Pattern and component motion selectivity in cortical area PMLS of the cat

Bing Li,* Yao Chen,* Bao-Wang Li, Lian-Hong Wang and Yun-Cheng Diao
Laboratory of Visual Information Processing, Institute of Biophysics, Chinese Academy of Sciences, Beijing 100101, P. R. China

Abstract

Visual motion perception is one of the most prominent functions performed by the mammalian cerebral cortex. The moving images are commonly considered to be processed in two stages. The first-stage neurons are sensitive to the motion of one-dimensional orientated components, and their outputs are combined at the second stage to perceive the global motion of the whole pattern. Alternatively, the pattern motion may be signalled by monitoring a distinctive feature of the image, such as a line-end or a corner. In the present study, a series of 'random-line' patterns were used to measure the direction-tuning responses of 138 neurons in the posteromedial lateral suprasylvian area of the cat. The novel stimuli comprised identical thin line segments, with a length : width ratio no less than 10 : 1, which were moved perpendicularly or obliquely to their common orientation during the recordings. When the component lines were much shorter than the size of receptive field, the majority of cells were selective to the direction of pattern motion while only a small subset was sensitive to the direction of component motion. However, the response profiles of most cells became more component-motion selective with the increment of orientation element in stimulus by elongating the component lines in the patterns. These findings imply that the two-stage theory might be incomplete for modelling the visual motion analysis. Even at relatively low levels of the visual system, some kind of nonorientation-based processing may coexist with the orientation-sensitive processing in a dynamic competition, where one rises as the other falls depending upon the strength of the orientation element in the stimulus, so that under some circumstances it becomes possible to signal the veridical direction of pattern motion.

Introduction

Direction-selective neurons in the visual cortex view image variations in the environment through the 'windows' of their receptive fields. Therefore they are inevitably subject to the so-called aperture problem: the true direction of movement of an elongated contour can not be unambiguously determined if it is viewed through an aperture (Marr & Ullman, 1981). For example, if a vertically orientated bar moves up and to the right across a small receptive field, the local motion detector can measure only the rightward component of motion, as the upward component provides no time-varying information. Solutions to this inherent ambiguity are thought to be computed at two sequential stages in a hierarchical process, which have been tentatively identified with specific neuronal populations in the brain (Adelson & Movshon, 1982; Movshon *et al.*, 1985; Welch, 1989; Derrington & Suero, 1991; Albright & Stoner, 1995). The first stage, consisting of analysis of object features as one-dimensional components, occurs in early visual areas and depends on orientation-selective mechanisms sensitive to the motion of individual component contours (i.e. component motion or CM). A second stage, supposedly involving higher extrastriate cortical areas, is required to integrate the outputs of the CM analysers to reconstruct the actual direction of coherent pattern motion (PM).

During the last two decades, the two-stage processing theory has gained support from neurophysiological and psychophysical studies using plaids formed by superimposing two differently orientated moving gratings (for review see Albright & Stoner, 1995), and computational models have been established to simulate the process of motion detection and integration (Wilson *et al.*, 1992; Nowlan & Sejnowski, 1995; Heeger *et al.*, 1996; Simoncelli & Heeger, 1998). However, much physiological evidence suggests that different mechanisms are involved in direction and orientation selectivity in the striate cortex (e.g. Creutzfeldt *et al.*, 1974; Hammond & MacKay, 1977; Sillito, 1977, 1979; Hammond, 1978; Bishop *et al.*, 1980; Eysel *et al.*, 1988; Wörgötter *et al.*, 1990). Several nonorientation-dependent models (the phrases 'nonorientation-based' and 'nonorientation-dependent' in this paper imply that it is not essential to extract information of orientated components in a pattern in the mechanism or model of visual motion processing.) were proposed to account for motion direction discrimination (Barlow & Levick, 1965; Torre & Poggio, 1978; van Santen & Sperling, 1984; also see Albright, 1984).

A number of psychophysical and theoretical studies found that, in many cases, one-dimensional orientated cues alone are not integrated by the visual system into the correct global motion percept, indicating a necessary role for localized information (such as point-like cues) in early motion mechanisms (Nakayama & Silverman, 1988; Rubin *et al.*, 1995a, 1995b). Specifically, Lorenceau *et al.* (1993) reported that the perceived direction of straight lines translating obliquely, relative to their orientation, is biased toward the motion component

normal to the lines (i.e. CM-sensitive) at long line length, short duration and low contrast. They proposed that such errors can be accounted for by a competition between contour motion processing units and line terminator processing units (Castet *et al.*, 1993; Lorenceau *et al.*, 1993). This controversy calls for further investigations on these issues.

The posteromedial lateral suprasylvian area (PMLS) of the cat is often considered as analogous functionally, even homologous, to the middle temporal area (MT) of the primate (Zeki, 1974; Spear, 1991; Payne, 1993; Dreher *et al.*, 1996). Substantial populations of PM-selective cells have been found in the MT, therefore, it may underlie, at least partly, the integration of motion signals in the second processing stage (Movshon *et al.*, 1985; Rodman & Albright, 1989; Stoner & Albright, 1992; Albright & Stoner, 1995). In contrast, studies with drifting plaids rarely found any PM cell in PMLS, and it was proposed that in this area, the response to the direction of motion is secondary to the determination of orientation and the motion signals are integrated in other parts of the cats' cerebral cortex (Movshon *et al.*, 1985; Gizzi *et al.*, 1990). As an area assumed to be involved mainly in higher functional aspects of motion processing, it seems questionable that the global percept of pattern motion is completely absent in PMLS. On the other hand, there is a disagreement in the literature concerning the presence or absence of orientation selectivity in the PMLS (for review, see Spear, 1991). Previous studies using short bars or spots have shown that few, if any, PMLS cells are orientation sensitive (Spear & Baumann, 1975; Camarda & Rizzolatti, 1976; Toyama *et al.*, 1994). However, when stimulated with long bars or gratings, the great majority of PMLS neurons are orientation selective (Blakemore & Zumbroich, 1987; Hamada, 1987; Gizzi *et al.*, 1990; Danilov *et al.*, 1995; Dreher *et al.*, 1996). All these points led us to question whether direction selectivity in this area is always secondary to orientation sensitivity and to examine the possible role that nonorientation-based mechanisms may play in mediating the direction preference of PMLS cells. Since PM- and CM-direction selectivity may not be readily distinguished with plaids (see Discussion), we developed a family of novel stimuli, termed 'random-line' patterns, in which the orientation element was adjusted by changing the length of the component lines. Using these stimuli, we found that many PMLS neurons were able to signal the true direction of pattern motion when the orientation element was relatively weak, and that the direction-selective behaviour of most cells varied with the stimulus pattern.

Materials and methods

Animal preparation and maintenance

The general procedures were similar to those described in a recent report (Li *et al.* 2000). Experiments were performed in compliance with the NIH guidelines on the care and use of laboratory animals. Briefly, experiments were carried out on normal adult cats weighing 2.0–4.0 kg. 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 ($\approx$ 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 the 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 the medial bank of the middle suprasylvian sulcus at Horsley–Clarke coordinates P2–A6, according to the division of PMLS by Palmer *et al.* (1978). Glass-coated tungsten microelectrodes were used to penetrate the cortex tangentially through the medial wall of the sulcus, so that the electrode tracks were roughly parallel to the cortical surface folded inside. Neuronal activity was recorded extracellularly with a programmable amplifier (CyberAmp 380, Axon Instruments, Foster City, CA, USA), and fed on-line into a computer via a laboratory interface (CED model 1401+ with a 1401–18 discriminator card; Cambridge Electronic Design, Cambridge, UK), by which the single-unit action potentials were isolated and stored in terms of firing times. The stimulus markers were also sent via the interface and recorded through an individual channel to synchronize the data. Occasionally, electrolytic lesions were made by passing a small direct current (10 μA for 10 s) through the electrode for histological identification of the electrode tracks at the end of experiments.

Visual stimulation

For each cell, the receptive field was first approximately plotted with hand-held stimuli (small patch, spot, short bar, etc.). In quantitative sessions, stimulation was carried out using moving bars and, as termed, 'random-line' patterns, generated on-line by a PII 266 computer with a graphics acceleration card (WinFast 3D L2300, Leadtek Research, Taipei, Taiwan) installed, and displayed on a 21-inch monitor (Brilliance 201P, Philips Elec. Industries, Taoyuan, Taiwan) with a resolution of 800 $\times$ 600 pixels and a refresh rate of 85 Hz. The luminance was 10–20 cd/m^2 for stimulus patterns and 0.5 cd/m^2 for background. The screen was placed 57 cm in front of the animal, covering the receptive field optimally. In the bar test, the conventional method was used i.e., a light moving bar was swept across the receptive field in 24 pseudorandomly interleaved directions at 15° steps, with the other parameters (size, velocity, contrast, etc.) qualitatively decided so as to elicit optimal responses. A blank control test was included to measure the spontaneous activity. The whole repertoire was repeated for five or ten trials to allow averaging of the data.

