



Spatial and temporal visual properties of the neurons in the intermediate layers of the superior colliculus[☆]

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ABSTRACT

Although the visual perception depends on the integration of spatial and temporal information, no knowledge is available concerning the responsiveness of neurons in the intermediate layers of the superior colliculus (SCi) to extended visual grating stimuli. Accordingly, we set out to investigate the responsiveness of these neurons in halothane-anesthetized cats to drifting sinewave gratings at various spatial and temporal frequencies. The SCi units responded optimally to gratings of low spatial frequencies (none of the analyzed SCi units exhibited maximal activity to spatial frequencies higher than 0.3 c/deg) and exhibited low spatial resolution and narrow spatial frequency tuning. On the other hand, the SCi neurons preferred high temporal frequencies and exhibited high temporal resolution. Thus, the SCi neurons seem to be good spatio-temporal filters of visual information in the low spatial and high temporal frequency domain. Based upon the above summarized results we suggest that the SCi units can detect large contours moving at high velocities well, but are unable to distinguish small details. This is in line with the generally held view that the SCi could possess visuomotor function, such as organizing the complex, sensory-guided oculomotor and skeletomotor responses during the self-motion of the animal.

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The superior colliculus (SC) is a multilayered structure of the mammalian mesencephalon, which plays an important role in visually guided behavior and is involved in the orienting response of the head and the eyes toward the object of interest of any modality [33]. The superficial layers of the (SCs) seem to play a role in the central processing of visual information, visual attention and motion perception. The intermediate layers of the SC (SCi) are regarded as important structures for the control of saccadic eye movements [33] and in cross-modal integration [15]. Besides being a crucial part of the oculomotor system, these layers are involved in the control of head movements and goal-directed arm movements.

Despite numerous studies focusing on visual receptive field organization and the response properties of the SC neurons, no information is available concerning the responsiveness of the SCi neurons to extended visual stimuli, such as sinewave drifting gratings. The sinusoidally modulated gratings are regarded as elementary components of the visual scene in the sense that

any two-dimensional visual object can be represented by an appropriate combination of these gratings [9]. Since theoretical considerations suggest that spatial and temporal frequency sensitivity functions fully describe the responsiveness of neurons to any kind of stimuli we set out to investigate the responses in the SCi to drifting sinewave gratings of a wide range of spatial and temporal frequencies. A description of the spatio-temporal filter properties of the intermediate layers of the SC neurons could contribute to a better understanding of the role of the SC in visual information processing and the related behavioral visuomotor actions.

Four adult cats were used in this study. All experimental procedures followed the European Communities Council Directive of 24 November 1986 (86 609 EEC) and the National Institute of Health guidelines for the care and use of animals for experimental procedures. The experimental protocol had been accepted by the Ethical Committee for Animal Research of Albert Szent-Györgyi Medical and Pharmaceutical Center of the University of Szeged. The animal preparation and the surgery were described in detail in our earlier papers [21,22,30].

A craniotomy was made above the occipital cortex overlying the SC. Extracellular single-cell recordings were made in the SCi layers with tungsten microelectrodes (AM Systems Inc., USA) with an impedance of 2–4 MΩ. Single-cell discrimination was performed with the help of a spike-separator system (SPS-8701, Australia). The

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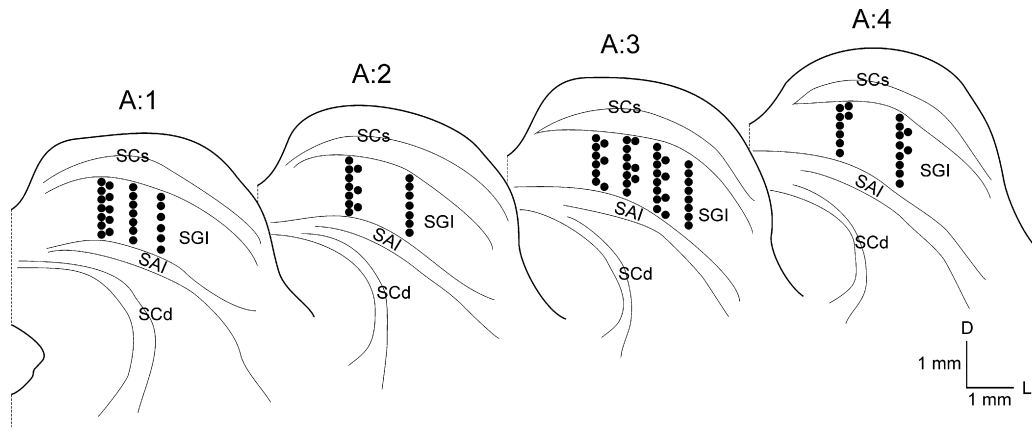


