

Response properties of neurons in cat dorsal lateral suprasylvian cortex to optic flow fields

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Single neurons in the dorsal lateral suprasylvian cortex (DLS) of the cat were tested with large field optic flow stimuli simulating translation and spiral motion (including radiation and rotation) in different directions. Most cells were responsive to both kinds of movement with fairly good direction selectivity. Generally, the responses were better to spiral motion than to translation, and better to radiation than to rotation. Moreover, the direction tuning

for spiral was broader than that for planar motion. The dot size in the stimulus patterns had no certain influence on the responses and direction preference. These results suggest that DLS might be substantially involved in the detection and analysis of complex optic flow information, and to some extent, in favor of the radiation component inside. *NeuroReport* 15:1019–1023 © 2004 Lippincott Williams & Wilkins.

Key words: Cat; DLS; Optic flow; Spiral motion; Translation

INTRODUCTION

Optic flow fields are normally generated by relative motion between an observer and the environment as the dynamic changes of images across the retina, which are critical for human beings and animals in perceiving the direction of self-movement and the structure of environment [1,2]. Previous studies have shown that the medial superior temporal area (MST) of the primate is directly involved in the processing of optic flow information [3–8]. At a higher level, several cortical areas that receive projections from MST (e.g. area 7a, the ventral intraparietal area, the anterior superior temporal polysensory area) were also proposed to contribute to optic flow analysis and self-movement perception [9–11]. In the cat, the lateral suprasylvian cortex (LS) is regarded as a likely substrate for analogous functions [12,13] and some investigators have reported that many LS neurons respond selectively to simulated optic flow stimuli [14–19].

As designated by Palmer *et al.* [20], the LS consists of six retinotopically organized sub-areas. The previous studies on this region of cortex were mostly carried out in its posteromedial part (PMLS). Recently we have reported some differences among sub-areas PMLS, PLLS and AMLS in their neuronal responsiveness and selectivity for different optic flow stimuli, implying that they may perform partly distinct functions [15,17]. Another LS sub-area, DLS, receives strong afferences from PLLS and may lie at a higher level in the hierarchical structure of cat visual system than PMLS and PLLS [21,22]. It is plausible to suppose that DLS plays an important role in visual analysis during self-movement. However, little has been done to investigate the

visual responses of DLS cells and it remains unclear about the similarities and differences between DLS and the other LS sub-areas. In the present study single DLS neurons were tested for their response properties to different optic flow patterns, in order to explore its function in visual information processing.

MATERIALS AND METHODS

Experiments were carried out on 12 normal adult cats (weighing 2.5–3.8 kg). The general procedures for animal preparation, maintenance and recording have been described previously [15,23]. Adequate measures (light anesthesia, paralysis, continuous monitoring of physiological conditions, protection of eyes, and so on) were taken to minimize pain and discomfort of the cats, in compliance with the NIH guidelines on the care and use of laboratory animals. Glass-coated tungsten microelectrodes were advanced perpendicularly or with a small inclination into the area DLS between Horsley-Clarke coordinates P2–A2 and L10–L16. Occasionally electrolytic lesions were made for histological identification of the electrode tracks.

The receptive fields (RFs) of single neurons were plotted approximately with hand-held stimuli on a tangent screen placed 57 cm in front of the eyes. The visual stimuli used in quantitative measurements were principally as same as given in a recent work [17]. The stimulus patterns were composed of small light dots against a dark background. Usually 250 dots were distributed randomly within a virtual circular window subtending 30° in diameter, while the window was individually centered on the RF being tested.

A set of optic flow stimuli consisted of spiral motion in 12 directions and translation in 12 directions. The 24 directions of stimulation, and a blank background for measuring the spontaneous activity as a control, were pseudorandomly interleaved and presented for ≥ 5 trials. Each sweep lasted 2000–3000 ms, succeeded by a pause period of 2000–3000 ms without any stimulus. In addition, some cells were also tested with conventional moving bar stimuli for direction tuning curve.

The spiral motion was defined in a similar way as in the literature [5,11], though more intermediate directions were included for a better measurement of tuning (see Fig. 1a for a schematic illustration). The instantaneous velocity of each dot was proportional to its distance to the center. The dot size was also varied with its position, within the range of $0.05\text{--}1.0^\circ$. In the translation mode, all the dots moved in a same direction and at the mean velocity in the spiral motion, but the size was randomized to match the spiral stimuli.

