Neuronal Responses to Optic Flow in the Monkey Parietal Area PEc

Area PEc, a high order association area, is located in the dorso-caudal portion of the superior parietal cortex. PEc neurons encode visual motion signals, especially the direction of stimulus motion. The present study tested if PEc neurons also process visual correlates of self-motion. The extracellular activity of single neurons in response to optic flow stimuli was recorded in two monkeys (Macaca fascicularis) trained in a fixation task. The stimuli were produced by random dots simulating planar motion, radial expansion and radial contraction. A substantial number of PEc neurons were specifically activated by radial optic flow and were selective for the position of the focus of expansion with respect to the fovea. Eccentric positions of the focus of expansion were preferred. Almost all neurons showed opponent excitatory–inhibitory activity to expanding–contracting visual fields. Planar motion elicited very weak responses. Optic flow responsiveness is not entirely explained by classical bar sensitivity in PEc neurons, suggesting that optic flow and classical bar responses could serve different mechanisms in the integration of visuo-motor signals to prepare body movements.

Introduction

In the posterior parietal cortex, signals from different modalities arriving via visual, tactile, auditory, vestibular and proprioceptive inputs are combined to create an abstract representation of space that can be used to plan and control body movements [for a review, see (Andersen et al., 1997)]. Optic flow field patterns occur whenever an observer moves through the environment, and the position of their focus of expansion (FOE) is an important cue for heading perception (Gibson, 1950). Neurons in many areas of the posterior parietal cortex are known to respond to optic flow stimuli. Many studies have shown that the visual analysis of self-motion has the largest expression in the inferior parietal lobule, such as area 7a (Siegel and Read, 1997) and the ventral intraparietal area (VIP) (Schaafsmadby and Duysens, 1996) and in the medial superior temporal (MST) area (Tanaka and Saito, 1989; Duffy and Wurtz, 1991a,b; Orban et al., 1992). Heading perception is believed to take place in MST, because its neurons are selectively activated by the position of the FOE with respect to the fovea (Duffy and Wurtz, 1995).

The dorsal portion of the superior parietal lobule, named area 5 (Brodman, 1909) or area PE (von Bonin and Bailey, 1947), was recently subdivided into area PE and PEc (caudal portion of area PE) (Pandya and Seltzer, 1982). PE neurons showed activity related to tactile and other proprioceptive stimulation (Duffy and Burchfield, 1971; Sakata et al., 1973; Mountcastle et al., 1975). PEc neurons are activated by classical visual stimuli (Squatrito et al., 2001) and are involved in early coding of reaching arm movements (Ferraina et al., 2001). These activities can contribute to the perception of body orientation in extra-personal space. Area PEc receives via cortico-cortical connections, visual signals from area V6a (Shipp et al., 1998) and directly projects to the frontal premotor area F2 (Matelli et al., 1998). Area F2 is involved in planning reaching movements and is considered an important link between visual signals and motor acts [for a review, see (Wise et al., 1997)].

Since PEc visual neurons are able to encode the direction of stimulus movement (Squatrito et al., 2001), it seems possible that the visual analysis performed by PEc neurons contributes to the planning and control of reaching movements to visual targets. We were therefore interested in determining if heading information from visual cues might contribute to this control system. The present study aimed to test if PEc neurons encode optic flow stimuli, in order to verify whether this cortical area could take part in the fronto-parietal cortical network that plans and controls body movements in space. We found that PEc neurons are significantly activated by radial optic flow. They show selectivity for the position of the FOE with respect to the fovea and strong preference for eccentric positions of FOE.

These results have been previously presented in abstract form (Raffi et al., 1999).

Materials and Methods

Experiments were carried out on three hemispheres of two Java monkeys (Macaca fascicularis) weighing 3.8–5.0 kg. All experimental procedures were conducted according to the European Communities Council Directive for the use of animals in scientific research (86/609/EEC) and under strict control of the veterinary staff.

Surgery

A metal recording chamber (1.8 cm in inner diameter) was implanted on the skull midline under sterile conditions and deep thiopenthal anesthesia (15 mg/kg i.v.). The chamber center was placed at stereotaxic coordinates AP-14, left -3.5 in one animal and AP-14, left zero in the other. Analgesics were administered for several days after surgery. After complete recovery, the bone at the bottom of the chamber was removed, under deep anesthesia, in order to drive glass-coated eldgyo microelectrodes (Suzuki and Azuma, 1976) through the intact dura mater. Experimental sessions started 1 or 2 days afterwards.