The random-line stimuli were similar to the matrices of lines used by Lorenceau *et al.* (1993) in psychophysical experiments but had been modified for the purpose of this electrophysiological study. The patterns were composed of a number of thin line segments (width 0.1°) with identical length (L) and orientation, distributed randomly within a circular window subtending 30° in diameter (for an imaginary example see Fig. 1A). For some cells, the size of the window and the number of lines were adjusted proportionally for a better coverage of the receptive field so as to elicit good responses. Procedures similar to the bar test were performed: a complete trial was composed of sweeps in 24 pseudorandomly interleaved directions with a blank control, such trials were repeated for five or ten times to obtain a direction tuning curve. During each sweep, all the lines drifted coherently at the same velocity (usually 15–30°/s) and direction so that no relative displacement occurred between individual components. Normally, each sweep lasted about 2000 ms and was followed by a 500-ms pause (blank background) to remove 'OFF-responses'. It should be emphasized that (i) during each measurement, the orientation of the component lines was altered with the moving direction so that the angle between them was kept at a constant value ϕ; (ii) all lines moved within the virtual but stereotyped window, and a wrap around procedure was used so that
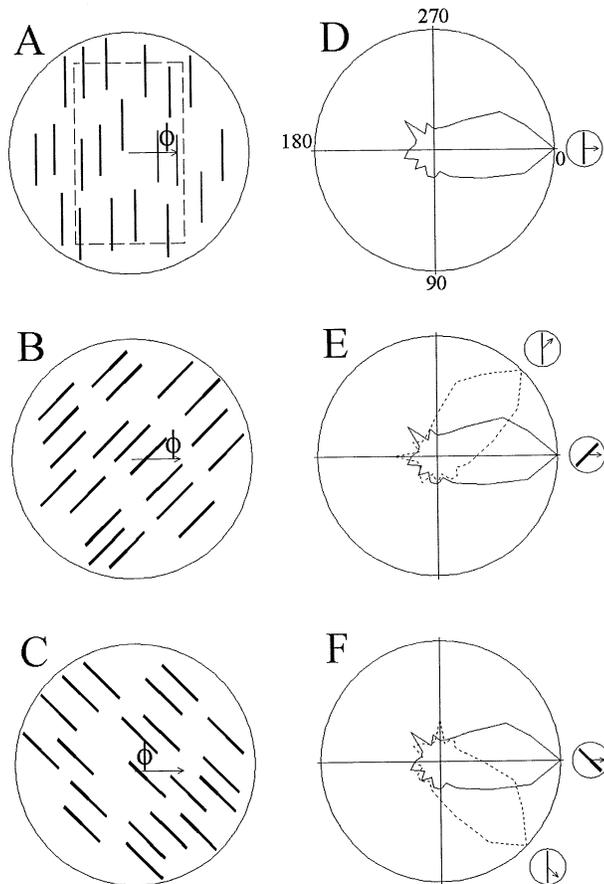
FIG. 1. Schematic illustration of the 'random-line' patterns used in the experiments and the prediction for PM- and CM-direction-selectivity. The stimuli are defined by two parameters: the length of the component lines (*L*) and the angle between the moving direction (shown with thin arrows) and the orientation of the component lines (ϕ). (A–C) 20 line segments of $L = 6°$ are distributed randomly within a circular window of 30° diameter and moved rightward (corresponding to 0° of direction in following polar graphs), perpendicularly (A, $\phi = 90°$) or obliquely ($\phi = 45°$ in B, 135° in C) to their common orientation. An imaginary receptive field is drawn in dashed line in A. The tuning curve in D depicts a typical response profile to the perpendicularly moved pattern. In E and F, the direction-tuning response shown in D is plotted again in solid lines, which are considered as the predicted profiles for fully PM-selectivity. The dashed lines predict the fully CM-selective response to the patterns moved obliquely and shown in B and C. The small panels in D–F display the optimal stimuli in a simplified mode (with only one line and an arrow on it, representing the component orientation and the moving direction, respectively) for the original response and for each prediction, from which it can be seen that the preferred direction (PD) keeps unvaried (rightward) for PM-prediction, while for CM-prediction, the preferred orientation of component lines is constant (vertical) but PD changes.

once a line left the window, it was immediately assigned a new location at the opposite side of the circle.

As described above, the random-line patterns could be defined by two parameters (*L* and ϕ). Normally each cell was tested with both shorter- ($L = 1–1.5°$) and longer- ($L = 3–4°$) line patterns. To keep a constant mean luminance within the patterns, the number of component segments was in inverse proportion to *L* (e.g. a pattern should have 120 lines when $L = 1°$, 40 lines when $L = 3°$, and 20 lines when $L = 6°$ as shown in Fig. 1). For each line length *L*, three tuning curves were measured with all the segments moved

perpendicularly ($\phi = 90°$) or obliquely ($\phi = 45°$, 135°) to their orientation (see Fig. 1). Some cells were also tested with patterns of additional line length and/or moving texture composed of random dots.

Data analysis

Neuronal response strength was determined as firing rate over the duration of measurement. Some cells fired very vigorously over a short period soon after stimuli were given. As the random-line and texture patterns covered a large area in the visual field, these transient responses might have been partly evoked by the general variation on the screen (luminance, contrast, or the emergence of motion) rather than the direction or orientation cue in the stimuli. To standardize measurements of different cells, discharges within 0–200 ms were excluded for all the samples in the analysis described below, except for the final part of the Results section in which an additional analysis was performed on the initial 200 ms to check the PM/CM selectivity in the earliest phase of responses.

Responses to random-line patterns were classified as PM- or CM-selective using the partial correlation analysis developed by Movshon *et al.* (1985) and revised afterward (Rodman & Albright, 1989; Movshon & Newsome, 1996). For each obliquely moved stimulus, the PM-selective prediction was derived by assuming that the response profile was the same as the tuning curve for the corresponding, perpendicularly moved pattern, and the fully CM-selective response profile was predicted by shifting this tuning curve by 45° so that the preferred orientation of component lines kept unchanged (see Fig. 1).

To compare the goodness of fit of the two predictions, the partial correlation coefficients R_p (for PM-prediction) and R_c (for CM-prediction) were calculated using the standard formulae:

$$R_p = \frac{r_p - r_c r_{pc}}{\sqrt{(1 - r_c^2)1 - r_{pc}^2)}}$$

$$R_c = \frac{r_c - r_p r_{pc}}{\sqrt{(1 - r_p^2)1 - r_{pc}^2)}}$$

where r_p and r_c are the simple correlation coefficients between the actual response and the PM- and CM-predictions, respectively, and r_{pc}, between the two predictions. A parametric statistical value *t* showing the significance of difference between R_p and R_c was calculated using:

$$t = \frac{z_p - z_c}{\sqrt{2/(n - 3)}}$$

in which

$$z_x = \frac{1}{2}\ln\frac{1 + R_x}{1 - R_x} \qquad x = p, c, \ n = 24$$

The *t*-value was used as a single index to quantify the status of PM/CM selectivity. Whilst lower *t*-values indicate higher CM-sensitivity of the cells, higher *t*-values represent more significant PM-selectivity. Qualitatively, the responses were classified into three categories at the significance level of $P = 0.05$ (see Fig. 3).
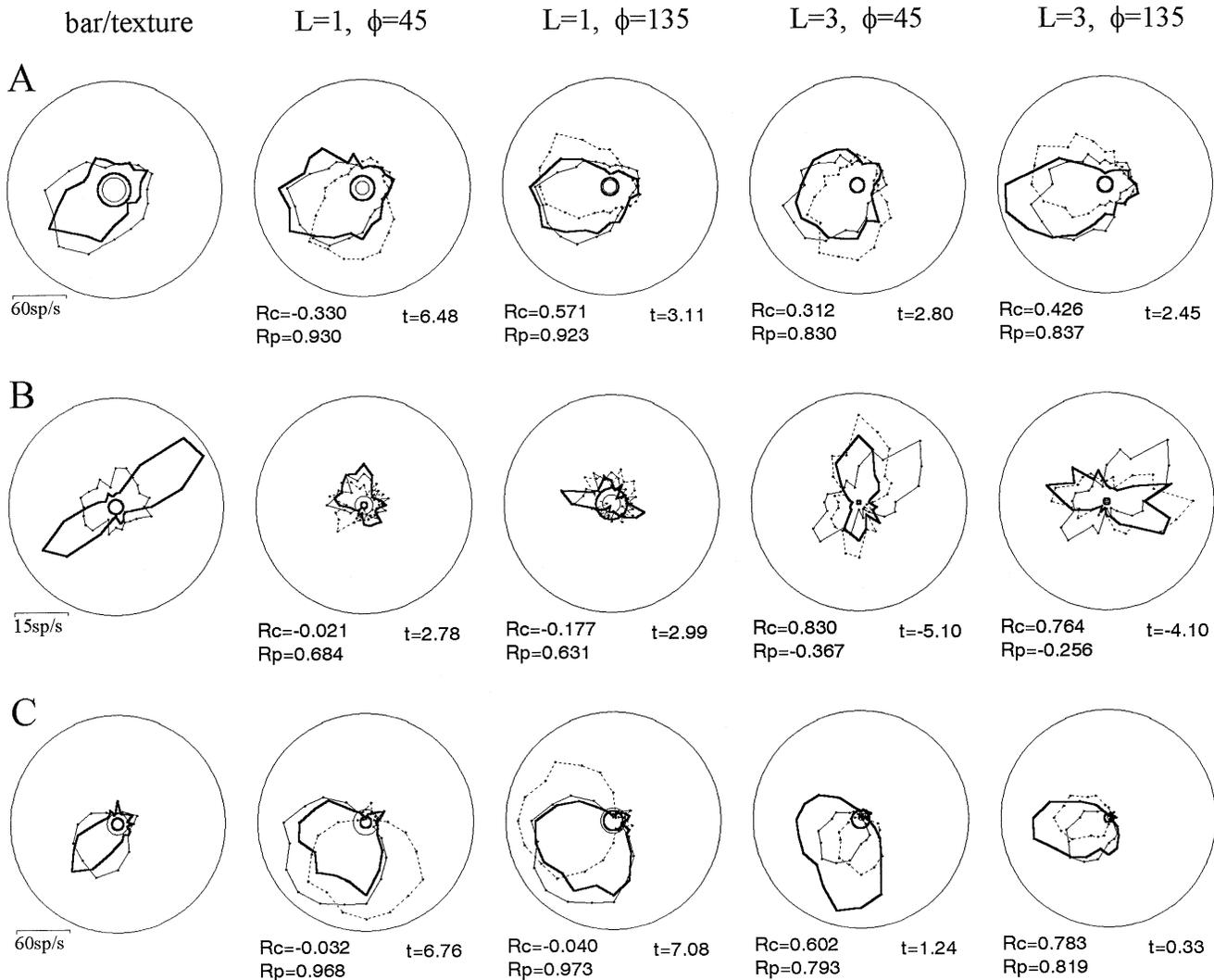
FIG. 2. Polar graphs illustrating the direction tuning curves of three representative PMLS neurons to different stimuli drifting in 24 directions. The leftmost column, responses to moving bar (thick line) and texture (thin line). The other columns, responses to random-line patterns moving obliquely (thick line), with the values for ϕ and L given in degrees at the top. In each panel, for a random-line stimulation of the same line length, the response to a pattern moved perpendicularly is plotted as a thin line as the prediction for a fully PM-selective unit, while the dashed line represents the predicted profile to the pattern moved obliquely for full CM-selectivity (cf. Figure 1). The spontaneous activity levels are shown as small central circles. (A) There was a close correspondence among the tuning curves no matter which stimulus was applied (though the tuning was sharper for moving bar), indicating that the cell was orientation-cue insensitive and PM-selective, which was also confirmed by the R_p and R_c values for each pattern moved obliquely. However, the difference between R_p and R_c (the statistical value t) was smaller for 3°- than for 1°-line patterns. (B) Significantly PM-selective to 1°-line patterns. For the 3°-line patterns moved obliquely, the major peak obviously shifted toward the CM-prediction, though the comparison between correlation coefficients resulted in an unclassified unit. The neuron seemed to prefer large field texture stimuli rather than a single bar. (C) The responses to 1°-line patterns were weaker and short of clear direction preference, and were unclassified in the partial correlation analysis. But when 3°-line patterns were applied, the cell turned out to be significantly CM-selective as the major peak shifted to opposite sides in the panels for $\phi = 45°$ and 135°.

Results

A total of 138 PMLS neurons were successfully recorded for their direction-tuning responses, with a moving bar and a series of random-line patterns. For the latter stimuli, the length of component line segments was altered to assess the dependence of direction tuning on the orientation element, which is presumably stronger with longer-line patterns, and even stronger with long contours. The receptive field properties were in general similar to those reported previously (for reviews, see Spear, 1991; Payne, 1993). Compared with striate cells, these neurons were usually more motion-sensitive, had larger receptive fields (ranging from < 10° to ⩾ 30°), and preferred higher velocities (10–40°/s). All the cells tested quantitatively were at least direction-biased or bi-directionally tuned to the moving bar, most of them showed strong direction selectivity (see below). 106 cells were completely measured with both shorter- and longer-line patterns, the others with only one of the two line lengths as their responses faded during further recordings. In most cases there was a good correspondence between a cell's tuning curves to a moving bar and, either a shorter- or longer-line pattern moved perpendicularly, and the preferred directions were close to each other. However, direction tuning was usually somewhat broader with shorter-line patterns (see examples in Figs 2 and 5). For each cell and every obliquely moved pattern, the tuning curve was compared with that of a pattern, of the
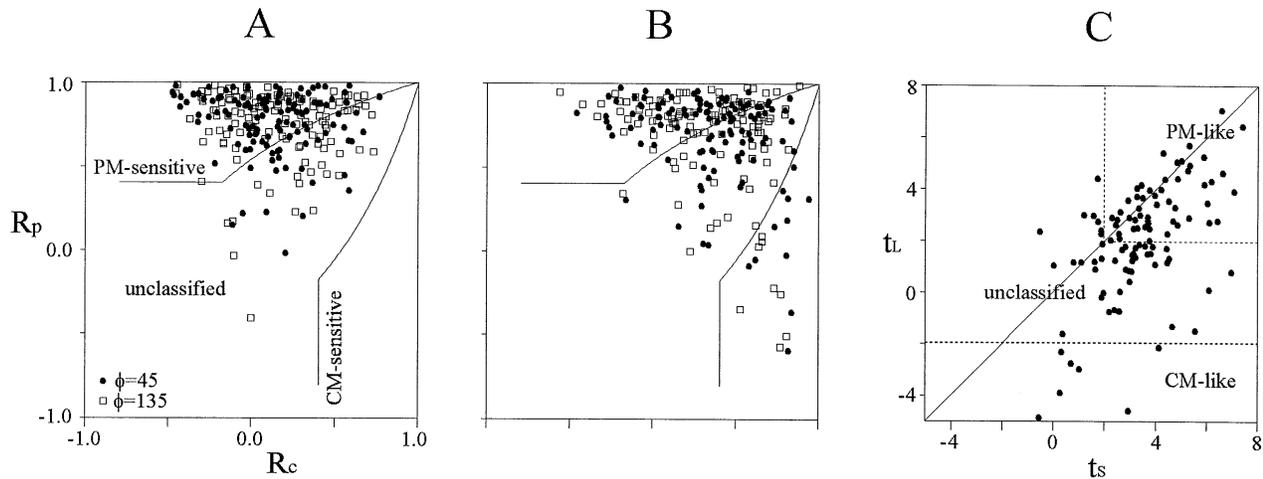
FIG. 3. Scatter plots for PM- and CM-selectivity of PMLS neurons to random-line patterns. (A and B) Partial correlation coefficient R_p against R_c. The data space is divided into three statistical regions by the boundaries defined as the significant difference between R_p and R_c, between R_p and 0, or between R_c and 0, at $P = 0.05$. (A) Data measured with shorter-line patterns ($L = 1–1.5°$, 124 cells). (B) Data measured with longer-line patterns ($L = 3–4°$, 120 cells). (C) t-value, the parametric statistical difference between R_p and R_c, for longer-line patterns (t_L) against that for shorter-line patterns (t_S). For each of the 106 cells and every line length, the t-values for $\phi = 45°$ and for $\phi = 135°$ were averaged instead of being plotted individually, since there was no obvious difference between them (see A and B). The significant level of $P = 0.05$ is shown as dashed lines, outlining the regions in which the cells are defined as PM-like or CM-like. Note that most samples fall below the diagonal, indicating a shift in favour of CM-selectivity when longer-line patterns were presented.

same line length but moved perpendicularly and classified by the partial correlation coefficients between the PM- or CM-prediction and the observed data.

