaluated by measuring the maximum firing rate (highest spike count in a single bin) and the average firing rate (AFR). The calculation was performed for the period between the onset and offset markers. Both measures gave comparable results, but in the present paper all data are represented as AFR because many neurons showed both a phasic and a tonic response and maximum firing rate does not represent tonic components well. The latency of the responses was based on a comparison between the response and the background activity in the 500-ms period before the onset of stimulation. The point at which the response first crossed a level corresponding to 4 times the SD of the background activity was taken as the latency.

To determine the optimal direction and the tuning width (TW) of the neurons for translation, eight different directions were tested. The responses were plotted in a polar plot and then fitted (Levenberg-Marquardt nonlinear regression; Press et al. 1992). A simple cosine profile [response \( R(\phi) = b + k \cos(\phi - \phi_0) \), where \( b, k, \) and \( \phi_0 \) are the fit parameters] could not be used for sharply tuned neurons. Thus in this paper a Batschelet distribution (Batschelet 1981) was used. For further details see RESULTS.

Histology and reconstruction

At the end of the series of recording experiments the first monkey was killed with an overdose of pentobarbital sodium. Formaldehyde 10% was used to perfuse the brain, which was later put in a sucrose solution. Serial sections of 40 μm were made in the coronal plane to allow tract reconstruction. Alternating sections were treated with cresyl violet for cell body staining and with the Giemsa method for myelin staining.

Reconstruction of the tracts was based on multiple electrolytic microlesions as illustrated in Fig. 2. These lesions were made at the end of experiments in both hemispheres 1 wk before perfusion. The second monkey is still involved in experiments. The electrode coordinates were similar to the ones used for the first monkey. Moreover, the physiological characteristics (visual and somatosensory responsiveness) were the same for this second monkey; thus
the eight neurons from this third hemisphere could be classified as belonging to VIP.

RESULTS

This paper is based on a group of 52 neurons that could be measured long enough to obtain quantitative tests with several types of translation (33 neurons) and/or first-order optic flow (41 neurons) stimuli and could be fitted by a Batschelet curve. A total of 101 neurons gave significant responses to a moving light bar or a random dot flow field. They are a subset of a group of 161 qualitatively identified neurons in the intraparietal cortex. Table 1 provides an overview. These neurons could be classified on the basis of histology as belonging to either the lateral intraparietal area (LIP) or VIP. The LIP sample consisted of a total of six neurons that responded only in relation to saccades. All were located anterior to the main sample, at depths between 3.5 and 12.2 mm. The remaining neurons belonged to VIP. The main emphasis of the present investigation was on visual responses. Nevertheless, it was often possible to investigate the responses to other modalities as well. A total of 16 VIP neurons responded to smooth pursuit eye movements. We did not test systematically for somatosensory responses. Nevertheless, two neurons were found that responded only during tongue protrusion but were not visually driven. Their responses correlated with the monkey’s drinking liquid reward. Another neuron was only responsive when the monkey’s face was touched. The three identified somatosensory neurons (found in 2 hemispheres) were all within the posterior region of our sample, at a depth of 4–5 mm. Of the remaining neurons, there were three that were only responsive to the onset of the presentation of a fixation dot. These neurons resembled MTf MT) neurons with very small RFs as described by others (Komatsu and Wurtz 1988; Newsome et al. 1988). Another four neurons were responsive only to the onset of the presentation of a large dot pattern.

Evaluation of direction tuning

The responses of the quantitatively measured VIP neurons were plotted in polar plots and then fitted (Levenberg-Marquardt nonlinear regression; Press et al. 1992). The definition of the fitted Batschelet profile (Fig. 3) is response $R(\phi) = b \exp[k \cos(\phi - \phi_0) + \nu \sin(\phi - \phi_0)]$. Here $b$, $k$, $\nu$, and $\phi_0$ are the fit parameters and $\phi$ is the direction of the flow in polar coordinates. This function can be regarded as a generalization of the Gaussian to circular statistics. The tuning direction ($\phi_0$), the TW, and the fitted maximum response [FMR = $R(\phi_0)$] are a more convenient set of parameters to describe the fitted curve. TW $\{T W^2 = \int_0^{2\pi} \cos(2\phi)R(\phi)d\phi]^2 + \int_0^{2\pi} \sin(2\phi)R(\phi)d\phi]^2$ represents the broadness of the tuning curve in the same manner as the sigma represents the width of a Gaussian. Because the tuning direction was measured in relatively crude steps (45°), the use of this fitting procedure improved considerably the estimate of the preferred direction and the broadness of tuning.

