

Neuronal Responses to Looming Objects in the Superior Colliculus of the Cat

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Key Words

Looming object · Collision avoidance · Receptive field · Superior colliculus · Cat

Abstract

The superior colliculus (SC) in the mammalian mesencephalon is involved in avoidance or escape behaviors, but little is known about the response properties of collicular neurons to an object approaching on a collision course towards the animal. The present study identified two classes of looming-sensitive neurons, rho and eta cells, in the SC of the cat, but did not find any tau cell, which has been observed in the pigeon tectofugal pathway. The looming responses were characterized by distinct firing patterns, in which the neuronal discharge steadily increased as the object was approaching, and peaked approximately at the time of collision (rho cell) or some time earlier (eta cell). The response onset time of both rho and eta cells was linearly related to the square root of the diameter/velocity ratio of looming objects; whereas for eta cells, the response peak time was linearly related to the diameter/velocity ratio. The receptive fields of these collicular cells were composed of an excitatory center and a suppressive surround, but the occurrence and development of neuronal responses to looming stimuli were independent

of the receptive-field organization. Although the cell number was relatively small in the deep layers of the SC, the proportion of looming-sensitive neurons was close to that in the superficial layers. These results suggest that a population of collicular cells is involved in signaling impending collision of a looming object with the animal and the neural mechanisms underlying the collision avoidance behaviors are to some extent conservative across species from insects to mammals.

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Introduction

An object approaching on a collision course towards an animal usually signals danger for the observer and an escape or avoidance reaction is critical for survival [Rind and Simmons, 1999; Regan and Gray, 2000; Frost, 2010]. The collision avoidance behaviors elicited by looming stimuli have been investigated in a very wide range of species, for instance, in *Drosophila* [Tammero and Dickinson, 2002; Hammond and O'Shea, 2007], the fly [Holmqvist and Srinivasan, 1991; Jabłoński and Strausfeld, 2001], the locust [Robertson and Johnson, 1993; Simmons et al., 2010], the crab [Hemmi, 2005], the frog [Yamamoto

to et al., 2003], the monkey [Schiff et al., 1962; Maier et al., 2004] and humans [Ball and Tronick, 1971; Poljac et al., 2006]. Conceivably, the visual system plays an important role in processing the characteristic information of looming objects and producing the neural signals to trigger behavioral responses [van der Weel and van der Meer, 2009; Billington et al., 2011]. In fact, looming-sensitive visual neurons have been recorded in the moth [Wicklein and Strausfeld, 2000], the mantis [Yamawaki and Toh, 2009], the locust [Rind and Simmons, 1992, 1997; Gray et al., 2010; Rogers et al., 2010], the crab [Medan et al., 2007], fish [Gallagher and Northmore, 2006], the frog [Nakagawa and Hongjian, 2010] and the pigeon [Wang and Frost, 1992; Liu et al., 2008]. Further studies have characterized several specific movement detector neurons in the locust optic lobe [Hatsopoulos et al., 1995; Gabbiani et al., 1999, 2001, 2004] and three classes of visual neurons in the pigeon tectofugal pathway [optic tectum: Wu et al., 2005; nucleus rotundus: Sun and Frost, 1998; telencephalic entopallium: Xiao et al., 2006] by their distinct response patterns to looming stimuli, and it has been suggested that these cells might be involved in computation of different optical variables of approaching objects. In the meantime, the neuronal activities evoked by looming stimuli have been related with the actual behavioral responses of animals [*Drosophila*: Fotowat et al., 2009; the locust: Gray et al., 2001; Santer et al., 2006, 2008; Fotowat and Gabbiani, 2007; Fotowat et al., 2011; the crab: Oliva et al., 2007; fish: Preuss et al., 2006; the frog: Ishikane et al., 2005]. Although the species are very different in the view of evolution, there appears to be some kind of conservativeness in the neural mechanisms underlying the collision avoidance behaviors. Remarkably, most of the relevant findings were obtained in nonmammals. Even if a type of approach-sensitive ganglion cell has been identified in the mouse retina [Münch et al., 2009], little is known about how looming information is processed in the mammalian central visual system.

The superior colliculus (SC) is the principal retinorecipient nucleus in the extrageniculostriate visual system of mammals and plays an important role in multisensory integration and visuomotor coordination [Wurtz and Albano, 1980; Stein and Meredith, 1991; Sparks, 1999; May, 2005; Isa and Hall, 2009]. It is involved in visual attention and visually guided behaviors, such as initiation and control of eye and head movements towards objects of interest. Moreover, investigations with electrical stimulation, neurochemical stimulation or anatomical lesion have shown that the SC mediates defensive behaviors, for example avoidance or escape which would be appropriate

for an impending emergency, such as the appearance of a predator or an object approaching on a collision course [Dean et al., 1989; Brandão et al., 1994; Schenberg et al., 2005]. Therefore it is plausible to suppose that at least a proportion of collicular neurons would be responsive to looming stimuli. On the other hand, the SC is considered as a homologue of the optic tectum of nonmammalian vertebrates in both structural and functional aspects. Since looming-sensitive neurons have been observed in the optic tectum of the frog [Kang and Li, 2010; Nakagawa and Hongjian, 2010] and the pigeon [Wu et al., 2005], one may expect some kind of similar finding in the SC.

Altogether, the SC turns out to be a potential candidate which may substantially contribute to neural processing of looming information in mammals. By using single-unit recording and computer simulation techniques, the present study was conducted on the cat to examine whether and how collicular neurons would respond to an object approaching on a collision course towards the animal.

