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Response properties of PMLS and PLLS neurons to simulated optic flow patterns

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Abstract

The processing of optic flow information has been extensively investigated in the medial superior temporal area (MST) of the macaque. In the cat, the posteromedial area and the posterolateral area in the lateral suprasylvian cortex (PMLS and PLLS, respectively) have been suggested as likely participants according to their direction preferences to moving objects. In the present study, 203 PMLS and 123 PLLS neurons were tested with simulated optic flow patterns composed of random dots (including expansion and contraction, clockwise and counter-clockwise rotation, and translation) and moving bar stimuli. About 90% of the neurons were found to be excited by the optic flow stimuli and most of them were multiple-responsive to different flow patterns. Only 20–25% of the cells were selective to different optic flow modes, and in general, the direction preference was fairly modest. The selective cells showed stronger directionality to both flow field and moving bar than nonselective cells. However, the optic flow response properties in the PMLS and PLLS were not well correlated with the direction preference to moving bars. In accordance with previous findings, the PMLS was analogous to the middle temporal area of the macaque in many respects. As for the PLLS cells, they were sensitive to fewer types of stimuli, but responded better and more selectively to radial motion. All these results suggest that the two lateral suprasylvian areas are unlikely to be specialized for the analysis or discrimination of different flow patterns, but may play some kind of relay role in optic flow information processing.

Introduction

Optic flow fields are the image motion patterns that an observer encounters during locomotion, usually composed of multiple objects and covering the entire visual field. These patterns are critical for indicating the direction of locomotion, and also provide cues about the structure of the environment (Gibson, 1950; Koenderink, 1986; Wurtz, 1998). During the past two decades, intensive efforts have been made to explore the neural basis of optic flow analysis, especially in the medial superior temporal area (MST) of the macaque. MST neurons have been shown to respond to planar, radial and circular motion (the basic components of flow fields), some of them with selectivity for particular flow patterns (Saito *et al*., 1986; Sakata *et al*., 1986; Tanaka & Saito, 1989; Tanaka *et al*., 1989; Duffy & Wurtz, 1991a; Orban *et al*., 1992; Graziano *et al*., 1994; Lagae *et al*., 1994). These properties make MST neurons capable of processing optic flow information, and the recent report by Britten & van Wezel (1998) provides preliminary but direct behavioural evidence that this cortical area is actually involved in the analysis. In the cat, attention has been focused on the lateral suprasylvian cortex (LS), since the direction preferences in this area were found to be biased for matching the radial motion seen in flow fields (Blakemore & Zumbroich, 1987; Hamada, 1987; Rauschecker *et al*., 1987; von Grünau *et al*., 1987). However, few direct investigations have been conducted, except for the studies using optic flow movies designed to simulate natural scenes (Kim *et al*., 1997; Mulligan *et al*., 1997; Sherk *et al*., 1997). These experiments were mostly carried out in the posteromedial area of the LS (PMLS), and did not include circular motion in the stimulation.

Although there are other views on the subdivision (Sherk, 1986; Grant & Shipp, 1991), it is most widely agreed that the LS cortex consists of six visuotopically organized areas, including the PMLS and the posterolateral part (PLLS; Palmer *et al*., 1978). The two areas are similar in some general features, but different in their detailed receptive-field properties and connectivities (for reviews see Rosenquist, 1985; Dreher, 1986; Spear, 1991). The PMLS is usually considered an analogue of the middle temporal area (MT), which is at a lower level than the MST in the visual motion pathway of the primate (Zeki, 1974; Felleman & Van Essen, 1991; Payne, 1993). However, the possible counterpart of the PLLS remains unclear, though the MST and the fundal superior temporal area were suspected to be candidates (Payne, 1993). Since the cat has not been systematically tested with simulated flow patterns similar to those applied to the macaque, little is known about the similarities and differences between the two species and between the two LS areas in optic flow processing. The present study is aimed at these still unanswered questions.

In an earlier qualitative study in our laboratory, many PMLS cells were found to be sensitive to simple radiating or rotating patterns (Xie *et al*., 1997). In order to obtain further quantitative results, we improved the quality of flow stimuli, tested single cells in the PLLS, as well as the PMLS, for their responsiveness and preferences for the stimulus mode and direction, and analysed the differences between the two areas. The results are compared with previous findings in the MT and MST, and the possible functional implications and underlying mechanisms are discussed in the present report.

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Materials and methods

Animal preparation and maintenance

A detailed description of the procedures has been previously reported (Wang *et al*., 1995). Adequate measures were taken to minimize pain and discomfort, in compliance with the NIH guidelines on the care and use of laboratory animals. Briefly, experiments were carried out on 38 normal adult cats (weighing 2.0–4.5 kg) which were also used for recordings for other purposes. Anaesthesia was induced with ketamine hydrochloride (20–30 mg/kg, i.m.). Surgery was performed to enable continuous infusion of urethane (10–20 mg/kg/h), gallamine triethiodide (10 mg/kg/h) and glucose (200 mg/kg/h) in Ringer's solution through a foreleg venous cannula (~ 4.0 mL/h) and artificial ventilation through the trachea. Body temperature, end-tidal CO_2, electrocardiogram, and sometimes, electroencephalogram were continuously monitored. Pupils were dilated with homatropine and nictitating membranes were retracted with phenylephrine hydrochloride. The eyes were protected using contact lenses of appropriate refractive power and covered with 4 mm artificial pupils. The locations of the area centralis and optic disks were checked frequently with a reversible ophthalmoscope.

Craniotomy was performed over both banks of the middle suprasylvian sulcus at the stereotaxic coordinate P2-A6. The divisions and nomenclature of Palmer *et al.* (1978) were used to decide the position of the PMLS and PLLS. Glass-coated tungsten microelectrodes were used to penetrate the cortex tangentially through the medial or lateral wall of the sulcus, so that the electrode tracks were roughly parallel to the cortical surface folded inside. Neuronal activity was amplified and filtered with a programmable amplifier (CyberAmp 380, Axon Instruments, Foster City, CA, USA), and fed online into a computer via a laboratory interface (model 1401 plus with a plugged-in 1401-18 discriminator card, Cambridge Electronic Design, Cambridge, UK). With the accompanying multichannel data acquisition software (Spike 2, Cambridge Electronic Design, Cambridge, UK), the single-unit action potentials were isolated and stored as firing times. The stimulus markers were also sent via the interface and recorded through an individual channel to synchronize the data.

Visual stimulation

For each neuron, manually controlled light or dark stimuli (small patch, short bar, etc.) were first employed to estimate the position and size of the receptive field, the approximate preferred direction and the optimal velocity. Most of the cells had relatively large receptive fields of over $10° \times 10°$. However, the borders of the fields were difficult to determine exactly with the hand-held stimuli, and we did not try to measure them quantitatively to save time.

In quantitative sessions, the visual stimuli were generated on-line by a PII 266 computer with a graphics acceleration card (WinFast 3D L2300, Leadtek Research, Taipei, Taiwan) installed inside, and displayed on a 21-inch monitor (Brilliance 201P, Philips Elec. Industries, Taoyuan, Taiwan). The screen was placed 57 cm in front of the animal and covering the receptive field optimally. The optic flow patterns were composed of small light dots (illuminance 10–20 cd/m^2, diameter 0.05–0.5°) against a dark background (0.5 cd/m^2). Usually 250 dots were distributed randomly within a virtual circular window subtending 30° in diameter, but for some cells the dot number and window size were adjusted proportionally for a better coverage of the receptive field to elicit good responses. All dots started moving as soon as they appeared on the screen, and once a dot travelled out of the window, it was immediately assigned a new random location within the circle.

