

Analysis of Optic Flow in the Monkey Parietal Area 7a

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Environmentally relevant stimuli were used to examine the selectivity of area 7a neurons to optic flow using moving, flickering dots. Monkeys performed a psychophysical task requiring them to detect changes in translation, rotational and radially structured optic flow fields consisting of collections of moving dots which are free of form cues. The neurons in area 7a were selectively responsive to all the different types of moving stimuli. Two types of tuning for motion selectivity were found. Some neurons were tuned to distinguish a particular direction of optic flow (e.g. radial expansion versus radial compression), while others were tuned to distinguish between different classes of optic flow (e.g. radial motion versus planar rotation). The latter tuning was unlike that reported for area MST by others and may represent a novel representation of optic flow. The response of these neurons to translating bars was compared to that of optic flow fields. There appeared to be no similarity in the tuning to the two types of motion. Furthermore, there does not appear to be an identity between the neurons that could be classified as opponent vector and those selective for radial optic flow. Area 7a is involved in the further analysis of optic flow beyond the cortical areas MT and MST and provides a novel representation of motion. These results are consistent with the neurons in area 7a utilizing motion for the construction of a spatial representation of extra-personal space.

Introduction

Psychophysical studies in human subjects have shown that visual motion alone can provide salient cues to extract the two- and three-dimensional structure of the surrounding environment and of objects (Wallach and O'Connell, 1953; Ullman, 1979). Both *Homo sapiens* and *Macaca mulatta* appear to perform this perceptual analysis in terms of computations performed on the motion flow fields (Siegel and Andersen, 1988; Andersen and Siegel, 1990; Siegel and Andersen, 1990; Regan and Beverley, 1979; Longuet-Higgins and Prazdny, 1980; Siegel, 1988) and not upon the successive analysis of individual frames (Ullman, 1979). It is an open question how this neural computation actually occurs in cortex.

The neurons involved in the analysis of complex motion perception can be readily studied as the general anatomical and physiological outlines of the motion analysis pathway in the macaque monkey are known (Van Essen *et al.*, 1981; Maunsell and Van Essen, 1983c; Andersen *et al.*, 1990a; Felleman and Van Essen, 1991). Regions that respond to motion are the middle temporal area (MT/V5) (Spatz and Tigges, 1972; Allman *et al.*, 1973; Zeki, 1974; Van Essen *et al.*, 1981), the medial superior temporal area (MST) (Saito *et al.*, 1986; Duffy and Wurtz, 1991a,b; Treue *et al.*, 1993; Lagae *et al.*, 1994) and area 7a (Motter and Mountcastle, 1981; Steinmetz *et al.*, 1987). There are also motion-selective neurons in the temporal lobe (Bruce *et al.*, 1981; Perrett *et al.*, 1985). Neurons in MT respond primarily to translation motion and are responsive to disparity and transparency cues. Neurons in MST respond to translation,

although responses to more complex optic flow fields of planar rotation and radial motion also occur.

Area 7a in the inferior parietal lobule is at the apex of this motion pathway (Andersen *et al.*, 1990a); damage to the putative homologous region in human patients leads to profound deficits in spatial analysis (Critchley, 1953; Vaina, 1994). For example, human patients have deficits in navigation and spatial orientation, spatial memories, route-following and oculomotor control. This set of deficits, called 'parietal neglect syndrome' or simply 'hemispacial neglect', includes disturbances of the awareness of body, of the relation of body to the environment, and of the perception of the organization of the environment. Motion is a critical component of spatial perception; consider the visual signals available to a pilot landing an aircraft at night, or the driver of an automobile along a freeway lined with reflectors. Interestingly no studies have specifically examined the ability to use optic flow for navigation in the cortically compromised.

Earlier recording studies in the monkey using moving bars have suggested that area 7a neurons are involved in the analysis of motion evoked during locomotion or by the manipulation of objects by the hands (Motter and Mountcastle, 1981; Steinmetz *et al.*, 1987), and perhaps the extraction of three-dimensional shapes (Sakata *et al.*, 1980, 1984, 1986). The presence of such neurons primarily depended upon a simple stimulus protocol in which square stimuli translated across the visual field. Neurons were found which responded only when the stimulus moved towards the fixation point; these were termed 'inward opponent vector' neurons. A second class of 'outward' opponent vector neurons were also seen. It was hypothesized that the opponent vector neurons were activated during locomotion or reaching. An important and inherent assumption in this approach is that when the visual system is challenged with a more realistic, and complex, visual stimulus, the neurons will respond primarily based upon the principles elaborated from the simpler measurements. Thus it would be expected that the neurons activated by moving bars should be similarly activated by optic flow generated by locomotion or reaching. This assumption is not always born out (Allman *et al.*, 1985).

Comparative psychophysical studies using similar motion stimuli in both monkey and human subjects indicate that performance of the two species is similar (Golomb *et al.*, 1985; Siegel and Andersen, 1988, 1990; Andersen and Siegel, 1990). Thus, the study of the properties of neurons in the visual system in the macaque monkey is particularly well-justified in that (i) the monkey's visual system is psychophysically capable of performing the required analysis and (ii) the physiological results may be generalized to the human visual system.

In the present study, neurons have been tested with 'classical' stimuli (e.g. translating squares) to map their motion-selective properties. Furthermore, recordings were made while the

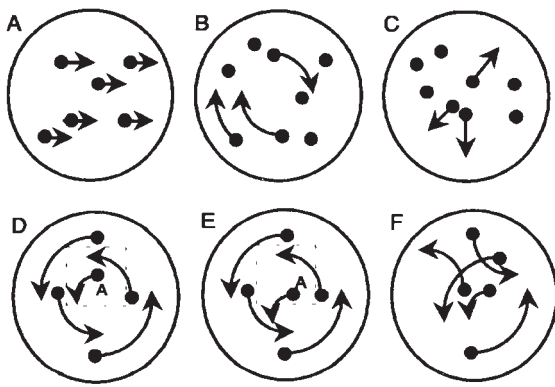


Figure 1. Visual stimuli used to test for structure-from-motion selectivity in area 7a neurons. (A) Translation. (B) Planar rotation. Each point is moved with a fixed angular velocity about the central point. The radius of each point is kept constant. The display typically consists of 128 points; each point had a point life of 533 ms. The display had a diameter of 20° or 40°. Both clockwise (cw) and counter-clockwise (ccw) rotational motion was tested. (C) Radial motion: in this display, points moved radially inwards or outwards at a fixed speed. A further modification of the stimuli (D–F) was made to provide a control condition that could be used to ‘ask’ monkey subjects behaviorally about the stimuli (Siegel and Andersen, 1988, 1990). This control condition is called ‘unstructuring’ of the motion stimuli, and is generated by moving entire motion trajectories randomly within a proscribed area. The process is illustrated for a planar rotation motion field of diameter ‘D’. One of the motion trajectories, labeled ‘A’, is randomly displaced within a box of size ‘W’ (E). This process is repeated for all the motion trajectories (F), greatly reducing the global percept of motion. A FOS of 0 would indicate an unstructured display, while a FOS of 1 would indicate a completely structured display.

animal performed the same task used in the comparative psychophysical studies. The physiological properties of neurons in area 7a were characterized using highly controlled optic flow patterns consisting of moving dots that have no form cues. These neurons have responses to all types of motion stimuli tested, although the response to the classical stimuli do not appear to correlate with those to the optic flow stimuli. The activation of the neurons is temporally correlated with the psychophysical detection and may underlie the perceptual event. The responses to optic flow suggest that area 7a neurons may be encoding spatial information from motion. The selectivity of optic flow in area 7a suggests a new representation not seen elsewhere in the visual system.

These results have been presented in abstract (Siegel, 1989; Siegel and Read, 1994; Read *et al.*, 1994).

Materials and Methods

Behavioral task

Two monkeys were trained to perform a reaction time task to detect changes in structured motion (Siegel and Andersen, 1988, 1990). Eye position was monitored at 30 Hz with an infra-red system centroid measuring device (Bach *et al.*, 1983) or an infra-red video system (ISCAN Co., Cambridge, MA) with the head fixed in place by an implanted holder. The monkey pulled back a lever at the onset of a 0.2° red fixation point at the center of the screen. The stimuli are summarized in Figure 1 (Siegel and Andersen, 1990). The stimulus, consisting of 128 white flickering dots, began 2000 ms after the initial fixation point (Fig. 1). The stimuli were specifically constructed to be free of all form cues other than the luminance border at the edge of the display. Each white point was on for 533 ms (32 video frames) with the initial point life randomly chosen over the interval [0, 533] ms. These points traveled along trajectories selected from the movement of an underlying structured object. In the initial portion of the motion stimuli, the complete trajectories were shuffled randomly in space to create an ‘unstructured’ motion percept. At a random time T , in the interval 3500–6000 or 2500–6000 ms after the

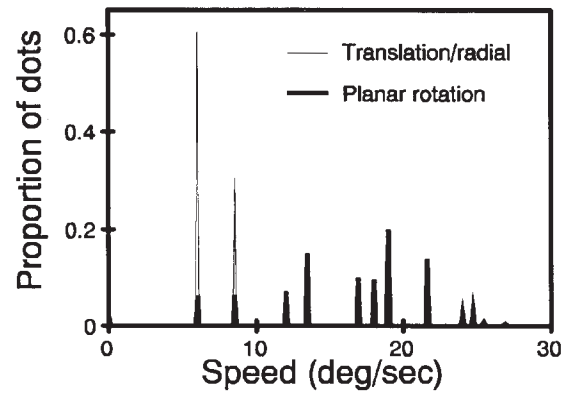


Figure 2. The distribution of speeds for translation, radial and planar rotation. The speed on a frame by frame basis was computed as: $\sqrt{(|x_i - x_{i+1}|^2 + |y_i - y_{i+1}|^2)}$. Note that the speed distributions are not the same for the planar rotation and radial stimuli.

onset of the dot stimuli, the shuffling of the stimuli began to be removed. At the time $T + 533$ msec, all the motion trajectories were in the correct position and a global form could be perceived from the motion (e.g. rotating disk). If the animal released the lever within $T + 150$ to $T + 800$ ms of the change to the structured stimulus (structured motion), he was rewarded with a drop of juice. Monkeys readily learned to perform this task at 90–100% correct trials. These parameters give optimal behavioral response (Siegel and Andersen, 1990).

The stimuli presented to the animal initially consisted of an ‘unstructured motion’ which changes to a ‘structured motion’. In an alternative version of the task sequence, animals were presented with an initially structured motion stimulus which changed to an unstructured motion stimulus. The unstructured motion consisted of the same motion trajectories as the structured motion, except that the trajectories were randomly shuffled within a window of width W (Fig. 1). The fraction of structure (FOS) was defined as $FOS = 1 - (W/2R)$, where R is the radius of the display, and is either 0 or 1 in this study.

A stimulus with a FOS of 0 does contain a small amount of structure in a planar rotation stimuli that can be used by the trained observer to distinguish direction of rotation. Thus the direction of clockwise planar rotation display with a FOS of 0 can be psychophysically distinguished from a counterclockwise rotation display with a FOS of 0. In order to obtain stimuli with no discernible FOS, it is necessary to increase the window W to extremely large values, resulting in negative values for the fraction of structure. The computational time for these displays increases almost exponentially with negative fraction of structure and thus it was not possible to construct stimuli with no discernible structure.

The equations governing the stimuli can be found in Siegel and Andersen (1990). The diameter of the stimuli were 20° in the first animal and 40° in the second animal. The angular velocity for the planar rotation was 60°/s; the speed of the dots for the translation and radial displays was 6° of visual angle/s. The distribution of speeds could be computed for these displays (Fig. 2). The distribution of speeds was matched for the translation and radial expansion stimuli. The distribution of speeds was different for the planar rotation. The distribution of speeds for the unstructured motions was also computed and exactly matched that of the structured motions.

Surgery

A 16 mm diameter chamber was implanted on the cranium and single unit recordings were made using platinum–iridium electrodes (Wolbarsht *et al.*, 1960) with standard physiological techniques. In one of the two animals, the placement of the chamber in both hemispheres was aided by the use of a magnetic resonance imaging scan (kindly performed by Charles Schroeder at the Albert Einstein College of Medicine.) After six or more months of study per hemisphere, the animal was killed with an overdose of barbiturate and perfused. Two animals were studied and recordings were made from a total of three hemispheres. All recordings

reported in this paper were taken from the upper few millimeters of the convexity of area 7a (Fig. 13A,B). Standard thionin and myelin (Gallyas, 1979) histology was performed on 30 μm frozen sections to verify chamber placement.

All procedures were performed in accordance with NIH guidelines on the use of animals in research and were approved by the Rockefeller and Rutgers University Animal Use Care Committees.