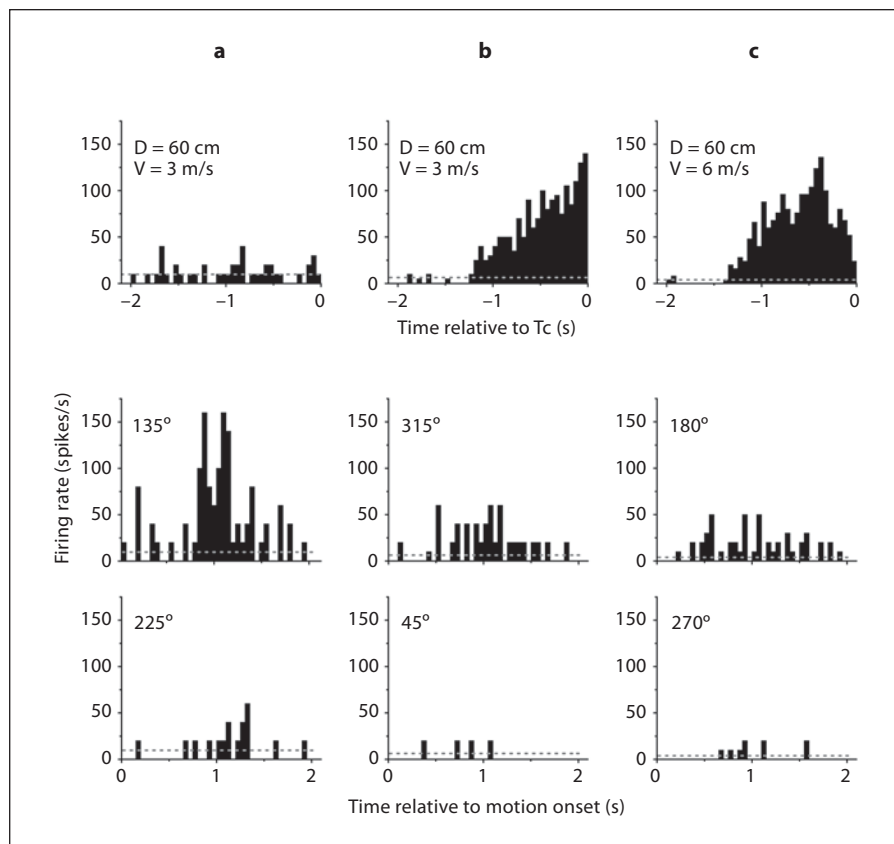
Materials and Methods

Animal Preparation and Maintenance

Experiments were carried out on 13 normal adult cats of either sex weighing 2.0–3.0 kg. The protocol was approved by the Animal Administration Committee, Institute of Biophysics, Chinese Academy of Sciences, and performed in compliance with the National Institutes of Health guidelines on the care and use of animals. The procedures for animal preparation and maintenance were conventional and adequate measures were taken to minimize pain and discomfort of the cats. Briefly, anesthesia was induced with ketamine hydrochloride (20–30 mg/kg, i.m.). Surgery was performed to enable continuous infusion of sufentanil citrate (0.15 µg/kg/h), propofol (4 mg/kg/h), gallamine triethiodide (10 mg/kg/h) and glucose (300 mg/kg/h) in Ringer's solution (10 ml/kg/h) through a foreleg venous cannula and artificial ventilation through a tracheal cannula. During experimentation, the expired CO₂, body temperature, electrocardiogram and electroencephalogram were monitored and maintained at appropriate levels by regulating the usage of drugs and a heating pad. The pupils were dilated with atropine sulfate and the corneas were protected with air-permeable contact lenses. The optics was corrected with suitable spectacle lenses to focus the eyes at a viewing distance of 57 cm.

Craniotomy was performed at Horsley-Clarke coordinates P2-A4 and L0–5 [Waleszczyk et al., 1999]. An epoxy-coated tungsten microelectrode (FHC Inc., Bowdoin, Me. USA) was lowered perpendicularly into the brain and then advanced into the SC (normally at least 12 mm below the cortical surface) for single-unit recordings. Neuronal activities were amplified and filtered with a differential amplifier (DAM80; WPI Inc., Sarasota, Fla., USA) and fed into a computer for on-line and off-line analyses. Once a collicular neuron was isolated, the receptive field was approximately plotted with hand-held light and dark spots.

Fig. 1. Response histograms of 3 collicular neurons to a ball approaching on a collision course towards the animal (top row, negative values on the abscissa indicate the time before collision) or a bar drifting on the screen plane in the preferred direction (middle row) or an orthogonal direction (bottom row). **a** Looming-insensitive cell. **b** Rho cell. **c** Eta cell. The spontaneous activity level is shown with dashed lines. Bin width = 50 ms.



The recording sites of some neurons were marked by passing a small amount of direct current (20 μ A for 20 s) through the electrode. At the end of experiment, the cat was perfused transcatheterially under deep anesthesia and the brain was removed from the skull. The colliculus was stereotaxically blocked and sectioned coronally at 40 μ m thickness on a freezing microtome. The sections were counterstained with cresyl violet and dehydrated for subsequent microscopic observation to reconstruct the electrode tracks and localize the recording sites [Waleszczyk et al., 1999; Hashemi-Nezhad et al., 2003].

Visual Stimuli and Data Analysis

Visual stimuli were generated on-line by a computer with a plug-in graphics acceleration card (NVIDIA Quadro FX 3400; Leadtec, China) and rear-projected onto a screen by a projector (XG-CN500X; Sharp, Japan). The screen was 200 cm in width and 150 cm in height, and placed 57 cm in front of the cat. During quantitative tests, the stimuli were presented to the dominant eye (mostly the contralateral eye, determined qualitatively with hand-held bar and looming stimuli) only.

