

Pattern motion and component motion sensitivity in cat superior colliculus

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Single neurons in the superior colliculus of the cat were tested for their direction-tuning responses to random-line patterns composed of identical short lines moving obliquely to their common orientation. A substantial population of cells responded primarily to the veridical direction of pattern motion while a few were sensitive to the orientation of component lines. Moreover, for most cells, the pattern motion sensitivity decreased when the orientation element was enhanced by elongating the component lines in

stimulus. Further analysis found that the initial transient responses after stimulus onset were relatively more sensitive to component motion than the subsequent sustained responses. These findings suggest that the superior colliculus is involved in the higher-order analysis of visual motion so that collicular neurons can signal coherent pattern motion in many cases. *NeuroReport* 16:721–726 © 2005 Lippincott Williams & Wilkins.

Key words: Cat; Component motion; Direction selectivity; Pattern motion; Random-line patterns; Superior colliculus

INTRODUCTION

Visual motion perception has been commonly considered as a two-stage sequential process. The first stage is characterized by analyzing object features as oriented contours and signaling the motion of individual one-dimensional components [i.e. component motion (CM)], and the outputs are integrated at the second stage to reconstruct the coherent pattern motion (PM) [1–3]. Because substantial populations of PM-sensitive neurons were found in several higher-order cortical areas but not in the striate cortex [2,4–7], the two stages were associated with the hierarchy of the visual cortex. Remarkably, Casanova and coworkers [8,9] reported that about 30% neurons in the lateral-posterior pulvinar complex (LP-pulvinar) of the cat exhibited PM-selectivity and proposed that the extrageniculate thalamic visual nucleus is involved in higher-order motion processing. On the other hand, a number of neurophysiological and psychophysical studies suggest that the two-stage theory cannot fully account for motion perception and the processing may, more or less, depend on other object features such as terminators, discontinuities, and so on [10–16].

The superior colliculus (SC), as a principal structure in the extrageniculostriate visual system of mammals, plays an important role in visual attention and visuomotor coordination [17,18]. Generally, collicular neurons have relatively larger receptive fields, exhibit strong preference for moving stimuli rather than stationary patterns, and are distinguished by their sensitivity to direction and velocity of motion [18–20]. Therefore, the SC appears to be mainly involved in motion detection and relevant information

processing (but see [21,22] for its postulated role in form/pattern discrimination). However, little has been done to examine the response properties of collicular neurons to pattern and component motion and the physiological substrate underlying the aforementioned functions of the nucleus remains unclear. The present study is conducted as an attempt to explore the unanswered questions.

MATERIALS AND METHODS

Experiments were carried out on 12 normal adult cats. The detailed procedures for animal preparation, maintenance and recording have been reported previously [12]. Adequate measures were taken to minimize pain and discomfort of the cats in compliance with the NIH guidelines. Craniotomy was made at Horsley–Clarke coordinates P2-A4 and L0-5 [19]. A glass-coated tungsten microelectrode was lowered perpendicularly into the brain and then advanced into the SC, normally at least 12 mm below the cortical surface. Once a single unit was isolated, the receptive field was approximately plotted with hand-held stimuli.

The visual stimuli used in quantitative measurements and the methods for data analysis were principally the same as those described in [12]. Briefly, the stimuli (termed as random-line patterns) were composed of a number of thin line segments (width 0.1°) with identical length (L) and orientation. The lines were distributed randomly within a virtual circular window, which was individually centered on the receptive field being tested. The number of lines was directly proportional to the window size (normally 30° in diameter, though for some cells appropriately adjusted to

elicit good responses) but inversely proportional to L . A complete trial consisted of sweeps in 24 pseudorandomly interleaved directions and a blank control for measuring the spontaneous activity, and at least five trials were presented to obtain a direction-tuning curve. Usually each sweep lasted 2000 ms and was succeeded by a pause of 2000 ms. During the stimulation period, all the lines moved coherently at the same velocity and direction to eliminate any relative displacement. In addition, the movement was restricted within the window, and a wrap-around procedure was performed so that once a line left the window, it was immediately assigned a new location at the opposite side of the circle. It should be emphasized that, during each measurement, the orientation of the component lines always varied with the moving direction so that the angle between them was kept at a constant value ϕ . Therefore, the stimuli could be defined with two parameters L and ϕ .

