Exp Brain Res (2002) 147:520–528
DOI 10.1007/s00221-002-1268-5

RESEARCH ARTICLE

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Responses of neurons in area VIP to self-induced and external visual motion

Received: 15 November 2001 / Accepted: 30 August 2002 / Published online: 26 October 2002

Abstract Single-unit recordings were obtained from directionally tuned neurons in area VIP (ventral intraparietal) in two rhesus monkeys under conditions of external (*passive*) and self-induced (*active*) visual motion. A large majority of neurons showed significant differences in directional tuning for passive and active visual motion with regard to preferred direction and tuning width. The differences in preferred directions are homogeneously distributed between similar and opposite. Generally, VIP neurons are more broadly tuned to passive than to active visual motion. This is most striking for the group of cells with widely different preferred directions in active and passive conditions. Response amplitudes to passive and active visual motion are not different in general, but are slightly smaller for passive visual motion if the preferred directions differ widely. We conclude that VIP neurons can distinguish between passive and active visual motion.

Keywords Parietal cortex · Awake monkey · Optic flow · Direction selectivity · Smooth pursuit

Introduction

Visual motion provides us with key information about the location and movement of objects in our surroundings. We use information from visual motion to navigate through our environment. In many situations, however, the visual motion pattern is ambiguous. For example, rightward image motion on the retina can be elicited by an object moving towards our right side, or by leftward eye or head movements. Several studies have convincingly demonstrated that the visual system uses extraretinal signals to determine the source of the motion in the visual field (Royden et al. 1992; Warren and Hannon 1988). To accomplish this task, we have to postulate the existence of neurons that can distinguish between self-motion and object motion in visual areas, which receive both visual and extraretinal inputs. The latter input then modulates the neuronal responses to visual motion when eye or head movements are involved. In fact, Erickson and Thier (1991) have found that most neurons in cortical area MSTd and many from area MSTl of macaque monkeys preferentially respond to externally induced visual motion, whereas up to area MT neurons make no distinction between visual motion due to object motion and self-induced visual motion. MSTd cells were also shown to be able to compensate, at least partly, for a shift in the location of the focus of expansion caused by pursuit eye movements (Bradley et al. 1996; Page and Duffy 1999) and head rotations (Shenoy et al. 1999) while viewing expanding patterns, simulating forward motion of the observer.

Neurons from area MT and MST both project to the ventral intraparietal area (VIP) (Maunsell and van Essen 1983; Ungerleider and Desimone 1986; Boussaoud et al. 1990). VIP neurons respond during pursuit eye movements (Colby et al. 1993; Schaafsma and Duysens 1996), and are thought to be involved in the brain's representation of near-personal space (Colby and Duhamel 1996; Duhamel et al. 1997, 1998). Especially in near-personal space, it is essential to distinguish between self-induced and externally induced visual motion because the time until action needs to be taken can be very short. It is not known, however, whether VIP neurons can actually make this distinction. In this study, we examined the responses of visually responsive VIP neurons to visual motion caused by a moving random-dot stimulus (the passive

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condition) or by smooth pursuit eye movements across a stationary random-dot stimulus (the active condition). Our results show that many VIP neurons discriminate between the two conditions, suggesting that VIP is involved in the computations underlying the distinction between visual motion caused by movement of the observer or of his surroundings.

Methods

The responses of 110 VIP neurons were recorded in three hemispheres in two awake male monkeys (*Macaca mulatta*) weighing between 6 and 8 kg.

Preparation

Surgery was done on the monkeys under general anesthesia; 50 mg ketamine and 0.25 mg atropine were used for initial anesthesia, while inhalation of Ethrane (enflurane) with a mixture of N_2O and O_2 was applied during surgery. During a first operation, a gold-plated polished copper ring was implanted on the monkey's right eye (needed for eye position recording). In a subsequent operation, a head-holding device was implanted, consisting of three bolts embedded in a skullcap made of dental cement placed around titanium bone screws. Then, monkeys were trained to do simple fixation and saccade tasks. A pursuit task was added at a later stage. When the monkeys were sufficiently trained to perform accurately the fixation and saccade tasks, in a third operation a trephine hole of 16-mm diameter was made and a stainless steel recording chamber was mounted on the skull over the parietal cortex at stereotactic coordinates 16.2 L, 3.3 P. During the experimental sessions, the recording chamber was filled with a saline solution to prevent cortical pulsations and to ensure stable recordings.

Recording sessions usually occurred on 3 days of a week. From the day prior to the experiments the animals were deprived of water, but received their regular amount of water during their working session. The monkeys were rewarded for correct fixation of a stationary target or for smooth pursuit eye movements within an adjustable electronic window (usually 5°×5°; note that a stricter criterion was used for accepting or rejecting single trials for offline analysis) around the fixation spot. On the remaining days, water supply was not limited.

All experimental protocols were approved by the local animal experimentation authority and were carried out in accordance with the European Community Council Directive of 24 November 1986 (86/609/EEC).