Neuronal response strength was determined as firing rate during stimulation. A cell was considered to be responsive to a stimulus if the significance level of $p < 0.05$ was reached in a t -test, in which the evoked activity was compared with the control. Each set of responses was then subjected to further analysis.

RESULTS

A total of 108 DLS neurons were tested for their visual responses to moving stimuli. Most of the receptive fields distributed in the binocular zone of the visual field. Generally, the RFs were quasi-rectangle or elliptical and somewhat larger than those of PMLS, PLLS [15] and AMLS [17] cells. The size was usually $< 30^\circ$, though it tended to be larger while the location shifted toward the periphery. The spontaneous activity level was 11.15 ± 1.18 spikes/s (mean \pm s.e.). All of these properties were similar to what had been reported before [20,24].

Excitatory responses to large optic flow field and/or moving bar stimuli were widely recorded in the experiments, and many neurons were sensitive to the change of direction. The tuning curves of two representative cells are shown in Fig. 1. The first cell (Fig. 1b) had significant responses to all the three kinds of stimuli with fairly good direction tuning. It responded best to spiral motion of 330° (an intermediate direction between counter-clockwise rotation and expansion), while the preferred direction (PD) to

planar motion was 180° (leftward). The second cell (Fig. 1c) responded better to translation than to spiral motion, but relatively weak to moving bar. The PDs were 0° (rightward) and 90° (contraction), respectively.

Principal response properties: Of the 108 cells, 84 (77.8%) were significantly responsive to the spiral motion stimuli. The mean maximal response strength (for each cell, corresponding to its preferred direction in the spiral space) was 40.98 ± 3.50 spikes/s. The distribution of the preferred direction is shown in Fig. 2a. No clear preponderance can be found in the histogram, though there are two small peaks at the positions for contraction and an intermediate direction close to counter-clockwise rotation.

In the same sample, 81 neurons (75.0%) had significant responses to the translation of random-dot patterns. A subset of 73 cells was also tested with moving bar, and 53 (72.6%) were responsive. The maximal response strengths were 33.11 ± 2.97 and 31.36 ± 3.54 spikes/s, respectively. The preferred directions to these two kinds of stimuli were usually close to each other, especially for the cells with good responses and moderate or sharp tuning (for examples see Fig. 1). As shown in Fig. 2b, the directions around 0° and 180° had an obvious advantage in the distribution of PD to translation, indicating that the DLS cells may prefer planar motion to the left and right sides rather than up and down.

The preference of DLS cells for the stimulus direction is actually more visible with the relative response strengths shown in Fig. 3. It can be seen that the responses to rotation were lower than those to spiral motion stimuli including a radiation component (Fig. 3a). For planar motion, 0° and 180° elicited stronger responses than the other directions (Fig. 3b). This tendency was even more obvious with a moving bar (Fig. 3c).

The direction index ($DI = 1 - R_{NPD}/R_{PD}$) is commonly used to evaluate the neuronal direction selectivity to moving stimuli. The statistics on the responsive cells resulted in 0.723 ± 0.027 (spiral motion), 0.754 ± 0.031 (translation) and 0.676 ± 0.040 (moving bar), respectively. The differences among the mean values were small and insignificant. As shown in Fig. 2c, 83.3% of the cells had DI values > 0.5 to spiral motion. For translation, the percentage was 84.0%. These data suggest that, in general, the DLS neurons have good direction selectivity to moving patterns. The bandwidth of direction tuning curve (quantified as half width at half height) was also measured for each responsive cell. The

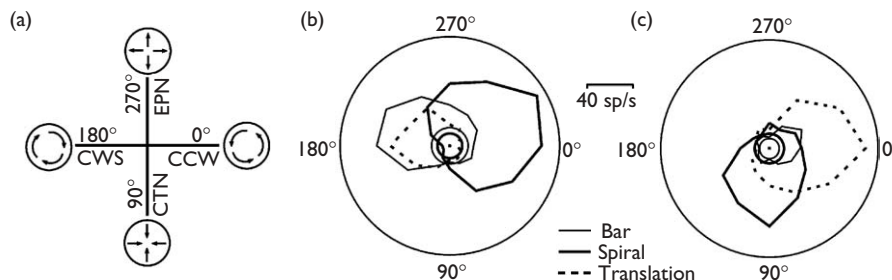


Fig. 1. (a) Cardinal directions of spiral motion and translation. The spiral motion was defined with the angle between the tangent line in respect to the center and the moving direction. For example, in contraction, the instantaneous direction of a dot was always 90° apart from the tangent line at its instantaneous position, i.e. always toward the center. In the present study, the spiral stimuli included four cardinal directions: counter-clockwise rotation (CCW), contraction (CTN), clockwise rotation (CWS) and expansion (EPN), and eight intermediate directions separated by 30° steps. (b,c) Direction tuning curves of two DLS neurons to spiral, translation and bar stimuli. The spontaneous activity levels are depicted as small central circles.