A total of 123 collicular neurons, mainly from the superficial layers, were tested with random-line patterns of $L=1^\circ$, 3° or 6° . Presumably, the orientation element in the stimulus increases with L . For each L , three tuning curves were measured with all the lines moving perpendicularly or obliquely to their orientation ($\phi=90^\circ$, 45° and 135° , respectively). As in an earlier study [12], the neuronal

discharges occurring within the first 200 ms of each sweep were excluded from the analysis until the final part of the Results section.

Each tuning curve obtained with an obliquely moved pattern was subjected to the partial correlation analysis between PM or CM prediction and the observed data (for details see [12]). The PM prediction was derived by assuming that the response profile was as the same as the tuning curve to the pattern of the identical L , but $\phi=90^\circ$, and the CM prediction was derived by shifting this tuning curve by 45° counterclockwise (for $\phi=45^\circ$) or clockwise (for $\phi=135^\circ$, see examples shown in Fig. 1). With the partial correlation coefficients R_p and R_c quantifying the fitness of actual response to PM and CM predictions, respectively, a parametric statistical value t was calculated to show the significance of difference between R_p and R_c .

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

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

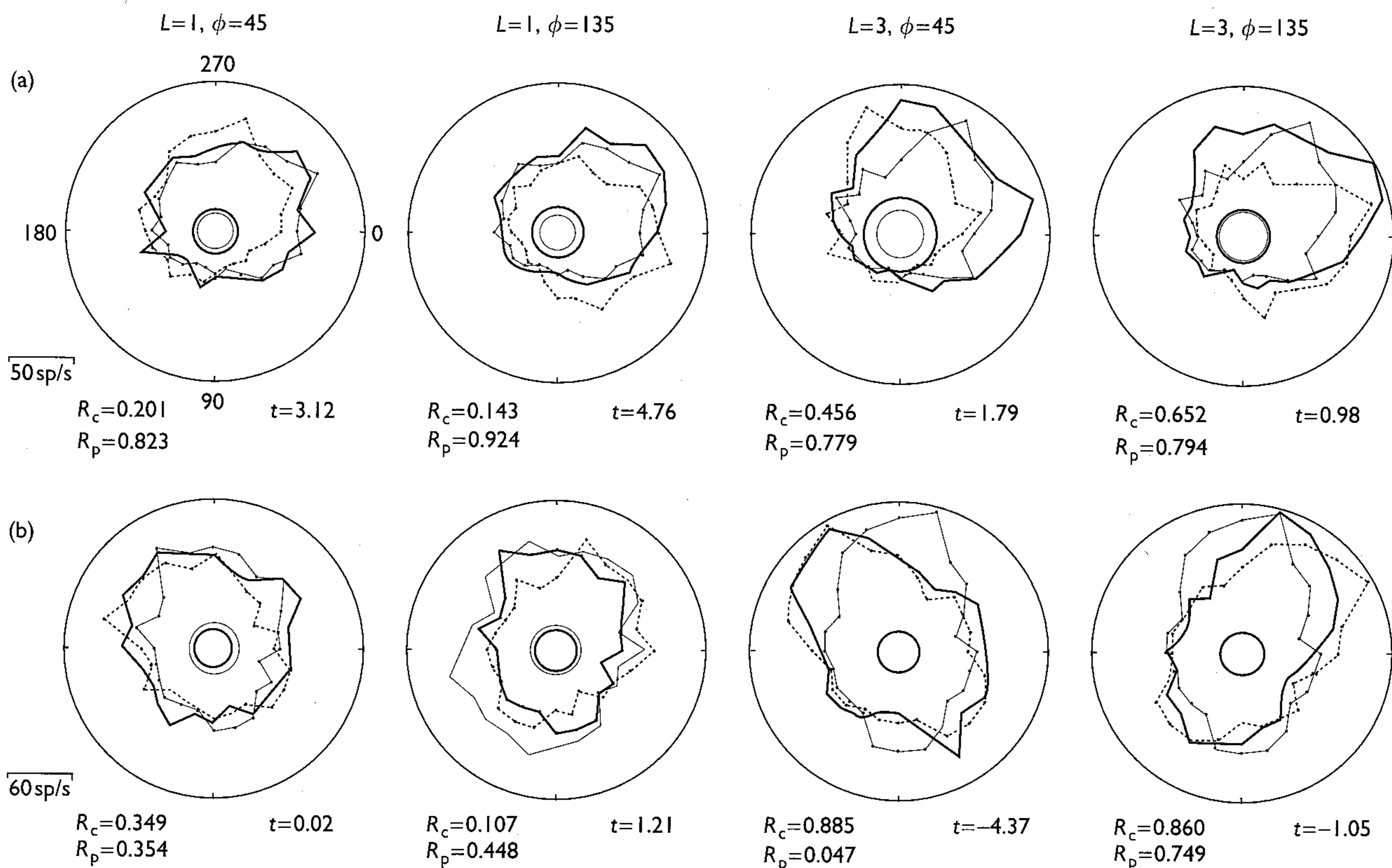


Fig. 1. Polar graphs illustrating the direction-tuning curves of two collicular neurons to random-line patterns with different parameters. In each panel, the response profile to the obliquely moved pattern (defined by L and ϕ values given at the top) is plotted in a thick line. In