Fig. 1. Positions of the analyzed SCI neurons (filled circles). The drawings depict coronal sections of the SC in the cat brain between anterior 1 and 4 according to the stereotaxic atlas of Reinoso-Suárez [24]. Bars in the right bottom corner provide size calibration and orientation in the dorso-ventral and medio-lateral aspect. *Abbreviations:* SCs, superficial layers of the superior colliculus; SGI, stratum griseum intermediale; SAI, stratum album intermediale; SCd, deep layers of the superior colliculus.

excitatory receptive field of an SCI neuron was defined as the area of visual space within which visual stimuli elicited an increased firing rate of the cell. The location and size of the receptive fields of the neurons were determined with the help of a hand-held lamp, by listening to the amplified neuronal electrical responses to visual stimulation through a loudspeaker. In case of determining the size of the excitatory visual receptive fields in the SCI neurons, light spots of different sizes ($1\text{--}10^\circ$) generated by a hand-held lamp, were used to stimulate the neurons. The hand-held lamp was equipped with a phosphor-based white light-emitting diode (operating at 3.6 V and 20 mA). Light spots were moved in different directions to determine the borders of the visual receptive fields. After converting the calculated Cartesian co-ordinates to polar co-ordinates according to the formulas published by Bishop et al. [4], the size of the receptive field in degrees² was estimated. For visual stimulation, an 18 in. color computer monitor (refresh rate 85 Hz; the screen was refreshed by progressive scanning) was placed 42.9 cm in front of the animal. Gray-scaled grating stimuli were presented on the monitor within a circular aperture with a diameter of 30° centered on the center of the receptive field of the investigated neuron. The mean luminance of the screen was 23 cd/m². The contrast of the grating was held constant at 96%. The presentation of a stimulus lasted altogether 2 s. During the first 1 s (prestimulus

time), a stationary grating was shown to the animal; while during the second 1 s (peristimulus time), the grating was drifting. The interstimulus interval was 0.5 s. Neuronal activities were recorded, correlated with the stimulus presentation and stored as peristimulus time histograms (PSTHs).

The spatio-temporal frequency profiles of the SCI neurons were assessed with the use of various spatio-temporal frequency combinations of optimally orientated gratings drifting in the preferred direction. The optimal direction was determined at the beginning of the recordings subjectively with a hand-held lamp and then by using eight different drifting directions of the sinusoidal gratings in 45° steps. The tested spatial frequencies ranged from 0.025 to 0.95 c/deg, while the temporal frequencies varied from 0.07 to 33.13 cycles/s (Hz). 110 spatio-temporal frequency combinations were presented in a random order. Each spatio-temporal frequency combination was presented at least 12 times. The spatial and temporal high-frequency cut-off, regarded as a measure of spatial and temporal resolution, was defined as the frequency at which the response of the neuron fell to one-tenth of the maximal, after the subtraction of the spontaneous activity determined from epochs of 500 ms preceding the grating movement. The spatial or temporal frequency tuning bandwidth was measured as the full width at half-height of the spatial or temporal frequency-tuning curve. In