As shown in Fig. 1 of Duffy & Wurtz (1991a), all motions in the three-dimensional space consist of combinations of translation along and/or rotation around the X, Y, and Z axes, which could be simplified into three categories of basic optic flow components: translation, rotation, and expansion/contraction (i.e. radiation). In the present study the three basic optic flow modes were simulated, each category with two possible directions opposite to each other. Therefore the neurons were tested with six types of flow stimuli: rotation (clockwise, counter-clockwise); radiation (expansion, contraction); and translation (forward, backward). A schematic illustration is depicted in Fig. 1. In forward translation, all the dots drifted along the preferred direction and at the optimal velocity, which had been qualitatively decided in advance. In backward translation, the dots moved along the opposite direction but at the same velocity. In rotation and radiation modes, the moving direction and velocity were varied frame by frame depending on the dot's instantaneous location. For each dot, the direction was always tangential in respect to the centre of the display window in rotation mode, and was radial in radiation mode. In both modes, the velocity was proportional to the dot's distance to the centre, with the mean value kept the same as that in translation mode. In radiation mode, the dot size was also varied with its position, simulating the approaching or receding objects in the field during locomotion.

The six types of stimuli and a blank background for measuring spontaneous activity as a control were pseudorandomly sequenced to compose a complete trial. Every sweep lasted either 2000 or 3000 ms, succeeded by a pause period of 500 or 1000 ms (blank background). Five or 10 such trials were repeated for averaging the activity. Before the optic flow measurement, cells were tested with moving bar stimuli for obtaining a direction tuning curve, in order to check if there is any relationship between the direction selectivity and the responses to the flow components. The conventional method was used; a light moving bar of optimal size and velocity was swept across the receptive field in 24 pseudorandomly interleaved directions at 15° steps. Similarly, a blank control test was also included, and the whole repertoire was repeated for 5 or 10 trials.

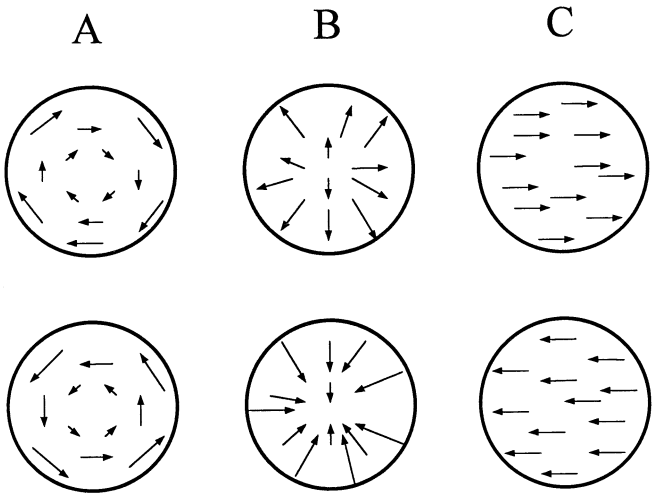

FIG. 1. Schematic illustration of the three basic optic flow modes used in the experiments. (A) rotation, (B) radiation, (C) translation. Each mode has two possible directions opposite to each other. Each arrow represents the instantaneous direction and velocity of a single dot at the location. As shown by the arrow length, the velocity was proportional to the distance to the centre of the circular window for rotation and radiation, with the mean value kept as the same as that for translation. The forward translation was along the approximate preferred direction and velocity, estimated with hand-held stimuli in advance.

Data analysis

Neuronal response strength was measured as firing rate, determined over the duration of stimulation. Many cells fired very vigorously during a short period soon after stimulus onset (see examples in Fig. 2). These spikes might be characteristic phasic responses to optic flow stimuli in some cases, but it was also plausible to suppose that they were, at least partly, evoked by the general luminance variation on the screen (for example see Fig. 2B). This possibility was even more realistic since our optic flow patterns were large field light stimuli, therefore the initial transient responses within 0–200 ms were excluded from spike counting.

A cell was considered to be responsive to a stimulus if the significance level of $P < 0.05$ was reached in a Student's *t*-test, in which the evoked activity during repeated presentations of the stimulus was compared with the activity recorded in an equal number of blank control trials. Besides normal excitatory responses, inhibitory effects were identified in a few cases in which the evoked activity was significantly below the spontaneous level (for example see Fig. 2A).