Experimental Paradigm and Stimuli

The monkeys performed a reaction time task while fixating a red target, consisting of a square pattern formed by two luminous vertical bars (0.17° wide) separated by a dark gap (0.17° wide). The target was presented in the middle of a 19" computer monitor placed 28.5 cm from the eyes. At the onset of the target the monkeys had to push a lever and begin to fixate. A 1000 or 1500 ms baseline period followed target onset and then the visual stimulus was presented. Trial duration was random, and varied between 3000 and 6000 ms. The monkeys had to detect a change in target orientation within 400 ms. The monkeys received a drop of water as the reward for each correct trial. Eye position was always at the primary position and was monitored monocularly, with a resolution of 0.2°, by an optoelectronic system that uses the corneal reflection of an infrared light beam (Ibach et al., 1983).

Extracellular activity of single neurons was recorded, during daily experimental sessions, from both the dorsal and the medial surface of the superior parietal lobule. When a cell was isolated, its visual responsiveness was initially assessed, by moving a luminous bar (3 cd/m²) on a dark background, with different speeds, sizes and peripheral locations around
the screen, in order to outline the receptive field. After the mapping each neuron was tested with optic flow stimuli formed by 1000 randomly distributed luminous dots. Each dot subtended 0.06°, with a luminous intensity of 3 cd/m². The dots moved radially in order to simulate expanding and contracting fields. The apparent average speed was ~10°/s. The sensitivity to this type of stimulus was assessed by positioning the FOE usually in a 3 × 3 grid at 10° distance from each point. Occasionally, wider inter-point distances were tested. For each cell, the random dot background was also moved tangentially to the frontoparallel plane, in eight directions at 45° angular intervals. For the planar stimulus the speed was 15°/s. Each neuron was also tested by the luminous bar, moving in eight directions at 45° angular intervals in order to compare the directional selectivity to the bar stimulus with the selectivity to the optic flow and planar motion. Each stimulus was repeated at least eight times. The dimension of the receptive field of each cell was determined by the response duration along the preferred direction (Squatrito et al., 2001).

**Histology**
At the end of the recording sessions, some electrolytic microlesions were performed at specific sites, to be used as landmarks for subsequent electrode track reconstruction. At the end of all recording sessions, the animals were killed with an overdose of anesthetic and then perfused. Their brains were then sectioned for histology. Coronal sections were made and the cytoarchitecture of one section every 200 µm was examined after staining with toluidine blue. Electrode tracks and the locations of recorded units were then reconstructed with the help of the coordinates of each penetration and the electrolytic microlesions.

**Results**

**Anatomical Localization of the Recording Sites**
According to the anatomical reconstruction, the recording region was limited to the dorso-caudal surface of the superior parietal lobule (Fig. 1A), extending to the first 3–4 mm of the medial bank of the hemisphere. We assigned each electrode track to a histological section, in order to assess the recording site. Samples of this reconstruction are shown in Figure 1B. Area PEC was identified according to the cytoarchitectonic criteria of Pandya and Seltzer (Pandya and Seltzer, 1982). Borders between area PEC and the neighborhood areas PGm (medial part of area PG), MIP (medial intraparietal area) and V6a were determined on the basis of both the cytoarchitectonic criteria and the Paxinos atlas (Paxinos et al., 2000).

**Optic Flow Responses**
The present study reports 147 electrode penetrations in three hemispheres (two left and one right) in which we encountered 211 single units. In these penetrations 129 cells responded to the preliminary hand-guided testing with visual stimuli. Of these, 49 neurons that showed signs of responding to expanding and contracting visual fields were collected and analyzed quantitatively.

A one-way ANOVA across all optic flow and planar motion stimuli showed significant ($P < 0.05$) differences for 43 units. The six units, with $P > 0.05$ were not considered for subsequent analysis. To assess if PEC neurons can signal the spatial arrangement of the FOE, a one-way ANOVA was performed across all FOE positions for both expansion and contraction directions. Results showed significant differences ($P < 0.05$) in responses for a great majority of them ($34/43, 79$%), implying selectivity for the FOE position. Out of this sample, for 88% ($30/34$) of the units the preferred FOE position was shifted with respect to the fixation point, while for 12% ($4/34$) it was concentric with the fixation point. The activity of neurons selective for FOE position was spatially organized. Firing rates were tuned to the FOE position, with opponent responses for expansion and contraction. Figure 2A shows the typical responses of a neuron to radial optic flow stimuli. When the FOE is at lower-left this neuron shows excitation during expansion and no response during contraction. With a FOE in the upper-right quadrant, there is inhibition during expansion and excitation during contraction. The responses were compared with those elicited by planar stimuli, to assess the specificity of cell responses for expanding and contracting stimuli. Out of 43 neurons that showed responses to radial optic flow, 37 were also tested with planar motion. In a majority of cases, responses to radial optic flow were stronger than those to planar motion. Figure 2B shows an example of responses to planar motion in comparison to radial motion. In this case, only two directions were mildly inhibitory, while in the other six the activity was not different from the spontaneous activity ($t$-test, $P > 0.05$).