PM- and CM-selective responses

The response profiles of three typical neurons are illustrated in Fig. 2. In Fig. 2A, the tuning curves to different stimuli were similar to each other in shape and the preferred directions were nearly identical, implying that this cell was insensitive to the orientation cue contained in the stimuli. Partial correlation analysis showed that this cell was PM-direction-selective to both 1°- and 3°-line patterns. The cell in Fig. 2B was significantly PM-selective to 1°-line patterns, but could not be classified as either PM- or CM-sensitive for 3°-line patterns as the observed major peak lay between the two predictions. The cell in Fig. 2C did not show clear direction preference to 1°-line patterns, but had significant CM-sensitive responses to 3°-line patterns. It should be noted that this cell had obvious bimodal tuning curves, having two preferred directions opposite to each other, to the moving bar and 3°-line patterns.

The classification of the whole sample is shown in Fig. 3. Of the 124 cells measured with shorter-line patterns, none was classified as CM-sensitive. The numbers of PM-sensitive cells were 93 and 90 for patterns of $\phi = 45°$ and $\phi = 135°$, respectively. 120 cells were tested with longer-line patterns. For $\phi = 45°$, 60 cells were PM-selective and another 11 cells were CM-selective. For $\phi = 135°$, the numbers were 72 and 8, respectively. In other words, the proportion of PM-sensitive cells decreased from $\approx 70\%$ to $\approx 50\%$ with the elongation of component lines, while a small subset of neurons ($< 10\%$) were identified as CM-selective, rather than nonselective. In Fig. 3C the responses to shorter- and longer-line patterns were considered jointly and the 106 cells tested with both line lengths were divided into three categories: PM-like, CM-like and unclassified. In Fig. 4A the response strength and direction index of these cells to the moving bar are shown as a scatter plot to allow comparison among the three categories. No obvious difference can be seen in the distributions of response strength, but for direction index values it seems that the PM-like and

CM-like cells are separate populations, while the unclassified cells cover the full range from close to 0 to above 1 (Fig. 4B). However, as shown in the figure, the relative PM/CM selectivity, evaluated by the parameter t_L, is significantly correlated to the direction index in a continuous distribution, of which the data space between PM-like and CM-like cells is filled up by the unclassified cells.

As shown in Fig. 3C, 52 neurons (49.1%) were PM-selective to both the shorter- and longer-line patterns, and in general, they were similar to the example shown in Fig. 2A. For most of the PM-like cells, the preferred direction remained almost unchanged when tested with the different stimulus patterns. In addition, all the direction index values of these cells were above 0.6 with only a few exceptions (for the moving bar see Fig. 4A, data not shown for other stimuli), implying that they had strong direction preference but were not sensitive to the orientation cue varied in the measurements. All these results indicate that these neurons might be able to signal the true direction of pattern motion in spite of interference of the component orientation, at least when the orientation element was not very strong.

A subset of seven neurons (6.6%), like in Fig. 2C, closely matched the prediction for CM-selectivity when longer-line patterns were applied, indicating that they processed the one-dimensional motion feature making up the stimuli. However, when tested with shorter-line patterns, most of these CM-like cells responded poorly and the direction preference was usually poor also. On the other hand, even though their responses to the moving bar were no weaker than those of the PM-like cells, their direction index values were much lower, within a range in which there was almost no PM-like cell (see Fig. 4). Further observation found that the low DI values resulted from the obvious bi-directional responses (with two preferred directions opposite to each other, as for the tuning curves to the moving bar and 3°-line patterns in Fig. 2C) instead of a 'real' poor direction sensitivity. Therefore, these cells might actually be orientation-selective and their direction-tuning responses based on the orientation mechanism, this would mean that they would hardly detect the direction of moving patterns when the orientation element was relatively weak, but when the orientation cue was clear enough, they would respond in an obvious CM-selective
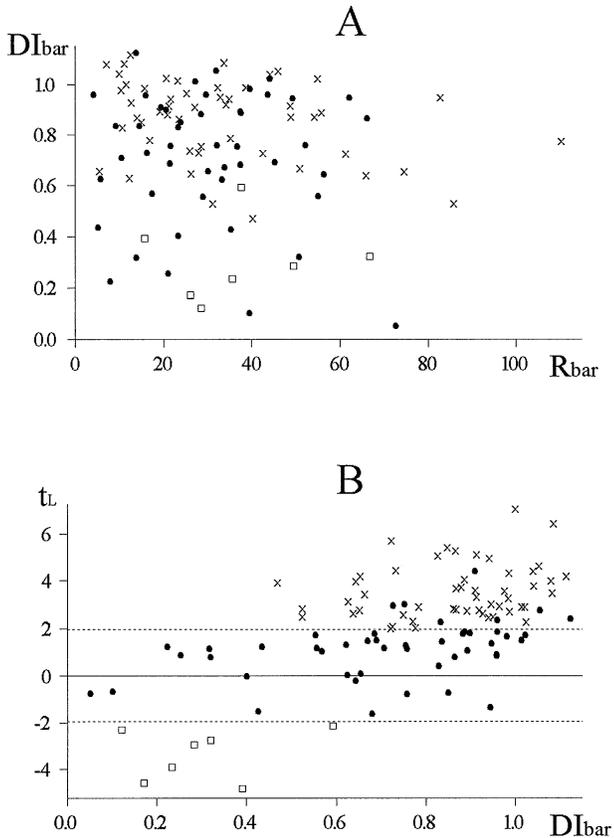
FIG. 4. (A) Distribution of response strength (R_{bar}) and direction index (DI_{bar}) to moving bar stimuli. Only the cells shown in Fig. 3C are included. For each cell, the conventional direction index was calculated as $DI_{bar} = 1 - R_{NPD}/R_{PD}$, where R represents the response strength for the preferred direction (PD) or its opposite direction (NPD), and R_{PD} was taken as R_{bar}. The spontaneous activity was subtracted prior to this calculation. All the response strength values, regardless of the cell category, are broadly distributed in the same range except for a few cases. The mean values and standard deviations are 33.11 ± 22.70 (PM-like, crosses), 37.24 ± 16.75 (CM-like, open squares), and 30.81 ± 16.72 (unclassified, dots) spikes per second. The differences are far from significant (Kruskal–Wallis χ^2-test, $P > 0.6$). However, the CM-like cells have much lower direction indexes than the PM-like ones (mean values 0.302 ± 0.156 vs. 0.846 ± 0.199, Kruskal–Wallis χ^2-test, $P < 0.0001$). For the unclassified cells, the points are more scattered with an intermediate mean value (0.713 ± 0.259). (B) t_L, as defined in Fig. 3C, is plotted against DI_{bar}. The sample points are broadly scattered rather than forming discrete clusters, and the two parameters are significantly correlated to each other ($r = 0.617$, $P < 0.0001$).

manner. It should be emphasized that such cells constitute only a small minority in our sample.

Variable PM/CM selectivity

Although PM-selectivity seems to have a preponderance in our sample, this advantage reduced when shorter-line patterns were replaced with longer ones. By this change, the responses of most cells became less PM-sensitive and more CM-like, with a few of them reaching the criteria for significant CM-selectivity (Fig. 3B, for examples see Fig. 2). This tendency, visualized in Fig. 3C as the generally lower t-values for longer-line patterns (Wilcoxon test, $P < 0.0001$), implies that the variation of the orientation element in the visual stimulus may affect the direction-selective behaviour of PMLS neurons. In order to confirm this still further, we tested a subset of samples with patterns composed of even longer random

lines. The results (for example see Fig. 5, for statistics see Fig. 6) demonstrated that the direction preference varied steadily in favour of CM-selectivity with the elongation of component lines, although only two out of 16 cells, and only when $L > 8°$, could be identified as significantly CM-selective.