Stimuli

Random-dot pattern stimuli were generated on a personal computer at a 60 Hz frame rate, and back-projected on a translucent tangent screen by a video projector (Barcodata 801). The awake monkey was sitting at a distance of 57 cm from the screen and its visual field extended 80°×80° in horizontal and vertical dimension. Each random-dot pattern contained 110 dots; each dot subtended 1.2° at 0.9 cd/m^2 against a background of 0.004 cd/m^2, with a standard lifetime of 167 ms. All stimuli were shown repeatedly (five to ten times) in random order.

Responses of VIP neurons to random-dot patterns were studied in two conditions (Fig. 1). In the *passive* condition, a stationary fixation target was switched on in the center of an otherwise dark screen and remained on throughout the trial. After 1 s, a random-dot pattern was displayed for 2 s, during which the dots were moving at a uniform speed of 16°/s. After the moving stimulus disappeared, the fixation dot was visible for another second. In the *active* condition, a stationary fixation target was switched on at a location

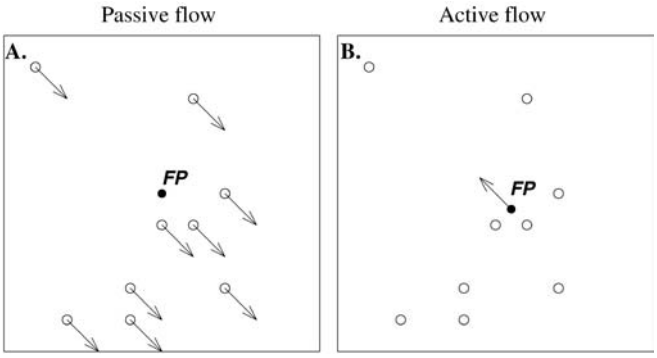


Fig. 1A, B The two experimental conditions. **A** Translation of random-dot pattern in one of eight possible directions with stationary fixation point *FP* (passive visual motion). **B** Fixation point *FP* moves in one of eight directions while random-dot pattern remains stationary (active visual motion)

16° eccentric of the center of the screen, and this target remained on for 1 s. After that, a stationary random-dot pattern was shown for 2 s, while the fixation target moved at a constant speed of 16°/s across the center of the screen, ending at a position 16° eccentric of the screen center on the other side. Motion of either the dots or the fixation spot was in one of eight directions, separated by 45°. On the retina, these two conditions created nearly identical motion patterns. Imperfections in the tracking eye movements of the monkey, such as small catch-up saccades (typically 1° to 2°, 2–3 per trial), were accepted. The visual stimulus covered 80° horizontally by 80° vertically. To avoid ocular tracking of the moving random dots, no dots were used in a small area (5° on all sides) around the target spot in either condition.

Recording techniques

Before each experimental session, the stainless steel chamber was flushed with sterile saline, and then a *x-y* micropositioner and hydraulic microdrive (Frederick Haer and Co., Bowdoinham, ME, USA) were mounted on the chamber. The activity of single neurons was recorded with home-made glass-coated tungsten electrodes (0.6–1.5 MΩ). Individual action potentials were identified by custom-made spike analyzers or two level detectors. Horizontal and vertical eye positions were recorded at 100 Hz using the double magnetic induction method (modified search coil technique with a resolution of 0.1°; see Bour et al. 1984). The time of occurrence of action potentials (using a 1-μs internal clock) and the vertical retrace of the video signal was recorded. Stimulus onsets and offsets were synchronized with neuronal and eye position signals. All data were collected by a special-purpose hardware interface comprising several 12-bit analog-to-digital converters and timers (time resolution 10 μs). A more detailed description has been given elsewhere (Schaafsma and Duysens 1996).

Experimental procedure

After the isolation of a single unit, the responses of the neuron and the location of the receptive field were first tested qualitatively with a hand-held projector. Using this projector, a light bar or a random-dot pattern was shown to test neurons for their sensitivity to visual motion such as translation, rotation, expansion or contraction. This allowed a rough judgment of both the optimal type of stimulation and the size and location of the receptive field. Generally, VIP neurons had large receptive fields, and responded well (and were direction-selective) to translation, while some also responded selectively to rotation or expansion. Quantitative testing of neuronal responses to passive and active directional visual motion

was performed using computer-generated stimuli. All stimuli were shown in random order and the interval between consecutive trials was 1–1.5 s. All neurons were tested binocularly.

Offline analysis

For every trial, mean firing rates in the middle interval of 1500 ms during the 2-s visual stimulation were computed and used for further analysis. By using only this middle interval, any initial differences in retinal motion due to the lag in the onset of the eye movement are discarded. All trials with imprecise fixations or pursuit eye movements (eye position >2° off the fixation or tracking target) in the interval of 1500 ms were rejected. We also verified that differences between retinal slip due to pursuit and due to stimulus velocity were smaller than 2°/s during the analysis interval. Trials in which pursuit velocity (in the active condition) differed from stimulus velocity (in the passive condition) by more than 2°/s were excluded from further analysis.