The main stimuli were constructed to simulate a collision course of an object approaching towards the animal at a constant velocity. As same as that in previous studies on the pigeon [Wang and Frost, 1992; Sun and Frost, 1998; Wu et al., 2005; Xiao et al., 2006], the computer was programmed to calculate the appropriate projective geometry, yield smoothly moving and transforming images and display the animation on the screen. The looming ob-

ject was designed as a 'soccer ball' with alternating black and white panels of equal areas, so that the overall luminance was unchanged during a trial. The luminance of black and white areas was 0.1 and 6.6 cd/m^2 , respectively. The ball was centered on the receptive field of the neuron under recording. It first stayed stationary on the screen for 1 s for measuring the spontaneous activity, then performed a simulated looming course of 4 s, and finally stopped at the moment when it virtually arrived at the eye (time of collision, T_c) and stayed there for an additional 0.5 s. Such a trial was followed by an interval of at least 5 s (blank screen) to allow the neuron to recover from any adaptation. Normally, each cell was stimulated with a number of objects with different diameters ($D = 12\text{--}120$ cm) and velocities ($V = 1\text{--}20$ m/s). In a quantitative test, 5–10 looming objects with different combinations of D and V ($D/V = 0.01\text{--}0.30$ s) were pseudorandomly interleaved to compose a block of stimulation, and 3–10 blocks were presented for data averaging.

Response patterns of collicular neurons to looming objects were plotted as peri-stimulus time histograms (fig. 1), in which the time was counted backwards from the end of the simulated looming course and the T_c was set to zero as the reference. In each histogram, the onset time of evoked response was determined at the bin from which the firing rate exceeded the spontaneous activity (mean + SD) continuously, and the peak time was determined at the bin with the highest firing rate. In addition, the drop-off in firing rate at T_c was calculated by the formula $(f_p - f_{tc}) / (f_p - f_s)$, where f_p , f_{tc} and f_s were the peak rate, firing rate at T_c and spontaneous rate, respectively.

In preliminary experiments, some collicular cells were also tested with an elongated bar drifting on the screen plane. The bar was moved at the optimal velocity in 8 pseudorandomly interleaved directions to outline the direction preference. In subsequent experiments, the excitatory receptive field (ERF) was mapped for some looming-sensitive neurons. A black square of 4° (visual angle) was moved at the optimal velocity, randomly along a series of parallel paths covering the whole visual space [Wu et al., 2005; Xiao et al., 2006; Liu et al., 2008]. A contour map was obtained by thin-plate spline interpolation to illustrate the spatial distribution of evoked responses, and the ERF size was determined as the geometric mean of length and width of the area within which the moving square elicited a significant increase in the firing rate of the cell. Since the spontaneous activity was often low in the cells, the suppressive region of the receptive field could not be accurately measured with this method. However, the presence of suppressive surround, usually several times larger than the excitatory region, was visible in many maps. When necessary, the extent of suppressive surround was estimated by gradually lengthening the square into a bar in the dimension perpendicular to that of motion until the firing rate evoked by the moving bar was reduced to a minimum [Wu et al., 2005; Liu et al., 2008].

Results

Looming-Sensitive Neurons in the SC

A total of 435 neurons were recorded from the SC. The peri-stimulus time histograms of 3 representative cells are shown in figure 1. Most of the cells ($n = 291$) responded only to stimuli moving on the screen plane but not to looming motion in depth (fig. 1a). The other 144 cells (33.1%) exhibited vigorous responses to an object approaching on a simulated collision course towards the viewing eye, while discharging much less to planar motion (fig. 1b, c). In addition, the response patterns were distinctive for looming objects (see below) but rather ordinary for planar stimuli.

All the looming-sensitive neurons started tonic firing at some time before collision but they were characterized by different response patterns. Two sorts of typical cells were observed and, in compliance with the terminology used in previous studies on the pigeon [Sun and Frost, 1998; Wu et al., 2005; Xiao et al., 2006], named as rho and eta cells, respectively. As shown in figure 2, the two classes of cells were similar in that both initiated earlier responses to looming objects of larger sizes and/or lower velocities but different in how the firing rates varied with time subsequently. For a rho cell, the evoked responses increased monotonically until T_c (fig. 2a, b), whereas for an eta cell, the firing rates displayed an interrupted ascending phase and then an obvious drop-off before collision (fig. 2c, d).

The classification of the whole sample of looming-sensitive neurons is illustrated in figure 3, in the same manner as that in the literature [Sun and Frost, 1998; Wu et al., 2005; Xiao et al., 2006]. The 144 neurons were clustered into two distinct groups: 21 rho cells (14.6%) and 123 eta cells (85.4%). Generally speaking, the firing rate of a rho cell peaked at a time close to collision so that the drop-off was quite low whereas for an eta cell the response grew to a peak earlier and then dropped off obviously before collision. The clear separation in the plot indicates that the two classes of cells differed from each other by the timing of peak responses. It should be noted that we did not find any tau cell, the third class of looming-sensitive neuron identified in the pigeon (a tau cell would fall close to the origin of the abscissa in the plot since it initiated responses at an approximately constant time independent of the size and velocity of looming objects).

Relationship between Timing of Responses and Looming Stimuli

Looming stimuli of different sizes and velocities were presented in quantitative tests and, as shown in figure 2, the main effect of varying the parameters occurred on the timing of evoked responses. Since an enlargement of the size and an increase in the velocity might lead to opposite changes in the response onset time (and the peak time of eta cells as well), the D/V ratio of looming objects was taken as a major concern. Actually for both example cells, the timing of responses consistently shifted backwards from T_c as D/V increased, suggesting that the ratio could be considered as a key factor to define the feature of a looming object.