addition, the tuning curve to the corresponding perpendicularly moved pattern (with identical L but $\phi=90^\circ$) is plotted in a thin line as the pattern motion (PM) prediction, while the dashed line represents the component motion (CM) prediction. The spontaneous activity levels are depicted as small central circles. (a) When $L=1^\circ$, a close correspondence was seen among the tuning curves for different ϕ values and the preferred directions were nearly the same. A similar response profile was observed while $L=3^\circ$ and $\phi=90^\circ$. However, for the obliquely moved 3° -line patterns, the major peak on the tuning curve shifted either counterclockwise (for $\phi=45^\circ$) or clockwise (for $\phi=135^\circ$) as it lay between the corresponding CM and PM predictions. (b) When $L=1^\circ$, the cell was short of clear direction tuning and it was hard to determine its preferred direction. Nevertheless, when $L=3^\circ$, it became well visible that the major peak shifted to opposite sides in the two panels to approach the corresponding CM prediction, though the fitness of the actual response to the CM prediction was very good for $\phi=45^\circ$ but insignificant for $\phi=135^\circ$.

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

in which

$$z_x = \frac{1}{2} \ln \frac{1 + R_x}{1 - R_x}$$

$$x = p, c, n = 24$$

where r_p and r_c are the simple correlation coefficients between the actual response and PM and CM predictions, respectively, and r_{pc} , between the two predictions. Qualitatively, the responses were classified into three categories at the significance level of $p=0.05$ (as shown in Fig. 2). Quantitatively, the t -value could be used as a single index to quantify the status of PM-CM sensitivity.