A direction sensitivity curve was fitted to the mean firing rates obtained for all eight directions of retinal motion. A Gaussian function of the form

$$freq = A \cdot e^{-\frac{(\varphi-\varphi_{Opt})^2}{2\sigma^2}} + b$$

(see Britten and Newsome 1998) was used for the fitting procedure, where *freq* is the predicted response to visual motion in direction φ, A is the response amplitude, φ_{Opt} is the preferred movement direction and center of the tuning function, σ is the width of the Gaussian, and b is the baseline response for directions far from the preferred movement direction. Directions of visual stimulus motion were defined according to the mathematical convention (0° = rightward, 90° = upward).

Since all movement directions were tested 5–10 times for each cell in both conditions, this resulted in a set of 5–10 fitted values for the preferred direction in a single condition for each individual cell. Using Rayleigh's test for uniformity (Mardia 1972) to determine whether a cell had a consistent preferred movement direction in a given condition, and Watson's F-test for circular means (Watson and Williams 1956), we then tested whether a cell had significantly different preferred directions for passive and active visual motion using a significance level of 5% probability.

Histology and reconstructions

At the end of the series of recording experiments, the monkeys were anesthetized with an overdose of pentobarbital. Formaldehyde 10% was used to perfuse the brain, which was later put in a sucrose solution. Serial sections of 40 μm of the first monkey's brain were made in the coronal plane to allow tract reconstruction. Alternating sections were treated for cell body (cresyl violet) and for myelin staining. Location of the tracts was aided by multiple electrolytic microlesions made at the end of the experiments in both hemispheres during the last week prior to perfusion. Sections of 25 μm, with an interspacing of 75 μm, were made from the second monkey's brain. The histology of the two brains confirmed that the recording locations were situated in area VIP.

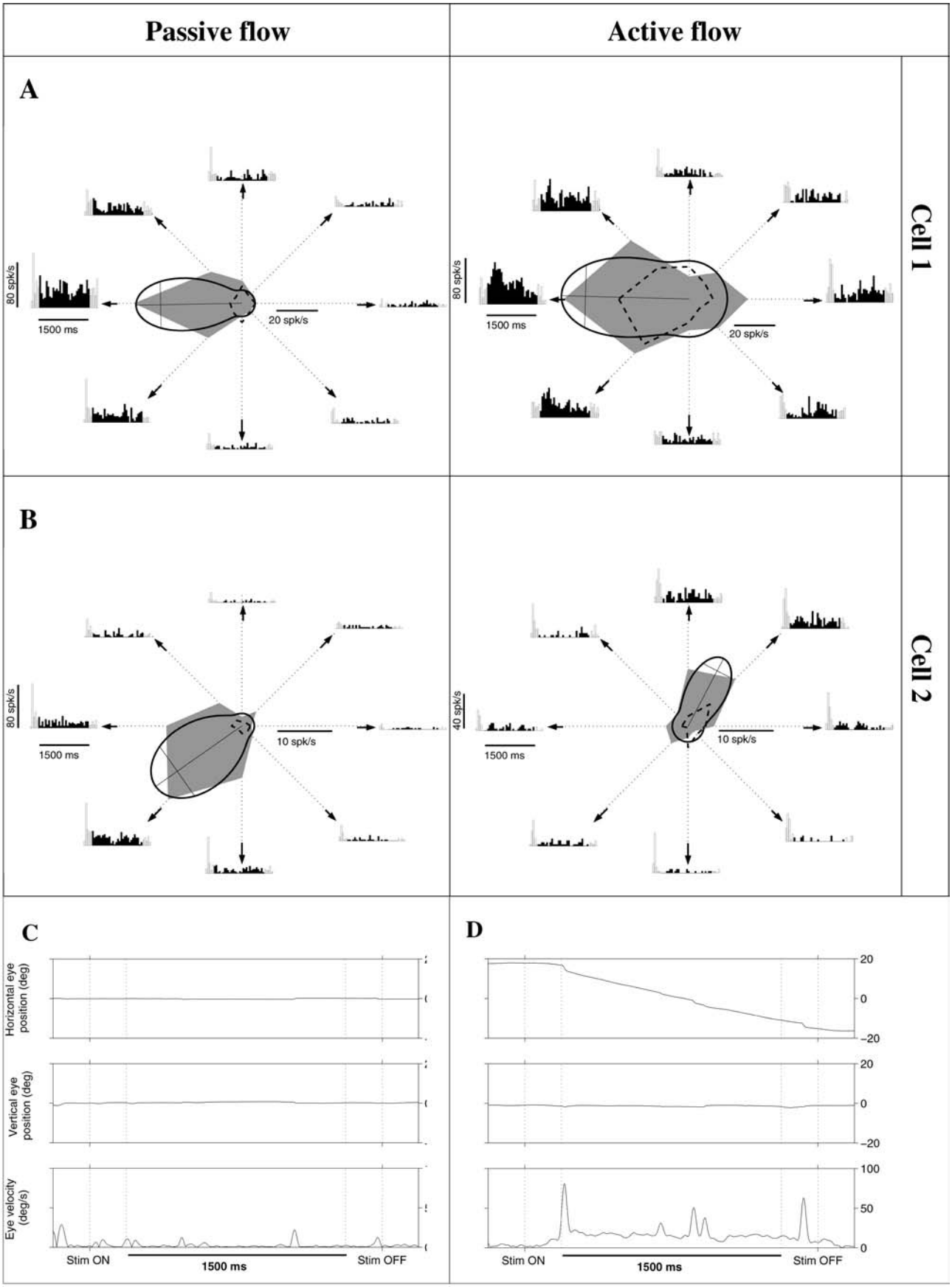
Results

Recordings were made from 110 neurons that were visually responsive to active and passive motion stimuli. Cells with responses exceeding their spontaneous firing rate by 2 SD for at least one stimulus condition were selected for further analysis (n=66). In the remaining cells, the slow motion of 16°/s needed for comparison of active and passive visual motion did not elicit a substantial response, and these cells are not considered in the present report.