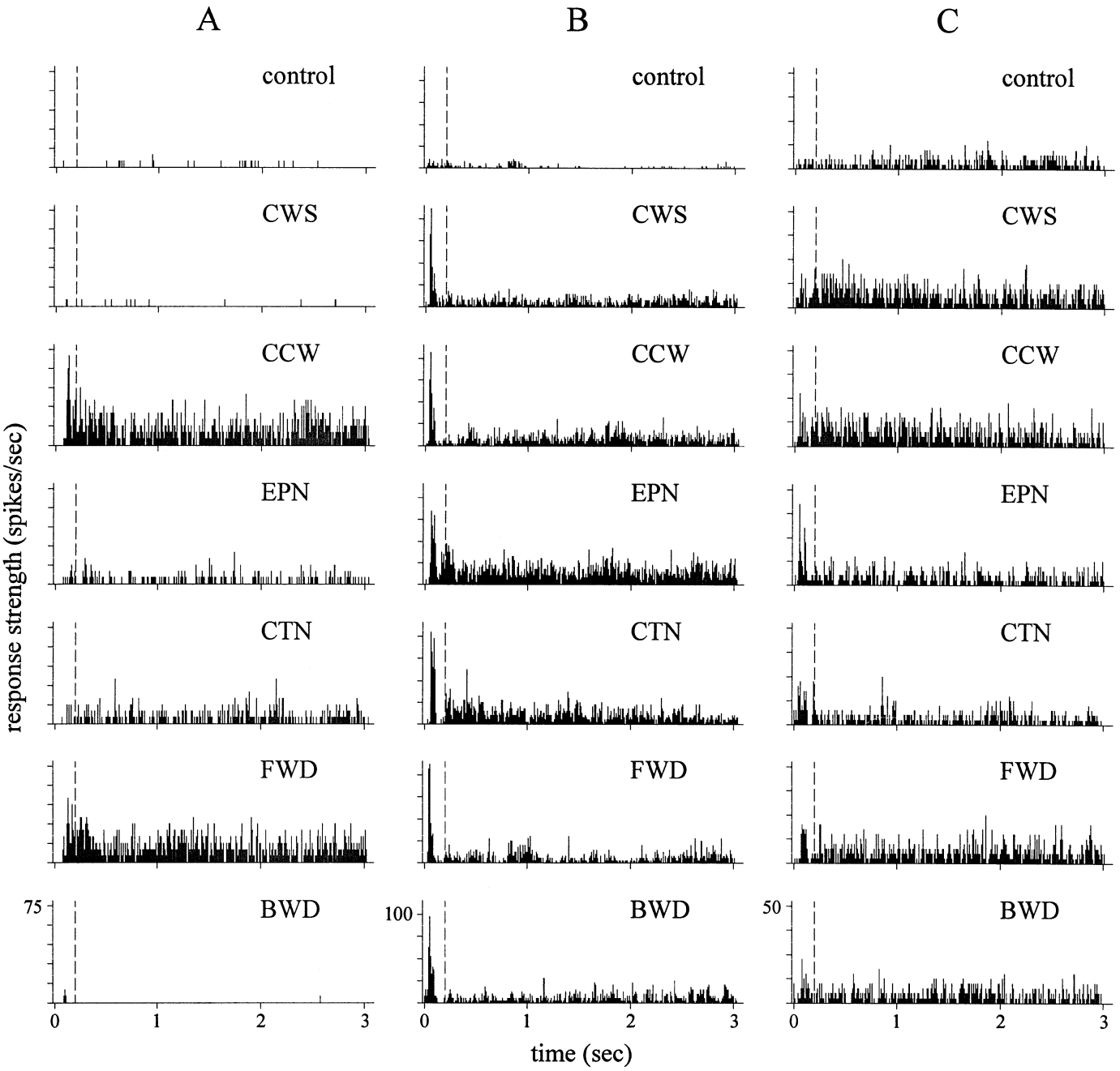

FIG. 2. PSTHs for three typical LS neurons. (A) A PMLS cell, significantly excited by counter-clockwise rotation (CCW), expansion (EPN), contraction (CTN) and forward translation (FWD), but inhibited by clockwise rotation (CWS) and backward translation (BWD). The cell had significant directionality to all the three optic flow modes but was not selective to any of them. (B) A PLLS cell, excited by all the six stimulus types presented. However, its responses to expansion were significantly higher than those to all the other stimulus types, so it displayed clear selectivity and directionality to radiation mode. Note that the firing of the cell was very strong during the first 200 ms after stimulus onset for all the stimuli (left of the dashed lines), which was probably caused by the general luminance changes on the screen instead of by the intrinsic characteristics of the stimuli. (C) Another PMLS cell, significantly excited by CWS, CCW and FWD, but with neither directionality nor selectivity to these optic flow modes.

The Student's *t*-test was also applied to each responsive cell to determine the significance of optic flow mode selectivity and directionality. Responses to different optic flow categories and to opposite directions were compared with each other. If the responses to a certain type of optic flow stimulus were significantly higher than those to the other types (except for that in the same category but with the opposite direction, which is treated in terms of directionality) as well as the spontaneous activity, the cell is regarded as significantly selective to this optic flow mode. Also, if a cell's responses to the two opposite directions of a certain flow mode were significantly different, the directionality of this cell is regarded as significant for this mode.

The direction tuning curve to moving bar was measured for all but seven cells. Among them eight cells did not respond significantly to the bar moving along any direction (*t*-test, $P > 0.05$), so they were excluded from further analysis on direction selectivity. For each responsive cell, the direction index was calculated as $DI_{bar} = 1 - R_{NPD}/R_{PD}$, where R represents the response strength for the preferred direction (PD) or its opposite direction (NPD). The spontaneous activity was subtracted prior to this calculation.

Non-parametric statistical tests were applied to check the significance of the differences between two or among multiple groups of data. The two-sample Mann–Whitney *U*-test was used for comparisons between PMLS and PLLS cells, the multisample Kruskal–Wallis χ^2-test, for comparisons among response properties to different visual stimuli.

Histology

After some recordings, electrolytic lesions were induced by passing a small direct current (10 μA for 10 s) through the electrode. At the end of the experiments, the animals were deeply anaesthetized and perfused for histological identification of the electrode tracks.

Results

Altogether, 203 neurons were successfully recorded in the PMLS, and 123 neurons in the PLLS. The receptive field properties were generally similar to what had been reported previously by others (Spear & Baumann, 1975; Camarda & Rizzolatti, 1976; Blakemore & Zumbroich, 1987; Rauschecker *et al*., 1987; von Grünau *et al*., 1987; Yin & Greenwood, 1992; for review see Spear, 1991). The receptive fields were usually circular or elliptical in shape, with diameters ranging from less than 10° to as large as 30° or more. Neurons in both areas were motion-sensitive, most of them were direction-selective and preferred relatively higher velocities (10–40 °/s). Generally, PLLS neurons tended to have larger receptive fields and were more active than PMLS neurons (mean spontaneous activity 12.59 ± 16.45 vs. 9.67 ± 8.87 spikes/s, for visual responses see Fig. 3), though many of the differences were insignificant due to the divergence of data especially for PLLS cells (larger standard deviations, see Fig. 3).

The overwhelming majority of the cells in our sample responded to at least one type of optic flow patterns by the criteria described in Methods. The responses of three typical cells are illustrated in Fig. 2, and the properties of the whole sample are elaborated in the following sections.

Inhibitory responses

Of all the neurons studied, there were only a small minority, i.e. 18 PMLS cells (8.9%) and four PLLS cells (3.3%), that showed significant inhibitory responses to one or more types of optic flow stimuli. Totally 31 sets of inhibitory effects (24 in PMLS, seven in PLLS) were detected, and Fig. 2A gives an example whose activity was depressed below the control level in two cases (clockwise rotation and backward translation). It should be noted that (i) about half of these sets of inhibitory responses were evoked by backward translation; (ii) in many cases, just like the cell shown in Fig. 2A, when an optic flow stimulus induced inhibition, the stimulus of the opposite direction elicited significant excitatory response, therefore the effect could be considered as sharpening directionality. Since inhibition could only be determined unarguably in a few cases, we did not analyse this effect in more detail.

Excitatory responses

Excitatory visual responses were widely elicited in the lateral suprasylvian area by the three optic flow modes used in the experiments. For each stimulus type except backward translation, over half of the recorded cells were significantly excited both in PMLS and in PLLS (see statistics in Table 1). Only about 10% of the

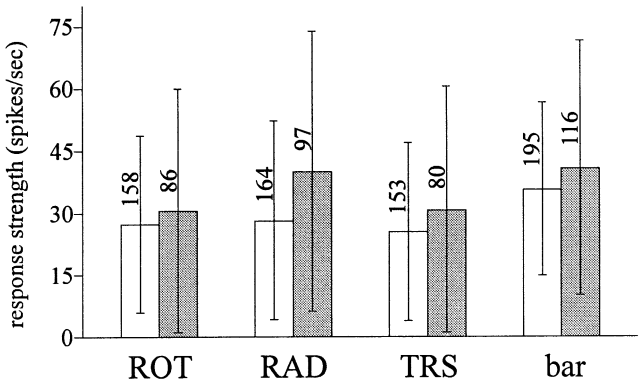

FIG. 3. The average response strengths and standard deviations of PMLS (light bars) and PLLS (grey bars) neurons to different optic flow modes and moving bar stimuli. Only the cells which were significantly excited are included, and the cell numbers are given next to each bar. The spontaneous activity has been subtracted. If the responses were significant to both directions of a mode, the stronger one was taken into account. The values are 27.26 ± 21.41 and 30.51 ± 29.53 (rotation), 28.11 ± 24.08 and 40.05 ± 33.93 (radiation), 25.41 ± 21.56 and 30.78 ± 29.82 (translation), 35.75 ± 20.99 and 40.85 ± 30.92 (moving bar), respectively, for PMLS and PLLS cells.