Although it seems reasonable to suppose that the PM/CM selectivity of a cell to a pattern moved obliquely may depend on its receptive field size, we failed to find an obvious relationship between the classification and the width/height of receptive field. It should be noted that all the data presented here were obtained using patterns of which the line length was much shorter than the receptive field width of the cell being recorded. Actually, the conventional tests were conducted with $1–1.5°$ and $3–4°$ lines, while the receptive fields were usually larger than $10°$ and sometimes even close to $30°$. Even when additional tests were performed, the maximal line length was limited to one-third or a half of the width of the receptive field, and no more than $9°$ (see Fig. 6). With this design, the lines composing a pattern would not be too few and there would be always a number of lines falling within the range of the receptive field during stimulation (see Fig. 1A). These settings may minimize the potential problems introduced by the purely positional information and the inhomogeneity in the pattern. Given such conditions, it would not be surprising to find that no significant correlation was detected between the PM/CM selectivity and the receptive field size.

The differences between PM- and CM-like cells and the correlation shown in Fig. 4B indicate that the PM/CM selectivity is related to the strength of direction bias. The more a cell prefers one direction over the opposite one, the more it is likely to be PM-sensitive, while the bi-directionally tuned cells tend to be CM-selective. On the other hand, the variable direction preference suggests that all the PMLS neurons may form a continuum of response selectivity and the identification of PM- or CM-sensitivity is, to some extent, dependent on the stimulus pattern. This idea is supported by the fact that the unclassified cells fill up the gap between PM-like and CM-like cells in the distribution of data (see Figs 3C and 4B). It is plausible to suppose that, with an increasing orientation element in the stimulus, there would be more and more PM-like cells being re-categorized as unclassified, and unclassified cells becoming CM-sensitive.

PM/CM selectivity during the initial phase of responses

All the results described above were obtained by analysing the sustained responses occurring later than 200 ms after the stimuli were given. Although those vigorous, early discharges may be induced partly by stimulus features other than motion direction and contour orientation, many cells had fairly good direction-tuned responses within the initial 200 ms and it would be interesting to compare the neuronal activities during these two periods of time. Therefore, the same procedures for PM/CM selectivity analysis were conducted on the initial transient responses and the results are shown in Fig. 7.

In Fig. 7C and D it can be seen that, for both shorter- or longer-line patterns, most cells had lower t-values during the initial phase than during the late part of responses. The means of the whole sample were significantly different (Wilcoxon test, $P < 0.0001$). These are in agreement with the findings of Lorenceau et al. (1993) that the accuracy of movement-direction discrimination of tilted lines is poor at short durations when the perceived direction tends to be at right angles to the to the lines. Pack & Born (2001) recently reported that MT neurons initially respond primarily to the motion component perpendicular to a contour's orientation, but over a period of approximately 60 ms the responses gradually shift to encode the true stimulus direction. All these data are in favour of the idea that the
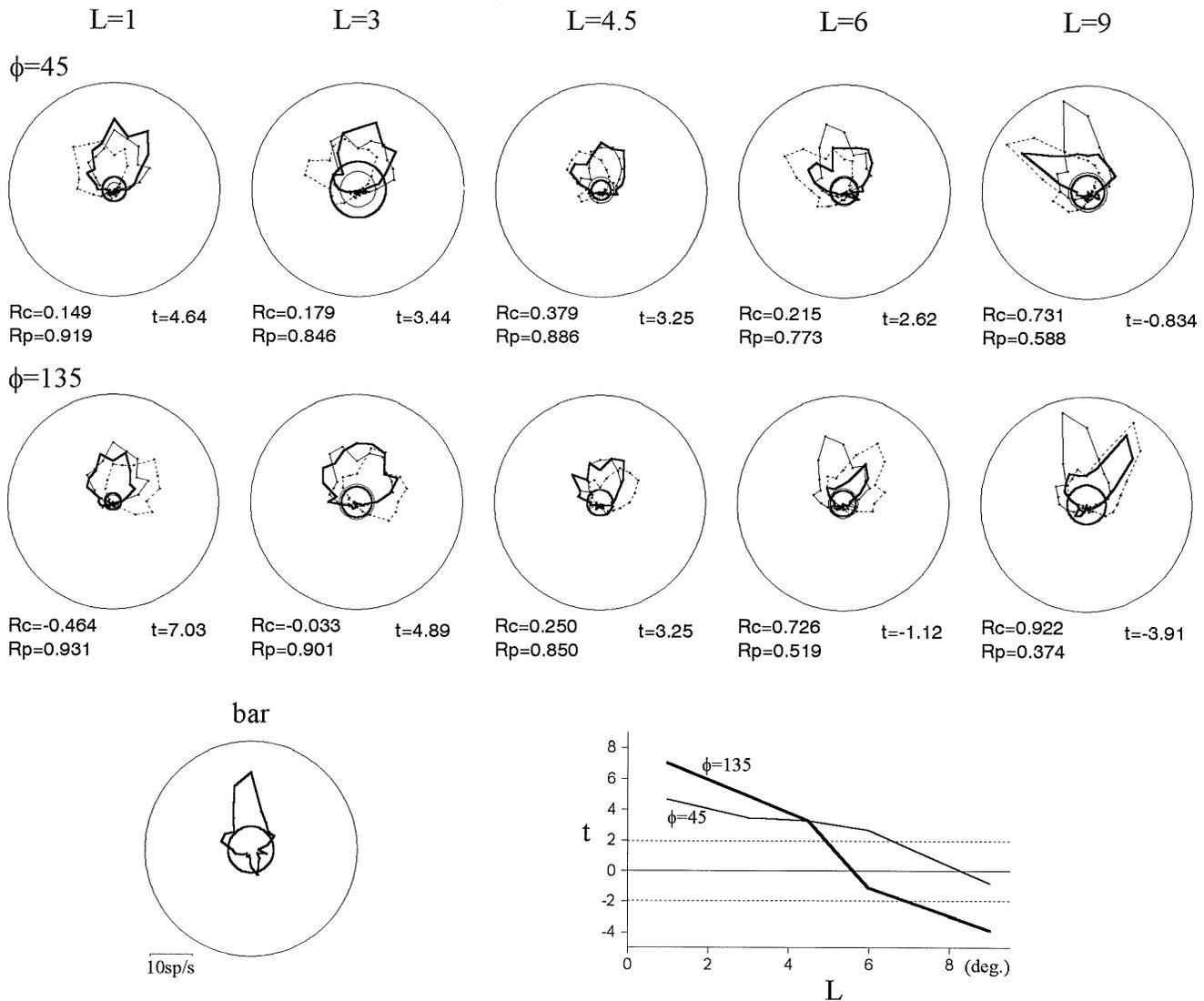
FIG. 5. Polar graphs illustrating the variation of direction-tuning responses of a PMLS neuron with the length of component segments (*L*) in random-line patterns. When *L* was equal to 1°, 3° or 4.5°, the responses could be identified as PM-selective, though the difference between R_p and R_c became smaller and smaller. For patterns with $\phi = 135°$, the tuning curve fell into the unclassified category when $L = 6°$ and changed to CM-sensitive when $L = 9°$. Note that with increasing *L*, the major peak shifted progressively to meet the CM-prediction. For patterns of $\phi = 45°$, the difference between R_p and R_c also decreased when *L* was increased, but the peak shifted to the opposite side. At the bottom row, the tuning curve to a moving bar is depicted for reference (left), and the difference between R_p and R_c (shown with the statistical value *t*) is plotted against *L* to show the variation more clearly (right).

neural solution to pattern motion is firstly estimated by computing the motion of orientated contours and then refined over time to progressively approach the veridical direction of stimulation. However, when compared with the classification shown in Fig. 3A and B (the sustained responses), there were far fewer PM-sensitive responses in the initial phase, only slightly more CM-selective responses in this phase and the vast majority of samples fell into the unclassified category (see Fig. 7A and B). Therefore, we are cautious to make any conclusion on this issue. Since the data were averaged over a much shorter period for the initial responses than for the sustained responses, there may be relatively more noise in the tuning curves. On the other hand, as mentioned above, the initial responses may be partly evoked by the variation of luminance or other features. Both of the two aspects may disrupt the regular direction tuning and increase the chance of unclassified responses, but probably can not fully account for the unexpected low appearance of CM-sensitive

responses. Further explorations on the dynamics of direction selectivity varying with time may help answer further questions.

Discussion

In the present study, a series of random-line stimuli were used to systematically investigate the direction selectivity of PMLS neurons. It is the first time, to our knowledge, that the substantial existence of PM-sensitive responses has been observed in this extrastriate visual area of the cat. In addition, our results show that the PM/CM sensitivity of a certain cell is variable with the orientation element in stimulation. These findings imply that the commonly accepted two-stage processing theory is probably incomplete for modelling the visual motion analysis in the cortex.