Instrumentation

All experimental control was via custom software on one IBM PC computer. Either a 25 MHz 386 or 66 MHz 486 machine was used. A variety of hardware interfaces were used to produce the stimuli, measure interspike intervals, monitor eye position, monitor the manipulandum, and provide the reward. The stimuli were generated using a Sergeant Pepper Number Nine board at 640×480 pixels and displayed on either a Zenith 1301 13 in. diagonal monitor or a Mitsubishi 1301 33 in. diagonal monitor. The stimuli were always white (32 cd/m^2 lux) on a dark background (0.25 cd/m^2). The room illumination was 1 cd/m^2 .

Voltage signals from the electrodes were amplified and discriminated in amplitude and time (BAK Co., Bethesda, MD). At times, more than one spike could be separated from a single electrode. Interspike intervals were measured using a Metrabyte CTM-05 board with a resolution of 0.1 ms (Ratzlaff and Siegel, 1990).

The analog signals from either of the two infra-red eye-tracking systems were measured using a DT-2831 (Data Translation Co.) board sampling at 30 Hz. The board also monitored digital signals corresponding to the position of the manipulandum and triggered the juice reward. If the animal made an eye movement during the trial of $>150^\circ/\text{s}$ the trial was terminated. Off-line analysis confirmed that the eye position did not change by more than 1.5° at stimulus presentation.

Statistical Analysis

Analysis of Variance

In order to quantify the responses of the neurons, we utilized an analysis of variance, *post-hoc* analysis and a variety of regression methods. The analysis of variance was used to determine whether a cell was sensitive, selective or had no response to the presented stimulus in order to provide a quantified implementation of the definition of selectivity in Table 3 of Van Essen (1985) in which various conditions for specificity of tuning of a neuron are defined. 'Selective' neurons responded differentially to at least one of the stimuli in the test set. We defined 'sensitive' neurons as those that respond equally to all the stimuli in a given test set.

Firing rates for a neuron were computed by counting the number of spikes that occurred during the 500 ms prior to a particular event (e.g. stimulus onset) and the number of spikes that occurred during the 500 ms after the event for every trial. These counts were then converted into firing rates. This computation controlled for possible changes in neural excitability over the recording period. This duration was chosen since many neurons in area 7a have both phasic and sustained tonic responses to visual stimuli (Mountcastle *et al.*, 1975; Lynch *et al.*, 1977; Robinson *et al.*, 1978; Sakata *et al.*, 1980; Motter and Mountcastle, 1981; Mountcastle *et al.*, 1981; Andersen and Mountcastle, 1983; Sakata *et al.*, 1984; Andersen *et al.*, 1985b).

A two-way analysis of variance was run for each neuron's response with one independent variable corresponding to the *class* of stimulus (e.g. optic flow type) and the other representing the time *period* of the firing activity (baseline versus evoked activity) as shown in Table 1. This analysis is referred to as the *standard analysis of variance* through the remainder of this paper. The significance level was taken as $P < 0.05$. With this experimental design, neurons that did not have an effect of either class or period were taken to be visually non-responsive (Type 0). Those neurons which had a significant effect of period alone were taken to be 'sensitive' to the stimulus, but not selective (Type 1). Neurons that had both a period effect and a class effect, but no interaction were classified as selective, as were neurons that had interaction effects (Type 2). There were a few neurons which had a significant effect of class alone to stimulus onset; these were always $\sim 5\%$ of the total neurons and arise from there being differences in the classes but not in the time-varying

Table 1

Different classifications for neurons using standard analysis of variance

Type	Before versus after	Class	Interaction	Description
0	-	-	-	not responsive
1	+	-	-	sensitive
2	+	+	-	selective-separable
	+	+	+	selective-interaction
	+	-	+	
	-	+	+	
3	-	-	+	
	-	+	-	
	-	+	-	statistical

The type is indicated in the first column. The two factors are 'before versus after' and 'class'. 'Before versus after' refers to the 500 ms period before and after the stimulus onset. 'Class' refers to the stimulus conditions. A '+' indicates that $P < 0.05$ while a '-' indicates $P \geq 0.05$.

properties of the neuron. In the analysis computed at stimulus onset, these are statistical outliers (Type 3) and are not dealt with further.

In other analyses, there was a substantial percentage of neurons with Type 3 effects. This occurred when the standard analysis of variance was computed as the animal detected the change in fraction of structure. Under these conditions, the firing rate was computed for the 500 ms prior to the change in fraction of structure, and also for the period of time from the beginning of the change to the time the key was released. The latter time was variable as the reaction time to release varied on a trial-by-trial basis. If the standard analysis of variance resulted in a Type 3 effect, then this would indicate a neuron which was selective to the type of stimulus (e.g. expansion versus compression), but did not change its firing rate when the structure was removed; these are discussed in the Results where appropriate.

A few comments are in order concerning the statistical analysis of the studies using the radial motion and planar rotations. The distribution of speeds was not identical between these two optic flow fields (Fig. 2). In addition, the trajectories are straight in the former and curved in the latter stimuli, which makes these stimuli perceptually different to the human subject. Since these stimuli are substantially different it would be inappropriate to analyze the response to both the radial and planar rotation in the same analysis of variance. Thus the analysis of the radial expansion/compression and the analysis of the planar clockwise/counter-clockwise motions were performed separately.

Sinusoidal Regression

The sinusoidal regression was performed with the function $Y = b_0 + b_1 \cos(\phi) + b_2 \sin(\phi)$. b_0 represents the mean firing rate, while $B = \sqrt{(b_1^2 + b_2^2)}$ is the peak modulation of firing activity (Steinmetz *et al.*, 1987). The parameters b_1 and b_2 represent the horizontal and vertical modulation of the firing rate. The direction of maximal response was given by $\phi_m = \tan^{-1}(b_2/b_1)$ with appropriate assignment of direction by quadrant. Unlike the previous study, the estimation of variables was performed using a non-linear minimization of the sum of squares of the residuals to calculate the best estimates of b_0 , b_1 and b_2 using a step-down procedure. The significance that each of the three parameters was different from 0 evaluated independently (procedure REG in the SAS statistical package.). Only parameters with a significance value less than the 0.05 level were used in the model. The procedure would enter and remove parameters until the best fit was obtained with significant parameters. The null hypothesis that the best representation of the data could be simply given by the mean was tested with an analysis of variance to compute a probability for the r^2 value (Zar, 1984) and rejection was set at a level of $P = 0.05$. (An example of such a fit is given Fig. 3D.)

Results

Response to Classical Bar Stimuli

Measurements were first made of the directional selectivity and the opponent vector selectivity using classical bar stimuli moving in linear trajectories in order to permit later comparison with the selectivity for random dot optic flow (Fig. 3). In these

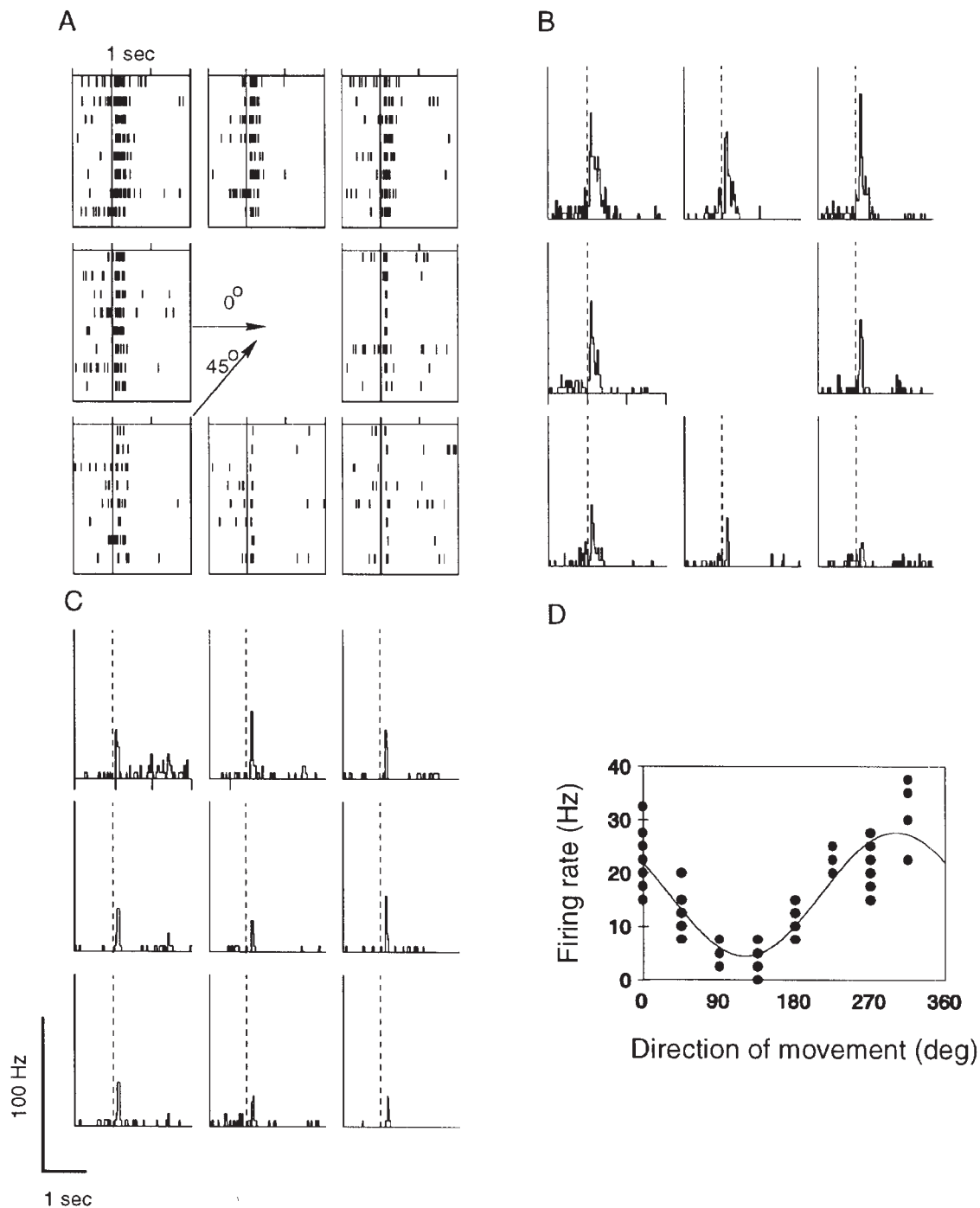


Figure 3. A neuron that exhibits both opponent vector properties and directional selectivity. (A) Raster plots of spike data 1 s prior to and 2 s after the onset of a translating bar. The location of each raster plot indicates the starting location for the translating bar on a $40^\circ \times 40^\circ$ grid. The directional arrows indicate the direction for two of the trajectories. The placement of the histograms follows the same conventions for the remainder of this figure. (B) Peristimulus time histograms of the data depicted in (A). The strongest responses are found when the stimulus starts in the upper contralateral visual field and passes across the fixation point. (C) Peristimulus histograms of the same neuron in response to stationary square stimuli used to map the receptive field. The squares are on for 1 s. Although there is a position-selective response to the light, it is substantially less than when the stimulus is moving. (D) Directional plot of the mean firing rate for the neuron in (A). See text for details of the analysis. The variance accounted for by the sinusoidal fit was 79%. Bin width 30.3 ms.

experiments, the squares came on 2000 ms after the fixation onset. The 5° or 10° squares were initially placed at eight positions on a square grid of 20° or 40° width respectively. As soon as the stimuli came on, the bar would move towards the fixation point at the center of the screen at speeds of 30 or 60°/s.

(No clear dependencies on the speed or size of the square were seen so these data were grouped.) These speeds were chosen to match those used in earlier studies of this property of parietal neurons (Steinmetz *et al.*, 1987). The bars would continue moving until they went off the edge of the screen. Note that the

duration of the movements along the diagonals would be longer by $\sqrt{2}$ than those along the vertical and horizontal meridians. The squares were always kept at a vertical orientation.

Some of the neurons that fit the opponent vector definition were directionally selective (Fig. 3). Although this neuron has a response to static stimuli (Fig. 3C) the vigorous response to the motion onset of the bar cannot simply be explained by the response of the neuron to static stimulus. Some of the other neurons tested with these stimuli responded equally from all directions during the inwards sweep, while others responded in a directional manner for both the inwards and outwards sweeps of the square.

To quantify the directional selectivity to the translating squares, we used a two-step statistical procedure. First the standard two-way analysis of variance was run to select neurons that had a visual response to the translating squares. Second, the directional tuning was computed for the cell by sinusoidal regression for the inwards and outwards components. The firing rate for the 500 ms prior to stimulus onset was computed, as was the firing rate during the period the bar moved either towards or away from the fixation point. The two segments of motion were treated separately. The independent variables were thus period of measurement (baseline versus evoked) and angle of movement. Three hundred and thirty-three neurons were examined in this way at a criterion probability level of 0.05.

Approximately half the neurons were visually responsive to either the inward or the outward movements (Table 2). Of these neurons, ~60% were selective to the direction of movement of the bars. This selectivity indicates that the neurons were not simply responding to the presence or onset of the bar, but to the bar's particular trajectory.

