

## Response properties of cat AMLS neurons to optic flow stimuli

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**Abstract** Spiral and translation stimuli were used to investigate the response properties of cat AMLS (anteromedial lateral suprasylvian area) neurons to optic flow. The overwhelming majority of cells could be significantly excited by the two modes of stimuli and most responsive cells displayed obvious direction selectivity. It is the first time to find a visual area in mammalian brain preferring rotation stimuli. Two representative hypotheses are discussed here on the neural mechanism of optic flow analysis in visual cortex, and some new viewpoints are proposed to explain the experimental results.

**Keywords:** optic flow, direction selectivity, AMLS, cat.

Compared with a stationary observer, one can see very different scenes when he is moving. Optic flow fields, such as rotation, expansion/contraction and translation, result from the dynamic changes of images on the retina induced by locomotion of an observer. The optic flow processing has been extensively investigated in several extrastriate visual areas of the macaque (MST, VIP, 7a and STPa)<sup>[1-7]</sup>. However, in the cat, there have been only a few studies on the response properties of cortical neurons to optic flow stimuli<sup>[8-10]</sup>, and they were carried out in the posteromedial and posterolateral areas of the lateral suprasylvian cortex (PMLS and PLLS). A recent report<sup>[9]</sup> proposed that PMLS might play a relay role in optic flow information processing while PLLS might be partly involved in the analysis of radial motion. AMLS is another important extrastriate area in the visual system of the cat, which receives projections mainly from PMLS and some nuclei of the thalamus<sup>[11]</sup>. Using hand-held stimuli, Toyama et al.<sup>[12]</sup> found that AMLS neurons responded best to higher velocities and 3-D motion, whereas PMLS cells preferred relatively low velocities and 2-D motion. Based on these results, AMLS is supposed to be suitable for the analysis of optic flow information.

During locomotion, the image changes on the retina rarely appear as pure rotation, pure translation or pure translation. On the contrary, the image motion patterns often consist of two or three of these optic flow modes. Currently, there are two representative hypotheses on the neural mechanism of optic flow processing in the visual cortex: (i) multi-channel decomposition hypothesis<sup>[2,3]</sup>, the optic flow stimuli are decomposed and analyzed by separate neuronal channels

which encode different basic optic flow components, such as rotation, radiation and translation; (ii) continuous sampling hypothesis<sup>[4]</sup>, different optic flow fields are sampled by neurons with a continuous array of preferred flow patterns, which is similar to that in the striate cortex<sup>[13]</sup>, the neurons show a continuous array of preferred directions rather than two orthogonal motion channels. Both of the two hypotheses were based on experimental evidence obtained in macaque MST. The present study is aimed at checking the response properties of AMLS neurons to simulated optic flow stimuli and exploring the similarities and differences between the cat and the macaque in their visual pathways. Furthermore, the results may help to understand the neural basis of optic flow information processing.

## 1 Materials and methods

### 1.1 Animal preparation and maintenance

Experiments were carried out on 14 normal adult cats (weighing 2.5—3.8 kg). The general procedures were similar to those described previously<sup>[9,10]</sup>. 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 and artificial ventilation through the trachea. End-tidal CO<sub>2</sub> was maintained at about 4% and body temperature near 38°C. Electrocardiogram and electroencephalogram were continuously monitored to ensure a stable condition of the animal during the experiment. 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 optic disks and area centralis were projected onto a tangential screen at 57 cm distance for monitoring the residual eye movement. Glass-coated tungsten microelectrodes (tip length 8—30 μm, impedance 2—5 MΩ) were advanced perpendicularly to sulcus fundus along the anteromedial bank of the lateral suprasylvian sulcus (A9—A13) to record single-unit activities in AMLS from both hemispheres. Electrolytic lesions were made by passing a small direct current (10 μA for 20 s) through the electrode for histological identification of the electrode tracks at the end of experiments.