A linear regression method was used in order to quantify the dependency of the responses on the horizontal and vertical position of the FOE in space. The dependent measure is the difference in firing rate between the baseline and the evoked responses expressed in spikes per second. The equation for this model was a linear modulation with horizontal and vertical position. Out of the sample of 34 neurons showing significant sensitivity to FOE position (ANOVA, $P < 0.05$), 94% ($n = 32$) had significant linear dependence for expansion and/or contraction position. Regarding expansion, 22 cells (65%) fitted

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**Figure 1.** Recording region. (A) Dorsal view of the posterior part of monkey brain. The gray areas indicate the recording regions. Horizontal lines (a, b, c) indicate the level of the sections shown in (B). (B) Example coronal sections through the recording region. Vertical lines indicate electrode reconstructions and filled circles mark recording sites of visual units responding to optic flow. POS, parieto-occipital sulcus; IPS, intraparietal sulcus; STS, superior temporal sulcus; LE, lateral fissure; CS, central sulcus; LS, lunate sulcus; PEC, caudal part of area PE; PGm, medial portion of area PG; MIP, medial intraparietal area; d, dorsal; l, lateral.
significantly with the model. Ten units (45%) fitted with a linear component in the horizontal or vertical dimension, while the other 12 (55%) fitted with a linear component in both dimensions. The response field fit shows that the activity of the cell during expansion (Fig. 3A) was greater when the FOE was located in the lower part of the visual field. This preference for the stimulus position was reflected on the slope of the response field fit, which increased in both $x$ and $y$ \[ P(x) = 0.02 \text{ and } P(y) = 0.0001 \]. Regarding contraction, 26 cells (76%) fitted significantly with the model. Fourteen units (54%) fitted with a linear component in the horizontal or vertical dimension, while 12 (46%) fitted with a linear component in both dimensions. Figure 3B shows the response field fit of the cell during contraction. In this case the increase in firing rate was greater when the FOE was in the upper-right field and only the horizontal dimension showed a significant fit \[ P(x) = 0.02 \], while there was no modulation in the vertical dimension. This is clearly visible in the example of Figure 2A in which the firing rate is shown by peri-stimulus time histograms.

The fitting of the data with a regression method was also used to quantify the modulation of the tuning in the horizontal or vertical meridian. The horizontal coefficients of the right hemisphere were multiplied by -1 in order to have all positive values in the contralateral hemifield. Figure 4 shows the scatter plot of the adjusted values for both expansion and contraction tuning. Optic flow responses of Pe neurons do not seem to be tuned for a specific hemifield or quadrant of the visual field.

To compare the strength of the responses between different kinds of stimulation (planar or radial), an index computed by the following formula was used:

\[
\text{preferred stimulus} = \frac{St_{1\text{max}} - St_{2\text{max}}}{St_{1\text{max}} + St_{2\text{max}}}
\]

where $St_{1\text{max}}$ is the maximum firing rate in one stimulus condition and $St_{2\text{max}}$ is the maximum firing rate in the other stimulus condition. A similar analysis has been performed using this index in area MST (Pekel et al., 1996): it produces values from -1 to 1 and was computed for the preferred direction of radial movement (expansion or contraction), versus the preferred direction of planar movement. Most of the cells (33/37, 89%) tested with both radial optic flow and planar stimuli gave positive indices (Fig. 5A), implying that radial optic flow stimuli elicited responses stronger than those of planar stimuli. In many cases (23/33, 62%) the index was ≥0.2, meaning a firing rate at least 50% higher with radial than with planar stimuli. Moreover, this index was also computed for both phases

Figure 2. Responses to optic flow stimuli. (A) Peri-stimulus time histograms of firing rates during stationary background presentation (SA) and expanding (EXP) or contracting (CONTR) radial optic flow stimuli, with nine different FOE. The $X/Y$ position of the FOE is reported below each rectangle (0/0 corresponds to the fixation point). (B) Responses of the same neuron to planar random-dot background motion in eight directions. Each arrow indicates the direction of the background motion.
of radial movement (expansion vs contraction) (Fig. 5B). Again, results showed a strong preference for one direction according to the FOE position in space.