To calculate the significance of our fit, we used the $F$ test (Judd and McClelland 1989). This test compares the reduction in variance brought about by our model (the Batschelet distribution) with the average reduction expected from a random set of numbers. We can think of this numerator $F$ as the average proportional reduction in error per parameter added divided by the average proportional reduction in error that could be obtained by adding all the remaining parameters. For the Batschelet distribution to be significantly better than the mean response model (this means no tuning), we want the average error reduction for the parameters added to be greater than the average error reduction we could get by adding the remains of the possible parameters. Thus, if $F \sim 1$, we are doing no better than we could expect on average. So a value of $F$ near 1 suggests there is no tuning in the response. Furthermore, we calculated the significance of the fit ($p$).

Table 1. Overview of neurons

<table>
<thead>
<tr>
<th>Area</th>
<th>$n$</th>
<th>Responses To</th>
</tr>
</thead>
<tbody>
<tr>
<td>LIP</td>
<td>6</td>
<td>Saccades</td>
</tr>
<tr>
<td>VIP</td>
<td>11</td>
<td>Smooth pursuit only</td>
</tr>
<tr>
<td>VIP</td>
<td>3</td>
<td>Somatosensory</td>
</tr>
<tr>
<td>VIP</td>
<td>4</td>
<td>on response only</td>
</tr>
<tr>
<td>VIP</td>
<td>3</td>
<td>Small slit (resemble foveal MT)</td>
</tr>
<tr>
<td>VIP</td>
<td>33</td>
<td>Unclassified</td>
</tr>
<tr>
<td>VIP</td>
<td>4</td>
<td>Smooth pursuit and moving light bar/dot pattern;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>no quantitative fit of tuning curves</td>
</tr>
<tr>
<td>VIP</td>
<td>1</td>
<td>Smooth pursuit and moving light bar/dot pattern;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>quantitative fit of tuning curves</td>
</tr>
<tr>
<td>VIP</td>
<td>45</td>
<td>Moving light bar/dot pattern; no quantitative fit</td>
</tr>
<tr>
<td></td>
<td></td>
<td>of tuning curves</td>
</tr>
<tr>
<td>VIP</td>
<td>51</td>
<td>Moving light bar/dot pattern; quantitative fit</td>
</tr>
<tr>
<td></td>
<td></td>
<td>of tuning curves</td>
</tr>
</tbody>
</table>

Total 161

$n$, number of neurons. LIP, lateral intraparietal area; VIP, ventral intraparietal area; MT, middle temporal area.

FIG. 2. Section in the coronal plane (9.1 mm anterior) with tract reconstruction guided by 4 lesions (circles). Three lesions were positioned inside VIP. One lesion was made well outside VIP to get a good direction estimate of the direction of the tracts. VIP is indicated by the dotted area, as based on our integrated estimate with the use of both physiological and histological data from the present and previous studies. LIP, lateral intraparietal area.
The criterion used for direction selectivity was based on the fit with the Batschelet distribution. All fits with $F > 1.5$ were accepted as following the Batschelet distribution and being direction selective. Note that if the fit parameter $k$ would not be significantly different from 0, the tuning curve could be simplified to $R(\phi) = b$. $F$ would approach 1, because the parameters $\nu$ and $\phi_0$ would not contribute much to improve the fit. Fitting a tuning curve is a stronger criterion for direction selectivity than the test based on the direction index calculated from the responses in the preferred and nonpreferred direction (Rodman and Albright 1987). Our criterion rejected neurons where the direction index was $>2$ if the tuning was very noisy. This criterion is optimal when more than two directions are tested, because it takes all data points into account and not just the two nearest to the preferred and nonpreferred directions. For the fitted parameters ($b$, $k$, $\nu$, and $\phi_0$) we also calculated their SD. For $\phi_0$, this SD indicates how precisely the tuning is measured. Note that this measure is not the same as $F$, which states how well the data follow the Batschelet distribution.