Figure 2A shows a typical example of the responses of a directional VIP neuron with similar directional preferences in the passive (*left* panel) and active (*right* panel) conditions. This neuron responded best to passive or active visual motion to the left. For easier comparison, peri-stimulus time histograms (PSTHs) are plotted with respect to retinal motion, implying that the eye's rotation was in the opposite direction. Response differences in the passive and active condition at the very start of the stimulation periods are presumably due to the latency of pursuit eye movements in the active condition. In the latency period (typically about 200 ms), visual motion is caused by the fixation target moving in the direction opposite to the resulting motion pattern, eliciting a small transient response. In contrast, visual motion starts instantly in the passive condition, resulting in a transient response with the same preferred direction as the sustained response. However, in the time interval chosen for data analysis (bar under left PSTHs of Fig. 2A, excluding the first and last 250 ms of the 2-s stimulus period), the average visual motion on the retina is the same within 1°/s in the passive and active conditions. Figure 2B shows an example of a second type of neuron, one that responded to passive (*left* panel) and active (*right* panel) visual motion but with the respective preferred directions almost opposite each other. In Fig. 2C, D, typical eye position and eye velocity traces are shown to give an indication of the fixation and tracking performance of the monkey under the two conditions.

To determine the difference in the preferred directions during the two visual motion conditions, we computed tuning curves for each cell by fitting a Gaussian function to the average firing rates in the analysis interval for each condition (see Methods section for details). For example,

Fig. 2A–D Direction tuning during passive and active visual motion, with typical eye position and eye velocity traces. **A**, **B** Polar plots in the middle of each panel (*gray shaded area*) show average firing rates over 1500 ms of visual motion in eight directions, and average firing rate in the 250 ms preceding each stimulus (*thick dashed lines*). The best-fit Gaussian (*thick solid curve*), $freq = A \cdot e^{-\frac{(\varphi-\varphi_{Opt})^2}{2\sigma^2}} + b$ characterizes a neuron's directional tuning, specifying preferred direction of visual motion ϕ_{Opt} (*solid line* extending from the origin of polar plot) and tuning width σ (line depicting width of curve). The length of the line representing φ_{Opt} depicts response amplitude (A) plus baseline (b) firing rate. Peri-stimulus time histograms (PSTHs; binwidth 50 ms) are shown at the end of each direction-of-motion axis for the time interval between stimulus onset and stimulus offset. *Black bins* represent responses in the analysis interval. **A** Typical neuron with identical preferred directions during passive (*left* panel) and active (*right* panel) visual motion. **B** Neuron with significantly different preferred directions in the two conditions. **C, D** Sample eye position (*upper* two panels) and eye velocity (*lower* panels) give an indication how comparable the stimulation in the two conditions is. The *dark bar* underneath indicates the analysis interval. **C** Passive condition; **D** active condition. In this case, gain of the pursuit movement was 0.88. Typically, gain would be between 0.85 and 0.90


Passive flow
Active flow
A
Cell 1
80 spk/s
1500 ms
20 spk/s
80 spk/s
1500 ms
20 spk/s
B
Cell 2
80 spk/s
1500 ms
10 spk/s
40 spk/s
1500 ms
10 spk/s
C
Horizontal eye position (deg)
Vertical eye position (deg)
Eye velocity (deg/s)
Stim ON
1500 ms
Stim OFF
D
20
0
−20
20
0
−20
100
50
0
Stim ON
1500 ms
Stim OFF

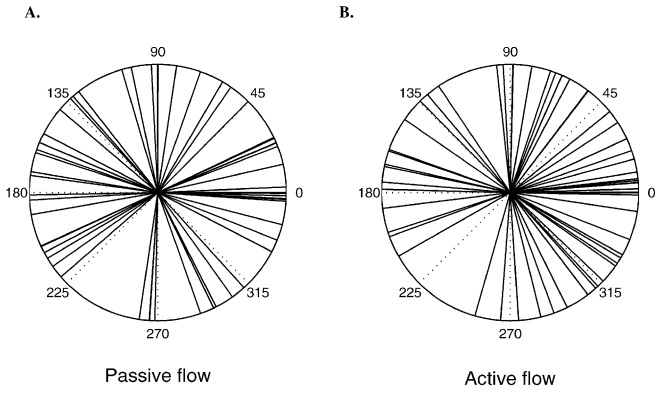


Fig. 3A,B Population distribution of preferred directions during passive (**A**) and active (**B**) visual motion. Data indicate no preference for any direction of visual motion in both conditions