Opponent Vector Cells

According to the original definition of Motter and Mountcastle (1981), opponent vector neurons responded only to inwards or outwards motion. In later papers, it was noted that these neurons could respond directionally during either the inward or outwards sweep (Steinmetz *et al.*, 1987). Thus a neuron that responded to outward flow and did not respond to inward flow would be classified as an outward opponent vector neuron and presumably would encode optic flow generated by forward motion.

The neurons studied in this paper were tested statistically for this property using the standard analysis of variance rather than the Student's *t*-tests used in earlier publications. The analysis of variance permitted direct comparison of the response of the neuron to bars and other optic flow stimuli using identical criteria. A significant response to the inwards sweep of the bar was determined by whether the neuron was classified as non-responsive (Type 0 or 3) versus responsive (i.e. sensitive or selective, Type 1 or 2). If the response during the inward sweep was significant and the outward sweep was not significant, the cell was termed inward opponent vector. Outward opponent vector neurons were similarly defined.

Of the 331 neurons to which this analysis could be applied, 100 neurons were inward or outwards opponent vector neurons. Fifty-six neurons responded only during the outwards sweep, while 44 responded to the inwards sweep (Fig. 4). Of the 100 neurons that could be classified as opponent vector neurons (i.e. responding only to the inward or outward sweep), about half had an equal response regardless of the angle of movement (Fig. 4A). The responses of the remainder depended significantly

Table 2

Distribution of neurons responding to different phases of the translating square movement

	Inward motion		Outward motion	
	<i>n</i>	%	<i>n</i>	%
Not responsive: Type 0 and Type 3	165	50	151	45
Sensitive: Type 1	66	20	69	21
Selective: Type 2	102	30	111	34
Totals	333	100	333	100

The trajectories of movement were separated into inward and outward segments and analyzed independently. Approximately half of the neurons did not respond to the stimuli. The majority of the neurons which responded to the light were selective to the angle of the movement.

on the angle of the movement and were thus termed direction-selective opponent vector neurons.

The directional selectivity on the angle of bar movement for these 26 inward opponent vector neurons and 27 outwards opponent vector neurons was computed. The numerical methods to quantify directional selectivity were similar to that of Steinmetz *et al.* (1987). As in the prior work, a sinusoidal regression was performed between the firing rate (termed *Y*) during the test period (e.g. during inwards motion) and the direction of movement (see Materials and Methods).

Of the 26 inward opponent vector neurons, 14 were appropriately (i.e. significantly) fit by the sum of a sine and/or cosine; the remaining 12 could not be modeled by this function (i.e. they have a significant lack of fit). For the 27 outward opponent vector neurons, 19 were significantly fit and eight neurons were not modeled by the function. The distribution of best directions is given in Figure 4B. There does not appear to be one direction which is preferred for inward or outward movement, nor does there appear to be an ipsilateral or contralateral preference. The population size is too small to make any further quantitative statements.

In summary, approximately one-third of the 300 neurons studied were opponent vector neurons. A further third of the neurons studied were visually non-responsive. Approximately half of the opponent vector neurons also had a dependence on the angular direction of movement for the bar. Two-thirds of these directional opponent vector neurons were well fit by a simple sinusoidal model, with the remainder having a significant, non-sinusoidal, dependence on angular direction.

Non-opponent Vector Neurons

The remaining 124 of the 331 neurons tested with translating bars had visual responses which did not fit the opponent vector definition. Twenty-five were not directionally selective to any phase of the translating bar. These could be responding simply to the visual stimulus in a large, non-specific receptive field. Fifteen neurons responded selectively to one phase of the movement, but responded in a non-directional and significant manner to the other phase. These 15 neurons are similar to the opponent vector neurons with the primary difference being that they always fire above baseline when a visual stimulus is on. Opponent vector neurons do not fire above baseline except when there is a directional response. The neurons with a significant background rate could provide similar signals to the opponent vector neurons. Of the remaining 84 neurons, 61 neurons were directionally selective to both the inwards and outwards movement. However, there was no correlation between the best direction for a response to the inward and outward movements (Fig. 4C). These neurons could not be

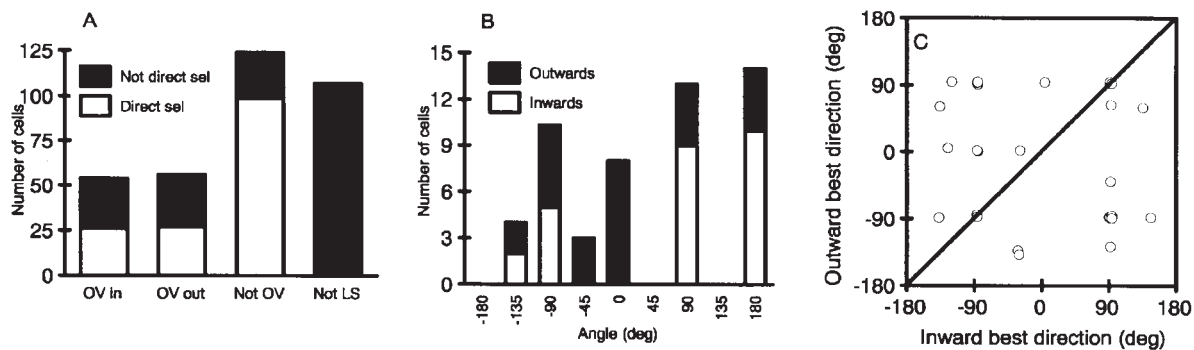


Figure 4. Properties of opponent vector neurons. (A) Distribution of directional response of the recorded population of inferior parietal lobule neurons. The inward category refers to the neurons which responded solely during the inward phase of the movement. Similarly the outward category refers to those neurons which would respond during the outward trajectory. Opponent vector neurons that were directionally selective are indicated by the open bars. Not light sensitive refers to the inability of the translating square stimulus to evoke a response from the neuron different from baseline levels. (B) Angles that evoked a maximal response from neurons with opponent vector properties in the inferior parietal lobule. 0° refers to a movement into the contralateral visual field, while 90° refers to an upwards motion. Only those neurons which were directionally selective and opponent vector are utilized in this distribution. (C) Directional tuning for neurons that are selective for movements both towards and away from the fixation point. The direction which yields a maximal response for the inward and outward segments of the sweep of the bar was determined by curve fitting. Directional conventions are as in (B) with the angles 180° and 360° appropriately transformed. The inward best direction is plotted against the outwards best direction for 33 neurons that were not opponent vector. The heavy line indicates the expected relationship between the directional tuning on the inwards and outwards sweep if the neuron had a uniform directional selectivity across the entire receptive field.

directionally selective neurons as might be found elsewhere in the dorsal stream (e.g. area MT).

Thus some of the neurons in area 7a were not well described by either the opponent vector model, or by a simple directional selectivity. The complicated motion responses of the neurons could be in part due to the interaction between static form cues and the motion cues.

Response to Optic Flow Stimuli

In order to further test the motion-selective properties of area 7a neurons, optic flow stimuli were utilized that had a constant luminance border and internal motion. The behavioral task was different when tests were being made with random dot stimuli. As before, the animal was required to fixate a central fixation point located at the primary position and pull back on the manipulandum. However, in the studies with random dots, the monkey's key release was contingent on changes in the movement of a field of random dots on the screen, rather than the dimming of the central fixation point.

Directional Selectivity to Translating Dots

We first considered whether inferior parietal lobule neurons were responsive to translating flickering dots. This was done by using a random dot field of 40° diameter which was turned on 2000 ms after the initial fixation point. The point life of the 128 dots in this display was 533 ms. The animal's behavior was contingent on the stimulus in that the dots would start moving in one of eight directions at onset and then stop 1500–4000 ms after their onset. Measurements of firing rates to stimulus onset always occurred prior to the stimulus cessation. The animal needed to release the key within a 800 ms interval from the time the dots stopped to receive his reward. As elsewhere, breaking of fixation terminated the trial. The speed was $6^\circ/\text{s}$, the point size was constant and 0.1° throughout the display. Directions of 0, 45, 90, 135, 180, 225, 270, and 315° were used.

The initial analysis of these neurons used the 'standard analysis of variance' (Table 3). The neurons were analyzed for their response relative to a baseline 500 ms prior to stimulus onset. The response over the first 500 ms following stimulus onset (defined as the early response) and that for 500–1000 ms after onset (late response) was computed.

Table 3

Sensitivity and selectivity of neurons tested with translating flickering dots

	First 500 ms		Second 500 ms	
	n	%	n	%
Not responsive: Type 0	45	48	50	55
Not responsive: Type 3	3	3	4	4
Sensitive: Type 1	23	25	21	23
Selective: Type 2	22	24	16	18
Totals	93	100	91	100

The standard analysis of variance was performed on the data with respect to a control period that was a period of 500 ms immediately prior to the stimulus onset. The test periods were the first 500 ms after stimulus onset and the second 500 ms after stimulus onset. Approximately 50% of the neurons were visually responsive to these stimulus, with about half of these selective for the direction of dot movement.

Of the 93 neurons tested under these conditions, approximately half had a significant early response (Table 3). Of these 45 neurons, 22 were directionally selective to the direction of the translating dots. These were further analyzed by fitting the data with the sum of a sine and cosine wave using the non-linear regression methods described above (Fig. 3). All but four neurons with a significant (Type 2) early response were well fit by this function (Fig. 5).

A late response over the interval of 500–1000 ms after stimulus onset was also found in these neurons for about half of the cells tested. Again many of these were directionally selective and 11 of the 21 were well fit by the sinusoidal model. The distribution of the directional selectivity for all neurons with a significant fit is illustrated (Fig. 6A). The directional selectivity for the population of neurons appeared to be weakly biased to the ordinal directions (up, left, right), although it difficult to support this conclusion on the basis of a small number of cells. A similar bias for ordinal directions was seen for the opponent vector neurons (Fig. 4B) which would support this finding. These biases may arise from selective visual experiences as has been suggested in other motion cortices (Van Essen *et al.*, 1984; Albright, 1989) although the discovery of a ordinal bias described here is novel.

The directional selectivity for the early and late responses were compared for the 10 neurons of the 93 tested which had

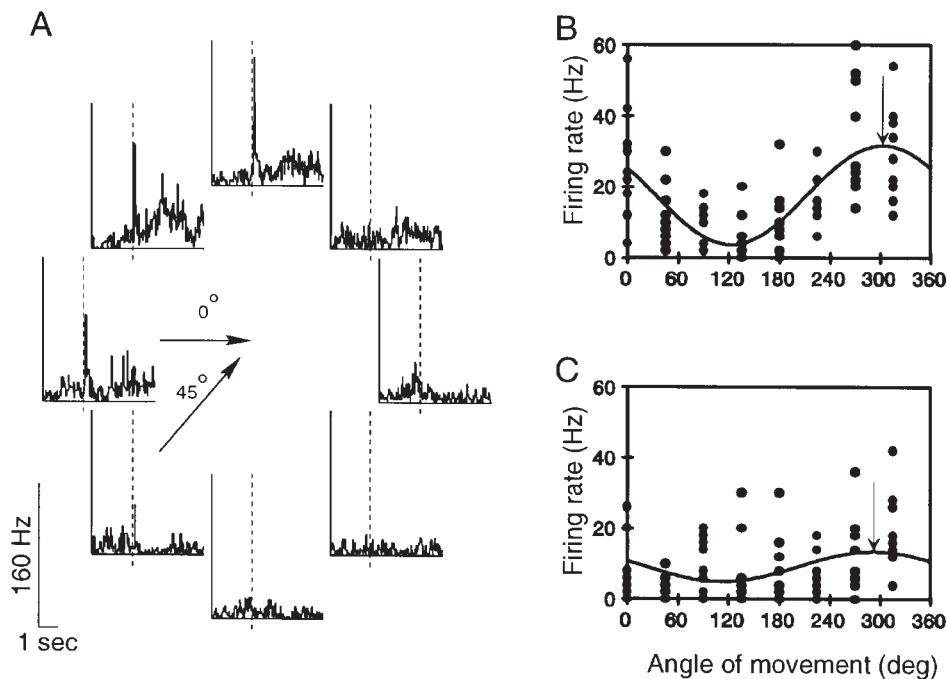


Figure 5. Directional selectivity to translating dots. (A) Peristimulus time histograms for a neuron that is directionally selective for the onset of a flickering translating random dot field. The stimulus comes on at 2 s and the dots stop between 3500 and 5500 ms. The location of the histogram indicates the direction of the motion rather than the more conventional origin of motion in order to remain consistent with Figure 3. (B) Analysis of early response to motion onset over first 500 ms following stimulus onset. (C) Analysis of late response from 500 ms after onset to 1000 ms after onset. The mean firing rate is computed over the 500 ms window. Individual points indicate individual trials. The solid line is the best fit of the sum of a sine and cosine function [$Y = b_0 + b_1 \cos(\phi) + b_2 \sin(\phi)$] using the non-linear minimization methods cited in Materials and Methods. The values for b_0 , b_1 and b_2 were 17.8 ± 1.2 , 7.43 ± 1.7 and -11.77 ± 1.7 Hz respectively for the early response. The angle with the maximal response was 302° . For the tonic response these values were 9.3 ± 0.96 , 1.58 ± 1.35 and -3.95 ± 1.35 Hz with a VAF of 55%. The angle with the maximal response was 292° .

were directionally selective for both the early and late response. Seven of these neurons had a significant fit during both periods. For this small number of cells there was a linear relationship between the early and late response (Fig. 6B).