Quantitative testing

Generally speaking, the quantitative analysis mostly complemented the qualitative analysis. However, for neurons with large RFs, the size of the RF was almost invariably larger in the quantitative test (computer) than in the estimate based on the qualitative stimulation (hand-held projector).

In the group of quantitatively tested neurons, significant tuning plots (as illustrated in Fig. 3) were obtained for 33 neurons tested for responses to translation in eight directions (Fig. 4A and B) and for 41 neurons tested for responses to first-order optic flow components (Fig. 4C and D).

For the group of 33 neurons tested for translation, all data could be represented well by a Batschelet curve. They showed a clear tuning in one direction (mean $F$ of 17). In Fig. 4 these neurons are represented by asterisks.

Among the group of 41 neurons tested for responses to first-order optic flow and fitted by a tuning curve, a total of 7 (open circles) were tested with four “directions” (expansion, contraction, clockwise rotation, and anticlockwise rotation), whereas the remaining 34 neurons (asterisks) were also tested with a mixture of these components (4 “spiral” directions). Of the seven neurons tested in four optic flow directions only, all could be fitted well by a cosine profile but not by a Batschelet profile. Another six neurons, excluded from this sample, yielded a fit with $F < 1.5$ and showed no direction selectivity. Fitting these neurons with a cosine profile (more sensitive to a broad tuning) confirmed this result.

Note that directions of 0, 90, 180, and 270° in Fig. 4, C and D, refer to preference for contraction, clockwise rotation, expansion, and anticlockwise rotation, respectively. In addition, most of these “divergence” neurons showed more reliable responses to expanding stimuli than to translating ones (the distance from the center is the inverse of the SD of the responses, compare Fig. 4, A and C). This illustrates that these neurons are more specialized for expansion than for translation. On the other hand, such specialization often was not very pronounced, because the TW for first-order optic flow was broad for most neurons (Fig. 4D). The data point belonging to the neuron illustrated in Fig. 3 is indicated by a separate arrow.

A total of 22 neurons was tested both with translation and first-order optic flow stimuli. In Fig. 5 the responses to these two types of stimuli are compared. There was no correlation between direction preference (translation) and preference for first-order optic flow (Fig. 5A). When TW was compared (Fig. 5B) it was evident that most neurons showed a broad tuning for both types of stimulation.
Divergence neurons

In our sample there were no true single-component neurons. However, there was a clear bias toward sensitivity for expansion. To illustrate the RF characteristics of this group of expansion-sensitive neurons (20 neurons with the largest responses for expansion when tested with 1st-order optic flow patterns), we describe two in detail. One of these neurons was a typical pursuit neuron; the other had no oculomotor-related activity.

The first example (neuron J7.5; Fig. 6) responded during smooth pursuit to the lower right of a small target in darkness. When tested during fixation, the neuron responded to moving random dot stimuli presented over the whole visual field. As found for other neurons in the divergence group, the neuron had a large RF (64 × 62°).

When tested with translating random dots over the whole field, the neuron responded optimally to movement to the right (Fig. 6A). Stimulation with expanding optic flow patterns yielded responses as well, but there was no response related to rotating or contracting flow fields. Thus this neuron would fit into the category of double-component planoradial neurons as described by Duffy and Wurtz (1991a). However, some combinations of divergence and rotation (spiral stimuli) (Graziano et al. 1990, 1994) evoked responses as well (Fig. 6B).