Further statistical analysis was performed on all the looming-sensitive neurons which had been fully tested with stimuli of 10 different D/V ratios. It revealed a strong linear relationship between the response onset time and the square root of the D/V ratio for both rho and eta cells (fig. 4a), as well as a strong linear relationship between the response peak time and the D/V ratio for eta cells (fig. 4b). Both classes of cells initiated earlier responses (and eta cells exhibited peak responses earlier) to looming stimuli of higher D/V ratio. On the whole, eta cells preceded rho cells in the timing of responses and the advantage was enlarged at a higher D/V ratio as the slope of the fitted line was shallower for rho cells. These results are analogous to what has been reported in the nucleus rotundus [Sun and Frost, 1998] and the optic tectum [Wu et al., 2005] of the pigeon.

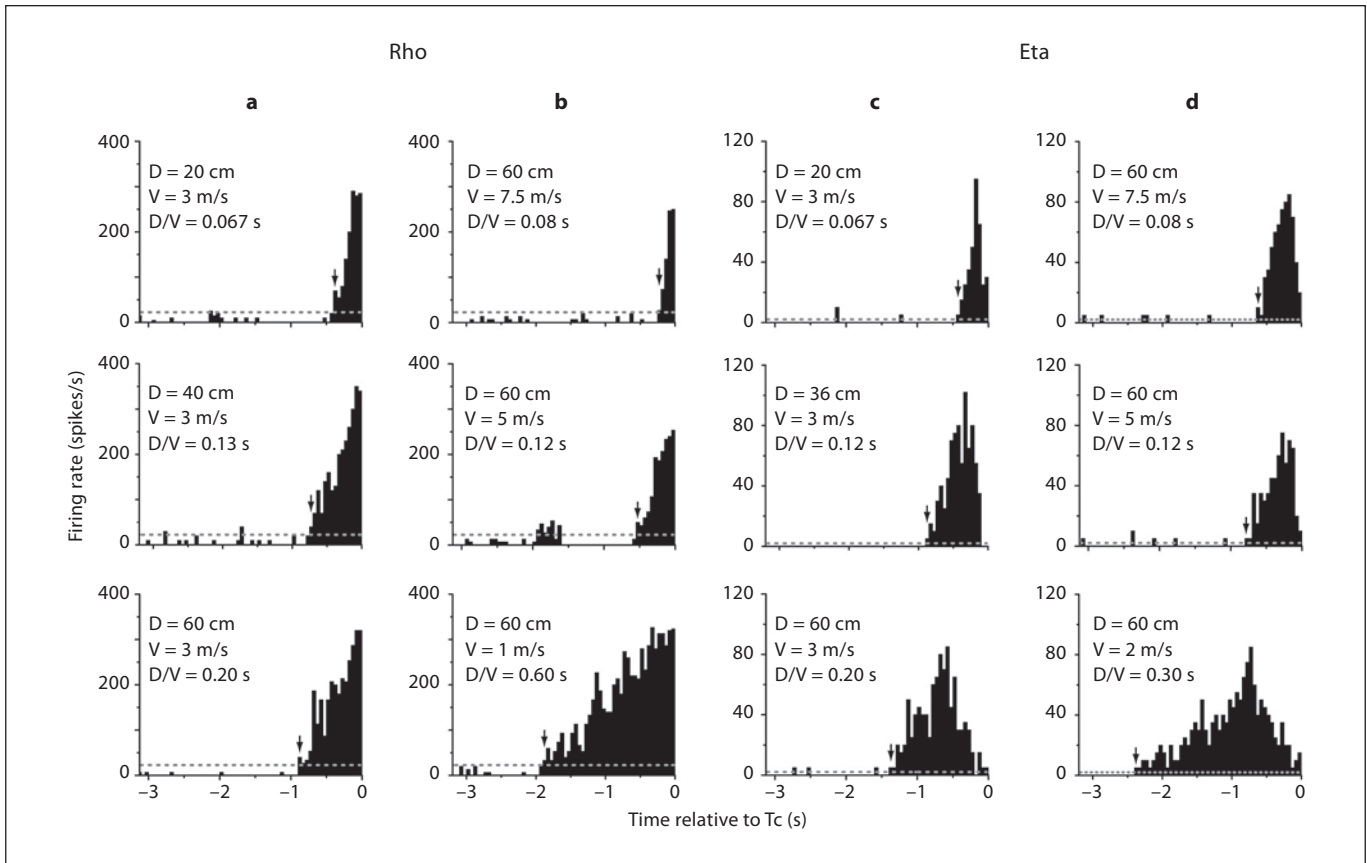
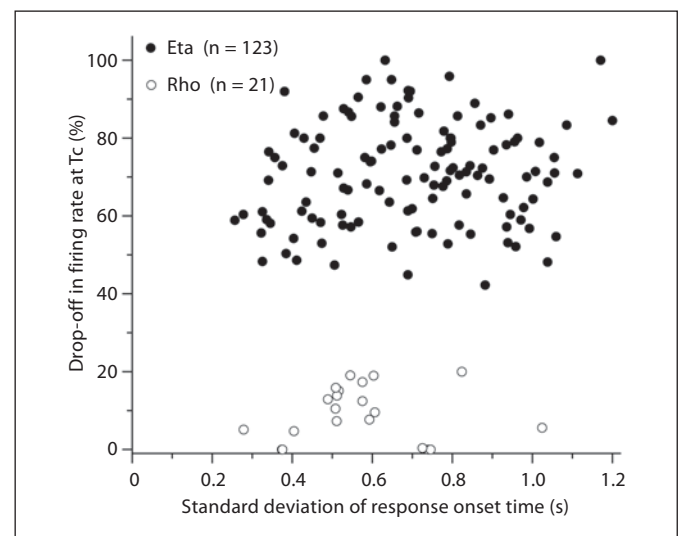