Considerations on stimulation: drifting plaid and random-line patterns

The drifting plaid, as a pattern comprising contours moving in two different directions, has been used in many studies to overcome the inherent ambiguity of one-dimensional motion and the results are taken as evidence for the two-stage processing theory (for review, see
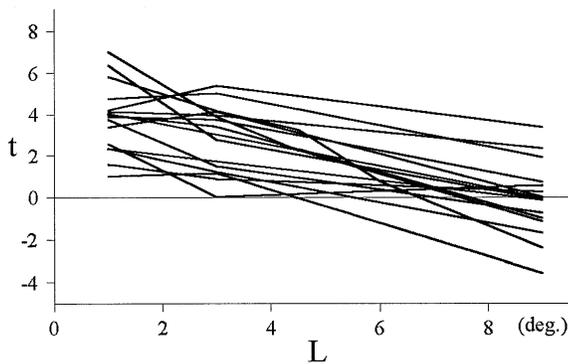

FIG. 6. Effect of increasing the length of component segments (L) in random-line patterns on the direction selectivity of 16 PMLS neurons tested with multiple line lengths from 1° to 9°. The t-value, averaged from those for $\phi = 45°$ and for $\phi = 135°$, is plotted against L. For most cells, t-value decreased monotonically with the increment of L, indicating that the direction tuning varied in favour of CM-selectivity when the orientation element in the stimulus was increased.

Albright & Stoner, 1995). One potential problem with this approach is that a plaid contains unambiguously moving local contrasts at grating intersections that may possibly be used as a cue in a nonorientation-based mechanism to signal the overall direction of pattern motion (Stoner *et al.*, 1990; Lorenceau & Shiffrar, 1992). However, in the relevant studies, the intersection cue might be not clear enough to prevail over the orientation element in the plaid. To explore the possible involvement of nonorientation-based processing, it is necessary to test the direction selectivity with stimuli containing a weaker and adjustable orientation element. The random-line patterns we used appeared to be appropriate for this purpose, provided that the elongated line segments in our stimuli were not misconceived by the neurons as the isotropic dots in conventional random textures. As shown in our results, about 50% of the cells tested were PM-selective to 3°-line patterns (length : width = 30 for each component line), and when even longer lines were used, there were still some cells giving PM-sensitive responses (see Figs 5 and 6). It is very unlikely that all these cells took the component lines as circular dots. This hypothesis may find support from the report by Henry *et al.* (1974) that some striate cells are sensitive to the orientation of a single flashing bar as short as 0.57° (width 0.29°, length : width = 2). There are no comparable data available for PMLS cells, probably due to the poor responsiveness to stationary stimuli. Since their receptive fields are usually larger, one may argue that a distinction between short lines and small dots of similar size might be not very clear especially when the pattern is moving. However, the minimal line length used in the present study was 1°
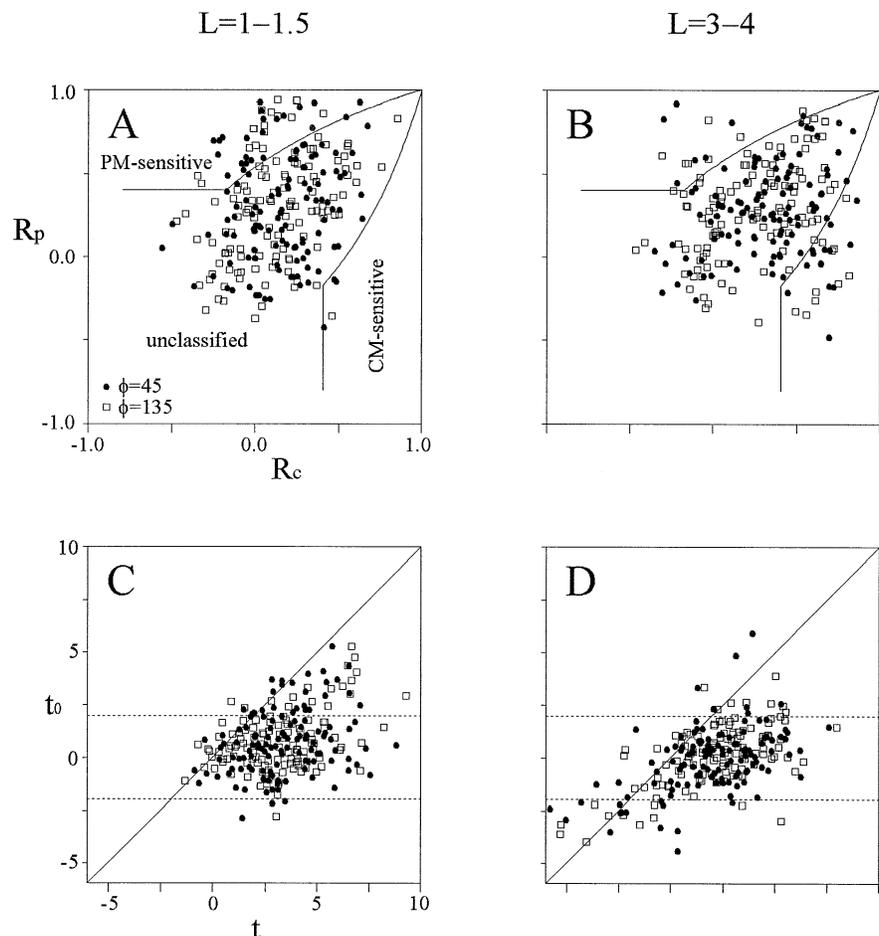

FIG. 7. PM/CM selectivity during the initial phase of responses. All the neurons shown in Fig. 3 were subjected to analysis again but the spike counting was performed within 0–200 ms after the onset of stimulation, the period which was excluded while preparing Figs 2–6. (A–B) Partial correlation coefficient R_p against R_c for L values of 1–1.5° (A) and 3–4° (B). Conventions are the same as in Fig. 3A–B. (C–D) t-values for initial responses (t_0) against that for subsequent sustained responses (t) for L values of 1–1.5° (C) and 3–4° (D). Most samples are distributed below the diagonal, indicating that the initial transient responses may be more CM-sensitive than the late part of responses.

which corresponds to a length : width ratio of 10 : 1, and for each cell, the receptive field was well covered by numerous randomly distributed component lines making the orientation cue more visible. In addition, the moderate velocity could help to overcome the ill-effects caused by motion (blurring, jerking, etc.). With all the settings, it is reasonable to believe that the random-line patterns were effectively anisotropic to the neurons in the orientation domain and to make the PM- and CM-predictions as described in Methods.

During the experiments, the drifting velocity of an obliquely moved pattern was always identical to that of the corresponding perpendicularly moved pattern, thus, the component vector normal to the line orientation was about 30% smaller than the physical speed. This setting should not affect the PM-prediction, but for the CM-prediction in which the cell is presumed to be sensitive to component orientation, the effective velocity vector is possibly no longer optimal for the cell and the responses may decrease. However, this effect would not vary with the line length and has little influence on the results of correlation analysis. One may expect that the CM cells have higher preferred velocity to patterns moved obliquely; probably due to the low appearance of CM-sensitive responses, so far we have not found reliable evidence for this hypothesis. It would be interesting to conduct this test in area V1, in which one may have a better chance in inducing CM-sensitive responses (see below).

Since random-line stimuli have rarely been used in relevant investigations, there are no data available from other sources for a direct comparison. To gain more confidence, each cell included in our sample was always tested with patterns oblique to opposite sides as shown in Fig. 1B and C. When the direction-tuning profiles were classified into different categories, the two obliquely moved patterns of the same line length frequently gave similar results (see examples in Figs 2 and 5, statistics in Figs 3A and B, and 7). When a neuron was not PM-selective, the major peak of its tuning curve usually shifted to the opposite sides for the two stimuli, no matter whether the criteria for significant CM-sensitivity were reached or not (Figs 2B and C, and 5). In addition, the cells were not tested in a stereotyped order (e.g. from shorter- to longer-line patterns, or from $\phi = 90°$, $45°$, to $135°$) but in an interleaved manner, especially for those measured with multiple line lengths. Therefore, one may exclude the possibility that the results presented here were artefacts but consider them as representing the direction-selective behaviour of PMLS neurons.