Responses to stimulation of RF subsections

To test the fine structure of the RF, the effective area of stimulation was subdivided into nine sections and the same translating stimulus was shown over each subsection. The result of this test is shown in Fig. 7A. It can be seen in Fig. 7A that each of the nine subsections of the RF still responded when stimulated in isolation. However, the responses were smaller than for whole field stimulation. This was confirmed for all 24 neurons tested in this manner. As was usually found, the RF was most sensitive in the central region. The RF was least sensitive in the upper contralateral corner (left corner in Fig. 7). Of all translation-responsive neurons, a total of 24 neurons was tested in the way illustrated in Fig. 7A. In all cases it was found that the smaller translation stimuli were effective in driving the neurons. For some subregions the responses were relatively small. This could indicate that such stimuli covered only part of the RF under such circumstances. There is indeed no reason to assume that the size of the RF fitted exactly the rectangular form of our stimulus area (see also Lagae et al. 1994 for MSTd).

We also tested the scale invariance for the preferred stimulus for other optic flow patterns such as divergence and rotation. To test scale invariance for divergence, the expansion pattern used in Fig. 6 was scaled down and presented over nine subregions of the RF (Fig. 7B). Responses were
found in six of the nine subregions; sensitivity was highest for the middle row.

A total of 27 neurons was tested with this type of test illustrated in Fig. 7B. In all cases the response to the preferred stimulus over the whole RF was not significantly different from the response to the preferred stimulus scaled down to the subregions. This is illustrated in Fig. 8A, in which the ratio of best subsection response over whole field response is plotted. Note that the mean ratio (0.93) was only slightly <1, indicating that overall the best subsection response was barely inferior to the whole field response. However, if all subfields are taken into account the situation is different. In Fig. 8B the mean ratio for all the subfields versus whole fields tested is shown (for each neuron a mean ratio was calculated on the basis of all subfields). The mean ratio for the whole population was 0.64, which was substantially lower than the mean ratio for the best responses (compare Fig. 8, A and B). Note that if the nine subfields were equal and if the whole RF had a homogeneous structure, both histograms would have looked the same.

**Test of direction mosaic hypothesis**

From the direction mosaic hypothesis one would expect that testing a divergence responsive neuron with smaller...
translation stimuli over parts of the RF would result in a tuning curve with the direction of translation following the flow in the divergence. For example, testing the right upper corner of the RF of an expansion-sensitive neuron with translation in various directions would yield larger responses for translation in the direction of the right upper corner than for other directions. For the VIP neuron, such as shown in Fig. 9, this was clearly not the case.

Most tuning curves in Fig. 9 for the smaller translation stimuli had the same direction preference as for translation over the whole RF (preference for movement to the right). This result is in conflict with the mosaic hypothesis. In total, five neurons were tested completely with this time-consuming method of small translating stimuli in a $3 \times 3$ grid, moving in eight different directions. In none of these neurons was there evidence of a radial arrangement of subfields.

A second approach to investigation of the RF organization consisted in masking parts of the RF (see also Duysens et al. 1985). This method was especially attractive for neurons with weak tuning for direction of translation (neurons inappropriate for exploring the variations in direction selectivity in subfields of the RF). An example of such a neuron is given in Fig. 10. This neuron was sensitive to first-order optic flow components but with no eye-movement-related responses.

The neuron shown in Fig. 10 responded vigorously to various types of moving stimuli such as a light bar or noise patterns. When full field translating dot fields were used, the neuron lacked a strong tuning for direction (Figs. 3A and 10A). When tested with rotating and diverging patterns over the full field, the neuron showed a distinct preference for expansion (Fig. 10B). Some spiral stimuli, constructed by a combination of rotation and expansion, were also quite effective. Contracting stimuli failed to yield either facilitatory or suppressive responses (in our sample, we actually encountered only 1 neuron that showed inhibition when stimulated with the nonpreferred first-order optic flow stimulus). Before the masking test was started, the neuron was first tested for scale invariance and for optimum stimulus size.