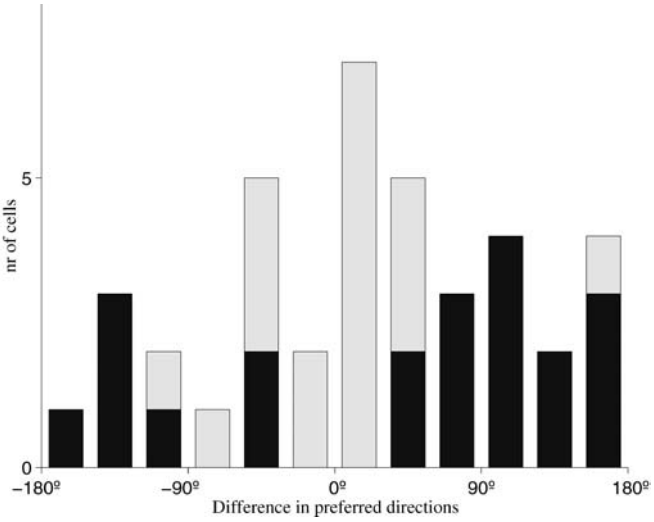


Fig. 4 Differences in mean preferred directions during passive and active visual motion for the population of VIP neurons with sufficient response in both conditions. A positive difference means that the mean preferred active direction is shifted clockwise relative to the mean preferred passive direction; a negative difference represents a counterclockwise shift of active motion relative to passive motion. *Dark bars* indicate statistically significant differences in mean preferred directions in the two conditions (Watson's *F*-test for circular means, confidence level 95%); *light bars* indicate statistically non-significant differences

the neuron shown in Fig. 2A yielded similar preferred directions in the two conditions, with a difference of only 1°, whereas the neuron illustrated in Fig. 2B had significantly different preferred directions (difference 146°).

The preferred visual motion directions of all neurons during passive (*left* panel) and active (*right* panel) visual motion are shown in Fig. 3. We applied a Rao spacing test for uniformity to test for a possible directional bias in the preferences of the two conditions (Batschelet 1981) but found no such bias in the preferred directions in either condition ($P>0.11$ and $P>0.54$ for passive and active conditions, respectively), indicating that there is no general preferred direction for the population of VIP cells in either the passive or active condition.

In a next step, we determined the differences in the preferred directions in the passive versus active visual motion condition for all cells yielding responses more than 2 SD above their spontaneous firing rate in both conditions (n=39, see Fig. 4). The population of cells showed the whole range of preferred movement directions from the same (0°) to opposite (±180°) directions during passive and active visual motion, as illustrated in the diagram of Fig. 4. Many neurons (21 of 39) showed preferred directions in the two conditions that were significantly different from each other (Watson's *F*-test, confidence level of 95%). For 14 of these cells, the preferred directions in the two conditions were more than 90° apart. For none of the cells that showed preferred directions less than 30° apart (9 of 39) was the difference statistically significant. A statistical analysis revealed that the differences in direction preferences of all cells did not deviate from a homogeneous distribution in the range between –180° and +180° (χ^2-test at a confidence level of 95%).

The difference between the preferred directions obtained in the passive and active visual motion conditions highlights only one aspect of direction selectivity, since it does not reflect other possible systematic changes in tuning properties of cells. For instance, a single cell may show a brisk, narrowly tuned response in one condition, and a smaller and more widely tuned response in the other condition; this is a difference that would be overlooked by looking at the preferred directions only. Therefore, we have examined mean firing rates and tuning widths for the population, to test whether there were any systematic changes in responses during the passive and active motion conditions.

Figure 5 shows the mean firing rates to the preferred motion direction during passive and active visual motion for each cell. The data points are scattered on both sides of the *dashed line* of Fig. 5, which indicates equal firing rates, with some clustering of *open dots* (depicting cells with widely different preferred directions; difference >90°) below the *dashed line*. To test for significant differences in mean firing rates in the two conditions, paired data from all cells in passive and active motion conditions were compared with respect to their mean firing rates. A Wilcoxon paired test yielded no significant difference for the population as a whole ($P>0.33$), but did reveal a significant difference for the group of cells with widely different preferred directions (difference >90°, $P<0.05$), showing a smaller response to passive than to active visual motion. Therefore, while a subpopulation of VIP cells responds more strongly to actively induced visual motion than to passively viewed visual motion, the population as a whole does not.

When comparing the tuning widths of the cells (Fig. 6) we found a striking difference. VIP cells are generally more broadly tuned for passive motion than for active motion. In Fig. 6, more data points are located above the *dashed line* (indicates equal tuning widths), especially in