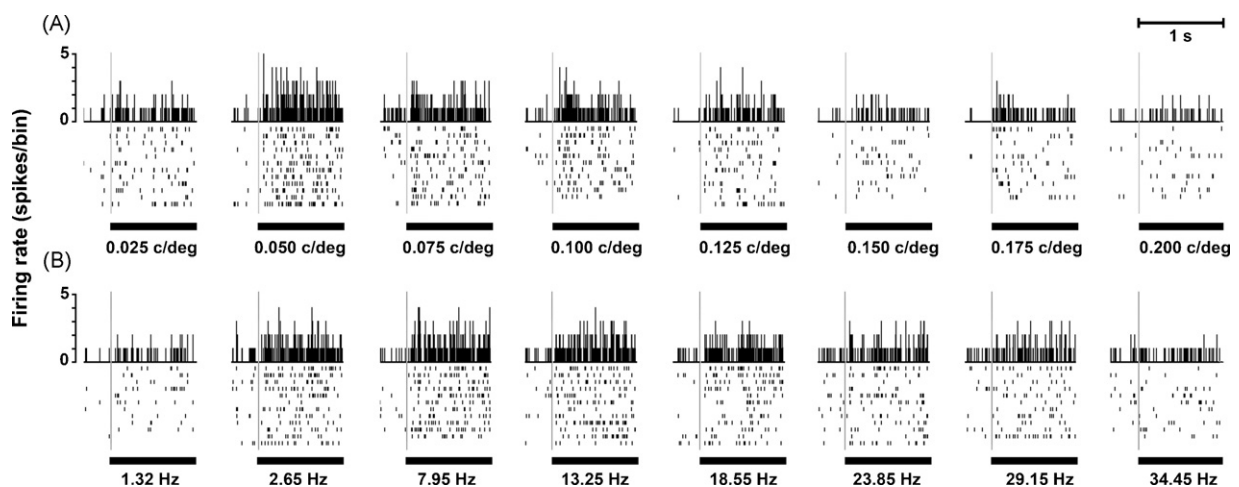


Fig. 2. Responses of an SCI neuron to drifting gratings. Peristimulus time histograms (PSTHs, bin width: 10 ms) and raster plots of a single SCI cell responding to drifting gratings with different spatial and temporal frequencies. The ordinate denotes the firing rate (spikes/bin). The thick black lines under the PSTHs indicate the duration of the stimulus movement for 1000 ms (peristimulus time). Corresponding spatial or temporal frequencies of the sinusoidally modulated drifting gratings are shown under the PSTHs. (A) Responses of an SCI neuron to eight different spatial frequencies (temporal frequency: 9.27 Hz). (B) Responses of the same SCI neuron to eight different temporal frequencies (spatial frequency: 0.025 c/deg).

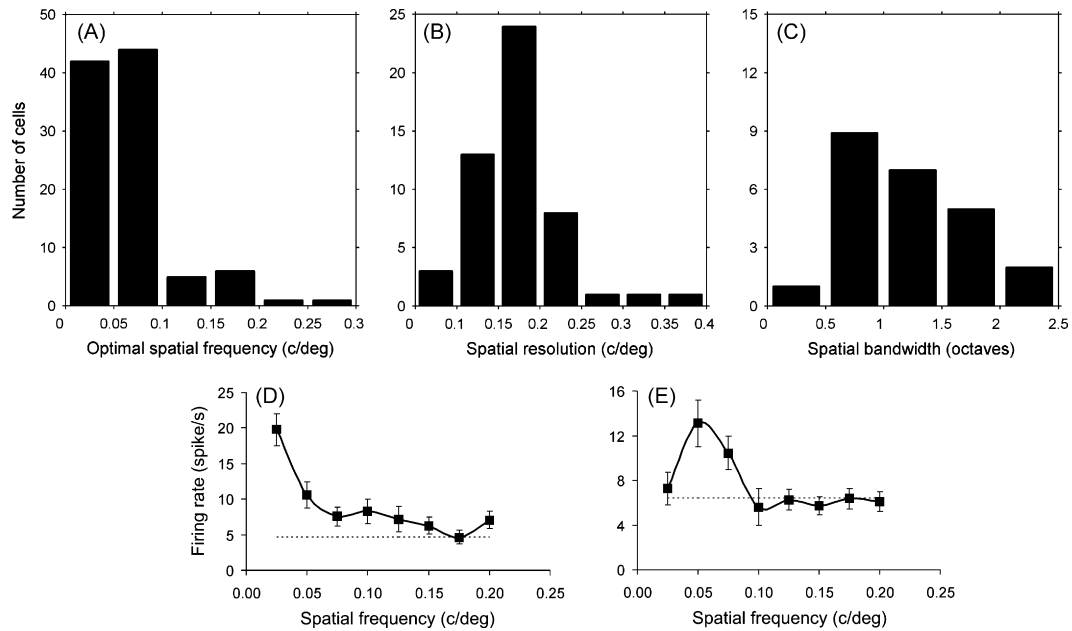


Fig. 3. Spatial visual properties of the SCI neurons. (A) Distribution of the optimal spatial frequencies, estimated from the spatial frequency tuning functions. (B) Distribution of the spatial resolutions. (C) Distribution of the spatial bandwidths. (D) Spatial frequency tuning curve of a low-pass unit. (E) Spatial frequency tuning curve of a band-pass SCI neuron. The tuning curves were fitted by using the cubic-spline technique. Peak values of the fitting curves were considered as the optimal spatial frequency for each unit. Each error bar corresponds to the standard error of the mean. The dashed lines indicate the level of the spontaneous activity.