TABLE 1. Responsiveness of LS neurons to three basic optic flow modes and the two opposite directions for each mode

Excited neurons in	Rotation			Radiation			Translation			
	CWS	CCW	Subtotals	EPN	CTN	Subtotals	FWD	BWD	Subtotals	Overall
PMLS ($n = 203$)	130	121	158 (77.8%)	135	129	164 (80.8%)	151	66	153 (75.4%)	184 (90.6%)
PLLS ($n = 123$)	64	67	86 (69.9%)	84	72	97 (78.9%)	79	34	80 (65.0%)	111 (90.2%)

The significantly excited cells (*t*-test, $P < 0.05$) were counted, the numbers and percentages are shown, respectively, for PMLS and PLLS. The last column includes all the cells responsive to any of the flow stimuli.

cells were nonresponsive to all the patterns tested, indicating that LS neurons are generally sensitive to optic flow fields. We could not totally exclude the possibility that some nonresponsive cells were missed from the sample due to the experimental protocol, but it was equally possible that for some cells the most effective stimulus was not among the patterns we used. Therefore it is unlikely that a substantial over-estimation was made about the proportion of responsive cells.

The present results confirmed the observation that many LS neurons respond to approaching or receding stimuli. The percentage of cells responsive to radial motion (about 80%) was higher than the 70% reported by Kim *et al*. (1997) and the 50–60% by Niida *et al*. (1997), probably due to the potential differences in methods and criteria (see Discussion). The texture movie used by Kim *et al*. (1997) is analogous to our translation stimulus in the sense that only a single moving direction can be seen in the pattern. From Fig. 3 in this paper it can be seen that many cells in their sample were responsive to texture movie and some of them even preferred this stimulus to flow movie (which could correspond to our radial motion), which are similar to our results.

The proposal that LS cortex might be involved in optic flow processing was initially based on the distribution of preferred directions measured with simple moving stimuli (bar, spot, grating, etc.). Since populations of LS cells were found with centrifugal or centripetal direction preferences (Blakemore & Zumbroich, 1987; Hamada, 1987; Rauschecker *et al*., 1987; von Grünau *et al*., 1987), it was expected that responses to radial stimuli should be predominant in the area. However, we found that the clockwise/counter-clockwise rotation was effective stimulus for about 75% of the cells recorded. As shown in Table 1 and Fig. 3, the number of responsive PMLS cells and the average response strength were nearly the same for the three different flow modes. In the PLLS, radiation was prevailing, but not very much, over rotation and translation. In addition, as shown by Mulligan *et al*. (1997) the obvious discrepancies between the direction-selective behaviour to moving bars and movies, we did not see any clear relationship between the optic flow responses and the preferred direction to the moving bar, implying that responses in LS to flow fields are not well correlated with responses to single objects moving against a blank background. In other words, the responsiveness to optic flow fields could not be predicted or explained with the cell's direction preference to single objects.

It should be noted that, both in the PMLS and in the PLLS, most of the cells were excited by more than one flow mode, and/or by the patterns of opposite flow directions of a same mode (see examples in Fig. 2). We found only 18 PMLS and 19 PLLS cells responded to a unique type of stimulus, but 47 PMLS and 20 PLLS cells were sensitive to all six types. In summary, we recorded a total of 732 sets of excitatory responses from the 184 responsive PMLS cells (3.98 per cell), and 400 sets in 111 PLLS cells (3.60 per cell). The widespread existence of multiple-responsiveness makes it necessary to check the cells for their selectivity and directionality to different flow fields.

Selectivity for different optic flow modes

According to the results of the *t*-test, all the cells were divided into three categories: selective; nonselective; and nonresponsive (Fig. 4). The largest group was the one comprising the nonselective cells (nearly 70%), which were sensitive to different types of flow stimuli without any significant preference. The selective cells, which responded best to a certain flow mode than the others, constituted a much smaller subset (20–25%) in the sample. In order to visualize the differences among the responses, a triangular space plot is depicted in Fig. 5 to show the relative contribution of each of the three modes. A

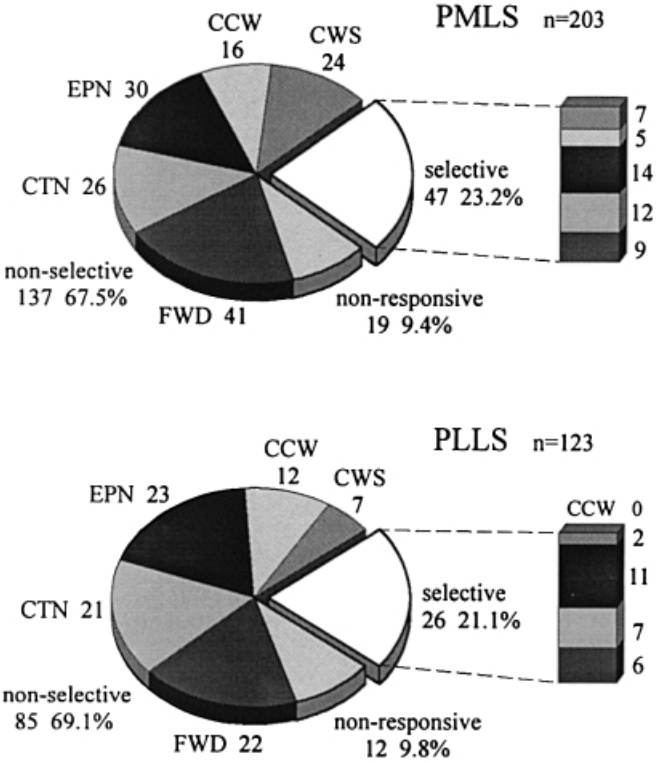

FIG. 4. Statistics for selectivity of PMLS and PLLS neurons to optic flow modes are shown in pie graphs. The cells are divided into three groups: selective, nonselective, and nonresponsive. For the first two groups, the cells are further classified according to the stimulus type which elicited the optimal responses.

cell's relative response strength to each motion mode is represented by the point's distance (P_X) to the corresponding vertex (for details see figure legends, also cf. fig. 6 in Graziano *et al*., 1994). The closer a point is to a vertex, the more the cell preferred the corresponding mode. To quantify the degree of selectivity, selective indexes ($SI_X = 1 - P_X^2$) were calculated for each cell and each motion mode to measure the cell's preferences. The statistic results are given in figure legends of Fig. 5.

As shown in Fig. 5, only a few points fall closely to the vertices, implying that there was rarely any cell responding exclusively to one particular motion mode. Most cells, including many selective ones, are distributed around the centre of the graph, indicating that they responded to all the three modes. All these results suggest that the selectivity for different optic flow modes is not good in the LS as a whole, and the area studied is unlikely to be specialized for discrimination of different flow patterns. However, there were indeed a small proportion of cells which could distinguish different modes fairly well, and the three categories of flow stimuli did make some differences in our sample.