RESULTS

The tuning curves of two representative neurons and the PM and CM predictions are shown in Fig. 1. For the first cell (Fig. 1a), the response profiles to different 1° -line patterns were very much alike and the analysis resulted in significant PM-sensitivity in both cases ($\phi=45^\circ, 135^\circ$), indicating that it responded primarily to the veridical direction of pattern motion. However, when the cell was stimulated with 3° -line patterns, its PM-sensitivity (t -value) dropped obviously and the responses fell into the unclassified category. The second cell (Fig. 1b) did not display clear direction preference to 1° -line patterns and was unclassified in the analysis. Nevertheless, the cell turned to be CM-sensitive to 3° -line patterns (though the normal significance level was yet to be reached for $\phi=135^\circ$), implying that the responses were more dependent on the component orientation in visual stimuli. Both neurons were also tested with 6° -line patterns (graphs not shown to save space). The first one was still in the unclassified category but the t -values decreased further; the second one had even better CM-sensitive responses, significant for both $\phi=45^\circ$ and 135° . In summary, the motion sensitivity varied with visual stimuli as both cells became relatively less PM-sensitive and more CM-sensitive when longer lines replaced shorter lines in the stimulus patterns.

The classification of the whole sample is displayed in Fig. 2. Because the differences between data (R_p, R_c, t) for cases of $\phi=45^\circ$ and cases of $\phi=135^\circ$ were insignificant (an exception was the mean R_c value for $L=6^\circ, \phi=45^\circ$, which was somewhat higher than that for $L=6^\circ, \phi=135^\circ$, Wilcoxon test, $p \approx 0.025$), the two sets of measurements were pooled together for overall statistics. As the outcome, when tested with 1° -line patterns, a substantial proportion of cells (48.8%) were PM-sensitive, while very few (1.2%) were CM-sensitive and the other $\sim 50\%$ of cells were unclassified. When $L=3^\circ$, the analysis resulted in 24.6% PM-sensitive cells and 3.0% CM-sensitive cells. When $L=6^\circ$, the percentages were 9.4% and 9.4%, respectively. Altogether, a number of collicular neurons responded preferably to the veridical direction of pattern motion rather than the component orientation when the orientation element was not very strong in the stimulus patterns, while few, if any, cells were significantly sensitive to the orientation cue.

It should be noted that, as classified in Fig. 2, the proportion of PM-sensitive cells decreased steadily with the elongation of component lines and the increment of orientation element in stimulus patterns, and meanwhile, there was a small increase in the number of CM-sensitive