Fig. 2. Response histograms of 2 collicular neurons to looming stimuli of different sizes (D) and velocities (V). Both the rho (**a, b**) and the eta (**c, d**) cells started tonic responses at hundreds of milliseconds before collision, and the response onset time (marked with arrows) became even earlier when the object was larger in size (**a, c**) or slower in velocity (**b, d**). Then the firing rates steadily

increased as the object was approaching, but the timing of peak responses was different. The rho cell had its highest firing rate approximately at T_c whereas the eta cell at some time before T_c . In addition, the response peak time of the eta cell also became earlier for a larger and/or slower stimulus. Bin width = 50 ms.

Fig. 3. Classification of looming-sensitive neurons in the SC. For each cell, the response onset time and the drop-off in firing rate at T_c were calculated for each looming object used in the quantitative test. The abscissa represents the standard deviation of the onset time values, and the ordinate the median of the drop-off values. The data points are distributed in two separate regions corresponding to rho and eta cells, respectively.



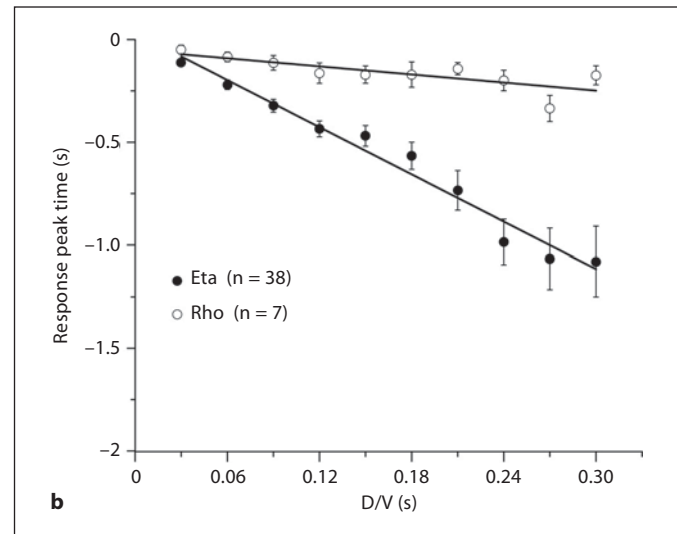
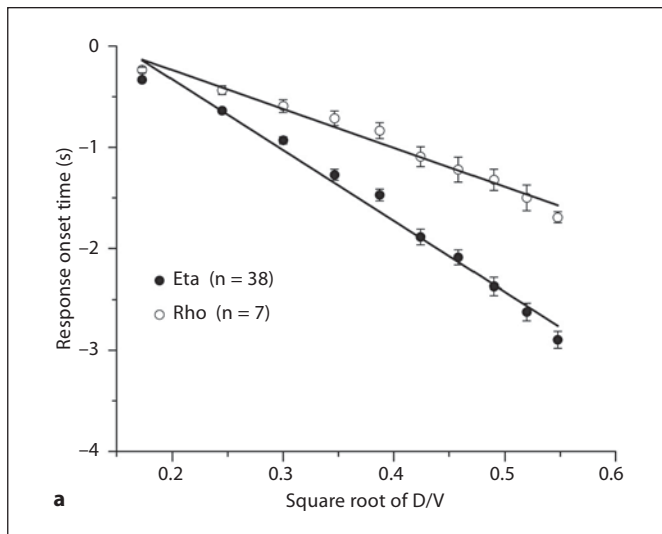


Fig. 4. Relationship between timing of responses and physical parameters of looming objects. **a** The response onset time was linearly correlated to the square root of the D/V ratio of looming objects for both rho (slope $p = -3.84$, correlation coefficient $r = -0.988$) and eta ($p = -6.99$, $r = -0.992$) cells. **b** The response peak time was linearly correlated to the D/V ratio for eta cells ($p =$

-3.82 , $r = -0.986$). The correlation was fairly good for rho cells ($p = -0.65$, $r = -0.775$), but the fitted line was rather flat and close to the level of $y = 0$, showing that the firing rates peaked approximately at T_c . As all the time values were obtained in reference to T_c , the negative slope values indicate earlier responses to higher D/V ratio. Error bars represent standard errors.

Receptive-Field Organization and Looming Responses

Normally, the looming-sensitive neurons in the SC were also responsive to stimuli moving on the screen plane and possessed a receptive field consisting of a moderate excitatory center and a much larger suppressive surround. The responses of the center to planar motion could be diminished or eliminated by stimulation of the surround. The ERF was mapped for 8 rho and 41 eta cells. The ERF size ranged between 8.6 and 15.8° for rho cells and 8.5 and 19.2° for eta cells. There was little difference between the two groups (12.3 ± 2.3 vs. $12.9 \pm 2.5^\circ$, mean \pm SD; t test, $p = 0.5$), suggesting that the distinct response patterns of rho and eta cells to looming stimuli might be irrelevant to receptive-field organization.