order to analyze the spatial frequency tuning properties the optimal temporal frequency of each unit was kept constant. Similarly, the temporal frequency tuning was measured at the constant optimal spatial frequency of each unit.

Statistical analysis of the data was performed with the Statistica[®] software. All mean values are accompanied by \pm standard deviations. Linear regression analysis was used to test a relationship between eccentricity and optimal spatial and temporal frequencies; p indicates the value of significance, while r indicates the Pearson correlation coefficient.

At the end of the experiments, the animals were deeply anesthetized with pentobarbital (200 mg/kg i.v.) and transcardially perfused with 4% paraformaldehyde solution. The brains were removed and sliced into coronal sections of 50 μ m, and the sections were stained with Neutral Red. The positions of the recorded SCI neurons were allocated on the basis of electrolytic lesions marking the deepest recording position of the electrode penetrations.

The visual responses of altogether 99 SCI neurons to drifting sinuswave grating stimulation were recorded and analyzed in detail.

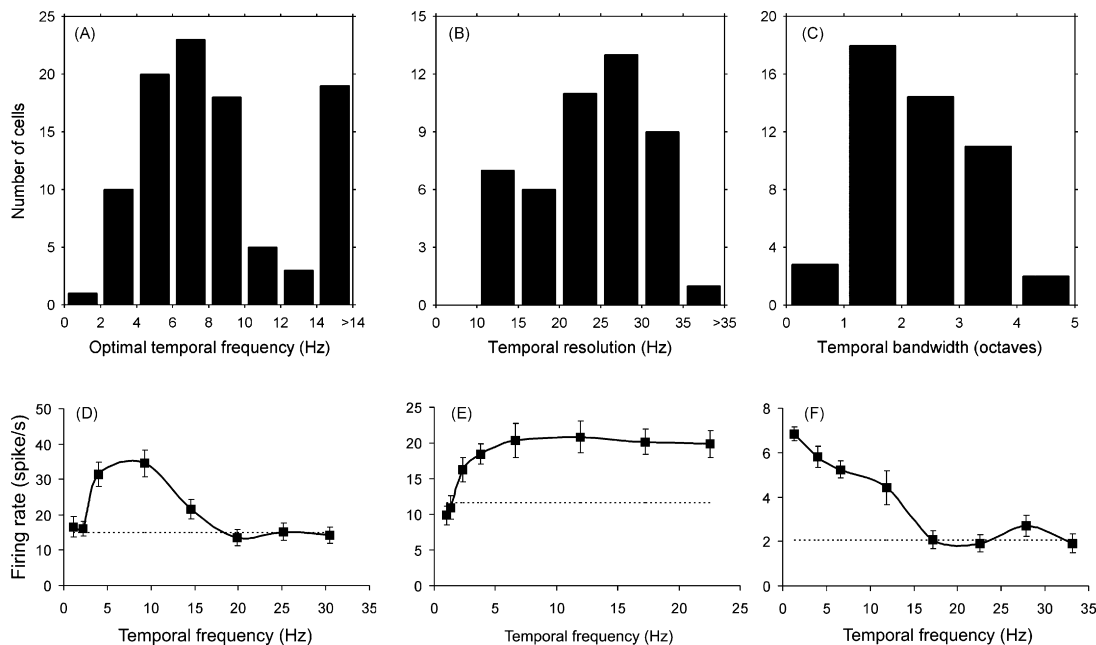


Fig. 4. Temporal visual properties of the SCI neurons. (A) Distribution of the optimal temporal frequencies of the cells, estimated from the temporal frequency tuning functions. (B) Distribution of the temporal resolutions. (C) Distribution of the temporal bandwidths. (D) Temporal frequency tuning curve of a band-pass SCI neuron. (E) Temporal frequency tuning curve of a high-pass SCI neuron. (F) Temporal frequency tuning curve of a low-pass SCI neuron. The conventions are the same as in Fig. 3.