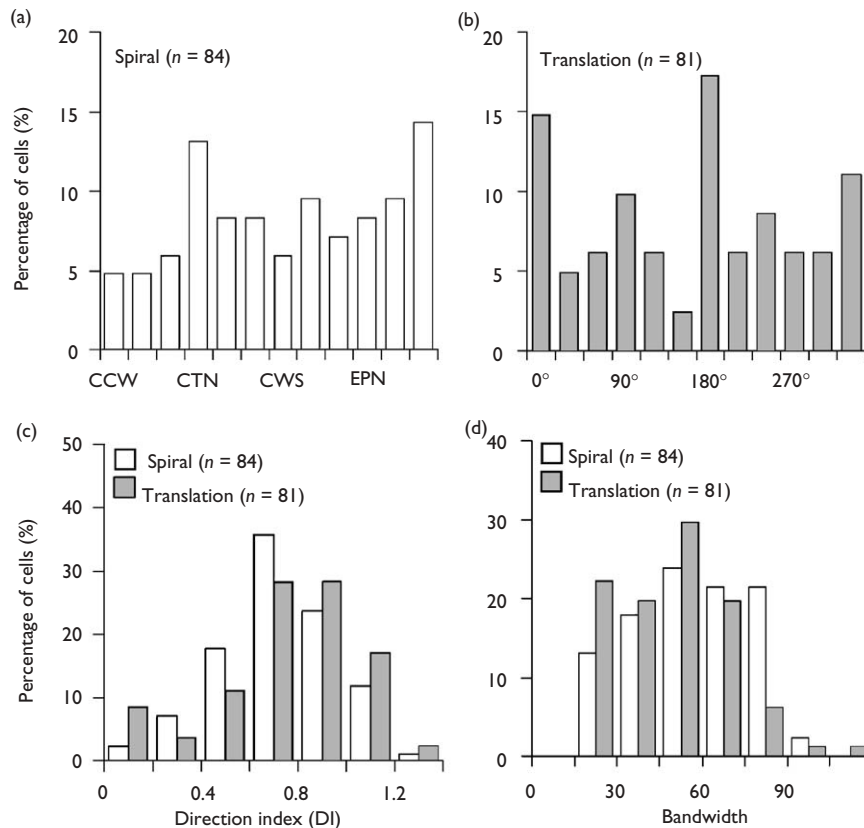


Fig. 2. Distribution histograms of neuronal response properties to large field optic flow stimuli. (a) Preferred direction to spiral motion. (b) Preferred direction to translation. (c) Direction index. (d) Bandwidth of direction tuning curve.

mean values were $56.95 \pm 2.26^\circ$ (spiral motion), $49.71 \pm 2.28^\circ$ (translation) and $40.88 \pm 2.84^\circ$ (moving bar), respectively, and the differences reached the significant level (Mann-Whitney *U*-test, $p < 0.02$ between spiral motion and translation, $p < 0.01$ between translation and moving bar). In other words, the DLS neurons had broader tuning for the direction of spiral motion than for planar motion (see Fig. 2d for the distribution), for large optic flow fields than for single moving bar. This result was also confirmed by the mean direction tuning curves shown in Fig. 3d. Further analysis on the 75 cells responsive to both motion modes displayed very weak positive correlation between the DI values for spiral and translation stimuli ($r=0.245$), and between the bandwidth values as well ($r=0.181$).

Preference for motion mode: To quantify the relative preference for spiral motion and translation, an index ($RI_{ST} = (R_{\text{spiral}} - R_{\text{translation}}) / (R_{\text{spiral}} + R_{\text{translation}})$) was calculated for the cells responsive to either motion mode or both. In Fig. 4a it can be seen that the distribution of RI_{ST} peaked at about 0.1 and averaged 0.130 ± 0.023 , which was significantly above zero ($p < 0.0001$). Eighteen cells (20.0%) had RI_{ST} values > 0.333 (i.e. R_{spiral} was at least twice that of $R_{\text{translation}}$), with only 3 cells (3.3%) giving the reverse result ($RI_{ST} < -0.333$). As above-mentioned, the mean response strength for spiral motion was somewhat higher than that for translation (*U*-test, $p < 0.1$). All of these indicate that spiral motion may prevail over planar motion in eliciting stronger responses of DLS neurons.