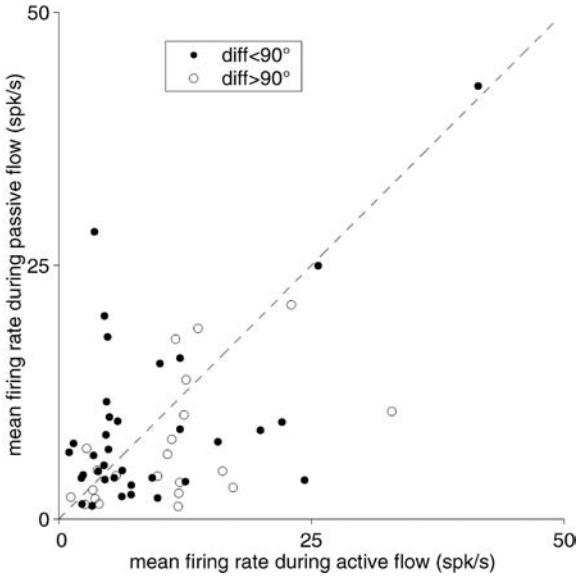


Fig. 5 Response rates for preferred directions of passive (*ordinate*) and active (*abscissa*) visual motion. Values obtained for neurons with preferred directions deviating by <90°and ≥90°. *Dashed line* indicates equal values of response rates for passive and active visual motion. Mean firing rates do not differ significantly in the two conditions

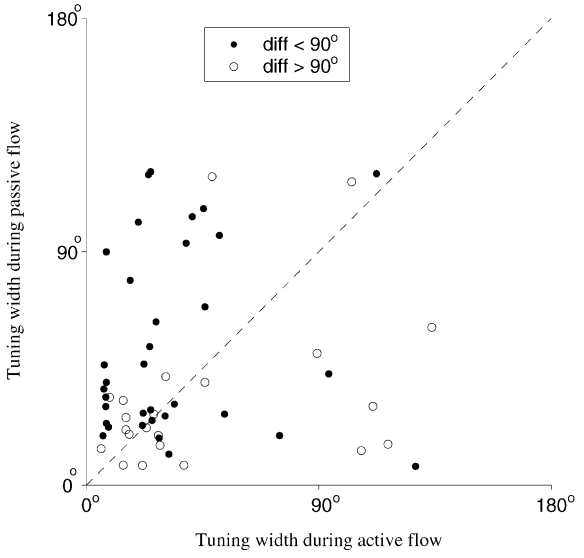


Fig. 6 Tuning widths for neuronal responses to passive (*ordinate*) and active (*abscissa*) visual motion. Symbols denote same cell groups as in Fig. 5. *Dashed line* indicates equal values of tuning widths during passive and active visual motion. Directional tuning is sharper during active visual motion for the entire population and for the subgroup with preferred directions deviating by <90°

the group of cells with a small difference in preferred directions (<90°, *solid dots*). A Wilcoxon paired test confirmed that there is a significant difference between the tuning widths in the active and passive conditions (P<0.01) for the entire population, with narrower tuning for active visual motion. This observation also held for the group of cells with preferred directions less than 90° apart (23 of 39 cells, P<0.001). However, for the cells with preferred directions more than 90° apart there was no significant difference in tuning widths for active and passive visual motion (P>0.60).

Since it is known that some cells in VIP discharge during pursuit eye movements (Colby et al. 1993), we tested a subset of the cells with responses in both the passive and the active conditions (20 of 39) with pursuit of the same target dot, but moving across a dark, unstructured background. For 5 of 20 cells, this elicited directionally selective activity, determined in the same analysis interval as that used for the passive and active conditions. The preferred directions for pursuit in the dark differed little from the preferred pursuit direction across a structured background (2° to 39°), while for these same cells the passive and active preferred directions differed by 36° to 169°. For none of the cells tested was the preferred retinal motion direction in the active condition (tracking across a structured background) the vectorial sum of the preferred direction in the passive condition and the opposite of the preferred pursuit direction. The described response differences in the passive and active conditions cannot, therefore, be ascribed to the addition of a smooth pursuit response to the visual motion response.

The speeds of the moving random-dot pattern in the passive condition and of the moving fixation target in the active condition were matched to ensure that the visual motion speed and direction on the retina were the same in both conditions. However, the two conditions differed in two other aspects: the eye's position in the orbit, and the position of the stimulated area on the retina. In the active condition, the eye rotates in the orbit, shifting the stimulated area across the retina, whereas it does not in the passive condition.

Stimulating only part of the receptive field of a particular VIP neuron can be expected to have a minor effect on its firing rate. At the beginning or end of the pursuit stimulus, which lasted 2 s, the maximum shift of stimulated retinal area would be 16°. This corresponded to a maximum shift of 12° at the beginning or end of the analysis interval, which excludes the initial and final 250 ms. Although VIP neurons generally have large receptive fields, this may still constitute a large shift of stimulated retinal area. However, for VIP neurons, reductions in stimulus size on the receptive field may be expected to have relatively small effects on their firing rate. In a previous study from this laboratory (Schaafsma and Duysens 1996), it was found in a sample of 27 VIP cells that a reduction in size to 11% of the total original surface reduced the peak response amplitude to 93% of the response to the total stimulus.