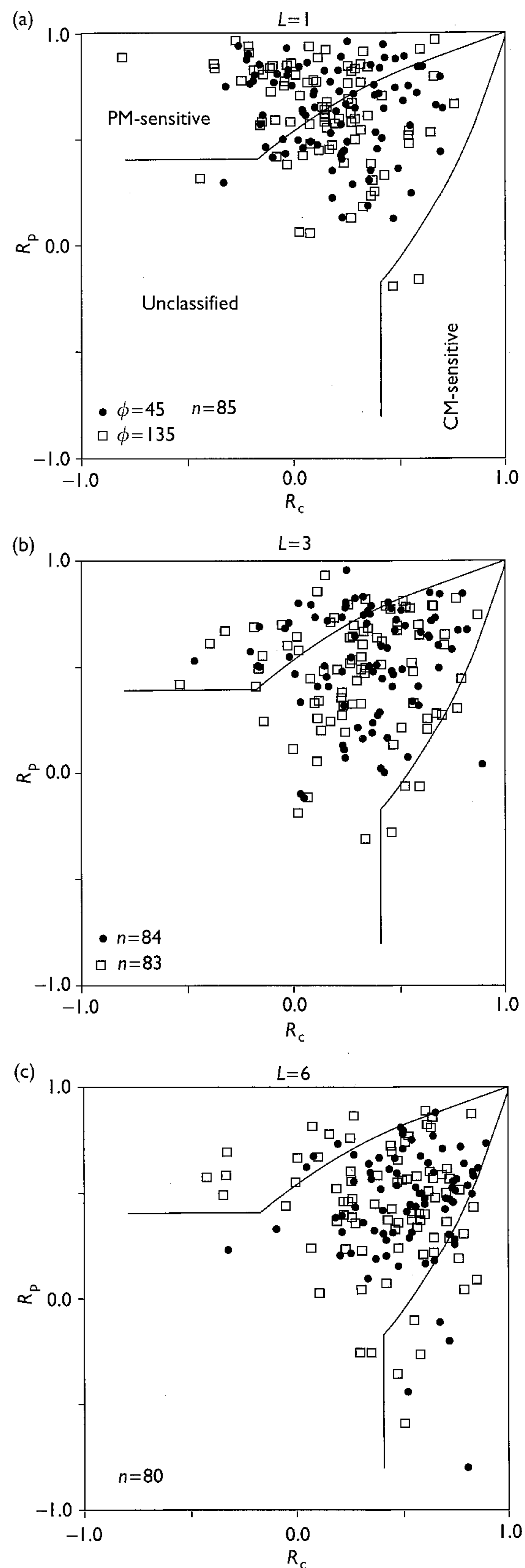


Fig. 2. Pattern motion–component motion sensitivity of collicular neurons to random-line patterns. Partial correlation coefficient R_p is plotted against R_c . The data space is divided into three statistical regions by the boundaries defined as the significant difference between R_p and R_c , between R_p and 0, and between R_c and 0, at $p=0.05$.