To test for scale invariance, the same neuron was presented with a scaled-down expansion stimulus over nine subsections of the RF. As seen in Fig. 11A, most of the subfields yielded responses to (scaled-down) expanding flow fields. Note that significant responses to expansion were obtained in eight of the nine sectors investigated. The presence of responses to expanding stimuli, shown in various divisions of the full field, excludes the possibility that the sensitivity to divergence of the whole field was generated through accidental activation of a small translation-sensitive subfield, as was observed in MT neurons ("elementary optic flow component sensitivity induced from a translation-selective RF"; Lagae et al. 1994). Furthermore, tests such as illustrated in Fig. 11 showed that the RFs were not homogeneous, as was also observed by others for MSTd neurons (Duffy and Wurtz 1991b; Lagae et al. 1994).

By testing several subfield sizes, it was found that optimal responses were obtained for stimulation over the right bottom
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The poor performance of the fitting algorithm for the neuron showed a significant bidirectional translation response, as indicated by the solid tuning curves. Preferred direction could be calculated for subfields of the RF (Fig. 11), where the outer circle represents a response of 80 Hz. This low response level (also relative to average) explains the poor performance of the fitting algorithm for some sections of the RF. For the area around the fixation point (right, middle) the neuron showed a significant bidirectional translation response.

After the most effective area for stimulation was carefully determined (both qualitatively and quantitatively: see Figs. 10 and 11), a series of tests with masking was performed. The aim of these tests was to investigate how important spatial summation was for these neurons and whether central and peripheral parts of the RF were equally effective. To explore these questions, only a part of the stimulus was shown (thus, in this case, the stimulus was not scaled down but there was simply a reduction in stimulated area).

To investigate the neuron illustrated in Figs. 10 and 11, the full expansion pattern was subdivided either into four (Fig. 12B) or nine sections (Fig. 12C), which were presented separately. As seen in Fig. 12C, the neurons kept responding even when only small subsections of the RF were stimulated. Furthermore, there was no indication that the periphery was more powerful than the center for VIP neurons that are sensitive to divergence.

Spiral neurons

To investigate whether there are VIP neurons with special sensitivity to combinations of rotation and divergence (spiral stimuli), a subset of neurons was presented with this type of stimuli. In the present study the spiral stimuli were optimal for 9 of the 34 neurons tested with eight conditions (see above). An example of such a spiral neuron in VIP is shown in Fig. 13.

Note that for this example, as for the other neurons in the spiral group (neurons for which the spiral stimuli yielded maximum responses), the selectivity for spiral stimuli was not very strict. All the neurons in this group showed sizable responses to other optic flow components as well.

DISCUSSION

In primate parietal cortex, VIP, located in the fundus of the intraparietal sulcus, has been shown to contain neurons that are well suited to the integration of information about self motion from several sources, including somatosensory and visual input. Neurons in this region respond to tactile or visual stimuli, potentially corresponding to objects moving toward the animal (Colby et al. 1993). In the present study, the somatosensory input to this area was confirmed. In addition it was found that, in agreement with previous studies (Colby et al. 1993; Duhamel et al. 1991), there is no saccade-related activity in VIP neurons. However, some neurons respond during smooth pursuit in darkness.

A primary new result of the present study is the finding that neurons in VIP respond well to first-order optic flow components, especially expansion. This finding fits well with preliminary communications of other groups on VIP of monkey (Graf et al. 1995) and humans (Kennedy et al. 1995). To be effective, the self motion component in the optic flow has to be linked to information from refer-
VIP resembles MSTd for optic flow

A: position scale test of expansion responses of VIP neuron D3.1. The stimuli were shown in a 3 X 3 grid of 38 X 34° each (inset at bottom right). A complete expanding flow field was shown for each of the 9 locations tested, as indicated by the dashed crosses in the bottom right corner. Size of the stimulated area is indicated by the dashed square in the top left corner. Radius of the solid circle corresponds to the response level. Dashed line represents the mean background activity during 0.5 s before stimulus onset. Error bars: SD.