Two more indices were also calculated to evaluate the relative response strengths for cardinal directions in the spiral space: $RI_{\text{RAD}} = R_{\text{radiation}} / R_{\text{spiral}}$, $RI_{\text{ROT}} = R_{\text{rotation}} / R_{\text{spiral}}$, and the distributions are shown in Fig. 4b. The mean value for radiation was significantly higher than that for rotation (0.713 ± 0.027 vs 0.595 ± 0.028 , Wilcoxon test, $p < 0.02$), implying that the DLS neurons had generally better responses to expansion/contraction than to rotation.

Influence of dot size in stimuli: The effect of changing the size of random dots was examined for a subset of 89 DLS cells. Two kinds of maximal dot size, 1° and 0.5° , were used in the experiments. Generally, little influence was observed on the response strengths and the preferred directions of the cells, for either spiral or translation stimuli. The statistics demonstrated that the difference, if any, was small and insignificant. In other words, the dot size in the stimulus patterns had no certain effect on the responses of DLS neurons.

DISCUSSION

It has been commonly accepted that the lateral suprasylvian cortex is involved in optic flow processing and a number of direct studies have been conducted in PMLS and provided important evidences [14–16,18]. However, the other LS sub-areas attracted little attention and, to our knowledge, no effort was made to investigate DLS on this topic. Our recent results suggest that PMLS and PLLS may play some kind of relay role in the processing [15] and AMLS might be,

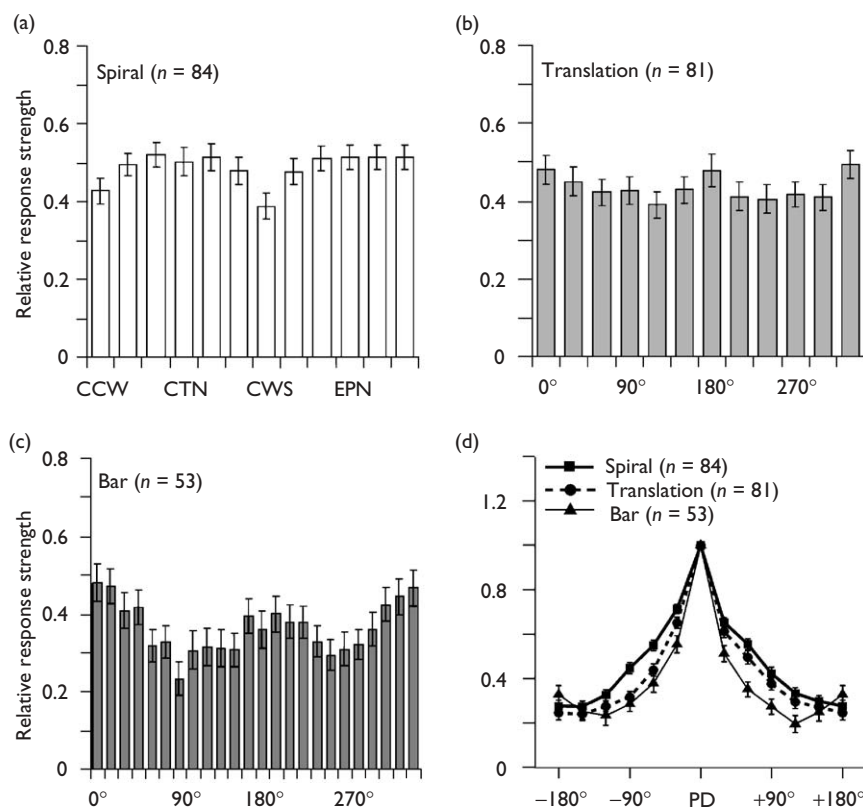


Fig. 3. (a–c) Mean relative response strengths for different directions of spiral and planar motion. All the responsive cells were included and, for each cell, the response values were individually normalized in respect to its maximal response strength before averaging. (d) Mean direction tuning curves for different stimuli. For each cell, the original tuning curve was individually normalized in respect to its maximal response strength and aligned to its preferred direction. It can be seen that the tuning bandwidth for spiral motion was broader than that for translation and moving bar.