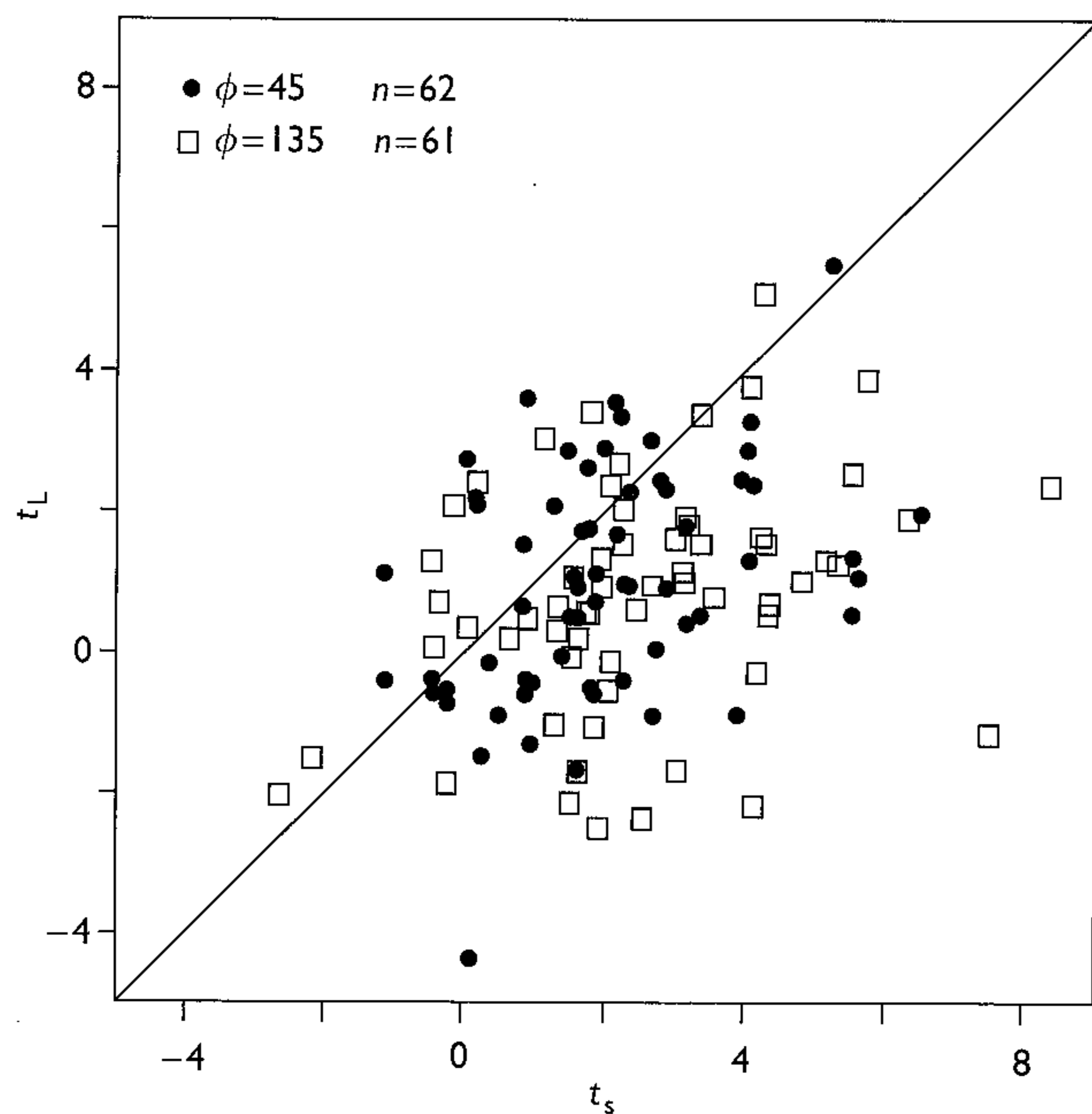


Fig. 3. Variation of pattern motion–component motion sensitivity of collicular neurons with the length of component lines in stimulus patterns. t -value, the parametric statistical difference between R_p and R_c , for 3° -line patterns (t_L) is plotted against that for 1° -line patterns (t_s). All the samples tested with both line lengths are included.

cells. This effect resulted from the variation of individual cells; as in Fig. 3, most samples fall below the diagonal with lower t -value for $L=3^\circ$ than for $L=1^\circ$ (the tendency would be even more pronounced if t -value for $L=6^\circ$ was plotted against that for $L=1^\circ$). Statistically, the t -values averaged at 2.149 ± 0.142 , 0.828 ± 0.122 and -0.102 ± 0.130 (mean value \pm standard error, all samples shown in Fig. 2 were included) for $L=1^\circ$, 3° and 6° , respectively, and the differences among them were extremely significant (Kruskal–Wallis χ^2 -test, $p < 0.0001$). All these findings suggest that, in general, the collicular neurons tend to be PM-sensitive to shorter line patterns but relatively more CM-sensitive to longer line patterns. In other words, the PM–CM sensitivity is dependent upon the length of component lines (or the strength of orientation element) in stimulation.

An additional test checked the receptive field size and electrode depth of the samples and found that the difference, if any, between PM-sensitive and CM-sensitive cells was small and insignificant.

The results described above were obtained by analyzing the sustained responses occurring later than 200 ms after stimulus onset, because the discharges within the early phase might be evoked partly by the general variation of luminance or contrast on the screen. However, previous studies suggested that the initial transient responses could be distinctive in direction tuning [10,12,23]. Therefore the same procedures for PM–CM sensitivity analysis were performed on this brief period and the results are shown in Fig. 4 as a comparison with the subsequent phase. It turns out that most samples fall below the diagonal in Fig. 4a, while the distribution is roughly around the corresponding line in Fig. 4c, and an intermediate situation is seen in Fig. 4b. Statistically, when $L=1^\circ$, the mean t -value for the initial period was significantly lower than that for the subsequent phase (0.323 ± 0.085 vs. 2.149 ± 0.142 , Wilcoxon