B: responses of VIP neuron D3.1 to diverging and rotating stimuli presented over lower right corner of the screen as indicated by the crossed area. Field size: 72 X 64°. The fitted values for the divergence/rotation Batschelet distribution are $\phi_0 = -179.7 \pm 8.3°$, $FMR = 65.4 \pm 7.3$ Hz, and $TW = 61.2 \pm 5.5°$, where $F = 9.4$ and $P = 0.049$.

ence copies and proprioceptive input (vestibular, muscle spindles, etc.), and this could well be the role of VIP. Neurons in MT project both to MSTd and VIP and are sensitive mainly to translating stimuli, to which they respond in a direction-selective manner (Albright 1984; Maunsell and van Essen 1983b). Nevertheless, MT neurons can respond to optic flow fields more complex than translation, but only when these flow fields contain translation components presented over the RF (Lagae et al. 1994). In contrast to VIP or MSTd neurons, those in MT do not respond to presentations of optic flow components over subsections of the RF (Lagae et al. 1994). The responses of many VIP neurons to optic flow stimuli are therefore most similar to those observed by others in MSTd. This could be due either to a similar type of internal processing of incoming MT input in both areas or alternatively to transmission of MSTd input to VIP. In view of this question it is essential to first compare the optic flow responses in the latter two areas in more detail.

Fig. 11. A: position scale test of expansion responses of VIP neuron D3.1. The stimuli were shown in a 3 X 3 grid of 38 X 34° each (inset at bottom right). A complete expanding flow field was shown for each of the 9 locations tested, as indicated by the dashed crosses in the bottom right corner. Size of the stimulated area is indicated by the dashed square in the top left corner. Radius of the solid circle corresponds to the response level. Dashed line represents the mean background activity during 0.5 s before stimulus onset. Error bars: SD. B: responses of VIP neuron D3.1 to diverging and rotating stimuli presented over lower right corner of the screen as indicated by the crossed area. Field size: 72 X 64°. The fitted values for the divergence/rotation Batschelet distribution are $\phi_0 = -179.7 \pm 8.3°$, $FMR = 65.4 \pm 7.3$ Hz, and $TW = 61.2 \pm 5.5°$, where $F = 9.4$ and $P = 0.049$.

Similarities and differences between MSTd and VIP

Both VIP and MSTd neurons have mostly large RFs, and both respond well when presented with expanding or rotating dot patterns over their RF (Duffy and Wurtz 1995; Komatsu and Wurtz 1988; Tanaka et al. 1986).

Second, VIP shows a predominance of responses to expansion. This is similar to related studies indicating a general preference of MSTd neurons for divergence (Andersen et al. 1993; Duffy and Wurtz 1995; Lagae et al. 1994; Tanaka and Saito 1989). Third, both MSTd and VIP neurons show “scale invariance” for the direction selectivity to first-order optic flow components. Neurons in MSTd keep responding when an optimal stimulus, such as rotation or divergence, is scaled down and presented over a smaller section of the RF (Andersen et al. 1993; Duffy and Wurtz 1991b; Graziano et al. 1994). This feature is considered to be specific for MSTd neurons (Lagae et al. 1994).

Fourth, both in MSTd (Tanaka and Saito 1989) and VIP (this study) it is sufficient to show only a small subsection.

Fig. 12. Effect of masking on responses of VIP neuron D3.1 to expansion presented in the lower right field. For the data shown in B and C, only sections of the stimulus were shown. Size of each section is indicated by the dashed squares in the top left corners of B and C (masking experiment). The responses are plotted in the center of the area where the stimulus is shown. Note that 1 section in B overlaps 4 sections in C. The stimulus size for the largest complete nonmasked stimulus (A) was 72 X 64°; the smallest area tested was 24 X 21° (C). For this masking experiment the responses were 1st tested over the same sensitive region of the RF as used for Fig. 11B. This subfield proved to elicit much higher responses than stimulation of the whole field (compare the responses to expansion in Fig. 10B).
of an expanding optic flow pattern to activate radial-sensitive neurons. Fifth, combinations of divergence and rotation (spiral stimuli) are effective both in VIP (present work) and in MSTd (Graziano et al. 1990, 1994). Sixth, both in MSTd and in VIP the responses of the neurons to first-order optic flow patterns are quite resistant to variations in speed and size of the dots in random dot patterns (Duffy and Wurtz 1991a; Tanaka and Saito 1989). Seventh, both in VIP (Colby et al. 1993; Duhamel et al. 1991; this study) and in MSTd (Dursteler and Wurtz 1988; Newsome et al. 1988) there are neurons that respond to smooth pursuit eye movements even in darkness.