Comparison between Optic Flow, Planar Motion and Moving Bar

We initially assessed the directional selectivity of each cell using the von Mises circular distribution computed by the formula:

\[ M(\theta) = A \exp\{k[\cos(2(\theta - \gamma)) - 1]\} \]

where \( A \) is the maximal firing rate for the preferred direction, \( \gamma \) is the preferred direction (radians), \( \theta \) is the stimulus direction (radians) and \( k \) is the parameter of concentration indicating the amplitude of the tuning curve (Batschelet, 1981; Swindale, 1998). This analysis was performed on units that showed a significant difference (\( t \)-test, \( P < 0.05 \)) in firing rate during stimulus presentation when compared to the spontaneous activity. The goodness of fit was assessed by a \( \chi^2 \) test (\( P < 0.01 \)).

A comparison of the preferred directions derived from planar motion and moving bar was also performed. The preferred direction was defined as the mean vector of the tested directions.
(Mardia, 1972; Batschelet, 1981) and only units with a significant directional selectivity were considered for this comparison. The analysis performed to compare directional selectivity to planar motion versus the moving bar showed that a majority of these neurons (15/20, 75%) had the preferred direction similar in the two types of stimulation. Therefore for this sample, the planar motion responsiveness might be predictable on the basis of the functional features of the receptive field.

On the contrary, the radial optic flow responsiveness is not completely explained by the functional features of the receptive field. An example of these findings is illustrated in Figure 6. Here, the responses to moving bar show a clear direction tuning (Fig. 6B), with preferred direction $-45^\circ$, across the whole receptive field. In this cell the receptive field includes the upper-right quadrant. This would imply a response to expanding optic flow, with FOE at the fixation point. Instead, the neuronal

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Figure 6. Neuronal response to optic flow, planar motion and moving bar. (A) Radial optic flow stimulation. On the left of the figure, the receptive field (RF) and four different positions of the FOE are indicated with a, b, c and d. In b the FOE and the fixation point (FP) are in the same location. On the right side, responses to expansion and contraction are shown by peri-stimulus time histograms. (B) Moving bar stimulation. The polar plot on the left shows the directional tuning. The histogram on the right illustrates the neuron’s response in the $45^\circ$ and $225^\circ$ directions. (C) Planar motion stimulation. On the left side, the void histograms illustrate the lack of neuron’s response to random-dot backgrounds moving at $45^\circ$ (left) and $225^\circ$ (right) directions.
response is excited by contraction when the FOE is in the upper-right quadrant (Fig. 6A). Moreover, translation of the whole background in the preferred direction of the moving bar stimulus does not elicit any response (Fig. 6C). Thus, it seems that the response to radial optic flow cannot be predicted by the effects of classical bar stimuli.

The neurons activated by radial optic flow show a mixed responsiveness to optic flow, planar motion or moving bar stimuli. Very few cells (n = 5) were activated by radial optic flow only. Many cells (n = 19) were activated by radial optic flow and moving bar and a similar number (n = 21) were activated by all stimuli. Finally, the index of equation (1) was computed in response to radial optic flow and moving bar in 37 neurons (Fig. 7). Most of the cells (21/37, 57%) tested with both radial and moving bar stimuli gave indices < -0.2, implying that radial optic flow stimuli elicited responses weaker than those of moving bar stimuli. The responses to the radial optic flow were weaker than those to moving bar, but stronger than those to planar motion. These data suggest that in this population of neurons there is a continuum of responses and no clear subdivision into separate functional groups.

**Discussion**

The anatomical reconstruction described in the results section show that the recording sites considered for this study were all within the cortical area named PEc by Pandya and Seltzer (Pandya and Seltzer, 1982). The recordings show that area PEc possesses a neuronal population representing optic flow signals. Area PEc has not been extensively studied by tactile or proprioceptive stimulation, however this portion of the superior parietal lobule was classically considered as a division of somato-sensory cortex especially on the basis on the somatosensoory-related activity and the cortico-cortical connections of area PE. The direct connection of area PEc with the premotor cortex, together with the neuronal activity related to visual stimuli and hand movement (Ferraina et al., 2001) may describe PEc as a visual area whose neurons are involved in the integration of visuo-motor signals. This sort of motion analysis, that carries the visual signal of self-motion, can contribute to the occipito-frontal cortical stream, linking visual input to motor output.