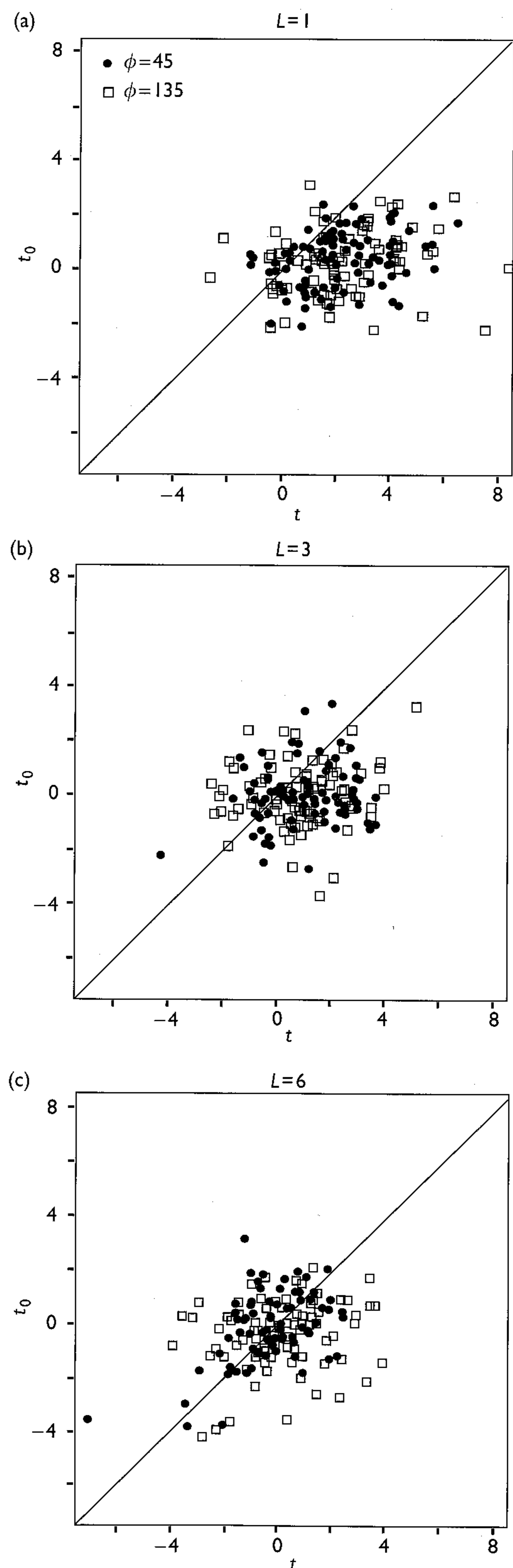


Fig. 4. Pattern motion–component motion sensitivity index for the initial transient responses (t_0) is plotted against that for the subsequent sustained responses (t). All the samples shown in Fig. 2 are included. It can be seen that the distribution ranges of samples in the three panels are displaced from each other along the abscissa (for t) but quite close along the ordinate (for t_0).

test, $p < 0.0001$), indicating that the transient responses were relatively more CM-sensitive than the sustained responses. When $L=3^\circ$, the difference decreased obviously (-0.045 ± 0.092 vs. 0.828 ± 0.122), though the significance level was still quite high ($p < 0.0001$). Nevertheless, when $L=6^\circ$, the difference (-0.291 ± 0.105 vs. -0.102 ± 0.130) was no longer significant ($p > 0.2$). In other words, with the increment of orientation element, the t -value for the initial transient responses did not drop as much as that for the sustained responses.

DISCUSSION

Considering the important role the SC plays in visual attention and visuomotor coordination, it is plausible to suppose that at least some collicular neurons can signal the veridical direction of coherent pattern motion. Perhaps because the responsiveness and direction preference of collicular cells to gratings/plaids (the stimuli widely used to identify PM- and CM-sensitivity in previous studies) are not as good as those of cortical neurons, few attempts were made to verify this assumption (but see [2] for a hint on the absence of PM-sensitive cells). On the other hand, the salient orientation cue in plaids may prevail over any other image feature (e.g. the intersections) that could possibly be utilized to perceive global motion, and this problem may lead to systematic underestimation of PM-sensitivity. Therefore, stimulus patterns composed of thin line segments have been employed in relevant experiments [10,12,13,23] and in the present study to explore the motion sensitivity of collicular neurons.