During a looming course, the stimulus image on the screen expanded continuously from a small dot to a large plate, and its size (i.e. the visual angle subtended by the approaching ball) enlarged approximately exponentially with time [Sun and Frost, 1998]. To examine whether the neuronal responses to looming stimuli were related to receptive-field organization, the angular size of the stimulus image at the response peak time was estimated for each cell and compared with the ERF size; the time when the stimulus image expanded to the ERF size was also calculated for each looming object as a reference. For a

rho cell, the looming response increased with time until collision, even though the edge of the object had entered the suppressive region of the receptive field. The inefficacy of suppression was even more pronounced with a large object as its stimulus image expanded very deeply into the surround but did not reduce the response strength (fig. 5a). Eta cells displayed an obvious drop-off in firing rate before collision, but at the response peak time, the edge of a looming object might fall either within the ERF (fig. 5b) or far beyond it into the suppressive surround (fig. 5c).

An overall view of the whole sample is displayed in figure 6. For all rho and most eta cells, the stimulus size at the response peak time was larger than the ERF (fig. 6a), in other words, the looming responses kept growing when the edge of an object had moved into the surround. Moreover, the time lag of peak responses was very diffuse among different cells and stimuli (see fig. 5a, c for examples and fig. 6b for statistics), and therefore could not be attributed to the latency of suppression. These results indicate that the surround was ineffective in suppressing the looming responses of these cells. On the contrary, for some other eta cells, the firing rates began decreasing before the stimulus image covered the ERF entirely (fig. 5b), and consequently before the suppressive surround might

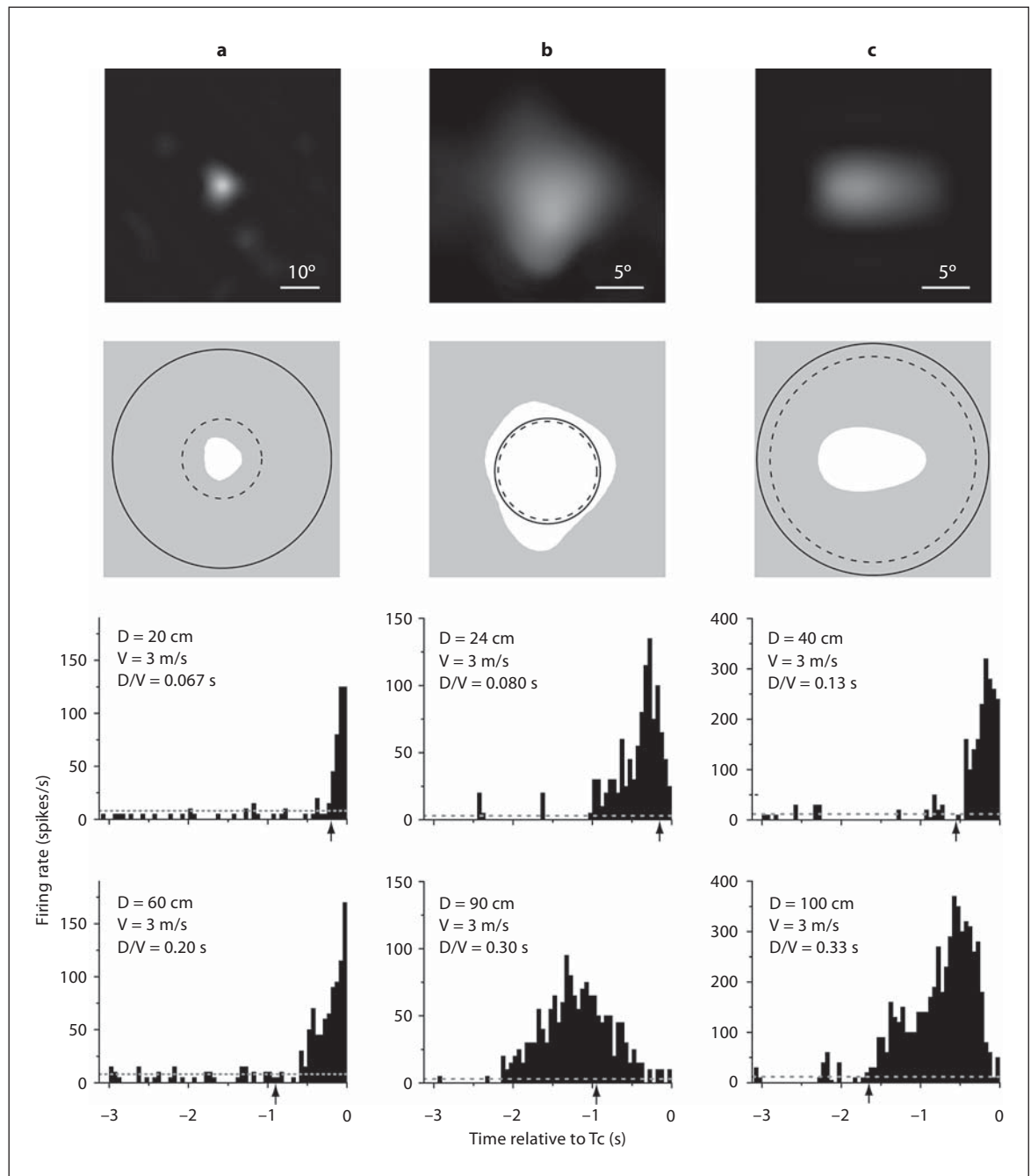


Fig. 5. Receptive-field organization mapped with planar stimulation and response histograms to looming objects. A rho cell (**a**) and 2 eta cells (**b, c**) are shown as examples. In the first row, the firing rates are coded in a gray scale to depict the appearance of the ERF (bright) and suppressive surround (dark). The regions are outlined in the second row (ERF in white, surround in gray), along with the locations of a small (dotted circle) and a large (solid circle) looming object on the screen at the corresponding response peak time. Neuronal activities evoked by the two objects

are displayed in the third and fourth rows, respectively, with arrows pointing to the time when the stimulus image expanded to the ERF size. Bin width = 50 ms. **a, c** The stimulus image had expanded into the suppressive region before the response reached the peak, sometimes even before the cell started tonic firing, indicating that the surround was incapable of suppressing the looming responses. **b** The stimulus image fell fully within the ERF at the response peak time, implying that the drop-off of looming responses was not initiated by activation of the surround.