### 1.2 Visual stimulation

Once a cell was isolated, its receptive field was qualitatively mapped with hand-held stimuli and the optimal velocity was approximately estimated. The visual stimuli used for quantitative measurement were generated on-line by a computer (Pentium II 400) with a graphics acceleration card (WinFast 3D L2300, 3Dlabs PERMEDIA™ 2) installed inside, and displayed on a 21-inch monitor (PHILLIPS Brilliance 201P). The screen was placed 57 cm in front of the animal, covering the receptive field optimally. The stimulus patterns were composed of 250 random dots (diameter 0.15°, illuminance 10—20 cd/m<sup>2</sup>) moving against a dark background (0.5 cd/m<sup>2</sup>). All the dots were distributed randomly within a virtual circular window subtending 30° in diameter. As

shown in fig. 1, a set of optic flow stimuli consisted of 24 different directions of movement, i.e. 12 directions of spiral motion (including four cardinal directions: clockwise rotation CWS, counter-clockwise rotation CCW, expansion EPN and contraction CTN, and eight intermediate spiral directions) and 12 directions of translation. For translation stimuli, the drifting directions were separated by  $30^\circ$  steps and all the random dots moved at the optimal velocity estimated in advance. For spiral stimuli, the directions, as defined in fig. 1, were also separated by  $30^\circ$  steps; the velocity of each dot was proportional to its distance to the center, with the mean value kept as the same as that for translation. The four cardinal directions in the spiral space ( $0^\circ$ ,  $180^\circ$ ,  $90^\circ$ ,