It is known that some VIP cells code for eye position (Bremmer et al. 1999). In our study, we chose the analysis interval such that the average eye position and the average stimulated area were as similar as possible in each condition. In 6 cells (of 66) we found a significant eye position effect, with different firing rates at the beginning and at the end of the trial in the active condition. The

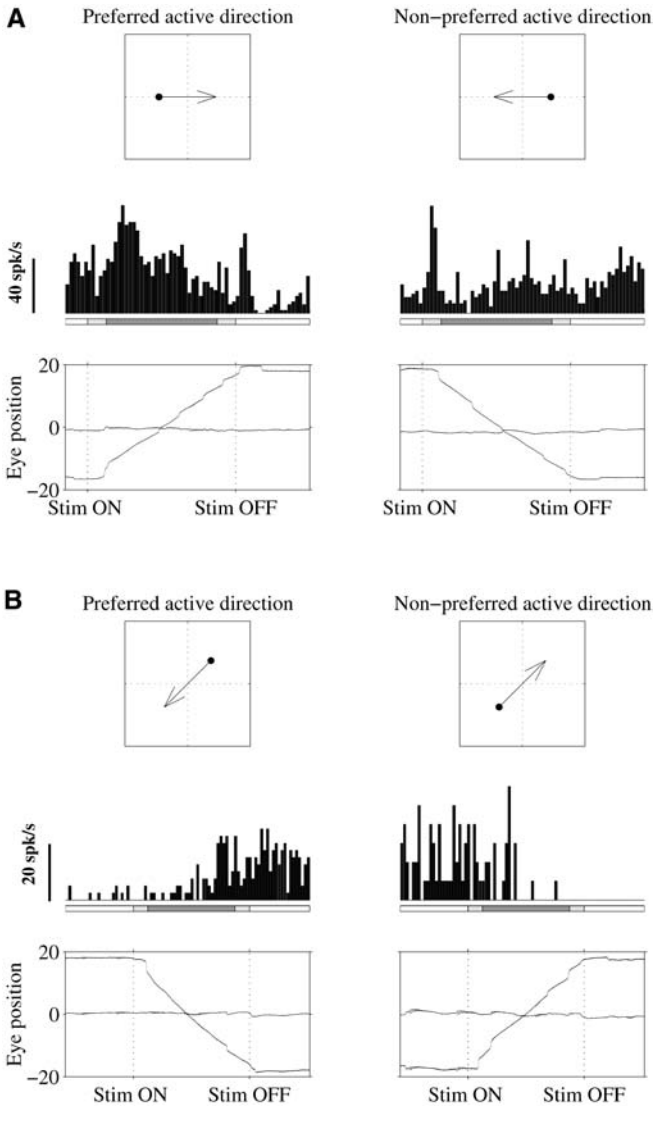


Fig. 7A,B Influence of eye position on the response in the active condition. **A**, **B** Eye movement causing the preferred and non-preferred directions of visual motion (*upper* panels), peri-stimulus time histograms (PSTHs) of the response in the active condition (binwidth 50 ms) (*middle* panels), and traces of eye position during one single trial (defracted into motion along preferred/non-preferred axis and perpendicular to that axis) (*lower* panels). The *bar* underneath the middle graph denotes the stimulus (*light gray*, from *Stim ON* to *Stim OFF*) and analysis intervals (*dark gray*). **A** Data from the same cell as in Fig. 2A; eye position effect visible in response during interval before and after stimulation, but relatively small when compared with response to visual motion. **B** Data from a cell with a strong eye position effect, driving most or all of the response during stimulation

average firing rates during fixation in an interval before stimulation (the 500 ms interval before stimulus onset) and in an interval after stimulation (the interval of 500–1000 ms after stimulus offset) were computed and compared (*t*-test; 95% confidence level). Figure 7 shows two examples of such cells. In the first case (Fig. 7A), representing the behavior of four of six cells, the firing rate is significantly different before and after stimulation, but the firing rate during the tracking response was significantly higher than before or after the tracking response. For these cells, the influence of the changing eye position on the firing rate during stimulation was relatively small. The differences in preferred direction in the active and passive conditions for all of these cells were not significant, indicating that any eye position-related effect on the firing rates can be excluded. In the other cases (Fig. 7B, illustrating the behavior of the other two cells), the firing rate in the analysis interval mainly followed the change in eye position. The measured response was compared with a predicted response that varied linearly with the eye position; a χ^2-test did not refute this at a confidence level of 95%. Since the two cells with this type of behavior could not be said to respond to the visual motion, they were excluded from the Wilcoxon tests on the response amplitudes and tuning widths, which were presented before (Figs. 5 and 6).

Discussion

The main results of this study are that the preferred movement directions of VIP cells can be different in active and passive visual motion conditions, and that tuning widths are larger for passive than for active visual motion. Differences in preferred movement directions in passive and active conditions range from 0° to ±180°. We did not find evidence that could reject the hypothesis of a homogeneous distribution of preferred directions.

There may be several reasons for the observation that a large fraction of the cells (21 of 39) prefer different directions in the active and passive conditions. An obvious suggestion to explain this observation might be that retinal slip due to the local motion of the fixation spot during imperfect smooth pursuit provides a directional cue opposite to the direction of the motion pattern. However, this explanation seems highly unlikely. Imperfect pursuit would cause differences in firing rate for opposite directions in the active and passive condition and cannot explain the orthogonal preferred directions in the active and passive condition. Since only a small number of cells had entirely opposite preferred directions for passive and active visual motion (5 of 39), this explanation does not account for the current results.