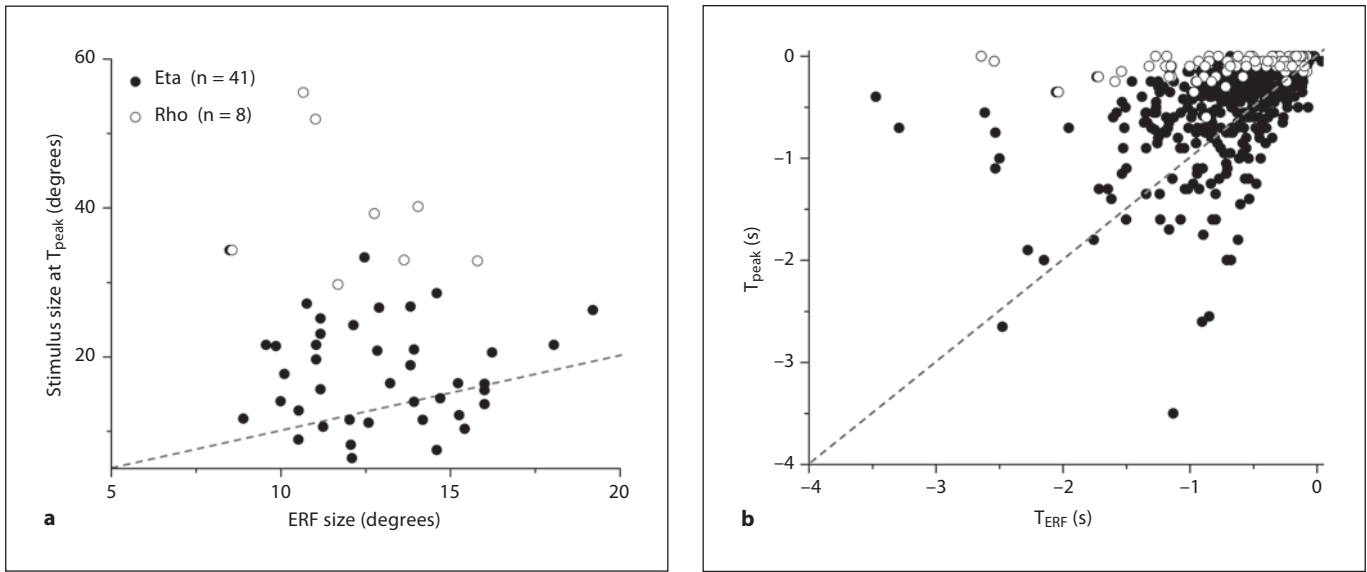


Fig. 6. Relationship between dimensions of ERF and occurrence of peak responses to looming stimuli. **a** For each cell, the angular size of stimulus image at the response peak time (T_{peak}) was estimated for each looming object used in the quantitative test, and the median is plotted against the ERF size. The correlation between the two variables was poor for both rho ($r = -0.32$) and eta ($r = -0.05$) cells, implying that the peak response was not related to the ERF size. The dashed line, on which the stimulus size is equal to the ERF size, represents the situation in which the peak

response appeared at the moment when the stimulus image covered the ERF optimally. **b** The response peak time is plotted against the time when the stimulus image expanded to the ERF size (T_{ERF}). The two variables were calculated for each cell and each looming object individually; therefore, the data points are much more than the cell number in **a**. T_{peak} was posterior to T_{ERF} in most cases (above the dashed line), but the time lag was very diffuse from zero up to a few seconds.