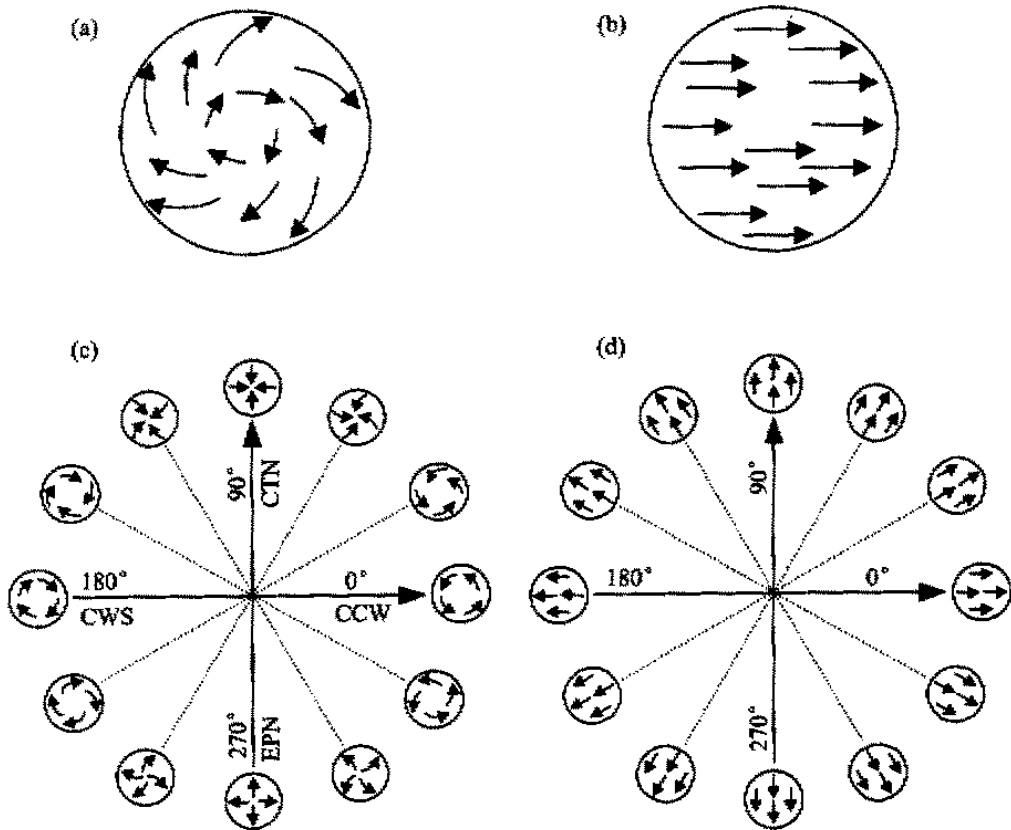


Fig. 1. Schematic illustration of the optic flow stimuli. (a) Spiral stimuli. (b) Translation stimuli. Each arrow represents the drifting direction of a single dot and its length indicates the velocity. (c) Distribution of the 12 spiral directions used in experiments. Each spiral stimulus is composed of certain portions of radiation and rotation. The drifting directions of the dots in a spiral pattern are decided upon the definition of the pattern in the spiral space. For the four cardinal directions,  $0^\circ$  corresponds to counter-clockwise rotation,  $180^\circ$  to clockwise rotation,  $90^\circ$  to contraction, and  $270^\circ$  to expansion. The angular difference between two nearby spiral directions is  $30^\circ$ . In a certain spiral pattern, each random dot moves to its next position according to:  $\Delta R = K_1 \times R \times \sin q_1$ ,  $\Delta F = K_1 \times 180/\pi \times \cos q_1$ , where  $K_1$  is a constant,  $R$  is the dot's distance to the center of the pattern,  $F$  is the angle in polar coordinate,  $q_1$  is the angular difference between the direction of the spiral pattern and the X axis (CCW). (d) Distribution of the 12 translation directions used in experiments. The angular difference between two nearby directions is also  $30^\circ$ . Each random dot moves to its next position according to:  $\Delta x = K_2 \times \cos q_2$ ,  $\Delta y = K_2 \times \sin q_2$ , where  $K_2$  is the velocity,  $q_2$  is the drifting direction of the dots.

$270^\circ$ ) were referred to the four directions of the two basic optic flow components in multi-chan-

nel decomposition hypothesis, i.e. rotation (CCW and CWS) and radiation (CTN and EPN).

The 24 directions of optic flow stimuli and a blank background for measuring spontaneous activity as a control were pseudorandomly sequenced to compose a complete trial. Each sweep lasted 2000 ms, succeeded by a pause period of 1000 ms without any stimulus. 5—10 such trials were repeated for averaging the data.

### 1.3 Data acquisition and analysis

The neuronal activities were sampled with a high impedance probe ( $\times 10$ ), amplified and filtered by a programmable amplifier (CyberAmp 380), and fed into a computer (PentiumII 266) via a laboratory interface (CED 1401plus). Using the multi-channel data acquisition software (CED Spike2), the analog signals were selected through a window-discriminator, the isolated single-unit action potentials were converted to TTL-pulses and stored as firing times. Many cells fired very vigorously during a short period soon after stimulus onset, which might be partly elicited by the general luminance variation on the screen. In order to avoid the potential ill-effects, the initial transient responses within 0 — 200 ms were excluded from spike counting for all samples. A cell was considered to be responsive to a stimulus if the significance level of  $P \leq 0.05$  was reached in a *t*-test comparing the evoked activities and the control. For each neuron, two direction tuning curves were plotted respectively for spiral and translation stimuli, and the preferred directions (PD) and direction indices (DI) were calculated for both curves. Similar to the previous studies,  $PD_s$  ( $PD_t$ ) was determined as the direction of spiral (translation) stimulus which elicited the maximal response,  $DI_s$  and  $DI_t$  were calculated as follows:

$$DI_s = 1 - SR_{np} / SR_p,$$

$$DI_t = 1 - TR_{np} / TR_p,$$

where  $SR_p$  and  $TR_p$  are, respectively, response strengths to the preferred directions of spiral and translation stimuli (with spontaneous activities subtracted, also for the other response strength values), and  $SR_{np}$  and  $TR_{np}$ , to the opposite directions. Thereafter  $DI_s$  and  $DI_t$  are used to quantify the cell's direction selectivity to spiral and translation motion, respectively.

In addition,  $RI_{rot}$  and  $RI_{rad}$  were calculated to show the relative response strengths of each neuron to rotation and radiation:

$$RI_{rot} = SR_{rot} / SR_p,$$

$$RI_{rad} = SR_{rad} / SR_p,$$

where  $SR_{rot}$  and  $RI_{rad}$  are, respectively, the maximal response strengths to rotation and radiation stimuli.

## 2 Results

A total of 253 AMLS neurons were quantitatively studied. The receptive field properties were generally similar to what had been reported before<sup>[14]</sup>. The receptive fields were usually within  $10^\circ$ — $30^\circ$  in size, most of them were located below the horizontal meridian in the contralat-

eral hemifield. The optimal velocities were usually above 60%, for some cells even higher than 120%. All the cells were individually recorded for their responses to 12 directions of spiral stimuli and 12 directions of translation stimuli to obtain the corresponding tuning curves.