In summary, many area 7a neurons were directionally selective to translating dots with a similar range of directions as compared to those tested with translating bars. Neurons tended to have respond more during the first 500 ms following stimulus onset, but some cells had a later more prolonged response.

Response to the Onset of Structured Optic Flow

Neurons were next tested with planar rotation and radial expansion optic flow. The animal performed a task in which the random dots came on at 2000 ms following the onset of the fixation point. At this time, the animal was holding the manipulandum back and foveating the central fixation point. Then, at a random time over the interval of 3500–6000 ms from fixation onset, the fraction of structure of the random dots changed.

Four types of optical flow were used: clockwise rotation, counter-clockwise rotation, radial expansion, radial compression. On half the trials, the animal was required to detect a change from structured motion (FOS = 1) to unstructured motion (FOS = 0), while on the other half the animal detected a change from unstructured to structured motion (Figs 7 and 9).

Neurons in area 7a responded to different events in the task. First, there was a light-sensitive response synchronized with the stimulus onset at 2000 ms (Figs 7A, 9A, 9D). This response could be selective to the type of stimulus. In the upper panel of Figure 7, the peristimulus time histograms are shown for the eight stimulus conditions. In all conditions, there was a 10–200 Hz

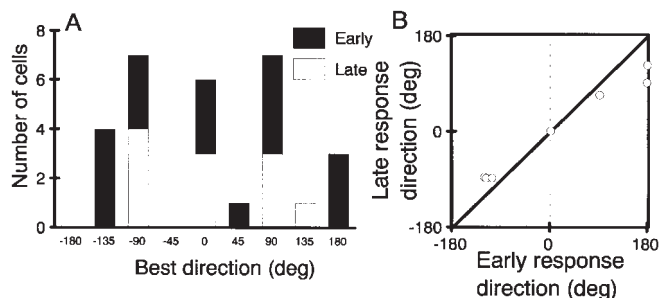


Figure 6. Directional selectivity of neurons tested with translating, flickering dots. (A) Distribution of directional selectivities for all responses that were selective to the early or late components of the neural response. The early and late components are presented separately. There is a propensity for the distribution to the major orthogonal axis (up, down, right, left). (B) Relationship between the directional selectivities for the early and late component of the responses. Only neurons which showed a significant fit to both the early and late components are illustrated. Although the number of neurons is small, a linear relationship exists between the directional selectivity to the early and late responses as would be expected from a constant directional selectivity throughout the neuronal response.

change in the peak firing rate occurring within the first 200 ms. Some of the neurons, such as the one illustrated in Figure 7, were selective to multiple stimuli. Strong responses were found to the onset of clockwise and counter-clockwise motion, while weak responses were obtained to all the other stimulus conditions. The angular velocity of the rotation stimuli was $60^\circ/\text{s}$ while the radial speed was $6^\circ/\text{s}$.

In the cell of Figure 7, a response was found at the stimulus onset to the clockwise and counterclockwise rotation. One possibility is that the difference in response to the planar

rotation and the radial stimuli arises because the former contained curved trajectories while the latter contained only straight trajectories. However, there was little or no response to the unstructured motion stimuli, indicating that the responses were indeed directly related to the planar rotation flow fields.

The first analysis determined whether the neurons were selective to the different types of optic flow. In order to ensure that the tangential speed distributions and curvature were the same for each comparison, the standard analysis of variance was performed separately for the rotation and radial expansion stimuli (see Materials and Methods). The experimental design for the standard analysis of variance was clockwise and counter-clockwise planar rotation as one categorical variable, with the second category being the time of measurement. A similar design was used for the radial motion.

Of the 271 neurons examined, about one-third (97 neurons) responded in some way to the onset of the four types of structured motion using the standard analysis of variance. One-third of these optic flow responsive neurons (42 cells) were selective for the stimulus (e.g. Fig. 8A), with the remainder unable to distinguish between the different types of optic flow. A similar analysis was performed on the 204 neurons which had been presented with unstructured motion at the beginning of the display. Under these conditions, 41% of the neurons responded to the onset of unstructured motion, with a quarter of these (20 cells) being selective to the unstructured motion. This small but significant selectivity to a FOS = 0 for these 20 neurons (11% of total) may indicate that there was an exquisite sensitivity for very small amounts of structure in the display.

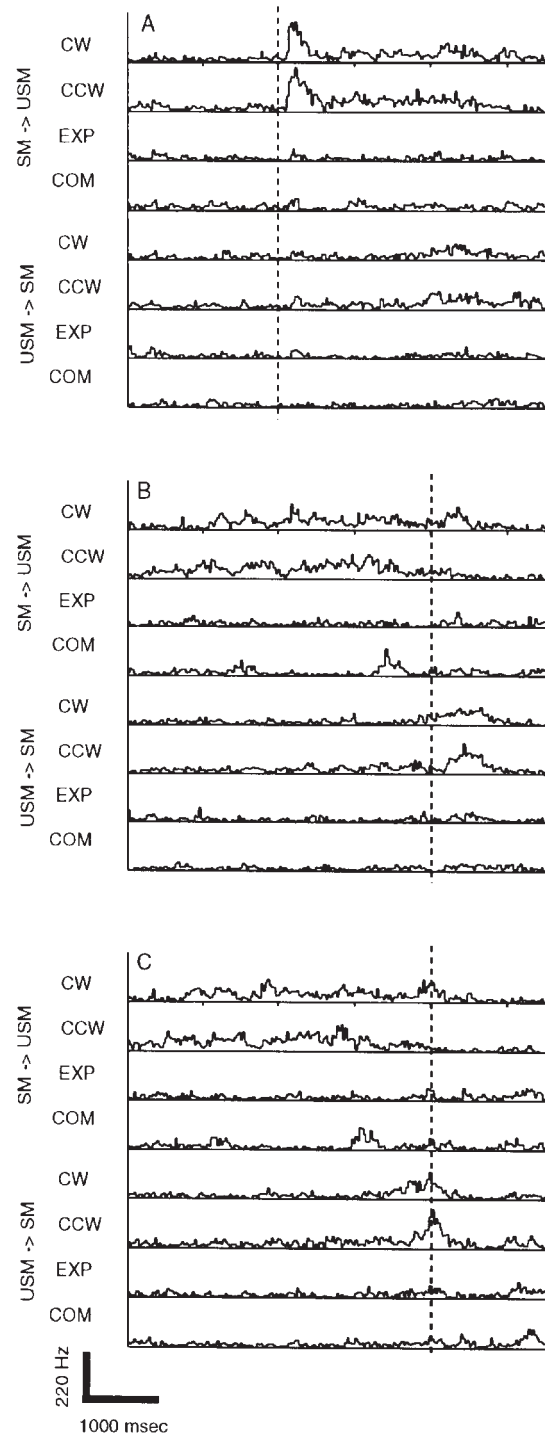
Response to Changes in the Fraction of Structure for Optic Flow Stimuli

In all of the above optic flow tests the animals were performing a detection task in which they needed to detect a change in the fraction of structure. The stimuli are devoid of secondary cues (e.g. luminance) at the time the change in fraction of structure occurs. This is a very rigorous test for the putative optic flow properties of the neuron because the only *visual* attribute that can alter the neuron's firing rate is the change in the fraction of structure.

Since the change from a fraction of structure of 0 to a fraction of structure of 1 occurs randomly during the trial, the spike

Figure 7. Example of a neuron that responds selectively to optic flow. The monkey was tested with four different types of motions: clockwise rotation (CW), counter-clockwise rotation (CCW), radial expansive (EXP) and radial compressive (COM). Two different sequences were presented to the animal for each type of motion. In one sequence the initial stimulus was structured motion (SM), which was followed by unstructured motion (USM). In the other sequence the initial stimulus was USM which was followed by SM. (A) The peristimulus time histograms are synchronized to the stimulus onset at 2000 ms following fixation point onset (indicated by vertical dotted line). When the initial motion is CW or CCW, the cell responds with a burst of activity. Under all other conditions, there is a weak or no response. The probability of distinguishing between clockwise and counter-clockwise rotation is 0.15 and between expansion and compression radial optic flow is 0.53. The probability of distinguishing between the radial and the planar motions is <0.001 . (B) The histograms are synchronized to the randomized times when the stimulus begins to change (indicated by vertical dotted line). Here a strong response is seen at the time the stimulus changes from unstructured rotation to structured rotation. (C) The histograms are synchronized to the time of key release (indicated by vertical dotted line). The neuronal response increases prior to key release only when the appropriate motion is presented. The upper histogram of each panel has small ticks indicating 1000 ms; the same calibration bars apply to all histograms. The selectivity index for the change from unstructured motion to structured motion is 0.75 for the planar rotation and 0.82 for the radial optic flow. The probability of distinguishing between the planar rotation and the radial optic flow at stimulus change is 0.002. Thus this neuron cannot distinguish the direction of motion but can distinguish the type of optic flow.

rasters needed to be synchronized to the 'change in structure'. To illustrate this, the histograms for each trial were synchronized on the time of the onset of the structured stimulus. A change in firing rate could be an increase or decrease depending on the neuron. Figures 7B, 9B and 9E illustrate the change in the rate of firing synchronized to the change in fraction of structure on a trial-by-trial basis. Although the only change in the visual stimulus was that in the fraction of structure, these synchronized responses could have been associated with eye or hand movement or attentional and changes that follow key release. To demonstrate simple motor responses, the data were



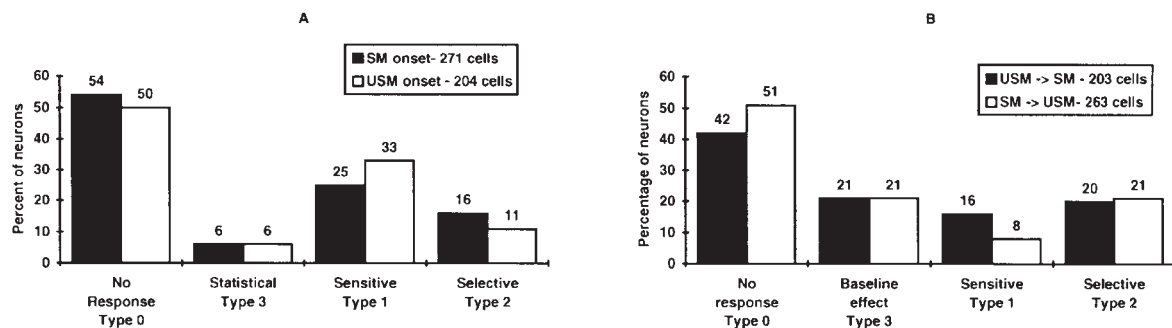


Figure 8. Sensitivity and selectivity of inferior parietal lobule neurons to optic flow. The standard analysis of variance was run on each neuron that was tested with optic flow stimuli. The analysis was run separately for each type of flow field as well as for the structured and unstructured motion. (A) Response of neurons to onset of structured and unstructured motion. The solid bars represent those neurons tested with the onset of structured motion. The open bars represent those tested with the onset of unstructured motion. (B) The neuron is evaluated during the period the animal is performing the psychophysical task. The solid bars depict data from neurons in which the initial stimulus is unstructured motion which changes to structured motion. The baseline effect reflects neurons that are differentially selective to the different types of unstructured motion. The selective neurons are those that change their rate with regards to a particular optic flow. The open bars depict data in which the initial stimulus is structured motion which changes to unstructured motion. The baseline effect represents neurons that fire tonically to the structured motion. The selective neurons are those that change their rate dependent on the fraction of structure.

also synchronized relative to key release. In the example of Figure 7, the increase in activity occurred prior to, and peaked at the time of key release. Since behavioral control of eye and hand position is maintained prior to key release, only visual, attentional and/or preparatory motor effects can account for the change in firing rate of the neuron.

The effect of a change in the fraction of structure upon the response of the area 7a neurons was quantified by utilizing the standard analysis of variance with one modification. As described elsewhere, the activity was typically averaged for 500 ms before and 500 ms after a stimulus event. However, in order to test the hypothesis that there was a change in activity associated with the change in fraction of structure, it was necessary to synchronize the action potential trains with the randomized time of stimulus change. The baseline period was taken to be the 500 ms prior to the stimulus change. The test period was taken to be the time after the stimulus change, but before the key release. This latter period is the reaction time, which varied from 300 to 800 ms depending on the stimulus condition. The number of spikes collected during each period were normalized by the data collection time, yielding the average firing rate in Hz. The use of the spikes that occurred during the reaction time, and not after, thus ensured a constant behavioral state (maintained fixation and external behavior) for the animal and the recording.