Although the cells responsive to radiation were only slightly more than those to rotation and translation (see Table 1), the radial motion took a clear preponderance in the group of selective cells (55.3% in the PMLS, 69.2% in the PLLS, see Fig. 4), and the average selective index was also significantly higher for radiation than for the other two modes ($P < 0.01$ for the PMLS, $P < 0.0001$ for the PLLS; see Fig. 5). Actually for the responsive but nonselective cells, the maximal responses were much often elicited by radial motion rather than by rotation and translation (40.9%, 29.2% and 29.9%, respectively, in the PMLS, and 51.8%, 22.4% and 25.9% in the PLLS; see Fig. 4). For all responsive cells, the average response strength to radial stimuli

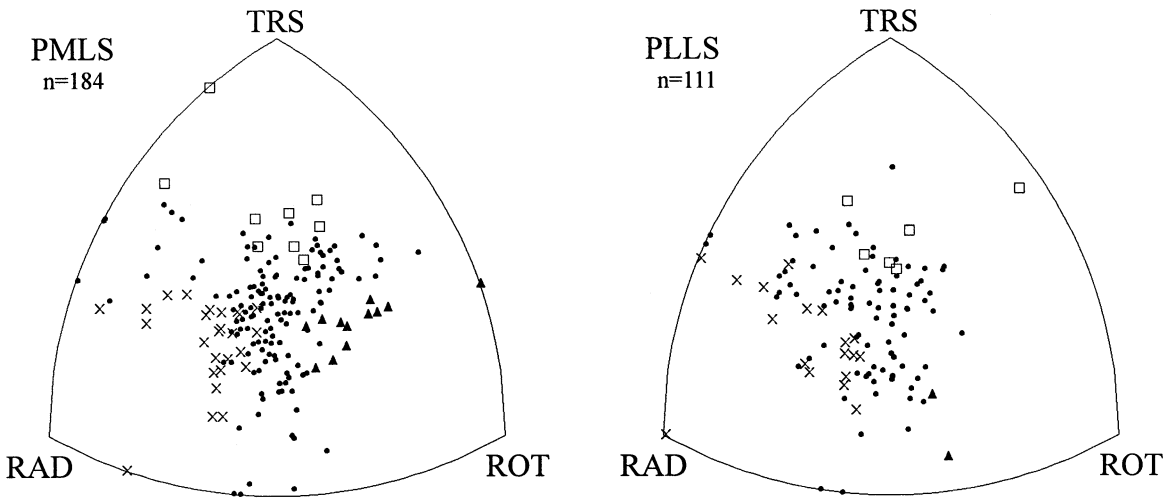

FIG. 5. Relative response strength to the three optic flow modes. Each point represents a responsive cell. A cell plotted close to one vertex responded best to the corresponding motion mode, and cells plotted near the centre responded equally well to all the three modes. The position for each point P was decided by the distances from the three vertices: $P_X = 1/(K \times R_X + 1)$, X = ROT, RAD or TRS, where K is a scaling factor individually calculated by numerically solving the three equations for each cell, R_X is the response strength to each motion mode. Only the responsive cells (both the selective and nonselective ones shown in Fig. 4) were included in this analysis. For each mode, the stimulus direction that elicited the significant or maximal responses was taken into account. The spontaneous activity was subtracted, and if a minus value was obtained, the R_X was set to be zero. The selective cells preferred different flow modes are marked with triangles, crosses, and open squares, respectively. Since the algorithm is nonlinear, the strength of selectivity is not proportional to the distance to a vertex and, as a result, many selective cells fall even closer to the centre than to the corresponding vertex. The selective indexes ($SI_X = 1 - P_X^2$) were calculated for each cell. The mean values and standard deviations are 0.620 ± 0.167 and 0.578 ± 0.172 (rotation), 0.670 ± 0.143 and 0.717 ± 0.117 (radiation), 0.604 ± 0.166 and 0.592 ± 0.163 (translation), respectively, for PMLS and PLLS cells. Compared with PMLS cells, PLLS cells had higher mean SI value to radial motion ($P < 0.005$), in accordance with the shift away from the rotation-translation axis seen in the graph for the PLLS.

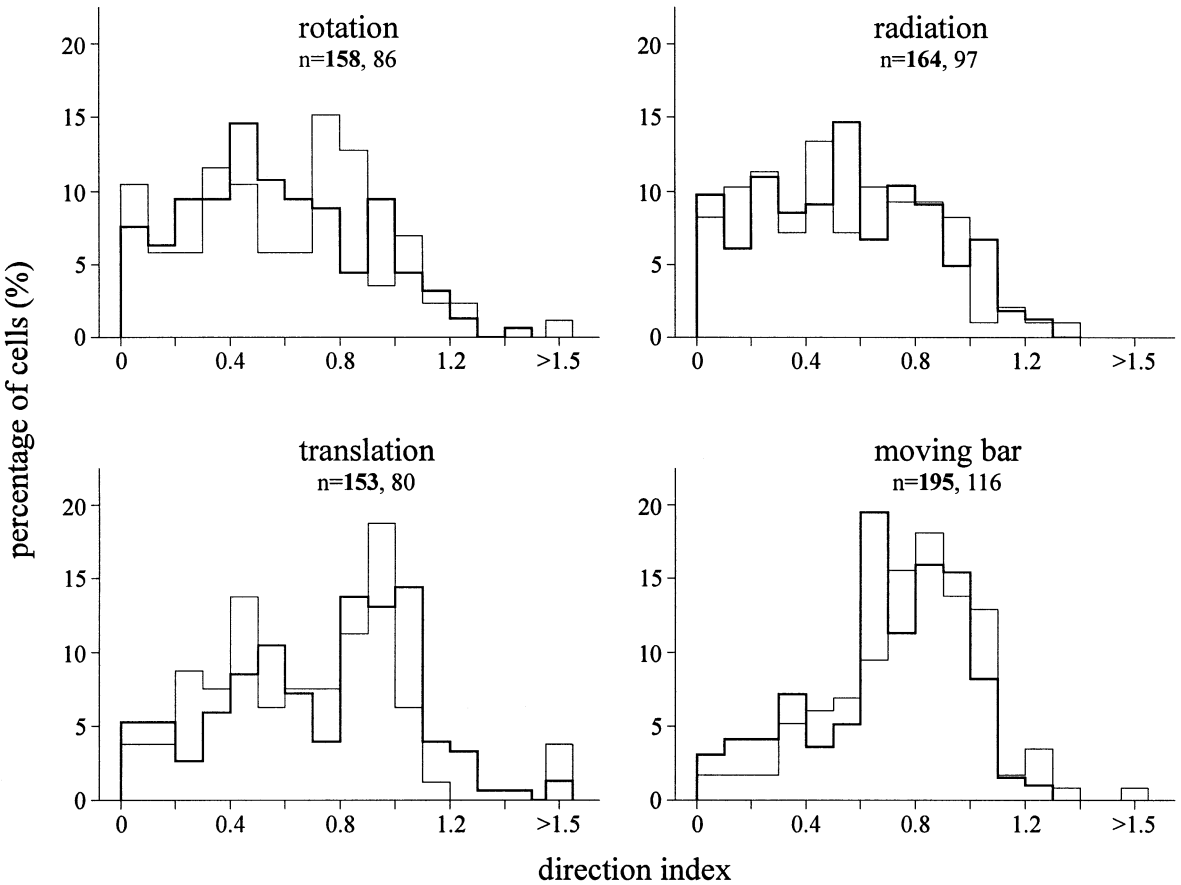

FIG. 6. Distribution histograms of absolute direction indexes for different optic flow modes and moving bar stimuli. Only the cells responsive to the corresponding mode are included. The mean values and standard deviations are: 0.558 ± 0.316 and 0.586 ± 0.350 (rotation), 0.540 ± 0.312 and 0.525 ± 0.312 (radiation), 0.725 ± 0.361 and 0.670 ± 0.343 (translation), 0.670 ± 0.302 and 0.745 ± 0.302 (moving bar), respectively, for PMLS (thick lines) and PLLS (thin lines) cells.

was the highest (see Fig. 3). These results indicate a preference for radial flow fields in the LS, but probably not as strong as one might expect from the previous reports (Blakemore & Zumbroich, 1987; Rauschecker *et al*., 1987).