Fig. 1 represents the positions of the recorded SCi neurons based on the histological reconstruction of the electrode tracks. We observed that the receptive fields in the SCi were large and they often covered parts of the ipsilateral visual field. The mean size of the receptive fields in the SCi was 2020.9 ± 949.3 degree² ($N=99$, range: 871.5–4643.9 degree²).

We performed statistical analysis to examine if there was a correlation between the eccentricities and the optimal spatial and optimal temporal frequencies of the SCi neurons. We could not detect any significant correlation ($p=0.89$) between the optimal spatial frequencies and the eccentricities ($r=0.01$). Similar results were obtained concerning the correlation between the optimal temporal frequencies and the eccentricities of the recorded SCi neurons ($p=0.91$; $r=-0.01$).

The SCi neurons responded optimally to low spatial frequencies (Fig. 2A). The mean optimal spatial frequency in the intermediate layers was 0.06 ± 0.02 c/deg ($N=99$, range: 0.025–0.3 c/deg; Fig. 3A). Since the optimal spatial frequency was at the lowest spatial frequency tested for 19 SCi neurons, the mean optimal spatial frequency could be overestimated.

Over half of the SCi neurons (53/99; 54%) displayed spatial low-pass tuning and there was either no or only a slight attenuation of the response at low spatial frequencies (Fig. 3D). Almost one-fourth of the SCi units (24/99; 24%) exhibited band-pass spatial frequency tuning (Fig. 3E). In these neurons, we observed an attenuation of the response to at least half the height of the maximum at low and high spatial frequencies within the tested range. We detected 10 (10/99; 10%) neurons with broad-band spatial frequency tuning. For 12 cells (12/99; 12%) there was no clear-cut spatial frequency tuning according to the above-mentioned categories. When calculating the high-frequency cut-off values of the SCi neurons, we could only take those neurons into consideration whose activity decreased under one-tenth of the maximal one. In case of the remaining neurons the activity did not fall under one-tenth of the maximal level, even when the highest stimulus frequencies were used. The mean spatial resolution of the SCi neurons was 0.17 ± 0.05 c/deg ($N=51$ [33 spatial low-pass and 18 spatial band-pass units], range: 0.06 and 0.37 c/deg; Fig. 3B). For the SCi neurons with spatial band-pass characteristics, the mean spatial frequency bandwidth was 1.06 ± 0.56 octaves ($N=24$, range: 0.1–2.18 octaves) (Fig. 3C).

The SCi neurons preferred the higher temporal frequencies (Fig. 2B), with a mean optimal temporal frequency of 9.06 ± 5.49 Hz ($N=99$, range: 1.71–31.93 Hz) (Fig. 4A). Almost half (48/99; 49%) of the neurons in the SCi exhibited temporal band-pass frequency

tuning (Fig. 4D), 16 SCi neurons (16/99; 16%) displayed high-pass (Fig. 4E) and 17 (17/99; 17%) low-pass temporal frequency tuning (Fig. 4F). We also detected nine neurons (9/99; 9%), which exhibited temporal broad-band tuning. For nine SCi neurons (9/99; 9%), a clear-cut temporal frequency tuning was not apparent when using the above categorization. The mean temporal high-frequency cut-off value was 22.2 ± 10.56 Hz ($N=47$ [35 temporal band-pass and 12 temporal low-pass neurons], range: 4.8–38.0 Hz) in the SCi neurons (Fig. 4B). For SCi neurons with temporal band-pass characteristics, the mean temporal frequency bandwidth was 2.32 ± 0.97 octaves ($N=48$, range: 0.25–4.29 octaves) (Fig. 4C).

Despite a large number of studies discussing the visual receptive field properties of the SC, no data are available concerning the spatio-temporal frequency response profile of the SCi neurons. Accordingly, in the present study we give a description of the spatial and temporal filter properties of the visually responsive SCi neurons and suggest their role in the control of visuomotor actions.