Implication of the present findings

In the two-stage processing theory, it was proposed that PM-selectivity is achieved by integrating the outputs of CM-selective units (Adelson & Movshon, 1982; Movshon *et al*., 1985; Welch, 1989; Derrington & Suero, 1991; Albright & Stoner, 1995; Nowlan & Sejnowski, 1995; Simoncelli & Heeger, 1998) and that CM and PM neurons are distinct subpopulations in the cortex (Rodman & Albright, 1989; Gizzi *et al*., 1990; Movshon & Newsome, 1996; Scannell *et al*., 1996; Gegenfurtner *et al*., 1997; Merabet *et al*., 1998). Here we have shown that PM- or CM-sensitivity may be not a fixed feature of certain cells, but the direction tuning of a PMLS neuron can vary with the orientation element in the stimulus. The scale of such variation could be different from cell to cell, within the range from fully CM-sensitive to fully PM-selective (Figs 3C and 6). Such dynamic variation would probably require dual underlying mechanisms. Besides the widely discussed orientation-sensitive mechanism, certain types of additional process, relatively independent of the one-dimensional orientation cue, may also be involved in determining the direction of motion. The two mechanisms would act simultaneously in a dynamic competition where one rises as the other falls, depending upon the strength of the orientation element in the stimulus. As a result, when one mechanism prevails over the other, it would respond like a PM- or CM-sensitive cell, otherwise, an unclassified one.

With the above hypothesis, the present findings are not contradictory with previous results obtained with drifting plaids where there was a population of CM cells but no PM cell in PMLS (Movshon *et al*., 1985; Gizzi *et al*., 1990; Merabet *et al*., 1998). Since a plaid is rich in orientation elements, the intersection cue it contains is probably not clear enough to prevail over the orientation-based mechanism and to signal the coherent motion of the composite pattern, so that no significant PM-selectivity was detected. However, the presence of a number of unclassified cells in all of the previous studies suggests that features other than orientation may also play an active role in evoking the direction-tuning responses. This proposition may also account for the disagreement on orientation selectivity of PMLS cells in previous studies with different stimuli (see Introduction). When the orientation element is not strong (such as in spots or short bars), the orientation mechanism might be not effective enough to elicit selectivity as clear as that found with long bars or gratings.

Although the detection of local orientated features has been demonstrated by numerous experimental evidence, a succeeding integration of the one-dimensional cues may result in incorrect global motion perception in many cases (Nakayama & Silverman, 1988; Ferrera & Wilson, 1990; Yo & Wilson, 1992; Rubin *et al*., 1995a, 1995b). Furthermore, many objects in the natural world do not possess such regular component orientations as that in plaids, and the estimation of orientation components in motion would become less reliable due to blurring or smearing as the speed increases. Therefore, some kind of nonorientation-based process may be necessary to detect motion of objects in the environment under various circumstances. Our findings, that many PMLS cells were PM-sensitive to shorter random-line patterns may indicate that such a process is probably present in this relatively lower extrastriate area which is believed to provide outputs for motion integration in higher level cortices (Movshon *et al*., 1985; Gizzi *et al*., 1990; Scannell *et al*., 1996).

Neural substrates for nonorientation-dependent processing

Based on their results of human psychophysical study, Lorenceau *et al* (1993) proposed a motion analysis model which relies on a dynamic competition between two different classes of signals, one originating from contour motion processing units, the other from line terminator processing units (Castet *et al*., 1993; Lorenceau *et al*., 1993). This theory is similar to our interpretation on the involvement of nonorientation-dependent mechanism but different on how the mechanism works. In their model, the competition occurs between two populations of units driven by orientation-dependent and nonorientation-dependent mechanisms, respectively, whereas, our results suggest that the two kinds of mechanisms may act simultaneously on a single cell and the competition between them enables the cell to demonstrate variable PM/CM selectivity to different stimuli. Nevertheless, it is also possible that the two competitions are in action together in the cortex to account for the dependence of direction discrimination on the characteristics of visual stimulus.

No matter how the nonorientation-dependent mechanism works, it requires the stimulus to contain certain identifiable features, other than an orientation cue, for tracking motion over time: this could be line ends (such as in our stimuli), corners, crosses, and so on (also see Zucker *et al*., 1990; Mingolla *et al*., 1992; Shiffrar *et al*., 1995; Shiffrar & Lorenceau, 1996). It was speculated that the end-stopped cells in areas 17 and 18 may signal feature points in motion, and the

activities of some specific neurons in area V2 of the monkey and area 19 of the cat were related to different pattern discontinuities (Castet *et al.*, 1993; Lorenceau *et al.*, 1993). Previous findings, that some striate neurons are highly sensitive to cross- or corner-like figures (Shevelev *et al.*, 1995, 1998; Sillito *et al.*, 1995), indicate the possibility of detecting such angular features in area 17. Besides these structural features, some motion cues may also contribute to nonorientation-based processing. For example, a recent psychophysical study suggested that motion streaks may provide a spatial code for motion direction (Geisler, 1999). Since lack of direct physiological evidence, these ideas are yet to be verified by new experiments.

The present study was carried out in PMLS because that, as an area mainly involved in motion perception and the putative analogue to MT, it may offer a better chance to encounter nonorientation-dependent responses, though area 17 is also of great interest. With the data available it remains unclear how the direction-tuning responses of PMLS neurons are modulated so that they could vary with the nature of stimulation. The aforementioned studies are in favour of the idea that nonorientation-dependent processing may occur as early as in striate cortex, but whether it is enhanced afterward in higher cortical areas remains to be answered. Recently, we conducted a number of similar experiments in area 17. The preliminary results show variable PM/CM selectivity for some striate neurons, but the PM-sensitive responses are not as pronounced as in PMLS, which seems to imply that the orientation-selective mechanism may play a more important role in this earlier cortical area.

Acknowledgements

Abbreviations

CM, component motion; MT, middle temporal area, PD, preferred direction; PM, pattern motion; PMLS, posteromedial lateral suprasylvian area.

References

Adelson, E.H. & Movshon, J.A. (1982) Phenomenal coherence of moving visual patterns. *Nature*, **300**, 523–525.

Albright, T.D. (1984) Direction and orientation selectivity of neurons in visual area MT of the macaque. *J. Neurophysiol.*, **52**, 1106–1130.

Albright, T.D. & Stoner, G.R. (1995) Visual motion perception. *Proc. Natl. Acad. Sci. USA*, **92**, 2433–2440.

Barlow, H.G. & Levick, W.R. (1965) The mechanism of directionally selective units in rabbit's retina. *J. Physiol. (Lond.)*, **178**, 477–504.

Bishop, P.O., Kato, H. & Orban, G.A. (1980) Direction-selective cells in complex family in cat striate cortex. *J. Neurophysiol.*, **43**, 1266–1283.

Blakemore, C. & Zumbroich, T.J. (1987) Stimulus selectivity and functional organization in the lateral suprasylvian visual cortex of the cat. *J. Physiol. (Lond.)*, **389**, 569–603.

Camarda, R. & Rizzolatti, G. (1976) Visual receptive fields in the lateral suprasylvian area (Clare–Bishop area) of the cat. *Brain Res.*, **101**, 427–443.

Castet, E., Lorenceau, J., Shiffrar, M. & Bonnet, C. (1993) Perceived speed of moving lines depends on orientation, length, speed and luminance. *Vision Res.*, **33**, 1921–1936.

Creutzfeldt, O.D., Kuhnt, U. & Benevento, L.A. (1974) An intracellular analysis of visual cortical neurones to moving stimuli: Responses in a co-operative neuronal network. *Exp. Brain Res.*, **21**, 251–274.

Danilov, Y., Moore, R.J., King, V.R. & Spear, P.D. (1995) Are neurons in cat posteromedial lateral suprasylvian visual cortex orientation sensitive? Tests with bars and gratings. *Vis. Neurosci.*, **12**, 141–151.

Derrington, A. & Suero, M. (1991) Motion of complex patterns is computed from the perceived motions of their components. *Vision Res.*, **31**, 139–149.

Dreher, B., Wang, C., Turlejski, K.J., Djavadian, R.L. & Burke, W. (1996) Areas PMLS and 21a of cat visual cortex: Two functionally distinct areas. *Cereb. Cortex*, **6**, 585–599.

Eysel, U.T., Muche, T. & Wörgötter, F. (1988) Lateral interactions at direction-selective striate neurons in the cat demonstrated by local cortical inactivation. *J. Physiol. (Lond.)*, **399**, 657–675.

Ferrera, V.P. & Wilson, H.R. (1990) Perceived direction of moving two-dimensional patterns. *Vision Res.*, **30**, 273–287.