Directionality for different optic flow modes

The preference for the direction of flow motion is another key property of optic flow responses. The results of *t*-tests (Table 2) showed that in both the PMLS and PLLS, for each of the three motion modes, only slightly over 50% of the responsive cells preferred one direction to the opposite. In order to quantify the directionality, optic flow direction index (*DI*) was calculated for each cell responded to each mode as follows.

$$DI_x = (R_A - R_B)/\max(R_A, R_B)$$

where X = ROT, RAD or TRS, A = CWS, EPN or FWD, and B = CCW, CTN or BWD. R_A and R_B are, respectively, response strengths for the two opposite directions of a same flow mode (X) with the spontaneous activity subtracted; max(R_A, R_B) is the maximum. This index is similar to the commonly used bar direction index, but the value could be either positive or negative, depending on which direction was preferred.

Since in translation mode the moving direction which evoked optimal responses was set as 'forward' for each individual cell, all the translation-sensitive cells preferred forward to backward motion and their DI_{TRS} values were always positive. As for the rotation- or radiation-responsive cells, no clear preference could be determined between the two possible directions. Cells responsive to expansion (see Table 1), selective to expansion (see Fig. 4), or preferred expansion (see Table 2), had only a small advantage over those responsive to, selective to, or preferred contraction, respectively. In cells responded to circular motion, we did not see any clear preference for either clockwise or counter-clockwise rotation. The average direction indexes and standard deviations are: 0.026 ± 0.643 and -0.012 ± 0.685 (rotation), 0.041 ± 0.623 and 0.047 ± 0.611 (radiation), respectively, for PMLS and PLLS cells. All the mean values are very close to zero (*t*-test, $P > 0.4$), also indicating no obvious preferred direction in either area.

The distribution histograms of absolute *DI* values are given in Fig. 6 to show the strength of directionality. For both rotation and radiation modes, the distributions were broadly scattered and the peaks were not obvious, and all the mean (and median) values were between 0.5 and 0.6, indicating that the directionality was not very good for most cells. However, the distribution for planar flow field (i.e. translation) was more clustered, and the mean direction index was somewhat higher ($P < 0.0002$ for the PMLS, but insignificant between translation and rotation for the PLLS), showing a relatively better directionality than that for radiation or rotation. The direction index for moving bar stimuli is also shown in Fig. 6. In contrast to that for radial and circular patterns, the distribution is clearly unimodal at higher value range, and the mean direction index is significantly higher ($P < 0.001$ for both the PMLS and PLLS).

Previously Niida *et al*. (1997) found that the corticotectal LS neurons tended to respond best to receding stimuli, whereas corticostriatal neurons tended to prefer approaching stimuli. If all the cells were pooled together, there was no overwhelming preponderance in LS as a whole. However, Kim *et al*. (1997) reported that 68% of the LS cells responsive to flow movies preferred radial-outward motion, which possibly corresponds to the expansion stimulus in our experiments. Furthermore, the same authors found that the LS cells had a stronger direction preference for flow movies than for moving bars, and the median value for Movie Direction Index was about 0.8 (see fig. 6 in Mulligan *et al*., 1997). It should be noted that their Bar Direction Index (median value 0.48) was much lower than the results reported by others (Blakemore & Zumbroich, 1987; mean value 0.77; Gizzi *et al*., 1990; Fig. 5C, value not given; Yin & Greenwood, 1992; mean value close to 0.75) and what we observed (see Fig. 6). These disagreements were probably due to different stimulus settings and sampling strategy in experiments. For example, the high Movie Direction Index obtained by Mulligan *et al*. (1997) probably came from the unusual stimuli they used. Our findings that for both radial and circular motion only about 50% cells distinguished between the two opposite flow directions, and that the *DI* values were fairly modest in general, suggest that the direction preference in the PMLS and PLLS for the two flow modes may not be as good as the direction selectivity to single objects (e.g. bar, spot, etc.) moving against a blank background.

Differences between PMLS and PLLS

Compared with PMLS cells, PLLS cells were less multiple-responsive to different optic flow patterns and the proportion of responsive cells to all the three flow modes were lower, though the differences were small. In the PLLS, more cells were responsive to radiation than to rotation and translation, while in the PMLS the cell numbers for these groups were much closer to each other (see Table 1). Although the percentage of selective cells in the PMLS and PLLS was very close, the composition was very different as the radiation-selective cells had a larger advantage in the PLLS (see Fig. 4). There were 12 PMLS cells (25.5%) which were significantly selective to rotation, but only 2 such cells (7.7%) were found in the PLLS. As shown in Fig. 3, the PLLS cells had higher mean response strengths to moving bar and all the three flow modes than PMLS cells, but only the difference for radial motion was significant ($P < 0.02$). This tendency in favour of radiation is more visible in Fig. 5 as the small shift away from the rotation-translation axis in the distribution of PLLS cells, and also confirmed by the mean selective indexes. The difference between the PMLS and PLLS in the direction preference to optic flow stimuli was small and insignificant (see

TABLE 2. Directionality of PMLS and PLLS neurons to optic flow patterns

Direction-sensitive neurons in	Rotation			Radiation			Translation		
	CWS	CCW	Subtotals	EPN	CTN	Subtotals	FWD	BWD	Subtotals
PMLS	44	38	82/158 (51.9%)	47	37	84/164 (51.2%)	93	0	93/153 (60.8%)
PLLS	21	25	46/86 (53.5%)	25	26	51/97 (52.6%)	43	0	43/80 (53.8%)

For each motion mode, the cells which preferred one direction to the opposite one (*t*-test, $P < 0.05$) were counted, respectively, for the two possible directions and the numbers are given separately. The sum of direction-sensitive cells and their percentage with respect to cells responsive to the particular mode are also given.

Table 2 and Fig. 6). However, the mean direction index for moving bar was significantly higher in the PLLS than in the PMLS ($P < 0.05$).

Generally, the PLLS cells were sensitive to fewer types of flow stimuli, but the responses were stronger especially to radial motion and they had the highest mean selective index to radiation. Most of the selective cells in the PLLS preferred expansion or contraction, few preferred rotation. These results suggest that the PLLS cortex might be relatively more specialized for radial motion whereas the PMLS cells are sensitive to various optic flow fields.

Differences between selective and nonselective cells

Comparisons were made on the response properties to moving bar as well as optic flow stimuli to check if there was any difference among the three groups of cells (selective, nonselective, and nonresponsive). All the data, from both the PMLS and the PLLS, were pooled together, as they showed almost the same tendency. The results are displayed in Fig. 7. For the cells nonresponsive to flow patterns, they gave fairly good responses to a single bar moving along the preferred direction (34.32 ± 29.48 spikes/s) and the mean bar direction index (0.690 ± 0.286) was only slightly lower than that for the nonselective cells.