Thirty-six percent of the 203 neurons tested were responsive to the change from unstructured motion to structured motion (i.e. increase in fraction of structure). About two-thirds of the neurons were selective to the type of motion (Fig. 8B). A number of neurons (~20% of the sample) showed a significant effect of the unstructured motion stimulus (Type 3), but did not change their rate with the change in fraction of structure. These neurons could be signaling the small amount of structure extent when the fraction of structure was 0.

The data set was also analyzed for 263 neurons that were studied when the stimulus changed from structured to unstructured motion (Fig. 8B). In effect, this analysis determines whether there is a response to the removal of structured motion and can be considered analogous to testing for an 'off response' in primary visual cortex. It was found that 27% of the neurons had a visual response to the decrease in fraction of structure, with 75% of these selective to the type of optic flow tested. Again it was found that many (21%) of the 263 neurons tested

were selective to the type of optic flow, but did not change their firing rate when the fraction of structure was decreased (Type 3). These neurons are cells that are differentially selective to the different types of optic flow, but did not respond, or responded with a long latency, to the change in fraction of structure.

Distribution of Neurons with Different Selectivities

The groupings of sensitivity and selectivity derived from the standard analysis of variance described above do not indicate how well a particular neuron can distinguish between any pair of experimental conditions. For example, a neuron classified as selective (i.e. Type 2) may be highly selective or weakly selective. Typically in the electrophysiological literature a selectivity index is derived and its distribution is presented across the population (Maunsell and Van Essen, 1983b; Mikami *et al.*, 1986; Graziano *et al.*, 1994). Such indices [e.g. $S = (F_{max} - F_{min}) / (F_{max} + F_{min})$, or $S = 1 - (F_{min} / F_{max})$, where F_{max} and F_{min} are the maximal and weakest mean responses to two stimulus conditions] have the desirable property of scaling across different mean firing rates and being nicely bounded. However, such indices do not take into account the variability in the response from trial to trial. Thus two neurons might have a similar selectivity indices, yet have very different discrimination properties depending on the variability (i.e. standard deviation) in the firing rate for each neuron. Receiver-operating characteristic analysis does take this variance into account; however, additional data are needed to perform this analysis. An additional possibility would be to use a *post-hoc* analysis such as a Bonferroni corrected *t*-test to determine which stimuli are different and by what magnitude. However, this test cannot be justified across the four stimuli as the velocity distributions are different for the planar rotation and radial optic flows.

To circumvent these issues, probability values computed in the standard analysis of variance were used as selectivity indices. The probability value takes into account the mean and variance of the firing rate, scales with firing rate, and is bounded between 0 and 1. The probability values for 'class' and 'interaction' were used for cells that were found to respond significantly to stimulus onset (Type 1, Type 2). If a cell had an 'interaction' term < 0.05 , then this value was used for the selectivity index. If the interaction term was not significant, then the probability value for the 'class' independent variable was used.

The selectivity index was tabulated for the 133 neurons that

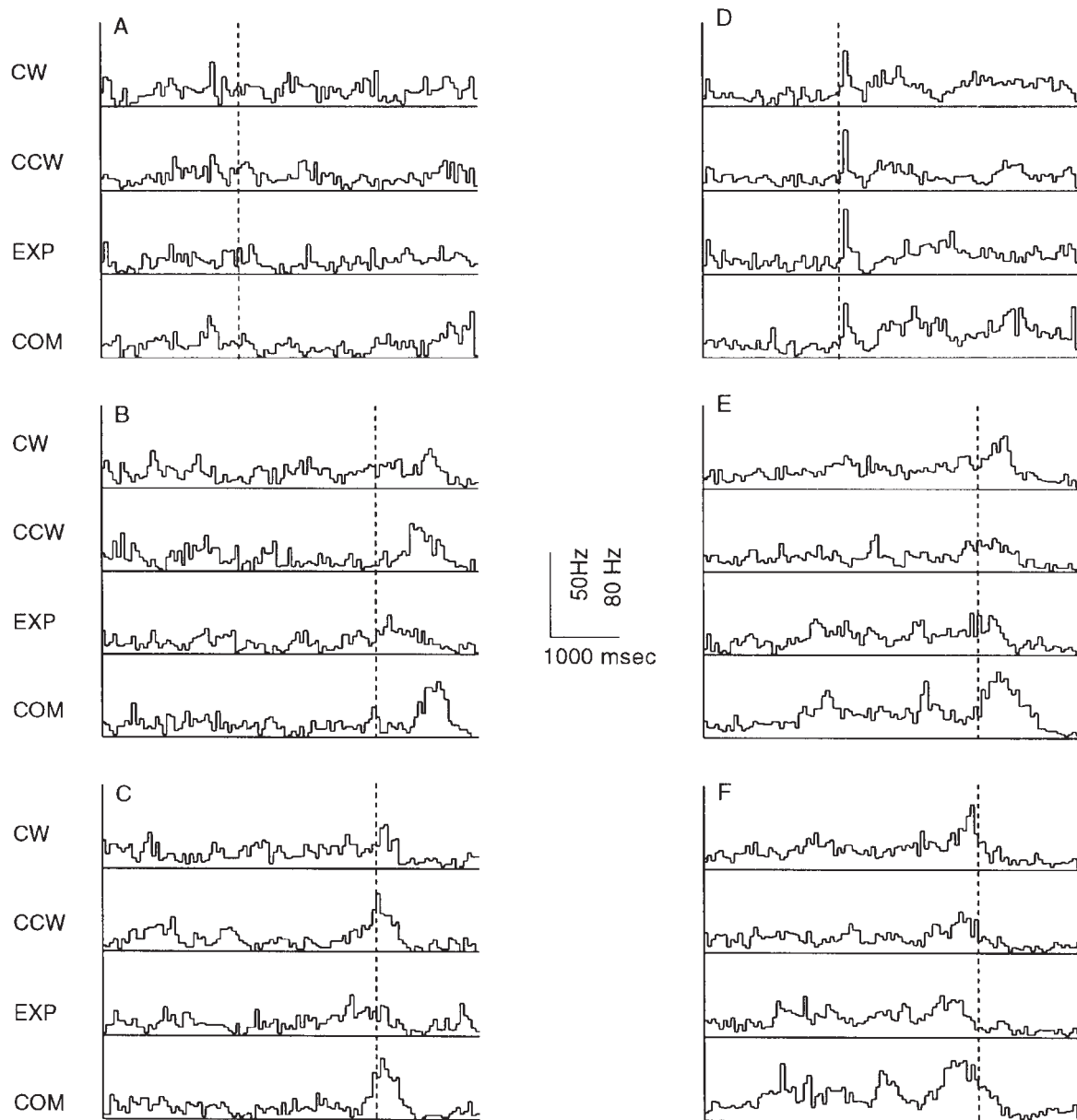


Figure 9. Area 7a neurons with selectivity to both radial and planar rotation when the monkey detects the change from unstructured to structured motion. Panels (A)–(C) are from a neuron which had no significant response to the onset of unstructured motion. (A) shows that peristimulus time histograms synchronized to stimulus onset. However, this neuron is selective to the different types of motion at the time the animal is performing the behavioral task. (B) shows the peristimulus time histograms generated by synchronizing the spike trains to the beginning of the change from unstructured to structured motion. There is a long latency increase in activity. This increase in activity peaks just as the key is released as shown in (C) in which the data is synchronized to the time the animal releases the key. Statistical analysis of the firing rate changes at stimulus change indicate that selectivity index is 0.03 and 0.0098 for the planar rotation and the radial motion respectively. Panels (D)–(F) show a similar analysis for a different neuron. This neuron responds to the stimulus onset; however, the response is non-selective for the type of optic flow. However, at the time the animal is performing the structure-from-motion detection, the neurons responds with a robust increase in activity. The selectivity analysis indicates a value of 0.025 and 0.0015 for the planar rotation and radial motion respectively. The dotted lines in (A) and (D) indicate stimulus onset. In (B) and (E) the dotted lines indicate the time of stimulus change. In (C) and (F) the dotted lines indicate the time of key release.

were sensitive (Type 1) or selective (Type 2) to the onset of rotation or radial motion (Fig. 10A). The directional index (i.e. probability) for the rotation stimulus was plotted on the abscissa, while the radial index was plotted on the ordinate. Only three of the 133 neurons that had a light response to the onset of the structured motion were selective to both. Many of the neurons which responded to the stimulus onset were found to be selective to either the radial or rotation optic flow. Fifteen and 28 cells were selective to the radial and rotational motion respectively. Eighty-seven cells were sensitive to both stimuli.

When the same analysis was performed on the response of neurons to the onset of unstructured motion, similar results were found (Fig. 10B). Few neurons were selective to both stimulus conditions, with many selective to either unstructured radial or rotation motion. The distribution of the neurons which were differentially selective to planar rotation and radial motion across the cortical hemisphere was generated (Fig. 13E,F; note that multiple neurons in a single penetration are indicated by only one symbol). Very few penetrations contained both types of neurons – in line with the idea that there are two separate

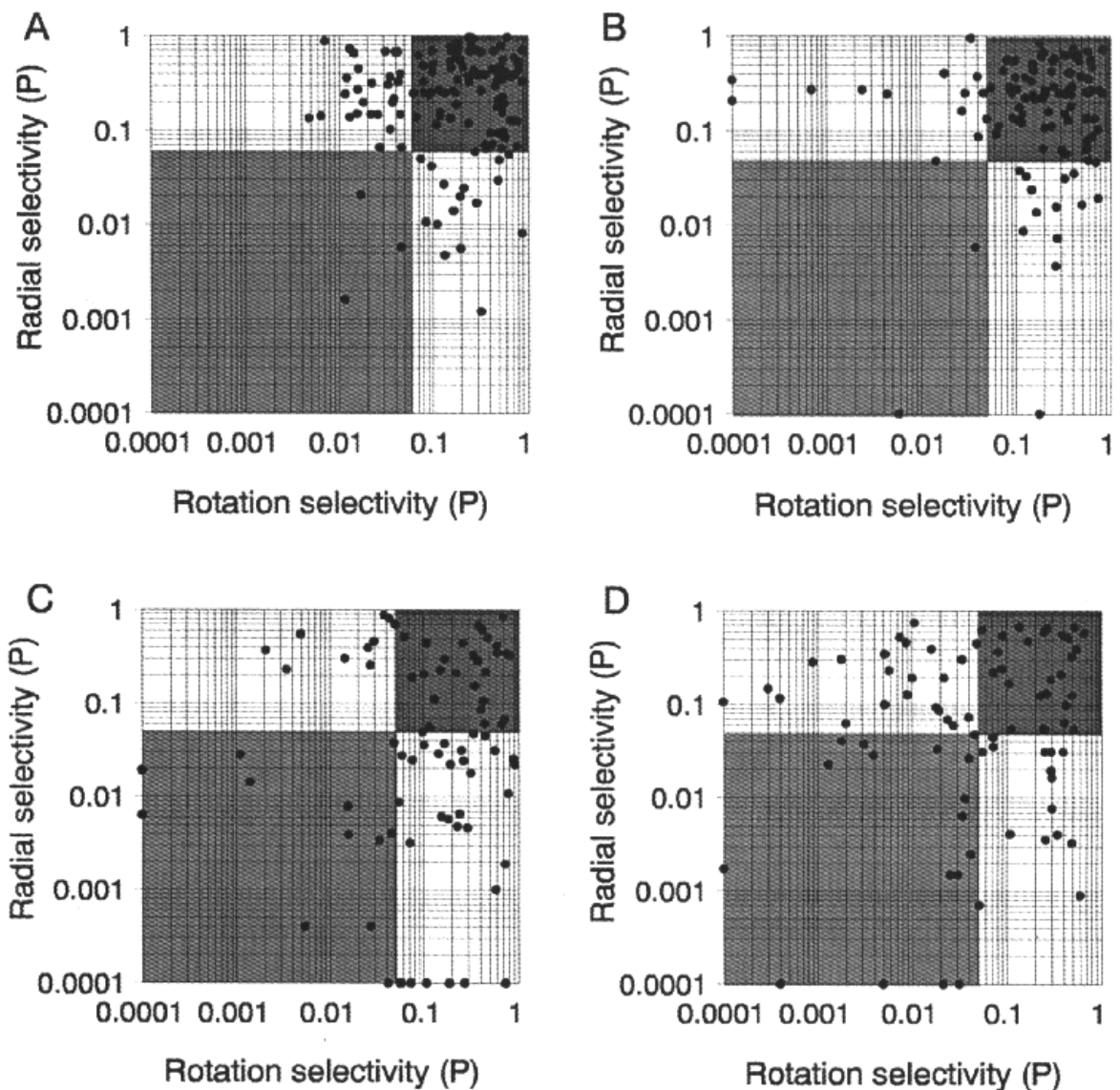


Figure 10. Distribution of radial and planar rotation selectivities. The probability value for each neuron to distinguish between either the two types of radial motion or the two types of expansion motion were determined and used as an index of the selectivity. Only neurons which showed a significant response to the onset of motion stimuli (upper panels) or change in motion (lower panels) were analyzed. (A) Cells which had a visual response to the onset of the optic flow stimuli when the fraction of structure was 1. (B) Cells which had a visual response to the optic flow stimuli when the fraction of structure was 0. (C) Cells which had a visual response to change from structured to unstructured motion. (D) Cells which had a visual response to the change from unstructured to structured motion. In all panels, the probability values for radial motion were plotted against that for planar rotation. The light gray region indicates all neurons which were significant at the $P < 0.05$ range for both radial and rotation motion. The dark gray region indicates all neurons which did not respond selectively to either the rotation or radial motion. The white region on the right of the graph indicates neurons which were only selective to radial motion and not selective to rotation motion, while the upper white region indicates neurons with selectivity to rotation but not radial motion.

populations (Fig. 13E,F). Furthermore, of the 31 different sites sampled, 20 sites had a neuron selective to the radial or the rotation stimulus, but not both. It would be expected if there was a single, heterogeneous population that neurons would be found evenly distributed in all penetrations. A χ^2 test rejects an even distribution at a probability of 0.05.