Apart from the somatosensory input, a main difference between MSTd and VIP lies in the absence of single-component neurons in VIP. In MSTd a small proportion of the neurons is only activated by a single first-order optic flow component. Duffy and Wurtz (1995) termed these neurons planar, radial, and circular neurons, and found that they represented 8, 8, and 2% of the population, respectively. In contrast, the neurons in VIP were sensitive to several first-order optic flow components. Additionally, they could always be driven by translating stimuli. One should keep in mind, however, that the present sample of neurons was more of an expanding optic flow pattern to activate radial-sensitive neurons. For the latter neurons it is easier to find a stimulus that is purely opposite to the optimal one and thus completely suppressive. In contrast, for multiple-component neurons, a stimulus in the nonpreferred direction is likely to contain components that facilitate rather than suppress the neural response.

A third difference between VIP and MSTd concerns the observation that the periphery of the RF has a special significance for MSTd, whereas this is less so for VIP. For example, one of the most interesting results of Tanaka and Saito (1989) was that the response to expanding patterns persisted even if only a peripheral annulus of the pattern was shown (their Fig. 3). Masking the central part had surprisingly little effect, whereas masking the periphery made the responses disappear. In our experiments there is no equivalent to the center being masked in isolation. However, by showing only the center of the stimulus and not periphery, an experiment was performed that closely mimics the center-without-annulus experiment of Tanaka and Saito (1989). In VIP such an experiment does not lead to the response being abolished. However, it remains to be seen whether this reflects a genuine difference between these areas or whether this is due to a difference in potency of the stimuli used in the two laboratories.

Overall, the similarities between VIP and MSTd are much more striking than the differences. This is especially true with respect to scale invariance.

Scale invariance

Position invariance is a neuron's consistent selectivity to a stimulus regardless of where the stimulus falls in the neuron's RF (Graziano et al. 1994). The general method to test neurons for position invariance is to show the optimal and nonoptimal stimulus over subfields of the RF. In MSTd the number of subfields tested varied considerably between the different studies \( [N = 4 \text{ (Saito et al. 1986); } N = 2-3 \text{ (Duffy and Wurtz 1991b); } N = 25 \text{ (Lagae et al. 1994); } N = 5 \text{ (Graziano et al. 1994)}] \). Although scale invariance is but one aspect of position invariance, it is of interest to compare the relevant data in VIP and MSTd.

In the present study it was shown that scaled-down versions of the optimal stimulus presented over nine subsections of the field was surprisingly effective in activating VIP neu-
rons. Our data show that when only 11.1% of the original stimulus area was stimulated, the response was on average ~64% of that of whole field stimulation (93% for the best subfield).

Position invariance is considered to be specific for MSTd neurons and is not seen in MT neurons (Lagae et al. 1994). For MSTd, it was recently pointed out by Duffy and Wurtz (1995) that this invariance was relative rather than absolute. For example, when the same divergence pattern is presented over different parts of the RF, there are usually positions where the responses are distinctly larger. Thus a sensitivity profile can be constructed (see Lagae et al. 1994), which explains the finding of Duffy and Wurtz (1995) that neurons with radial sensitivity have a graded preference for centers of motion.