For the selective cells, the responses to the preferred optic flow stimulus were significantly stronger than the maximal responses to moving bar (Wilcoxon test, $P < 0.01$), but for the nonselective cells, the mean response strength for bar was slightly higher than that for optic flow (Wilcoxon test, $P = 0.025$). In other words, the preferred optic flow pattern was probably the most effective stimulus for selective cells, whereas the nonselective cells responded to multiple types of visual stimuli without obvious preference, at least for those used in the present study. As compared with nonselective cells, the selective cells had higher mean selective index to optic flow as predicted (0.829 ± 0.050 vs. 0.757 ± 0.047, $P < 0.0001$), and the average direction indexes were also higher both for flow field (0.725 ± 0.309 vs. 0.649 ± 0.338, $P < 0.05$) and for moving bar (0.806 ± 0.247 vs. 0.706 ± 0.288, $P < 0.02$), indicating that the selective cells have stronger direction preference to both stimuli. However, the distribution of preferred direction to moving bar did not show any clear clustering for either cell group. Since the differences were not large, it is more likely that all the cells were recorded from a continuum of optic flow sensitivity rather than from discrete classes.

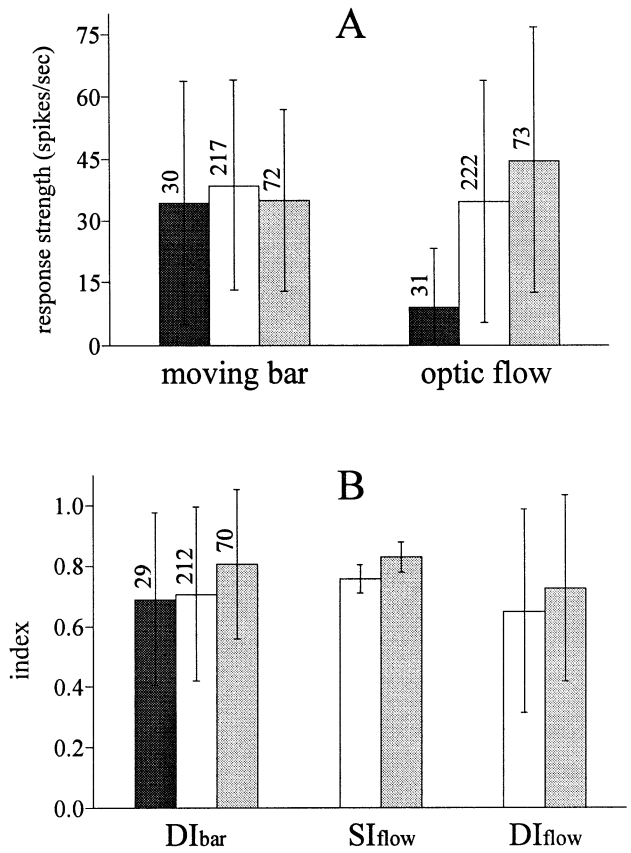

FIG. 7. Comparison among the selective (grey), nonselective (light), and nonresponsive (dark) cells, on response properties to optic flow and moving bar stimuli. (A) Response strength (R_{flow}, R_{bar}). (B) Direction index to moving bar (DI_{bar}), and selective and direction indexes to optic flow (SI_{flow} and DI_{flow}, not shown for nonresponsive cells since they make no sense). For R_{flow}, SI_{flow} and DI_{flow} values of each cell, the stimulus pattern which elicited the maximal responses was taken into account for the calculation. The optimal response to the moving bar was taken as R_{bar}. PMLS and PLLS cells have been pooled together. The cell numbers are given next to each bar, except for SI_{flow} and DI_{flow} since the numbers are the same as those for R_{flow}.

Discussion

In the present study, a set of rotation as well as radiation and translation patterns were used to systematically investigate the responses of single PMLS and PLLS neurons to optic flow fields. These stimuli were similar to the ones applied by others in macaque MT and MST (Duffy & Wurtz, 1991a; Graziano *et al*., 1994; Lagae *et al*., 1994), but different from those previously used in LS of the cat (Kim *et al*., 1997; Niida *et al*., 1997).

Comparison with previous studies of the LS cortex

The scheme for visual stimulation was an important difference between the present study and previous works in cat. Niida *et al*. (1997) adopted the simple method of varying the size of an iris diaphragm to mimic approaching and receding. Their stimuli were not provided with the multiple components one may encounter when moving through the environment, and therefore did not contain any spatial arrangement of moving directions. The variation of luminance might be one cause for the responses, and the edge might also lead to ill-effects. Sherk and coworkers designed a series of different movies to simulate the experience of a cat trotting across an endless plain covered with small balls (Kim *et al*., 1997), which were closer to natural scenes. However, it would be complicated to deal with the many variable elements in the flow movies, investigations with simulated stimuli composed of simple elements may have an advantage at easily focusing on a few key properties.

Probably because of the difficulties in designing matching stimuli, neither of the two groups took into consideration the circular motion, which is widely regarded as another basic optic flow mode in addition to radial and planar motion. On the other hand, Sherk *et al*. (1995) reported that a posterior population of cells in the LS tends to prefer tangential directions while an anterior population tends to prefer radial-outward directions, and suggested that cells in the former population might project to neurons that prefer circular or spiral motion. However, from the viewpoint of relating the direction preferences to the possible optic flow responses, it would be equally plausible to suggest that these cells might respond to circular motion themselves.

Another difference in stimulation concerns the centre of flow field, i.e. the origin of radial motion or the centre of circular motion. All the receptive fields studied by Sherk's group were located in the lower left quadrant of the visual field, and the virtual heading point was always kept at a constant position outside the receptive field (see fig. 2 in Mulligan *et al*., 1997). With such a setting, the moving directions

seen in a flow movie could cover only a limited range out of 0–360°. Consequently, the flow movie remained similar to a texture movie within a typical receptive field. Therefore Kim *et al.* (1997) suggested that some kind of surround mechanism could account for differentiating between the two stimuli. However, the spatial arrangement of different directions of movement was proposed to be a key factor in the optic flow analysis in MST (Tanaka *et al.*, 1989). Even in the vector field hypothesis (Duffy & Wurtz, 1991b), apparently different directions are also imperative to form the fundamental features (the curl of circular fields and the divergence of radial fields). To investigate optic flow processing in the cat in more detail, measurements with stimuli containing the full range of directions are necessary.

The sampling strategy was another key factor. Kim *et al.* (1997) made penetrations between A2 and the posterior end of the suprasylvian sulcus, with the great majority of recording sites within PMLS. Surprisingly, this is exactly where the posterior population lies, which was found to prefer tangential directions in an earlier study by the same authors (Sherk *et al.*, 1995; also see fig. 3 in Mulligan *et al.*, 1997). There was no explanation why the studies were not conducted in the anterior population which, according to their earlier results, should prefer radial-outward directions. The population of cells in the present study covered the whole range of PMLS and PLLS, yet we did not find a separation between the anterior and posterior parts as reported by Sherk *et al.* (1995). Anyway, the differences in sampling is one possible reason for the discrepancies between their results and the present ones.