### 2.1 Excitatory responses to optic flow stimuli

The overwhelming majority of AMLS neurons recorded in the experiments responded to at least one direction of spiral and/or translation stimuli (in comparison with control by *t*-test,  $P \leq 0.05$ ). Of all the 253 neurons, 228 cells (90.1%) had significant excitatory responses to one or more directions of spiral stimuli, the other 25 cells (9.9%) could not be excited by any spiral direction. 222 cells (87.7%) had significant excitatory responses to one or more directions of translation, the others (31 cells, 12.3%) could not be excited by any translation direction. 208 neurons (82.2%) responded to both spiral and translation, while only 11 cells (4.3%) were nonresponsive to all the optic flow patterns tested. A small subset of cells displayed significant inhibitory responses to some stimuli of certain directions, which might help to improve the direction preference. There was no cell being suppressed by all the stimulus directions. The responses of three typical neurons are shown in fig. 2. The first cell ((a), (b)) had significant excitatory responses to 12 spiral directions and 10 translation directions. The preferred directions, the direction indices, and the maximal firing rates to spiral and translation stimuli were  $0^\circ$  (CCW) and  $30^\circ$ , 0.84 and 0.72, 30.4 and 31.1 Hz, respectively. Since this cell showed obvious excitatory responses and high direction selectivity to both spiral and translation, it might be involved in the processing of these two modes of optic flow information.

The second cell ((c), (d)) was responsive to 11 spiral directions and 10 translation directions, of which the preferred directions, the direction indices, and the maximal firing rates were  $150^\circ$  and  $300^\circ$ , 0.87 and 0.83, 26.0 and 14.2 Hz, respectively. The maximal firing rate to spiral stimuli was much higher than that to translation, which may suggest that the cell's responses to complicate spiral patterns were based on the certain motion mode of optic flow rather than a match between the drifting direction of some random dots in spiral stimuli and the preferred direction for translation.

The third cell ((e), (f)) could be significantly excited by 7 spiral directions and 5 translation directions, of which the preferred directions, the direction indices, and the maximal firing rates were  $210^\circ$  and  $270^\circ$ , 0.48 and 0.89, 46.0 and 96.5 Hz, respectively. In contrast to the second cell, the maximal firing rate to translation was much higher than that to spiral stimuli, indicating that this neuron might be more suitable for the processing of the relatively simple translation information, but not for the complicate spiral patterns.

### 2.2 Direction selectivity for spiral stimuli

Most AMLS neurons were well tuned to the spiral stimuli, responding best to a certain direc-