The present study reveals that other factors may contribute as well. The presentation of a small peripheral section of an expanding pattern is sufficient to elicit a maximum response. From this it can be understood why expansion-sensitive neurons appear so robust with respect to displacement of the center of expansion (Graziano et al. 1994). From the present data, it is evident that neurons of this type can react even if the focus of expansion is outside the most sensitive area of the RF. However, this does not mean that these neurons are not able to code for the focus of expansion (see also Lagae et al. 1994).

Mechanisms underlying sensitivity to first-order optic flow in VIP

According to the classification of Duffy and Wurtz (1991b), there are basically two types of hypotheses to explain sensitivity for radial and circular motion: the direction mosaic hypothesis and the vector field hypothesis. The direction mosaic hypothesis assumes that the RF consists of a patchwork of subfields that are sensitive to planar motion and that vary in preferred direction depending on the type of neuron. For radial "expansion" neurons, all subfields have a preferred direction pointing outward from the center of the field. For spiral neurons, the preferred directions should be arranged in a spiral etc. In the present study, this hypothesis was tested directly by presenting local translations in various directions over the subfields of the RF of VIP neurons. It was found that none of the neurons had subfields arranged as predicted by the direction mosaic hypothesis. Instead, all neurons kept the same direction selectivity for translation irrespective of the position of the subfield in the larger RF. The present data are better accommodated by what Duffy and Wurtz (1991b) termed the vector field hypothesis, which is basically similar to the compartment model proposed by Saito et al. (1986). In these and related models (Zang et al. 1993) the local detection of rotation or divergence is achieved by projections of the appropriate afferents onto single branches of neurons.

A special case is the sensitivity to spiral stimuli. In MSTd there is an ongoing debate about the presence of neurons with special sensitivity to spiral stimuli. In contrast to pure radial neurons, which show a decrease in response when expanding patterns are mixed with rotation (Orban et al. 1992), spiral neurons are preferentially activated by spiral motions, which combine both expansion/contraction and rotation components. Graziano et al. (1990, 1994) found many examples of this type in MSTd, whereas others found them very rarely (Lagae et al. 1994). For some VIP neurons a spiral pattern constitutes the optimal stimulus. Nevertheless it would not be appropriate to label these neurons as "single-component" spiral neurons because they clearly are responsive to other optic flow components as well.

Functional considerations

Two hypotheses have been proposed with respect to the functional role of partial neurons in the analysis of optic flow. According to the "navigational" hypothesis, the responsiveness to optic flow patterns makes these neurons well suited for visual guidance during egomotion (Roy and Wurtz 1990; Saito et al. 1986). The large size of RFs and the predominance of expansion neurons (forward locomotion is more common than backward) are in favor of the suggestion that neurons in MSTd and in VIP can help in navigation during self motion. However, as was pointed out by Graziano et al. (1990, 1994), there are several discrepancies within this hypothesis. For example, although some MSTd neurons respond to full field stimuli, their RFs are not always large and sometimes are ~10° across. In agreement with Graziano et al. (1990, 1994), the present data on area VIP indicate that neurons with such apparently "small" RFs are able to respond to full field stimuli as well, but their response improved when the most sensitive part of the RF was stimulated selectively. Similarly, Duffy and Wurtz (1991b) found their MSTd neurons to be responsive to 100 × 100° stimuli, irrespective of their RF size.

Thus those and the present data of area VIP can also be viewed as supporting the "motion pattern" hypothesis, which states that MSTd neurons are involved in the analysis of motion of individual objects (Sakata et al. 1985, 1986). Actually, in many cases there is a combination of local and global motion. In the real world, every approaching object contains local texture features that also exhibit expansion. Therefore the detection of local expansion by VIP neurons can contribute to the detection of more global expansion, covering the whole RF. We conclude that the response to full field stimulation in VIP neurons clearly indicates that such neurons could contribute to a global (egomotion) analysis of the surround. However, stimuli shown over small portions of the RF (Figs. 10 and 11) elicit sometimes even higher responses than the stimuli shown over the whole RF. This suggests that some VIP neurons may play a dual role: detection of egomotion as well as object motion in three-dimensional space.

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