Comparison with MT and MST

The stimuli used in the present study were similar to those applied to MT and MST of the macaque in previous studies, and the results have yielded a number of similarities. In both the MT and the MST, many cells respond to multiple flow stimuli and all the neurons form a continuum of response selectivity rather than falling into discrete classes (Duffy & Wurtz, 1991a; Graziano *et al.*, 1994; Lagae *et al.*, 1994). In addition, the multiple-responsive MST neurons show weaker direction selectivity than the neurons respond to less kinds of optic flow components (Duffy & Wurtz, 1991a). All these results are very close to the present findings obtained in the LS. On the other hand, Duffy & Wurtz (1991a) reported that 23% MST neurons responded primarily to one component of motion and 63% responded to two or all three components. Carrying out the statistics in the same way as they did, we obtained only 9.9% single-component cells but 80.8% double- or triple-component cells in the PMLS, the percentages were 16.3% and 74.0% in the PLLS. Moreover, the points shown in Fig. 5 of the present paper are relatively more clustered around the centre, as compared with the distribution in Fig. 6 by Graziano *et al.* (1994). These facts suggest that the selectivity of LS neurons is generally weaker than that in the MST.

Lagae *et al.* (1994) made a series of comparisons between the MT and MST, and proposed that area MT responds to optic flow stimuli without analysing them whereas area MST analyses the optic flow. Comparing our results with their findings, it could be seen that the LS cells were similar to MT cells in some properties (the overall response strength to optic flow stimuli, the modest selectivity and directionality, etc.), but closer to MST cells in some others (the spontaneous activity, the relative predominance of radiation and rotation). However, the translation was not so effective in the LS as in either the MT or MST, and radial motion could excite relatively more LS cells. Taken the differences between the PMLS and PLLS, the PMLS may be even more similar to the MT, and the PLLS seems, to some extent, more specialized and closer to the MST. However, the differences between the PMLS and PLLS were not as obvious as those between the MT and MST, and we can not conclude that the PLLS actually functions like the MST.

Optic flow processing in the cat: a comparison with the macaque

One of the main results of the present study was that the PMLS and PLLS neurons were generally responsive to optic flow stimuli, but the selectivity and directionality to different patterns were not as good as supposed. Most cells could be excited by two or all three flow modes, or by both directions of a same mode, while only a few cells responded exclusively to one particular stimulus. Comparison with data obtained from the macaque show that the PMLS is mostly similar to the MT while the PLLS seems like an intermediate area between the MT and MST. These results indicate that the PMLS and PLLS are unlikely to be specialized for the analysis or discrimination of different optic flow fields, but instead may be a relay in transferring motion information to higher-level cortical areas. This role is analogous to the function supposedly performed by area MT in the macaque (Lagae *et al.*, 1994). Further investigations in other extrastriate areas receiving afferences from the PMLS and PLLS, may find neurons more suitable for precise analysis of optic flow.

In the primate, the dorsal pathway, V1→MT→MST is regarded as the principal visual pathway for motion processing. Based on the divergent projections from the MST to still higher level cortical areas, it has been suggested that this pathway can be further divided into two substreams, one toward the parietal lobe (area 7a, the ventral intraparietal area, etc.) and the other to the temporal lobe, in particular the superior temporal polysensory area (Boussaoud *et al.*, 1990; Baizer *et al.*, 1991). Optic flow selectivity, resembling that of MST neurons or even more pronounced, has been reported in both substreams (Schaafsma & Duysens, 1996; Siegel & Read, 1997; Anderson & Siegel, 1999). Siegel and coworkers have proposed that area 7a neurons may utilize flow motion for the construction of a spatial representation of extra-personal space, and that the anterior superior temporal polysensory area may be involved in the processing of forward locomotion and/or looming stimuli.

The visual system of the cat is similar to that of the primate in many aspects but has its own characteristics as well (Felleman & Van Essen, 1991; Kaas & Krubitzer, 1991; Payne, 1993). It is widely agreed that the LS cortex is essential for motion analysis and that the PMLS is analogous to MT (Zeki, 1974; Gizzi *et al.*, 1990; Dreher *et al.*, 1996). However, the existence of multiple visuotopic representations in the LS is intriguing for their functional implications. PMLS and PLLS neurons are alike in some general characteristics such as motion sensitivity and direction selectivity, and the differences between them seem to be less distinctive (Blakemore & Zumbroich, 1987; von Grünau *et al.*, 1987; Spear, 1991). Even in the present study, the optic flow responses in the two areas are similar in most respects. These led us to deliberate the possibility of parallel substreams for motion processing in the cat. Indeed, the PMLS and PLLS have very different afferent and efferent connections. Summarily, the PMLS receives its major inputs from area 17 and other striate-recipient structures (areas 18 and 19, and the lateral division of the lateral posterior nucleus), projects to areas 17, 18, 19 and 20a, and other LS areas. PLLS receives little input from striate–recipient structures, but instead is driven mainly by tectal inputs from the medial division of the lateral posterior nucleus, and projects to more remote extrastriate areas such as the anterior ectosylvian visual area. The reciprocal connection between the PMLS and PLLS is weak. (Rosenquist, 1985; Dreher, 1986; Sherk, 1986; Grant & Shipp, 1991; Scannell *et al.*, 1995) Unfortunately, the

relevant neurophysiological studies on extrastriate cortices of the cat are very limited so far and most of them were focused on PMLS, therefore the data are far from sufficient for verifying the idea.

The parallel processing assumption may correspond to the above-mentioned scheme proposed for the macaque, but with some obvious differences. In the macaque, the two substreams are divided beyond the MST, but in the cat, the supposed subdivision could appear much earlier at a subcortical level. The PMLS and PLLS probably lie at roughly equivalent stages in the hierarchy but in two substreams, so that the PMLS is not totally as same as the MT (for a major difference between the PMLS and MT see Gizzi *et al*., 1990) and the PLLS does not have a good counterpart in the macaque. In optic flow analysis, the areas that receive projections from the PMLS and PLLS, respectively, may function somewhat differently. For example, one may be involved in the processing of detailed flow information, but the other may just utilize the cues in flow patterns for relevant purposes. Moreover, this scheme may serve not only the optic flow analysis but also other aspects of motion perception, especially in the cat since it has less visual areas and simpler hierarchical relationships than the primate.

The neural mechanisms underlying optic flow processing still remains an open question. The two representative hypotheses, 'direction mosaic' and 'vector field', could hardly explain the position invariance and multiple responses of many MST cells (Duffy & Wurtz, 1991a; Graziano *et al*., 1994; Lagae al. 1994), therefore Duffy & Wurtz (1991b) suggested that the overlap of gradients of excitation and inhibition within a receptive field might account for the continuum of response types to flow fields. On the other hand, Duffy & Wurtz (1991a) found that the impact of inhibitory responses increased along the continuum from triple- to single-component neurons, indicating that inhibition may contribute to sharpen direction and component selectivity. The situation in the MT and LS may be not the same, since the optic flow selectivity in the two areas is not as good as that in the MST. Lagae *et al*. (1994) found that direction selectivity for flow components was not position invariant in MT cells, but did not discuss possible inhibitory effects. The presence of position invariance is yet to be tested in LS; however, in the present study, the inhibitory responses were much fewer than those reported by Duffy & Wurtz (1991a) in the MST. All these points suggest that the optic flow responses in the PMLS and PLLS may arise from a less specialized mechanism.

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Abbreviations

BWD, backward; CCW, counter-clockwise; CWS, clockwise; EPN, expansion; CTN, contraction; *DI*, direction index; FWD, forward; LS, lateral suprasylvian cortex; MST, medial superior temporal area; MT, middle temporal area; PLLS, posterolateral lateral suprasylvian area; PMLS, posteromedial lateral suprasylvian area; RAD, radiation; ROT, rotation; SI, selective index; TRS, translation.

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