With the random-line patterns, many posteromedial lateral suprasylvian (PMLS) cells and even some striate cells of the cat were found to be PM-sensitive when the lines were short and become more and more CM-sensitive when the lines were elongated [12,13]. As described in Results, a similar situation was observed in the SC but with some differences in detail. In summary, the overall PM-CM sensitivity of collicular neurons seems to be intermediate to that of PMLS and striate cells, as shown by the proportion of PM-sensitive cells (when $L=1^\circ$, $\sim 70\%$ in the PMLS, $\sim 50\%$ in SC and $\sim 40\%$ in striate cortex; when $L=3^\circ$, $\sim 50\%$, $\sim 25\%$ and $\sim 10\%$, respectively) and the distribution of t -value. At the moment, no comparable data are available from even higher areas in the extrastriate cortex, but in the light of the results obtained with plaids [4,6,7], the PM-sensitivity is probably more pronounced in the anteromedial lateral suprasylvian cortex (AMLS) and anterior ectosylvian visual area (AEV) than in the PMLS. Furthermore, one may conceive that the precise analysis of complex motion information is probably conducted in certain areas in higher-order extrastriate cortex, while relatively rougher motion detection could be achieved in the SC to direct coordinated behaviors such as attention, guidance and so on.

Despite these differences, we found that the SC was similar to the PMLS and striate cortex in the tendency that the PM-sensitivity decreased with the increment of orientation element in stimulus. As proposed previously [12], such variation would probably require dual underlying mechanisms that are dependent and independent of the one-dimensional orientation cue. This proposition has won support from a number of neurophysiological and psychophysical studies [10-16], and previous experiments have shown that the orientation-independent processing may

occur as early as in the primary visual cortex [13-15]. In addition, the terminators (endpoints) of long contours are mostly assumed as the critical feature for tracking, though corners, crosses and other types of discontinuities are potential candidates as well. Further investigation is required to find out the neural substrates for the dual mechanisms, and most interestingly, whether they stand for separate (parallel) information processing streams and whether different pathways are involved.

Also similar to the results obtained in the PMLS [12], significant differences were found between the initial transient responses and the subsequent sustained responses of collicular neurons concerning their PM-CM sensitivity (but not when $L=6^\circ$). These data, together with some previous findings [10,23], support the idea that the neural solution to pattern motion is firstly estimated by computing the motion of oriented contours and then refined over time to progressively approach the veridical direction of stimulation. This temporal evolution may indicate that the dual mechanisms discussed above have different time constants and courses. According to data obtained with different line lengths, the slower orientation-independent processing seems to be more susceptible to the alteration of stimulus than the orientation-dependent processing.

In the cat, the SC receives extensive direct retinal inputs and afferences from a number of visual cortical areas (including areas 17, 18, 19, 21a, areas located around the lateral suprasylvian sulcus and AEV; see [18,24]). Its outputs project back to the aforementioned visual cortical areas via the lateral geniculate nucleus and LP-pulvinar of the thalamus [9,20,25]. An intriguing but still open question is how the PM-sensitive responses are generated in the brain and modulated by the interactions among the SC and different cortical areas. It is possible that the dual mechanisms for motion processing are associated with different bundles of projections; for example, one may hypothesize that the dynamic motion sensitivity in the extrastriate cortex is produced with the convergence of the geniculostriate and the tectothalamocortical pathways (the latter is probably slower). On the other hand, previous studies have found that the major receptive field properties of collicular neurons, including the preference for moving stimuli and the direction selectivity, are dependent on the corticotectal inputs [18]. Therefore, it seems likely that the PM-sensitivity in the SC is determined mainly by corticofugal projections and the feedback from the lateral suprasylvian cortex might be essential. All these ideas are yet to be examined in new experiments.

CONCLUSION

The present study revealed the appearance of PM-sensitive and CM-sensitive neuronal activities in the SC and demonstrated that, similar to the situation in the cortex, the PM-CM sensitivity is stimulus dependent and might be processed by dual underlying mechanisms. Moreover, the SC may actively participate in the higher-order motion analysis in conjunction with a number of cortical areas.

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