A similar analysis was performed on all the neurons which had significant alterations in activity at the time of stimulus change. At this time, the monkey is detecting the change from structured to unstructured motion or vice versa. The result of the selectivity analysis was quite different (Fig. 10C,D). Thirteen of the 82 cells were selective to both the radial and rotational components when the stimulus changed from structured to

unstructured motion. When the order was reversed, approximately the same proportion of neurons (17/87) were selective to rotation and radial motion. The proportion of neurons with selectivity to both rotation and radial motion is thus dependent on the phase of the task. More neurons with dual selectivity were found at the time of change in the fraction of structure than at stimulus onset.

The locations of neurons that were selective to optic flow onset and those that were selective to change in the fraction of structure were plotted on the cortical surface (Fig. 13G,H). It was not possible to determine any topographic distribution of the neurons.

The above statistical analysis does not explore or detect the

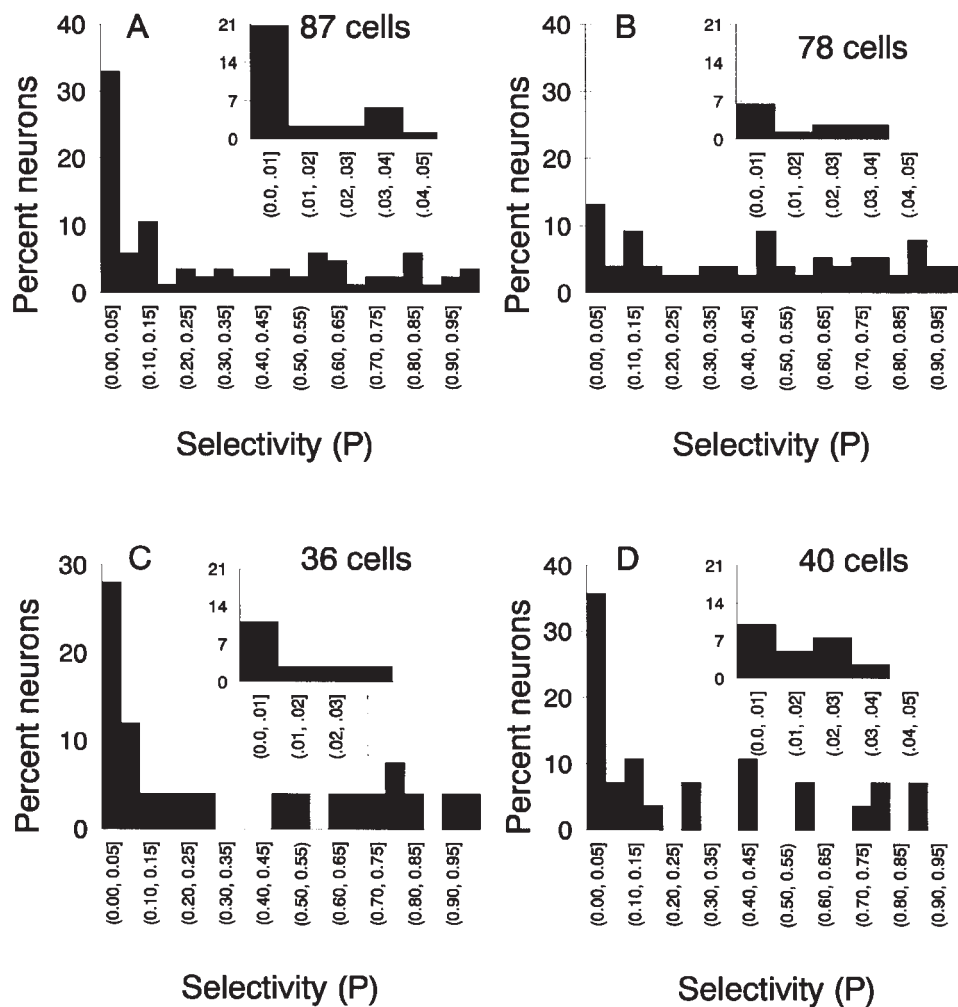


Figure 11. Selectivity indices for planar rotation versus radial motion. Only neurons which were *not* selective to the different radial motions and not selective to the different rotation motions were analyzed. (A) Cells which had a visual response to the onset of the optic flow stimuli when the fraction of structure was 1. (B) Cells which had a visual response to the optic flow stimuli when the fraction of structure was 0. (C) Cells which had a visual response to change from structured to unstructured motion. (D) Cells which had a visual response to the change from unstructured to structured motion. The responses were grouped across all radial stimuli (group 1) and across all rotation stimuli (group 2). A Student's *t*-test was used to evaluate the probability that the groups had different means. The insets show the distribution of *P* values < 0.05.

directional selectivity for radial versus rotation motion. The shortcoming of the prior analysis can best be illustrated with the neuron illustrated in Figure 7. This neuron has a selectivity index >0.05 for both the radial and rotation motion. (The probability of distinguishing between clockwise and counter-clockwise rotation is 0.15 and between expansion and compression radial optic flow is 0.53.) From the above analysis, one would conclude that this neuron does not distinguish between different types of structured motion. However, the peristimulus time histograms in Figure 7A indicate that the neuron is indeed able to provide information as to the different types of optic flow. Clearly additional *post-hoc* analysis is needed to determine whether the amplitude of the rotational responses is different from the response to the radial stimulus, that is to say whether the neuron can distinguish between radial and planar motion, but cannot distinguish between clockwise and counter-clockwise motion.

To examine the selectivity for radial as opposed to planar rotation motion, a second *post-hoc* analysis was performed for all neurons which were not selective to either the radial and rotation motion. The probability that the firing rate of the cell was different for the radial stimuli as opposed to the rotation

stimuli was computed by grouping the data within a stimulus type. This grouping is justified as a *post-hoc* analysis because the standard analysis of variance indicates that the response to the clockwise/counter-clockwise rotations are taken from one sampled group. A Student's *t*-test compared the difference of the means for the rotation versus radial stimuli. The distribution of the selectivities was computed by determining the distribution of the probability values (Fig. 11).

This analysis shows that many neurons have significant differences of the mean firing for rotation versus radial motion, even though these neurons are unable to signal differences within the type of radial or rotation motion. For the neuron of Figure 7A there is a probability of <0.001 that the firing rate with rotation is the same as with the radial motion. An appreciable proportion of the neurons were found that were able to distinguish between the onset of structured rotation and radial flow, while being unable to distinguish between types of either rotation (clockwise versus counter-clockwise) or radial motion (expansion versus compression) (Fig. 11A,B). A similar statement can be made for neurons that were tested with changes in the fraction of structure (Fig. 11C). However, the neurons tested

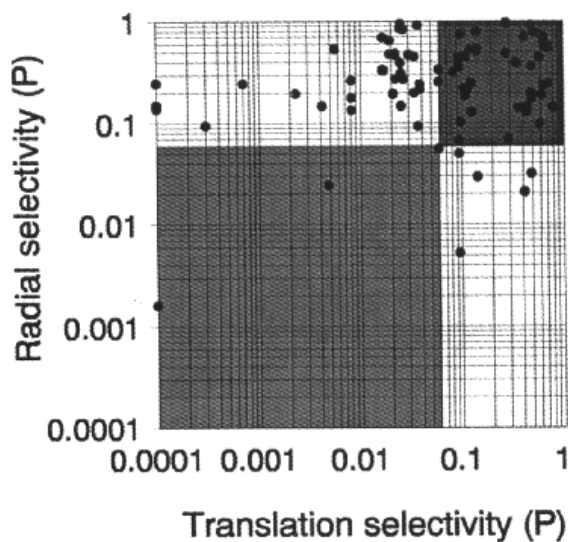


Figure 12. Comparison of selectivity for translation and radial optic flow. The two classes of stimuli were matched for all stimulus parameters. Only the data for stimulus onset is shown. Very few neurons were selective to both translation and radial motion. Further analysis of the neurons that were sensitive, but not selective, to the onset of the visual stimuli (in the darkest region) indicated that many of these neurons could distinguish between translation and expansion optic flows.

with the onset of stimuli with a fraction of structure of 0 had a low proportion of significant neurons (Fig. 11B).

In summary, the selectivity indices suggest that many neurons in area 7a may distinguish between two types of optic flow. These neurons appear to be similar to the single component MST neurons of Duffy and Wurtz (1991a,b, 1995). There appears to be an absence of double- and triple-component neurons that are described in MST. A new class of optic flow selective neurons does appear in area 7a; these can signal the broad class of optic flow while not being able to distinguish the direction of the optic flow. When the animal detects the change in fraction of structure, the tuning of the same population of neurons changes. At the time of key release, there is a greater proportion of neurons selective to more than one type of optic flow than at the onset of the motion.

Relationships Between Various Motion Selectivities

Having established that area 7a neurons are selective to different aspects of motion flow, it was next considered whether optic flow responses were predicted by the response to classical bar stimuli. Neurons were first selected that were tested with at least one of the following stimuli: (i) translating bars, (ii) translation optic flow, (iii) planar rotation or radial motion. In order to make a comparison between the selectivity to any two groups of stimuli (e.g. translating bars versus translating optic flow), all neurons that were tested with both groups of stimuli were culled. The number of neurons were determined that were (i) selective to both groups, (ii) selective to one group and sensitive to the other, (iii) not responsive to one group. When the number of neurons warranted, the selectivity distributions were generated.

Comparison of Translation Selectivity to Classic Bars and to Random Dot Fields

It was of interest to determine whether there was any relationship between the directional selectivity to the translating

bar and to the translating optic flow. This is because the response of the neurons could simply reflect the directional selectivity of neurons earlier in the visual system. For example, neurons of area MT appear to have similar directional selectivity to random dot fields and translating squares (Maunsell and Van Essen, 1983a).

Two-hundred and eighty-eight neurons were tested with both the translating bar and the translating dot stimuli. (In this study, either four or eight directions were utilized for the translating dots.) Of these, 67 were opponent vector neurons (29 inward, 38 outward), 69 were not responsive to the bars, and 153 had motion selectivity to bars that was not opponent vector.

Twenty of the 153 neurons also were directionally selective to the translating dots, with the remainder either responding equally in all directions (20) or not at all (40). Only seven neurons that were directionally selective to both stimuli had a match within 90° between the directional response to the dots and the bars. Thus only a few percent (6/288) of the neurons tested with both stimuli had a similar directional selectivity to classic bar stimuli and optic flow. The distribution of the neurons across the cortical surface indicates that populations that were directionally selective to classical bar stimuli and translating optic flow partially overlapped (Fig. 13C,D).

Comparison of Opponent Vector Tuning and Optic Flow Selectivity

The hypothesis by Steinmetz *et al.* (1987) that opponent vector neurons were also selective to the axis of radial motion was considered next. The set of all neurons that were tested with both of these stimuli was first selected (172 neurons). Twenty-six of these neurons had opponent vector tuning as defined above and five were radially selective to optic flow. However, only one neuron was opponent vector tuned and was selective to radial motion. The possibility that neurons with opponent vector tuning were selective to planar rotation motion was also considered for the 173 neurons tested with both sets of stimuli. Twenty-six of these had opponent vector tuning and 16 were planar rotation selective. However, only one of these neurons was opponent vector tuned and planar rotation tuned. Thus opponent vector selectivity to bars does not appear to predict optic flow selectivity to dot stimuli.

Comparison Between Directional Selectivity to Translating and to Radial Optic Flow Motion

A comparison of the selectivity to optic flow for translating dots and radially moving dots was made since some neurons in MST encode both translation and expansion (Saito *et al.*, 1986; Duffy and Wurtz, 1991a,b, 1995; Lagae *et al.*, 1994). The stimuli used to test the neurons for these conditions were precisely matched with all parameters, including the tangential speed of the points. Eighty-six neurons were tested under both conditions and were visually responsive to at least one of the stimuli. A plot was made of the probability from the standard analysis of variance under the two types of optic flow (Fig. 12). Of this population, 38 neurons were selective to translation optic flow, while seven were selective to expansion radial motion. Only two neurons were selective to both types of stimuli.