Gegenfurtner, K.R., Kiper, D.C. & Levitt, J.B. (1997) Functional properties of neurons in macaque area V3. *J. Neurophysiol.*, **77**, 1906–1923.

Geisler, W.S. (1999) Motion streaks provide a spatial code for motion direction. *Nature*, **400**, 65–69.

Gizzi, M.S., Katz, E., Schumer, R.A. & Movshon, J.A. (1990) Selectivity for orientation and direction of motion of single neurons in cat striate and extrastriate visual cortex. *J. Neurophysiol.*, **63**, 1529–1543.

Hamada, T. (1987) Neural response to the motion of textures in the lateral suprasylvian area of cats. *Behav. Brain Res.*, **25**, 175–185.

Hammond, P. (1978) Directional tuning of complex cells in area 17 of the feline visual cortex. *J. Physiol. (Lond.)*, **285**, 479–491.

Hammond, P. & MacKay, D.M. (1977) Differential responsiveness of simple and complex cells in cat striate cortex to visual texture. *Exp. Brain Res.*, **30**, 275–296.

Heeger, D.J., Simoncelli, E.P. & Movshon, J.A. (1996) Computational models of cortical visual processing. *Proc. Natl. Acad. Sci. USA*, **93**, 623–627.

Henry, G.H., Bishop, P.O. & Dreher, B. (1974) Orientation, axis and direction as stimulus parameters for striate cells. *Vision Res.*, **14**, 767–777.

Li, B., Li, B.-W., Chen, Y., Wang, L.-H. & Diao, Y.-C. (2000) Response properties of PMLS and PLLS neurons to simulated optic flow patterns. *Eur. J. Neurosci.*, **12**, 1534–1544.

Lorenceau, J. & Shiffrar, M. (1992) The influence of terminators on motion integration across space. *Vision Res.*, **32**, 263–273.

Lorenceau, J., Shiffrar, M., Wells, N. & Castet, E. (1993) Different motion sensitive units are involved in recovering the direction of moving lines. *Vision Res.*, **33**, 1207–1217.

Marr, D. & Ullman, S. (1981) Directional selectivity and its use in early visual processing. *Proc. R. Soc. Lond. B*, **211**, 151–180.

Merabet, L., Desautels, A., Minville, K. & Casanova, C. (1998) Motion integration in a thalamic visual nucleus. *Nature*, **396**, 265–268.

Mingolla, E., Todd, J.T. & Norman, J.F. (1992) The perception of globally coherent motion. *Vision Res.*, **32**, 1015–1031.

Movshon, J.A., Adelson, E.H., Gizzi, M.S. & Newsome, W.T. (1985) The analysis of moving visual patterns. In Chagas, C., Gattas, R. & Gross, C.G., (eds), *Pattern Recognition Mechanisms*. Ponticifica Academia Scientiarum, Vatican City, pp. 117–151.

Movshon, J.A. & Newsome, W.T. (1996) Visual response properties of striate cortical neurons projecting to area MT in macaque monkeys. *J. Neurosci.*, **16**, 7733–7741.

Nakayama, K. & Silverman, G.H. (1988) The aperture problem. II. Spatial integration of velocity information along contours. *Vision Res.*, **28**, 747–753.

Nowlan, J.J. & Sejnowski, T.J. (1995) A selection model for motion processing in area MT of primates. *J. Neurosci.*, **15**, 1195–1214.

Pack, C.C. & Born, R.T. (2001) Temporal dynamics of a neural solution to the aperture problem in visual area MT of macaque brain. *Nature*, **409**, 1040–1042.

Palmer, L.A., Rosenquist, A.C. & Tusa, R.J. (1978) The retinotopic organization of lateral suprasylvian visual areas in the cat. *J. Comp. Neurol.*, **177**, 237–256.

Payne, B.R. (1993) Evidence for visual cortical area homologs in cat and macaque monkey. *Cereb. Cortex*, **3**, 1–25.

Rodman, H.R. & Albright, T.D. (1989) Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT). *Exp. Brain Res.*, **75**, 53–64.

Rubin, N., Hochstein, S. & Solomon, S. (1995a) Restricted ability to recover three-dimensional global motion from one-dimensional motion signals: Psychophysical observations. *Vision Res.*, **35**, 463–476.

Rubin, N., Solomon, S. & Hochstein, S. (1995b) Restricted ability to recover three-dimensional global motion from one-dimensional local signals: Theoretical observations. *Vision Res.*, **35**, 569–578.

van Santen, J.P.H. & Sperling, G. (1984) Temporal covariance model of human motion perception. *J. Opt. Soc. Am. A*, **1**, 451–473.

Scannell, J.W., Sengpiel, F., Tovée, M.J., Benson, P.J., Blakemore, C. & Young, M.P. (1996) Visual motion processing in the anterior ectosylvian sulcus of the cat. *J. Neurophysiol.*, **76**, 895–907.

Shevelev, I.A., Lazareva, N.A., Sharaev, G.A., Novikova, R.V. & Tikhomirov, A.S. (1998) Selective and invariant sensitivity to crosses and corners in cat striate cortex neurons. *Neuroscience*, **84**, 713–721.

Shevelev, I.A., Novikova, R.V., Lazareva, N.A., Tikhomirov, A.S. & Sharaev, G.A. (1995) Sensitivity to cross-like figures in the cat striate neurons. *Neuroscience*, **69**, 51–57.

Shiffrar, M., Li, X. & Lorenceau, J. (1995) Motion integration across differing image features. *Vision Res.*, **35**, 2137–2146.

Shiffrar, M. & Lorenceau, J. (1996) Linking of motion signals decreases with contrast, duration and bar width. *Vision Res.*, **36**, 2061–2068.

Sillito, A.M. (1977) Inhibitory processes underlying the directional specificity of simple, complex and hypercomplex cells in the cat's visual cortex. *J. Physiol. (Lond.)*, **271**, 699–720.

Sillito, A.M. (1979) Inhibitory mechanisms influencing complex cells orientation selectivity and their modification at high resting discharge levels. *J. Physiol. (Lond.)*, **289**, 33–53.

Sillito, A.M., Grieve, K.L., Jones, H.E., Cudeiro, J. & Davis, J. (1995) Visual cortical mechanisms detecting focal orientation discontinuities. *Nature*, **378**, 492–496.

Simoncelli, E.P. & Heeger, D.J. (1998) A model of neuronal responses in visual area MT. *Vision Res.*, **38**, 743–761.

Spear, P.D. (1991) Functions of extrastriate visual cortex in non-primate species. In Leventhal, A.G., (ed.), *Vision and Visual Dysfunction*, **Vol. 4**, The Neural Basis of Visual Function. Macmillan, London, pp. 339–370.

Spear, P.D. & Baumann, T.P. (1975) Receptive-field characteristics of single neurons in lateral suprasylvian visual area of the cat. *J. Neurophysiol.*, **38**, 1403–1420.

Stoner, G.R. & Albright, T.D. (1992) Neural correlates of perceptual motion coherence. *Nature*, **358**, 412–414.

Stoner, G.R., Albright, T.D. & Ramachandran, V.S. (1990) Transparency and coherence in human motion perception. *Nature*, **344**, 153–155.

Torre, V. & Poggio, T. (1978) A synaptic mechanism possibly underlying directional selectivity to motion. *Proc. R. Soc. Lond. Series B*, **202**, 409–416.

Toyama, K., Mizobe, K., Akase, E. & Kaihara, T. (1994) Neuronal responsiveness in areas 19 and 21a, and the posteromedial lateral suprasylvian cortex of the cat. *Exp. Brain Res.*, **99**, 289–301.

Welch, L. (1989) The perception of moving plaids reveals two motion-processing stages. *Nature*, **337**, 734–736.

Wilson, H.R., Ferrera, V.P. & Yo, C. (1992) A psychophysically motivated model for two-dimensional motion perception. *Vis. Neurosci.*, **9**, 79–97.

Wörgötter, F., Gründel, O. & Eysel, U.T. (1990) Quantification and comparison of cell properties in cat's striate cortex determined by different types of stimuli. *Eur. J. Neurosci.*, **2**, 928–941.

Yo, C. & Wilson, H.R. (1992) Perceived direction of moving two-dimensional patterns depends on duration, contrast and eccentricity. *Vision Res.*, **32**, 135–147.

Zeki, S.M. (1974) Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. *J. Physiol. (Lond.)*, **236**, 549–573.

Zucker, S.W., Iverson, L. & Hummel, R.A. (1990) Coherent compound motion: Corners and nonrigid configurations. *Neural Comput.*, **2**, 44–57.