Another possible explanation would be that small catch-up saccades, which inevitably occurred in the pursuit condition, might account for the irregularities in the neuronal responses. Again, this seems unlikely. There is no evidence from previous studies (Colby et al. 1993; Schaafsma and Duysens 1996) that saccades elicit activity in VIP. In the present study there was no relationship between the occurrence of catch-up saccades and enhanced or suppressed neuronal firing.

A third possibility is that eye position plays a role in the observed differences. Bremmer et al (1999) found an effect of eye position in about half of the VIP neurons (40 of 74) by fitting a regression plane to the firing rates measured at nine different fixation locations. In our

experiments, we found an eye position effect in only 6 of 66 cells by comparing firing rates measured at two fixation locations: those at either end of the preferred active direction, as the eye position varied in the active but not in the passive condition. This low number of cells with an eye position effect may be due to the limited sample size and the less rigorous eye position analysis in the present study. The average eye position was the same for all movement directions in the active and passive conditions. Therefore, if the relationship between firing rate and eye position was linear, the mean firing rate related to eye position would be the same for all movement directions, which would rule out any effect of eye position on differences in preferred direction for the active and passive conditions. If the relationship between firing rate and eye position was nonlinear, or if the eye position related activity dropped to zero in the inner 12° of the oculomotor range, the mean firing rate in the active condition could depend on movement direction, which would cause a bias in mean firing rate. Such an effect could erroneously suggest a different preferred visual motion direction for the active condition. However, the eye position-related firing rate component of the six cells, which showed evidence for eye position effects on firing rate, was small and did not have any effect on preferred direction since these were not significantly different for the active and passive conditions.

As a fourth possibility, an oculomotor signal may provide the VIP cells with the information needed to distinguish between active and passive visual motion. The assumption that VIP neurons receive extraretinal input seems plausible for several reasons. As indirect evidence, areas MT and MST, both projecting to area VIP (Boussaoud et al. 1990), are known to receive extraretinal input (Dursteler et al. 1987; Komatsu and Wurtz 1988; Newsome et al. 1988). More direct support comes from studies showing that many VIP cells discharge during smooth pursuit eye movements (Colby et al. 1993; Schaafsma and Duysens 1996). For example, Colby et al. (1993) reported that 59% of VIP cells respond during smooth pursuit of a small target, and that the most frequent combinations of preferred directions for passive visual motion and pursuit were either similar or opposite. In our study, we found that 25% (5 of 20) of VIP neurons responded during pursuit in the dark, and that 59% (39 of 66) of visually responsive VIP neurons responded in the active condition, but we could not show that similar or opposite preferred directions occurred more frequently than other combinations. These differences may be due to limited samples in both studies (Colby et al. 1993 reported activity during pursuit of a small target in 10 of 17 cells; 5 of 20 cells showed pursuit-related activity in the present study).

The results of the present study on area VIP are different from the results in areas MSTl (Erickson and Thier 1991; Thier and Erickson 1992) and MSTd (Erickson and Thier 1991; Bradley et al. 1996; Page and Duffy 1999), which provide input to VIP. In the study on MSTl by Thier and Erickson (1992), which used mostly hand-held stimuli and some computer-controlled stimuli, the most frequent combinations of preferred directions for visual motion and pursuit eye movements were "similar" (19 of 22 cells) or "opposite" (2 of 22) directions. The large proportion of cells (19 of 22) with similar preferred directions in MSTl is different from the more or less homogeneous distribution of differences in preferred direction over the range from 0° to 360°.

Bradley et al. (1996) found that some cells in MSTd compensate fully or partially for pursuit eye movements, responding mainly to externally induced visual motion. This finding has recently been elaborated by Page and Duffy (1999), who showed that 85% of MSTd cells had a significant change in tuning properties for the focus of expansion during ocular pursuit compared to that in a stationary eye condition. None of these studies, however, examined the neurons' directional tuning by comparing them in passive and active conditions. In general, if cells are spatiocentric, that is if they respond only to visual motion after having accounted for pursuit eye movements without responding to the eye movement itself, they will be expected to respond less strongly and less sharply tuned to self-induced *active* visual motion than to external *passive* motion. On the other hand, if cells are not either fully spatiocentric or fully retinocentric, they may be expected to respond to externally induced visual motion in addition to responding to an oculomotor signal, giving rise to a less clear-cut combination of response-tuning properties. The brain would then have to use this complex information to come to a fully spatiocentric representation of space at a later stage, either in VIP itself or higher up in the brain. The present study seems to confirm the latter.

Conclusions

The present data demonstrate the existence of area VIP neurons capable of distinguishing between passive and active visual motion. The preferred directions for passive and active visual motion are significantly different for the majority of cells (21 of 39), and the tuning width is significantly narrower in active visual motion conditions than for passive visual motion conditions.

Acknowledgements We gratefully acknowledge the experimental and technical assistance provided by G. van Lingen, V. Langeveld, C. van der Lee, T. van Dreumel and H. Kleijnen. We also thank H. Arndts, M. Faassen, A. Peters and F. Philipsen for the animal care, and F. van der Werf for histology. This work was supported by the Foundation for Life Sciences and the Netherlands Organization for Scientific Research.

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