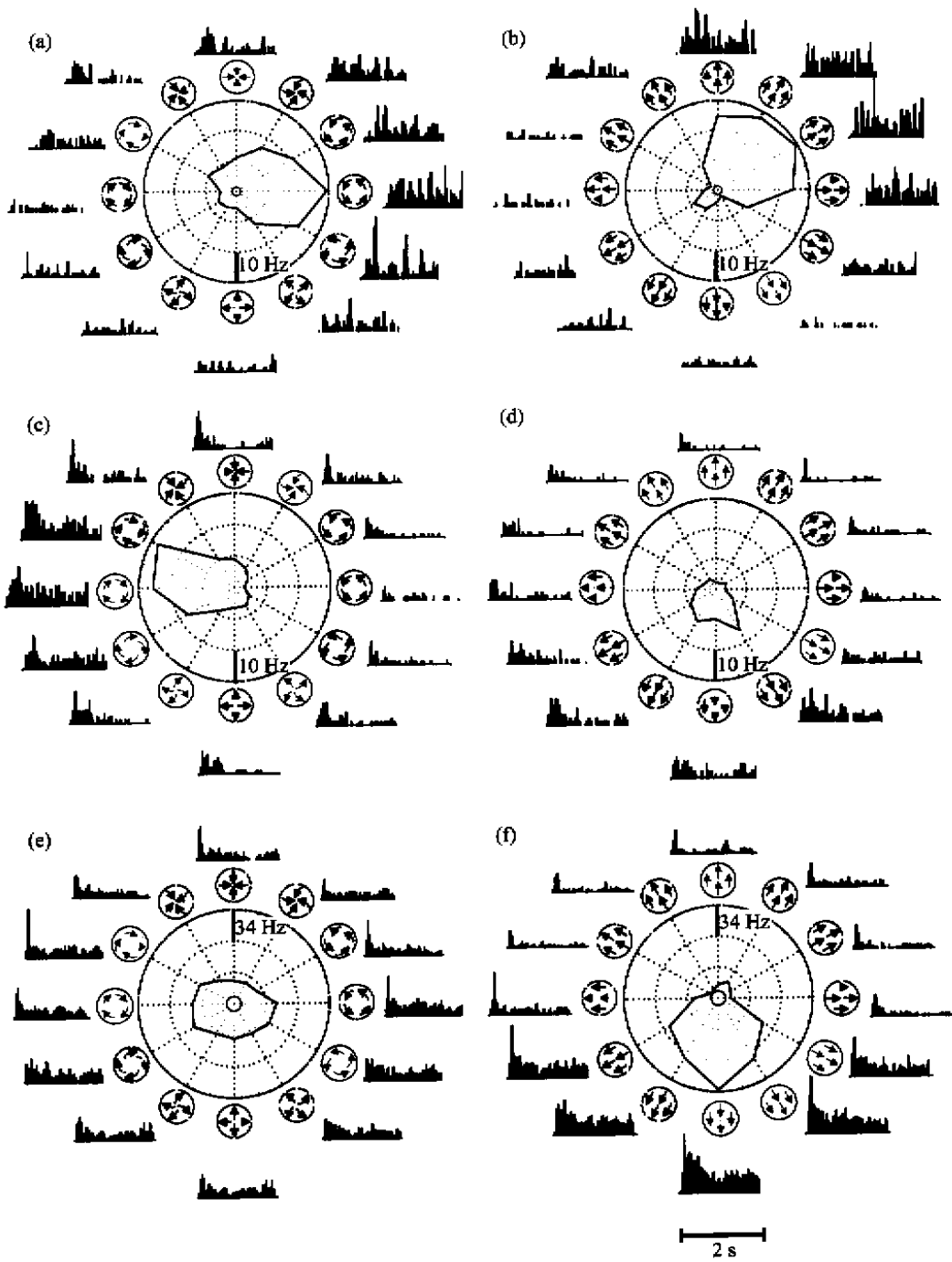


Fig. 2. Responses of three typical neurons. (a) and (b) Direction tuning curves of the first neuron to spiral and translation stimuli, respectively. The spontaneous activities are shown as small circles in the center. Each sweep of stimulus lasted 2 s. All the firing rates are given in Hz (spikes/s). (c) and (d) Tuning curves of the second neuron. (e) and (f) Tuning curves of the third neuron.

tion in the spiral space. For example, the three cells shown in fig. 2 had their maximal firing rates at spiral directions of  $0^\circ$ ,  $150^\circ$  and  $210^\circ$ , respectively. As a whole, the cells preferred rotation instead of sampling all the 12 spiral directions equally. Of all the 228 neurons responsive to spiral stimuli (fig. 3(a)), 79 cells (34.6%) preferred two cardinal directions, i.e. clockwise rotation (16.2%) and counter-clockwise rotation (18.4%), and there was no significant difference between the two directions ( $P > 0.05$ ). The percentages of the neurons preferring the other 10 directions (expansion, contraction and 8 intermediate spiral directions) were much lower. The values were 8.0% for expansion and 5.1% for contraction.

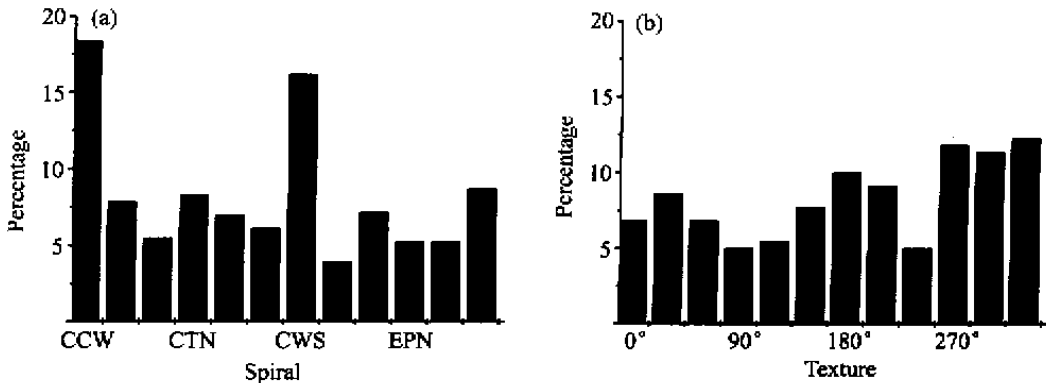


Fig. 3. The percentage of neurons preferring different directions of spiral and translation stimuli. (a) Abscissa represents the 12 spiral directions used in experiments. Only the four cardinal directions are marked. Refer to fig.1(c) for the settings of the eight intermediate directions unmarked. (b) Abscissa represents the 12 translation directions used in experiments. Similar to (a), only the four axial directions are marked and fig.1(d) could be referred to for the settings of the unmarked directions.