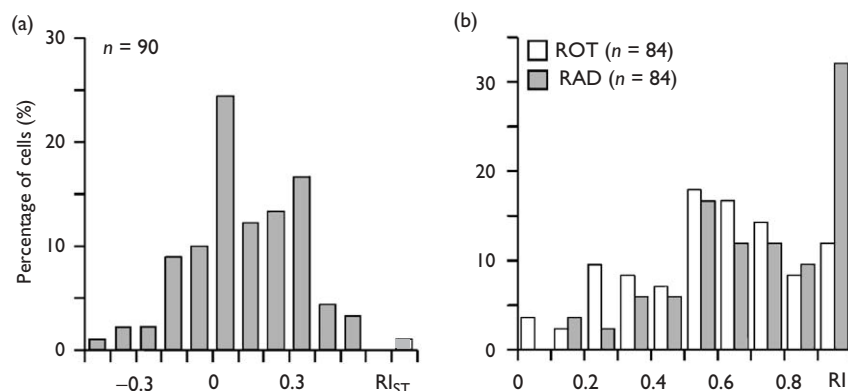


Fig. 4. (a) Distribution of the relative preference for spiral motion and translation. (b) Distribution of the relative response strengths for radiation and rotation stimuli, respectively.

to some extent, specialized for the analysis of rotation component in optic flow fields [17]. Here we proceed with these works and find that DLS is different from the three sub-areas on some response properties, especially the preference for motion mode.

Similar to PMLS, PLLS and AMLS, DLS neurons were generally responsive to large field optic flow stimuli, and most cells could be activated by different motion modes. Moreover, the neuronal selectivity for direction of motion was fairly good in all the sub-areas. As shown in Fig. 1 and Fig. 2, the majority of DLS cells had relatively high DI values

and moderate direction tuning curves, indicating that they might be potential candidates for encoding the relevant stimulus features. It is notable that, in the distribution of preferred direction to spiral motion (Fig. 2a), the four cardinal directions did not have a clear advantage over the intermediate directions. This phenomenon was also observed in MST [5] and AMLS [17], and was proposed as evidence against the hypothesis that optic flow is analyzed by decomposing its components into separate and discrete channels [5]. However, the spiral space is not represented evenly. More or less, some extent of imbalance has been

reported in several cortical areas of macaque and cat [5,11,17], and now in the present results as well.

As we have reported, different optic flow modes (translation, radiation and rotation) induced nearly equal influences in PMLS, radial motion had a slight advantage in PLLS by driving more cells and eliciting stronger responses [15], while in AMLS, rotation turned out to be the prevailing mode [17]. The situation was much different in DLS, where the general neuronal responsiveness was significantly better to spiral than to planar motion, to expansion/contraction than to rotation (Fig. 3a, Fig. 4). In other words, as compared with the other three sub-areas, the DLS cells displayed more preference for radial motion as a whole. Although both AMLS and DLS are proposed to be higher than PMLS and PLLS in the hierarchy of cat visual cortex, they have very different afferent and efferent connections. AMLS receives its major inputs from areas 17, 18 and PMLS, and projects to area 21a. DLS receives strong afferences from PLLS and projects mainly to AES and VLS [21,22]. We once suggested that PMLS and PLLS may lie at roughly equivalent hierarchical level but in two substreams of parallel processing, and the subsequent structures in the two substreams may function somewhat differently in visual perception [15]. Now the differences between AMLS and DLS add further support to this idea. Both areas may participate in the detection and analysis of complex optic flow information, but with partly distinct performance. While AMLS seems to be more important for rotation component, DLS probably works in favor of radial motion. However, the specificities of neurons in the two areas are unlikely to be good enough, and it may rely on further processing in even higher cortical areas to extract all the necessary and useful information in the visual field of the observer.

CONCLUSION

In the present study, 70–80% of the DLS neurons were responsive to large field optic flow stimuli, most of them to both spiral and planar motion modes. Generally, the responses to spiral motion were better than those to translation, and the responses to stimuli including radiation component were better than those to pure rotation. Most DLS cells were sensitive to the direction of moving stimuli with relatively high DI values and moderate direction tuning curves. As a whole, the cells preferred planar motion to the left and right sides rather than up/down and the intermediate directions. In comparison with the other LS sub-areas been studied, DLS turns out to be more specialized for radial motion in the cortical processing of optic flow information.

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