We found that the neurons located in the SCi responded optimally to very low spatial frequencies, and displayed low spatial resolution and low-pass spatial tuning. Similar properties have been observed earlier in the neurons of the SCs [5,16,23,30]. These findings indicate that the neurons in both the superficial and the intermediate SC layers act as good spatial filters in the low spatial frequency domain. The unique interlaminar connections within the SC may furnish an explanation for the similar spatio-temporal frequency characteristics of the superficial and the intermediate collicular layer neurons [12]. The spatial frequency properties found in the SCi are not only similar to those of the SCs, but they also resemble the properties of neurons in other structures of the extrageniculate visual pathway – the lateral posterior-pulvinar complex (LP-Pul) [6], the lateralis medialis-supragenulate nuclear complex (LM-Sg) [22], the caudate nucleus (CN) [21] and also the properties of the W- and Y-type neurons in the dorsal lateral geniculate nucleus (LGNd) [25–27] of the feline brain. Table 1 presents the quantitative visual spatial and temporal frequency properties of neurons in different cortical and subcortical visual areas of the feline brain. Neurons in the lateral suprasylvian (LS) cortices [10,34], and in the anterior ectosylvian visual (AEV) area [20], cortical areas that receive visual information from the SCi through the posterior thalamus, also prefer very low spatial frequencies. However, the mean optimal spatial frequency and spatial resolution of the recorded SCi neurons were much lower than those of the X-type neurons in the lateral geniculate nucleus (LGN) [25,26] and area 17 (A17), in which X input predominates [14,19], and the neurons in area 21a (A21a) [17,28].

Table 1
Quantitative spatial and temporal visual properties of cortical and subcortical structures in the feline brain.

| | Optimal spatial frequency (c/deg) | Spatial bandwidth (octaves) | Optimal temporal frequency (Hz) | Temporal bandwidth (octaves) |
|-----------------|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|
| SC intermediate | 0.06 | 1.06 | 9.06 | 2.32 |
| SC superficial | 0.10 | 1.84 | 6.81 | 2.37 |
| CN | 0.05 | 1.31 | 10.6 | 1.38 |
| LM-Sg | 0.05 | 1.07 | 8.53 | 1.66 |
| LP-Pul | ~0.20 | 2.20 | ~5.00 | 2.32 |
| LGN X cells | 0.85 | – | 2.50 | – |
| LGN Y cells | 0.14 | – | 5.20 | – |
| LGN W cells | 0.07 | – | 2.70 | – |
| A17 | 0.90 | 1.50 | 2.90 | 1.70 |
| A18 | 0.22 | 1.49 | 3.20 | 1.50 |
| A19 | 0.17 | 1.90 | 3.00 | 2.90 |
| A21a | 0.27 ^a , 0.36 ^b | 1.60 ^b , 1.79 ^a | 3.25 ^a , 7.00 ^b | 1.92 ^a , 2.90 ^b |
| A21b | 0.08 | 2.20 | 3.20 | 3.30 |
| PMLS | 0.16 | 2.20 | 5.00 | 2.00 |
| AES cortex | 0.20 | 1.40 | 6.30 | 1.10 |

^a Ref. [17].

^b Ref. [28].

In relevance to the temporal frequency properties of the neurons in the SCi, we found that the mean optimal temporal frequency and the temporal resolution of these cells were high. The mean optimal temporal frequency found in the SCi neurons is comparable to those in the LM-Sg [22], the CN [21], the AEV [20], the LS cortex [18,34], but higher than those in other visual cortical and subcortical areas [see Table 1; [2,17,25,29]]. These results may suggest that the SC is an important source of visual information in the high temporal frequency domain, relayed via the posterior visual thalamus to the CN and to the cortical neurons in the lateral suprasylvian areas and the AEV, structures, which take part in motion analysis [1,11,13,20,25,34].

The low spatial and high temporal frequency preferences of the cells in the SCi suggest that they receive strong visual inputs characteristic of Y and probably W channels presumably from the visual associative cortices and the SCs [3,7,8]. This correlates well with the findings that the AEV and the LS cortex, the main cortical input structures to the SCi of the feline brain are also dominated by Y inputs [31,32]. The preference of the low spatial and high temporal frequencies suggests that the neurons in the SCi can specialize in detection of rapid changes in the visual field, but because of the absence of high spatial frequency sensitivity, they are unable to distinguish small details of the visual image. This is in line with the generally held view that the SCi and the connected ascending tectofugal system could possess a visuomotor function, such as organizing the complex, sensory-guided oculomotor and skeletomotor responses during the self-motion of the animal.

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