Interestingly, there were 43 neurons that responded to the onset of both types of visual stimuli but were non-selective to the direction of motion stimuli. These cells were further analyzed to determine whether they could distinguish between translation and radial motion. For each neuron, the responses to all the translating stimulus conditions were grouped, as were those to

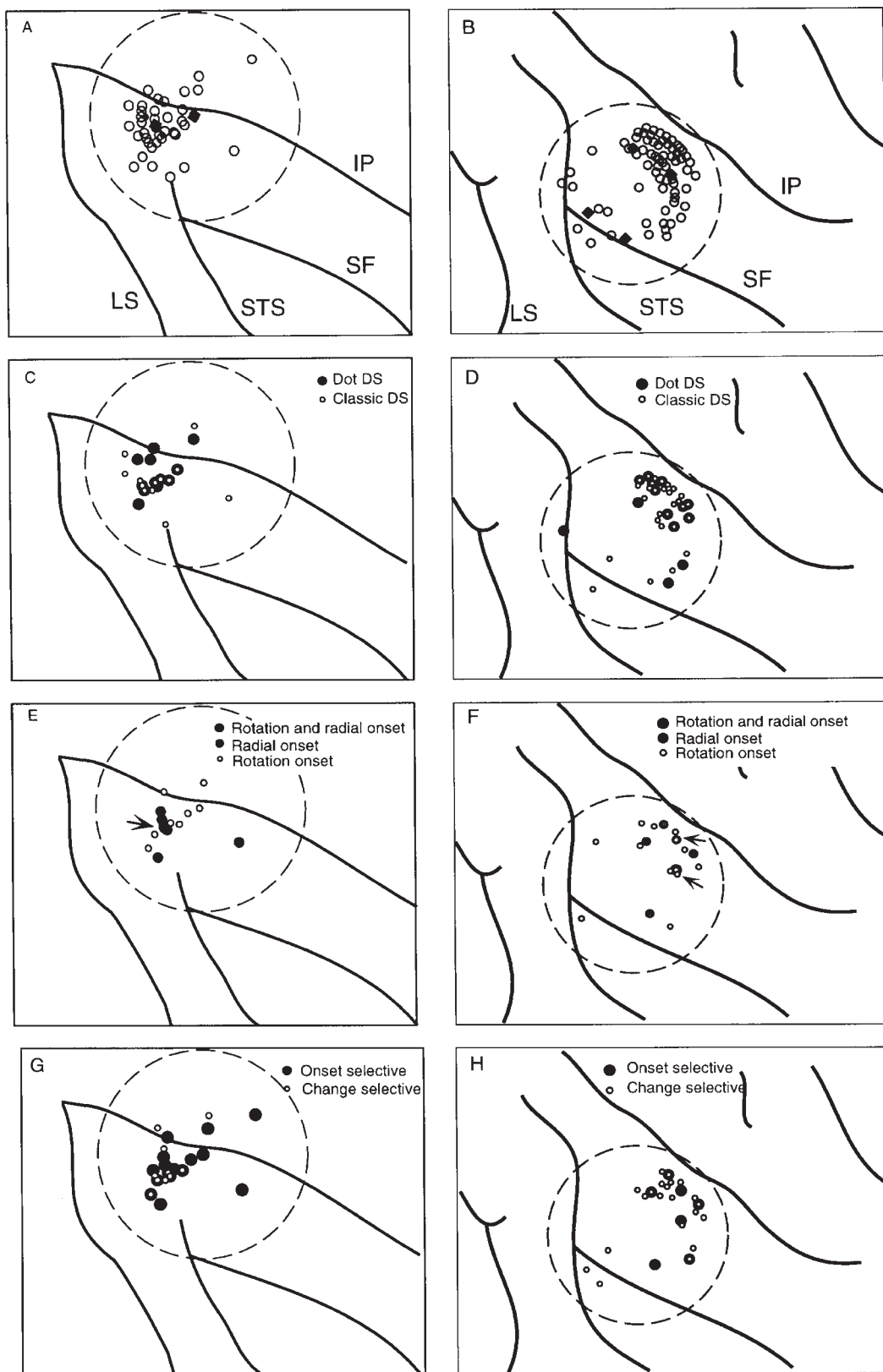


Figure 13. The distribution of various properties of neurons recorded in the right hemisphere (right panels) and the left hemisphere (left panels) of monkey 1. Panels (A) and (B) provide the recording sites. The diamonds indicate the location of the guidepins used for positioning. Panels (C) and (D) illustrate all neurons that were directionally selective (DS) to either the onset of dot and bar stimuli. There was a substantial overlap in the location of these neurons. Panels (E) and (F) illustrate the locations of neurons that were selective to rotation or radial stimuli. The arrows indicate the three neurons selective to both radial and rotation. Panels (G) and (H) indicate the location of neurons selective to the onset or the change of optic flow stimuli. Due to the nature of chronic recordings over many months and shrinkage during perfusion, the actual relations between the sulci and the chamber may vary somewhat (STS, superior temporal sulcus; LS, lunate sulcus; IP, intraparietal sulcus; SF, Sylvian fissure). The diameter of the chamber is 16 mm.

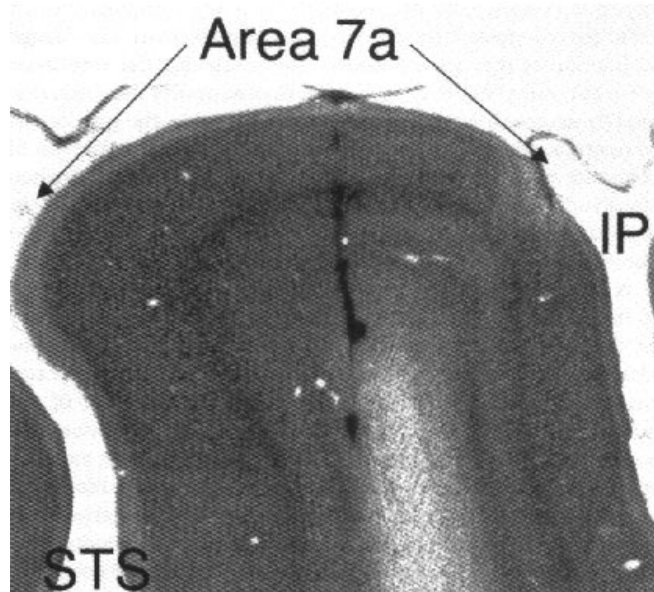


Figure 14. Electrolytic lesion in area 7a from the right hemisphere of monkey O. The lesion in the coronal section illustrates the location of some neurons selective to optic flow. IP, intra-parietal sulcus; STS, superior temporal sulcus.

all the radial stimuli. A Student's *t*-test was then used to determine if the two groups were different. The firing rates for 27 cells were significantly different for the translation and the radial motion stimuli. In summary, half the neurons tested (50%) were selective to either translation or radial optic flow. A third of the neurons tested were able to distinguish radial and translation optic flow, but were not selective to the type of radial flow nor the direction of the translation.

Localization of Recording Sites

Eight-hundred and forty-six neurons were recorded in 208 penetrations in three hemispheres. Lesions were made by passing 5 μ A of current for 5 s through the recording electrodes during the last few weeks of recording. Figure 13 shows a series of lesions located in area 7a (dark streak). Neurons were found at this recording site that are selective to different types of optic flow. After perfusion, but prior to the removal of the skull, the dura was removed and landmarks were taken of the sulcal positions within the chamber to enable orientation of the microdrive coordinate system with the cortex.

The distribution of the recording sites and some of the important properties of the area 7a neurons are presented (Fig. 13). A penetration site was considered to exhibit a particular property if at least one neuron was found to be selective to the stimulus parameter. The depth distribution of these neurons will form the basis of an additional report.

Discussion

We report recordings from neurons in area 7a of the parietal lobe in the behaving monkey in response to a variety of visual stimuli that are involved in the analysis of optic flow. These results indicate that the inferior parietal lobule is critical in the analysis of extra-personal space using motion.

The present study quantifies the terms 'sensitive' and 'selective' with respect to visual stimuli based on criteria initially suggested by Van Essen (1985). This analysis is based on the assumption that the mean rate represents the strength of

response of the neuron. Other measures may be used (Gerstein *et al.*, 1985; Strehler and Lestienne, 1986; Optican and Richmond, 1987; Siegel, 1990). Without suggesting that these other measures should be rejected as alternatives, the use of the mean firing rate is a simple, easily replicated measure with well understood statistical properties. To compute the mean rate a duration of 500 ms was generally used. Different durations may have been used to emphasize the phasic or tonic nature of the response (cf. Duffy and Wurtz, 1991a,b, 1995); however, the chosen duration combines both the tonic and phasic responses. Because of this choice, it is possible that there were clear differential responses of the neuron to a few spikes occurring over a very short time period which were not detected as significant using the 500 ms duration. However, rather than modifying the analysis on a cell-by-cell basis, the choice of a fixed duration was used for a conservative analysis of the data.

In addition, this work introduces the inclusion of variance in the selectivity measurement for an individual neuron, rather than simply using the mean as often is found in the literature (Maunsell and Van Essen, 1983b; Mikami *et al.*, 1986; Graziano *et al.*, 1994). This approach should lead to the development of computational models in which the contribution of each neuron to a distributed representation is scaled by its probability, leading to a probabilistic (i.e. Bayesian) approach to population measures. With this interpretation, neurons with 'probability values' >0.05 would contribute to the population response, and the distributions of probability given here would be able to assist computational neuroscientists in the creation of Bayesian models. Whether the cortex uses such information is an open question (Woodward, 1960; Födiák, 1992; Julesz, 1995; Landy *et al.*, 1995; Geisler and Albrecht, 1995).

Classical Stimuli

We have demonstrated opponent vector neurons using similar moving bar stimulus as prior workers (Motter *et al.*, 1987; Steinmetz *et al.*, 1987). Different statistical analyses were used here to select neurons that exhibited opponent vector properties. In the earlier studies, bin-by-bin Student's *t*-tests were utilized to compare the selectivity to motion in different directions for the same retinal location. These multiple comparisons require the use of correction factors. To avoid these corrections, a two-way analysis of variance was performed. Although the Student's *t*-test analysis was not performed on the neurons identified as opponent vector by the analysis of variance, it appears that both analyses identify the same population of neurons in terms of the qualitative appearance of the neurons and the proportion of neurons deemed opponent vector in the two studies. Furthermore, both studies have revealed a population of opponent vector neurons that were also directionally selective.

The present study adds to the prior description by further examining the properties of those neurons that did not fit the opponent vector description. These were of two groups – those that were uniformly responsive to motion throughout the visual field and those that were directionally selective throughout the visual field. The latter group of neurons were further examined with respect to their directional selectivity during the inward or outward sweep of the bar. This was to determine if they were simply uniformly directionally selective neurons as described in the cortical area MT. Few of the neurons tested had motion-selective properties similar to that of area MT, suggesting that additional processing of the visual signals from MT to the

area 7a neuron via MST or LIP (Seltzer and Pandya, 1984; Cavada and Goldman-Rakic, 1989; Andersen *et al.*, 1990a) has occurred.

Optic Flow Stimuli

The optic flows used in the study of structure from motion were derived from original descriptions by Gibson (1957, 1966), Ullman (1979), Koenderink (1986) and others in order to represent the mathematical transformations of the external environment upon the retina by egocentric motion. These mathematical transformations are called *translation*, *div*, *curl* and *def*, corresponding to translation motion, radial motion, planar rotation and shearing motion. These four transformations can be used as a set of orthogonal basis functions to represent any flow (either contrast or motion) and are quite similar to a mathematical basis set referred to as Lie germs (Lie, 1893; Hoffman, 1966; Gallant *et al.*, 1993).

Area 7a neurons are directionally selective to the simplest of the optic flow form of Lie germs – translating optic flow. The stimuli have constantly changing form cues because the dots of the random dot display constantly flicker on and off at different positions. The luminance border of the displays were round and constant across all stimulus conditions. Although such neurons have been found in other cortical areas, this is a novel finding for area 7a. Due to the properties of the stimuli, this selectivity can incontrovertibly be attributed to the optic flow. Recently, two positron emission tomography studies have reported changes in regional blood flow in human parietal cortex with translating full field optic flow or random motion (Cheng *et al.*, 1995; Bonda *et al.*, 1996). The present results may provide the physiological single cell exemplars that underlie the increase in the activation of parietal cortex in human subjects.

A number of lines of evidence derived from use of the other optic flow stimuli suggest that area 7a neurons are selective for planar rotation and radial optic flow. First, these neurons are directionally selective to the type of optic flow at motion onset. At onset the display changes from a dark one to one full of moving, flickering dots. The selectivity of the neurons for one or more types of the optic flow indicate that the neurons were not simply coding the onset of the visual stimulus. Careful attention was paid to the statistical analysis to ensure that the selectivity was not caused by differential distributions of speeds or curvature of the trajectories as may have been the case in other studies (Saito *et al.*, 1986; Duffy and Wurtz, 1991a,b, 1995; Lagae *et al.*, 1994).