Previous investigations on optic flow processing mainly focused on MST VIP, 7a, STPa of the macaque and PMLS, PLLS of the cat and found that, in general, these visual areas preferred expansion stimuli. Many of these studies<sup>[2,3,9,10]</sup> took only the basic optic flow components (rotation and radiation) as stimuli. Alternatively, in the present study, rotation and radiation represented only four cardinal directions in the spiral space while 8 intermediate directions were also included in stimulation. For the neurons preferring one of the intermediate directions (fig. 3(a)), their responses to radiation might be stronger than that to rotation. In order to make sure whether the AMLS cells preferred rotation, the firing rates to rotation and radiation stimuli were compared with each other for all the responsive cells. The mean values for  $RI_{\text{rot}}$  and  $RI_{\text{rad}}$  were significantly different ( $0.847 \pm 0.171$  vs.  $0.770 \pm 0.180$ ,  $t$ -test,  $P < 0.01$ ). From fig. 4 it can

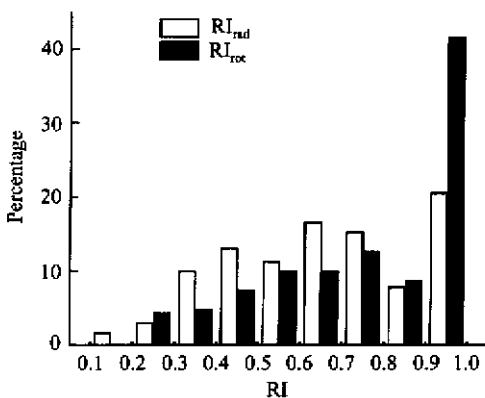


Fig. 4. Distribution of the relative response strengths to rotation and radiation stimuli. As a comparison between the two parameters, more  $RI_{\text{rot}}$  values were larger than 0.8 while more  $RI_{\text{rad}}$  values were smaller than 0.8, indicating that neurons had better responses to rotation than to radiation in general.

From fig. 4 it can be seen that the distribution of  $RI_{\text{rot}}$  values is shifted towards higher values (around 1.0) compared to  $RI_{\text{rad}}$  values (around 0.7-0.8). This indicates that neurons generally have stronger responses to rotation than to radiation.

be seen that, as compared with  $RI_{rad}$ , more cells had  $RI_{rot}$  values larger than 0.8. The significantly different distribution of  $RI_{rot}$  and  $RI_{rad}$  indicates that AMLS neurons have better responses to rotation than to radiation.

As mentioned in the methods, the direction index  $DI_s$  is used to evaluate the direction selectivity for spiral stimuli. The neurons with the  $DI$  value larger than or equal to 0.5 could be regarded as direction selective. Thus, the first and the second cells shown in fig. 2 were direction selective for spiral motion while the third cell was not. As shown in fig. 5, about 80% of the AMLS neurons were selective to the direction of spiral motion, which is supposedly suitable for processing the large-scale spiral optic flow information.

### 2.3 Direction selectivity for translation stimuli

In a spiral pattern, the drifting direction and velocity are distinctive for each random dot, therefore it is considered as a mode of complicate and high-level motion<sup>[1,4]</sup>. Meanwhile, translation is another basic optic flow component frequently encountered by animals during locomotion. The direction selectivity for translation is an important property for neurons processing optic flow information. All the three cells shown in fig. 2 were responsive to translation with obvious direction selectivity. Statistically, of all the 222 neurons responsive to translation stimuli, only 74 cells (33.3%) preferred the four axial directions ( $0^\circ$ ,  $90^\circ$ ,  $180^\circ$  and  $270^\circ$ ). It can be seen from fig. 3(b) that, in contrast to that for spiral stimuli, the distribution of the preferred directions to translation was relatively even without clear peak or valley, indicating that in AMLS the translation information might be analyzed in a different way from the spiral information. Although the four axial directions did not prevail over the intermediate directions in the distribution of preferred directions, it should be noted that the cells that responded best to downward translation were 2.4 times of those that preferred upward translation. This result might be relevant to the practice that a cat usually walks on the ground, since when it moves forward, the objects on the ground would mainly go down in its visual field.