The main inputs to PEc arise from the superior parietal areas PEA (part of area PE in the medial bank of the intraparietal sulcus), PECi (part of area PE in the caudal part of the cingulate sulcus), PE and MIP. Area V6a is the primary source of visual input (Shipp et al., 1998). The visual properties of V6a neurons are well documented (Colby et al., 1988), but there are no reports about their optic flow responsiveness. Area V6a receives a major input from the extrastriate areas PGM, PEA and MIP, but weaker connections are described with parietal visual areas 7a and VIP (Matelli et al., 1998; Shipp et al., 1998; Caminiti et al., 1999). It was interesting to establish whether there was a relationship between translation directional selectivity to bars and that of dot planar motion for PEc neurons to help establish the source of this motion selectivity. PEc neurons showed similar directional selectivity for these two types of stimuli. PGM neurons are activated by combinations of visuo-manual and oculomotor signals and seem to be involved in the generation of arm movements (Ferraina et al., 1997). MIP neurons are activated by both visual and tactile stimulation and they fire during arm movements (Colby and Duhamel, 1991). PGM and MIP have not shown the same characteristics in response to planar and classical visual stimuli, therefore it is not clear which is the source of this tuning for PEc neurons. It is possible that the tuning could result from a projection, direct or indirect, to PEc from some dorsal stream area such as 7a or MST. It is possible to speculate that PEc forms motion tuning de novo from disparate visual inputs.

It was also important to determine if the optic flow responsiveness to more complex motion depends on the functional features of the receptive field. In the present study, the optic flow responsiveness is not entirely explained by the moving bar sensitivity in PEc cells, suggesting that optic flow and moving bar responses might serve different mechanisms in the integration of visuo-motor signals to prepare body movements. The analysis of optic flow is very common in parietal stream areas. However, each region has a specific tuning which builds on earlier representations. MST neurons respond to one or more types of optic flow stimuli (Saito et al., 1986; Tanaka and Saito, 1989; Duffy and Wurtz, 1991a,b) and they show selectivity for the position of the FOE, suggesting a role in heading percep-

Figure 7. Comparison of firing rates for radial optic flow and moving bar. Frequency distribution histogram of activity indices (see text) of responses to the best direction (expansion or contraction) of optic flow versus the preferred direction of moving bar. Negative values on the abscissa mean a greater firing rate with moving bar than with optic flow.

The results of this study support the role for the superior parietal lobule in the integration of visuo-motor signals to plan and control movements. Area PEc probably represents visually derived self-motion signals, since its neurons represent forward and backward body movements. Furthermore, the selectivity for the FOE position with respect to the fovea could provide the system with detailed visual information about heading. Thus the information about heading, together with that from moving bars, could be useful for behavioral conditions in which self-motion...
and object motion interact, such as intercepting or avoiding visual targets during locomotion. An alternative hypothesis for the use of this representation of motion is that moving bar responsiveness, especially the directional selectivity shown by these cells, could play an important role in guiding locomotion. Recent observations have led to the hypothesis that the perception of single objects can be useful in the estimation of heading (Cutting, 1996; Cutting et al., 1999; Wang and Cutting, 1999). This hypothesis is supported by recent results on human subjects. Vaina and Rushton (Vaina and Rushton, 2000) report that patients with a lesion in the superior parietal cortex have difficulty with navigation, but are able to use the relative movements of objects in the visual scene to obtain information about heading. Human psychophysical studies further show that subjects are able to judge their heading in the presence of a single object moving in a portion of space, but they make some error when a moving object crosses the observer’s path (Warren and Saunders, 1995; Royden and Hildret, 1996). Only a few studies have examined how the detection of a moving object is possible in the optic flow field (Royden et al., 2001). Elucidating the conditions that permit us to perceive a moving object from the other parts of the optic flow field and how this is integrated with visuo-motor signals is beyond the scope of this study, but the previously discussed response characteristics make PEC neurons a possible candidate for this perception.

**Notes**

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Address correspondence to Salvatore Squatrito, M.D., Dipartimento di Fisiologia Umana e Generale, Università di Bologna Piazza di Porta S. Donato, 2-1-40127 Bologna, Italy. E-mail: squatrito@biocfarm.unibo.it.

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