A second line of evidence indicating that these neurons are selective to optic flow is the response of the neurons when the monkey was performing the structure from motion psychophysical task (i.e. when the animal was detecting the change in fraction of structure). Following the change, but prior to key release, there was no variation in the average luminance of the display. Only the fraction of structure of the radial or rotational optic flow changed. Many neurons showed statistically significant changes in activity that were correlated to the change in fraction of structure. The change in rate occurred after the change in fraction of structure, yet before the release of the key by the animal. Over this time period, the animal's observable external behavioral state was constant – the central red point was fixated and the key remained held. In some neurons, there was a change in activity that was independent of the type of optic flow. These neurons may encode either the ensuing release of the key or the change in the fraction of structure.

In another population of neurons that responded when the fraction of structure changed, the response of the neuron also

depended on the type of optic flow. This latter population may be in part modulated by the upcoming key release or the change in fraction of structure; however, the result that these neurons were also tuned to the type of optic flow supports the claim that area 7a neurons encode optic flow. Interestingly, the proportion of neurons selective to the optic flow at the time the fraction of structure changed was greater than the proportion found when the structured flow initially came on. This would be consistent with the task requirement for attention to be on the optic flow altering the selectivity of the population of area 7a neurons.

A third line of evidence for the role area 7a neurons may play in the analysis of optic flow may be obtained from the synchrony of the change in firing rate and the time that the stimulus changes. Qualitatively it appears that the firing rate increases prior to the animal's behaviorally indicated detection of the stimulus and generally peaks at the time the key is released. In some cells, the synchronous peaking of firing rate and key release suggests that these neurons may be receiving a reafferent signal indicating the motor act. Thus one possible scenario is that the area 7a neurons are receiving neural signals encoding the type of optic flow from motion processing cortices (Saito *et al.*, 1986; Duffy and Wurtz, 1991a,b, 1995; Lagae *et al.*, 1994) and signals indicating the progression of the animal's behavior from premotor and subcortical structures (Andersen *et al.*, 1985b, 1987). To date, unstructured motion has not been tested in MST or other cortical regions, so the source of the selectivity for unstructured motion and the source of the signal that indicates the change from unstructured motion to structured motion remains open. Thus the qualitative correlation in time between the change in fraction of structure and the behavioral detection is consistent with a role of area 7a neurons in the perceptual task.

The fourth and final line of evidence for the selectivity of these neurons to different types of optic flow was obtained using the degraded, unstructured motion stimuli. The activity of the neurons showed a statistically significant differentiation between unstructured optic flows. This is a novel finding in monkey visual cortex and was unexpected as the unstructured motion has little perceptual salience to the naïve observer. This result lead to further behavioral investigation of the optic flow stimuli with a fraction of structure of 0. Although there are no formal psychophysical studies on the primate's ability to determine direction of optic flow from the unstructured motion, extensively trained human observers can correctly report the direction of flow. It is possible that the monkeys will make the same judgment. Thus the directional selectivity of the area 7a neurons to unstructured motion would be commensurate with an exquisite selectivity to optic flow which might serve as the neural correlate of the perceptual event.

An alternative explanation for the directional selectivity to the unstructured motion is that there are specific features in the random dot patterns that activate the neuron. In area MT, such an explanation may account for specific temporal patterns of interspike intervals that could be found on a trial-by-trial basis (Bair *et al.*, 1994). Visual inspection revealed no such patterns in the interspike intervals of area 7a neurons with the optic flow stimuli. Furthermore, the random seeds used to create the optic flow fields were changed each day of recording, which would reduce the likelihood of a particular aberrant stimulus dominating the entire study.

Modulation of Selectivity for the Neuronal Population by Locus of Attention

Two sets of directionality measures were obtained when the

animal was performing the structure-from-motion task – during stimulus onset, and during the change in fraction of structure. During these two phases of the task the animal may direct its attention differentially. At stimulus onset, the subject could be solely attending to the fixation point. At the change in fraction of structure, he could be solely attending the optic flow stimulus. Interestingly there were different distributions of selectivity to the optic flow during these two phases of the task. This suggests that the attentional state may modulate the optic flow selectivity of the neuron. This change in selectivity could be modulated by subcortical projections (Mesulam *et al.*, 1977; Seltzer and Pandya, 1984; Andersen *et al.*, 1985a, 1990a; Asanuma *et al.*, 1985; May and Andersen, 1986; Selemon and Goldman-Rakic, 1988; Cavada and Goldman-Rakic, 1989, 1993), via other cortical projections, or via cortical circuitry intrinsic to area 7a (Motter and Mountcastle, 1981; Mountcastle *et al.*, 1981, 1987).

Source of Neural Signals for Area 7a Optic Flow Selectivity

Neurons selective for translation, radial or rotation optic flows have been found in area MT and MST by others (Saito *et al.*, 1986; Tanaka *et al.*, 1986; Duffy and Wurtz, 1991a,b; Lagae *et al.*, 1994) using somewhat different stimulus conditions. MT projects to MST and LIP, which in turn project to area 7a (Pandya and Seltzer, 1982; Andersen *et al.*, 1985a, 1990a; Cavada and Goldman-Rakic, 1989). These projections might serve as a conduit for signals encoding structured optic flow. Little is known about the motion-selective properties of LIP (Andersen *et al.*, 1990b; Schaafsma *et al.*, 1995); however, it is possible to compare the neuronal subpopulations of area 7a and MST.

MST neurons respond to one or more types of optic flow (Saito *et al.*, 1986; Duffy and Wurtz, 1991a,b, 1995; Lagae *et al.*, 1994). Some area 7a neurons appear to be tuned primarily to only one type of optic flow (e.g. expansion versus compression). We term these flow-particular (FLO-P) neurons. These are similar to the single component neurons of area MST. Some properties of area 7a neurons differ from those of area MST. First, there were very few area 7a neurons which are selective to both radial and planar rotation, whereas most neurons in area MST respond to more than one optic flow (termed MST double- or triple-component neurons). Second, there is also a novel class of area 7a neurons consisting of about one-quarter of those responding selectively to optic flow. These neurons appear to differentiate between radial motion and planar rotation while being unable to distinguish the direction of the motion of either (e.g. Fig. 7). These neurons, which we term flow-general (FLO-G), represent a novel class of neurons from those of area MST. Thus area 7a has taken the analysis of motion one step beyond MST: in one sense the broadly distributed motion selectivities of MST have given way to neurons that represent singular aspects of the moving visual environment.

This new reduced representation of the moving visual environment was also seen in the comparison between radial and translation motion. These two stimuli were completely matched with respect to the straightness of the motion trajectories and the speed of movement. Unlike MST, just 2% of the neurons in area 7a were selective to both radial and translation optic flow. The majority of the neurons were selective to only one of these stimuli (i.e. FLO-P), or had signals which could only be used to differentiate between radial motion and translation motion (i.e. FLO-G) without differentiating the direction of either the radial or translation motion.

Thus it appears that area 7a neurons have two types of

neuronal populations to represent optic flow. The FLO-P population responds with a selectivity across one type of motion flow, be it translation, expansion, compression, clockwise or counter-clockwise rotation, and may represent direct projections from MST. The FLO-G population is able to distinguish between the type of optic flow without being selective to the direction of optic flow. A neuron in this FLO-G population might carry a visual signal indicating that the subject was moving along a line perpendicular to the frontal plane without being able to signal if the subject was moving forwards or backwards. The direction of motion would be carried in the distributed responses of the FLO-P neurons.

In both the earlier MST studies and the present area 7a study, the question arises as to the mechanism for the optic flow selectivity. MST neurons maintain their optic flow selectivity regardless of the locus of the flow field (Saito *et al.*, 1986; Duffy and Wurtz, 1991a,b, 1995; Lagae *et al.*, 1994). Using methods similar to the MST studies, placement of the center of optic flow in multiple retinotopic locations does not alter motion selectivity for area 7a neurons (Siegel and Read, 1994; H.L. Read and R.M. Siegel, in preparation). In MST, additional evidence has been presented that the selectivity arises from non-linear interactions from different regions of the receptive field of the neuron and not from directional selectivity to local patches of motion (Saito *et al.*, 1986; Tanaka *et al.*, 1986; Duffy and Wurtz, 1991b; Lagae *et al.*, 1994) as proposed by Siegel (1988) based on modeling studies. In area 7a, the presence of FLO-G neurons argues against the optic flow selectivity arising from local directionally selective patches. However, it will be necessary to map out the receptive fields of area 7a neurons in detail with small patches of motion in order to test further this particular hypothesis for motion selectivity in area 7a.

Comparison of Selectivity to Classic Bar Stimuli and Optic Flow Stimuli

Having established that the methods above were able to delimit both opponent vector and radial motion optic flow-selective neurons, the question as to the equivalence of the two populations was addressed. Very few neurons that were opponent vector tuned were also selective to optic flow. One interpretation of this result is that opponent vector neuron selectivity does not predict the response to optic flow. However, the optic flow stimuli in this study differed in a number of substantial ways from the more classical moving bar stimuli described above.

First, while the bar stimuli had moving luminance boundaries, the optic flow stimuli were built up of many small dots, with the average luminance within the movement field constant (i.e. the spatial frequency distributions of the two displays were different). Second, the speed of motion in the bar was ~10 times that of the optic flow display. Third, in the moving bar experiment the monkey was required to attend to the central fixation point, while in the optic flow study he was required to attend to the dots. Fourth, the total luminance for the bars was ~100 times that of the optic flow stimulus.

Although these are substantial differences, counter-arguments can be presented for all but one possibility. For the first point, neurons are found in MT that have similar directional selectivity to bars and random dot fields (Maunsell and Van Essen, 1983a). For the second point, opponent vector neurons do not drastically alter their directional properties with speed (Motter *et al.*, 1987). Third, attention appears primarily to alter the strength of the response rather than its selectivity to visual stimuli (Lynch *et*

al., 1977; Robinson *et al.*, 1978; Motter and Mountcastle, 1981; Mountcastle *et al.*, 1981; Moran and Desimone, 1985; Robinson *et al.*, 1986; Posner and Presti, 1987; Fuster, 1990). It is only the issue of luminance and size of the display which have no counter-example in the literature and will require additional control experiments.

Neurons were also found using the classical bar stimuli that were directionally selective to translating bars, but did not fit the opponent vector definition. It is possible that these directionally selective cells represent an indirect projection of MT neurons via LIP or MST to 7a (Pandya and Seltzer, 1982; Andersen *et al.*, 1985a, 1990a; Cavada and Goldman-Rakic, 1989). However, a comparison of the directional selectivity to translating optic flow and classical stimuli indicates that the directional selectivities are different with the two types of stimuli unlike those of area MT (Van Essen *et al.*, 1981; Maunsell and Van Essen, 1983b). This conclusion is subject to the same cautions as to the role of speed, luminance and attention as noted above.

A comparison of the locations of these neurons is not consistent with two physically separate populations or subdivisions in area 7a. Indeed penetrations were found that yielded both classical bar and optic flow-selective neurons. However, localization is difficult over the 1–2 years of recordings from these animals. A laminar analysis might reveal differences, but this is difficult to do with precision.

Implications for the Role of Area 7a Neurons in Spatial Perception

A number of properties of the area 7a neurons could be used for spatial perception and spatial localization depending on the motion of the observer relative to the environment. The processing of motion in area 7a differs from the other regions that project to area 7a and may represent a synthesis of the representations present in MT, MST and LIP to form novel representations of motion (the FLO-G population). The flow particular neurons could be used to indicate the direction of a particular motion (clockwise versus counter-clockwise rotation), while area 7a optic flow general (FLO-G) neurons may simply indicate that a particular type of motion is occurring without indicating its direction (rotation). This latter novel motion representation can be thought of as a rectifying operation upon collections of neurons from area MST. The FLO-G neurons could in principle be used to extract the optic flow uniquely tied to a particular egocentric movement. Furthermore, these studies provide a new, biologically motivated approach for modeling egocentric motion from optic flow in which the signals are not represented as an orthogonal 'Lie-germ like' basis set, but as a collection of neurons that represent different environmentally relevant aspects of motion perception.

It is curious that motion-processing deficits are not observed in conjunction with parietal damage in human patients (Critchley, 1953; Vaina, 1994) as are seen with extensive occipital-temporal damage (Zihl and von Cramon, 1983; McLeod *et al.*, 1989; Baker *et al.*, 1991). It may be that different tests are needed to tease out difficulties in spatial perception from motion. One possible clinical test would be to require patients with parietal syndrome to extract spatial information from optic flow. A prediction of our work is that the patient would not show a frank motion deficit, but would be unable to localize the center of a radially expanding flow pattern in their neglected hemifield. Given that area 7a projects directly to prefrontal Walker's area 46 and 8 (Seltzer and Pandya, 1984; Cavada and Goldman-Rakic, 1989; Andersen *et al.*, 1990a), damage to the parietal cortices

may prove to alter the guidance of eye and other body movements relative to the moving environment. Further understanding of the involvement of inferior parietal cortex in motion perception may then aid in developing strategies to assist those with parietal syndrome.

Notes

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