About 90% of the neurons were selective to the direction of translation with a direction index value larger than 0.5 (see fig. 5).

### 2.4 Comparison between response properties to spiral and translation stimuli

Of all the 242 neurons responsive to optic flow stimuli, the average response strength to spiral was higher than that to translation, but the difference was insignificant (39.7 vs. 36.8 Hz,  $t$ -test,  $P > 0.05$ ). The relative response strength  $R_{st} = (SR_p - TR_p) / (SR_p + TR_p)$  was calculated for each

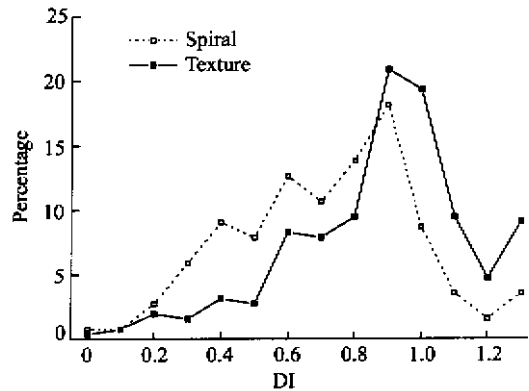


Fig. 5. Distribution of direction indices to spiral or translation stimuli. Only the responsive cells are included.



neuron to evaluate the preference to the mode of optic flow, where  $SR_p$  and  $TR_p$  were the maximal firing rates to spiral and translation stimuli, respectively. It is shown in fig. 6 that most  $R_{st}$  values were close to zero, and the average was 0.047. In other words, there were more cells that responded best to spiral than to translation, but the difference was small. Here the cells with  $R_{st} \geq 0.2$  are regarded as preferring spiral motion (the response strength to spiral was 1.5 times as that to translation), the ones with  $R_{st} \leq -0.2$  as preferring translation (the response strength to translation was 1.5 times as that to spiral), and with  $-0.2 < R_{st} < 0.2$ , as having no preference. The three examples shown in fig. 2 are representative for these three types of cells. Of all the 242 responsive neurons, 58 cells (24.0%) preferred spiral, 31 (12.8%) preferred translation, and 153 (63.2%) did not show obvious preference.

In summary, as compared with translation, spiral stimuli could activate more AMLS cells and evoke better responses, and there were more cells that preferred spiral motion (24.0% vs. 12.8%,  $P < 0.05$ ). All these results suggest that AMLS neurons might be mostly involved in the processing of complicate spiral patterns.

### 3 Discussion

In the present study, large-scale optic flow stimuli were first used to investigate the response properties of AMLS neurons. It was found that the cells tended to respond best to two cardinal directions in the spiral space, i.e. clockwise and counter-clockwise rotation, rather than sampling the spiral space equally. The preference for rotation patterns has never been reported in the previous studies in MST<sup>[1-4]</sup>, 7a<sup>[6]</sup>, VIP<sup>[5]</sup>, STPa<sup>[7]</sup> of the macaque and PMLS<sup>[8-10]</sup>, PLLS<sup>[9]</sup> of the cat.

#### 3.1 Neural mechanism of optic flow processing

In early studies<sup>[2,3,15]</sup> it was suggested that the optic flow information could be decomposed into three basic components, i.e. rotation, radiation (expansion and contraction) and translation, which might be processed by three types of cortical neurons, respectively. This idea is the key point of multi-channel decomposition hypothesis. However, in macaque MST, only a minority of neurons is selective to a certain optic flow component, while most cells respond well to two or three components<sup>[2,3]</sup>. The existence of these multiple responses is inconsistent with the decomposition hypothesis. On the other hand, the continuous sampling hypothesis proposed by Graziano<sup>[4]</sup> could hardly explain the present result that AMLS neurons tend to prefer rotation stimuli. Recently, Anderson et al.<sup>[7]</sup> reported that, of 84 macaque STPa neurons selective to spiral stimuli,

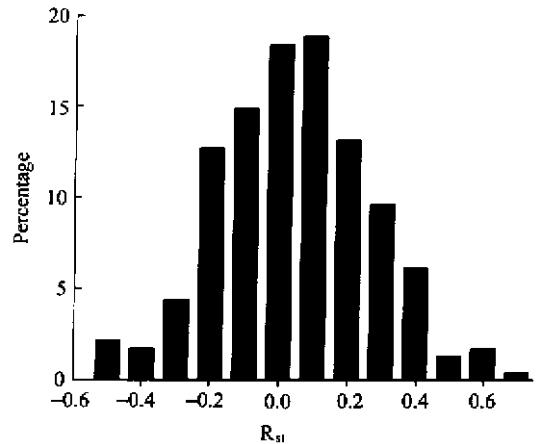


Fig. 6. Distribution of the preference for spiral or translation stimuli. The relative response strength was calculated as  $R_{st} = (SR_p - TR_p) / (SR_p + TR_p)$ .

78.6% of them preferred the cardinal directions while the other 21.4% preferred intermediate spiral directions. Moreover, Morrone et al.<sup>[16]</sup> found in psychophysical studies that, the human beings tend to process the basic optic flow components (e.g. radiation and rotation) during locomotion. Therefore as our viewpoints, a number of extrastriate visual areas might be involved in the processing of optic flow information, but each area may have its own characteristics. The relatively low areas (e.g. cat PMLS and macaque MT) may not show clear preference for the direction in the spiral space. The relatively high areas may prefer some certain cardinal directions, for example, some areas (cat PLLS and macaque STPa) may prefer radiation, while some other areas (e.g. cat AMLS) may prefer rotation. The processing of translation information may exist in multiple extrastriate visual areas.

### 3.2 Comparison between responses to spiral and translation stimuli

The drifting direction and velocity are distinctive for each random dot in a spiral pattern, while in translation all the dots move in a same direction and at a same velocity, therefore spiral is considered as a more complicate optic flow mode. In the extrastriate cortex of the macaque, especially in STPa<sup>[7]</sup>, most neurons have better responses to spiral than to translation stimuli. In PMLS and PLLS of the cat<sup>[9]</sup>, it has been found that the majority of cells responded better to radiation and/or rotation than to translation. It is plausible to suppose that many PMLS and PLLS cells would give even stronger responses if some kinds of spiral stimuli were used. There might be two reasons for the neurons showing better responses to spiral than to translation. First, the cells might be sensitive to the distribution of drifting directions of different random dots in the spiral patterns. Second, the cells might be sensitive to the speed gradients in the spiral patterns. The distribution of different drifting directions and the speed gradients may provide some kind of depth information which is very important for an animal during locomotion to determine its heading direction. Toyama et al.<sup>[12]</sup> found that AMLS neurons tend to analyze the three-dimension motion information, which is consistent with the present result that AMLS cells prefer spiral stimuli containing three-dimensional information.

### 3.3 Comparison with the macaque visual cortex

for visual motion processing, and MST is considered as the first step in the analysis of optic flow information<sup>[1-4]</sup>. MST not only processes optic flow information, but also transmits it to several higher level cortical areas, such as VIP<sup>[5]</sup>, 7a<sup>[6]</sup> and STPa<sup>[7]</sup>. Although the neurons in these three areas are similar to MST cells in their response properties to optic flow stimuli, each area has its own characteristics. MST may process large-scale optic flow information as well as detect the motion of single objects<sup>[4]</sup>. VIP may process the optic flow information but not analyze the motion of single objects. Area 7a may process the optic flow information and utilize the flow information as well for analyzing the spatial representation of extra-personal space. STPa may mainly process the radial motion information as well as detect the looming stimuli in the visual field.

In the visual pathway of the cat, PMLS is commonly considered as analogous to MT of the primate<sup>[17]</sup>, though the parallel processing pathway in the cat extrastriate cortex is somehow different from that in the macaque brain<sup>[18,19]</sup>. Generally, the response strengths of PMLS neurons to the three basic optic flow components are about the same, thus PMLS may play a relay role in optic flow processing<sup>[9]</sup>. PLLS cells respond better to radiation stimuli than to rotation or translation<sup>[9]</sup>. The present study has found that AMLS cells display a preference for rotation patterns. All these results indicate that the optic flow information processing in the cat extrastriate cortex is very different from that in the macaque. These differences might be relevant to the projections the areas receive. PMLS mainly receives inputs from LGN, areas 17, 18 and 19. AMLS receives little input from area 17, its major afferences come from PMLS and a number of thalamic nuclei, e.g. centro-lateral (CL), pulvinar (P), lateral posterior (LP), medial interlaminar (MIN), lateral dorsal (LD) and ventral anterior (VA). Therefore, the responses of AMLS neurons to optic flow stimuli may result from the integration of all the information received from PMLS and the subcortical nuclei.

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