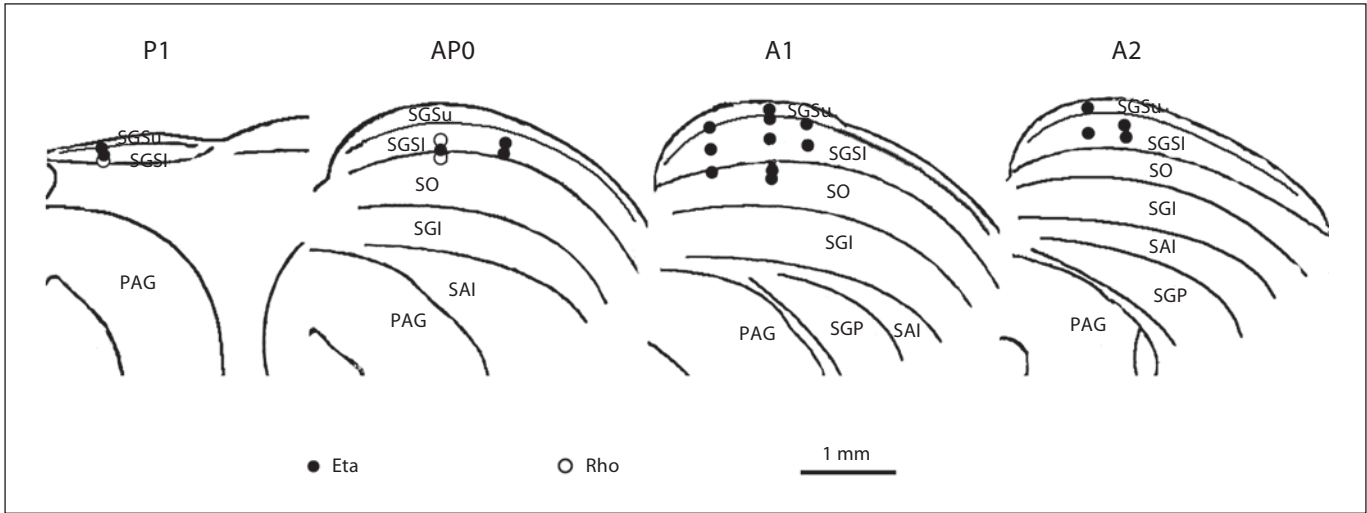


Fig. 7. Topological distribution of recording sites of 3 rho and 19 eta cells in the SC. The locations were reconstructed onto four coronal sections between Horsley-Clarke coordinates P1 and A2. By convention [Wurtz and Albano, 1980; Stein and Meredith, 1991; May, 2005], the SC is divided into the superficial layers consisting of stratum zonale (outermost but too narrow to be shown), stratum griseum superficiale (subdivided into upper and lower

sublaminae, SGSu and SGSI) and stratum opticum (SO), and the deep layers consisting of stratum griseum intermediale (SGI), stratum album intermediale (SAI), stratum griseum profundum (SGP) and stratum album profundum (deep white layer, not shown). PAG = Periaqueductal gray. The marked sites were localized in SGSu, SGSI and SO.

Table 1. Laminar location of looming-sensitive (rho and eta) and insensitive neurons in the SC and percentage of looming-sensitive neurons

Layer	Cell number				Looming-sensitive
	rho	eta	insensitive	sum	
SZ	0	0	7	7	
SZ/SGSu	0	0	3	3	
SGSu	2	19	67	88	23.9%
SGSu/SGSl	1	11	18	30	40.0%
SGSl	7	47	91	145	37.2%
SGSl/SO	1	5	7	13	46.2%
SO	7	31	65	103	36.9%
SO/SGI	0	0	3	3	
SGI	3	8	23	34	32.4%
SAI + SGP	0	2	7	9	22.2%
Total	21	123	291	435	33.1%

SZ/SGSu, SGSu/SGSl, SGSl/SO, SO/SGI: the location was around the boundary between two layers and could not be reliably identified. On the whole, the proportion of looming-sensitive neurons was 33.7% in the superficial layers (from SZ to SO: 18 rho, 113 eta and 258 insensitive cells) and 30.2% in the deep layers (from SGI to SGP: 3 rho, 10 eta and 30 insensitive cells).

be activated. Generally, the occurrence of peak responses to looming stimuli was not determined upon the dimensions of the ERF, and the drop-off of firing rates was not associated with expansion of the stimulus image into the surround.

Laminar Distribution of Looming-Sensitive Neurons

The recording sites of 3 rho and 19 eta cells were marked by electrolytic lesions and their locations in the SC were reconstructed on a stereotaxic atlas of the brain (fig. 7). All of them were distributed within the superficial layers, i.e. the upper (SGSu) and lower (SGSl) sublaminae of stratum griseum superficiale, and stratum opticum (SO), but none in stratum zonale (SZ). To complete an overall examination, the laminar location was approximately determined for each collicular cell, upon the depth differences among recording sites and the positions of electrolytic lesions [Waleszczyk et al., 1999; Hashemi-Nezhad et al., 2003]. As shown in table 1, the majority of looming-sensitive neurons were located in the superficial layers SGSu, SGSl and SO, the remainders in the deep layers, i.e. stratum griseum intermediale (SGI), stratum album intermediale (SAI) and stratum griseum profundum (SGP), but none in the outermost layer SZ. The

proportion of looming-sensitive neurons in SGSu was smaller than that in SGSl and SO ($p < 0.05$), while the difference was insignificant among the layers from SGSl to SAI and SGP.

Discussion

The SC has long been thought to mediate avoidance or escape behaviors [Dean et al., 1989; Brandão et al., 1994; Schenbergh et al., 2005], and has recently been shown to respond to looming stimuli by functional magnetic resonance imaging of the human brain [Billington et al., 2011]. However, direct evidence is lacking for the presence of looming-sensitive neurons in this nucleus or any other structure in the mammalian central visual system (Westby et al. [1990] claimed that a small proportion of rat collicular cells fired vigorously to ‘looming’ stimuli but did not provide the details). The present study reveals that a population of cat collicular neurons (about 33% in the whole sample) responded to an object approaching on a simulated collision course towards the animal. These cells were characterized by distinct firing patterns, in which the neuronal discharge steadily increased as the object was approaching, and peaked approximately at Tc or some time earlier (fig. 2, 5). The looming-sensitive neurons were also responsive to stimuli moving on the screen plane, but typically with less discharge and a plain firing pattern (fig. 1). Moreover, planar motion of an object elicited excitatory responses in the ERF and inhibitory responses in the suppressive surround of a collicular cell whereas symmetrical expansion of the image of a looming object into the suppressive surround was not associated with a reduction of firing rates (fig. 5, 6). Generally, the looming responses reported here were clearly different from the neuronal activities evoked by planar stimuli. The occurrence and development of these responses were independent of the receptive-field organization of the cells, indicating that they were elicited by motion in depth of a looming object but not by lateral motion of the object edge on the screen plane.

The looming-sensitive neurons in the SC could be classified into two groups, rho and eta cells, by the criteria established in the pigeon. The two groups were distinct in their response patterns, especially the timing of peak responses. Rho cells have been recorded in the optic tectum [Wu et al., 2005] and the nucleus rotundus [Sun and Frost, 1998] of the pigeon. Eta cells, which constituted a majority in our samples, have been found throughout the pigeon tectofugal pathway [Sun and Frost, 1998; Wu et

al., 2005; Xiao et al., 2006]. There was no comparable classification in previous studies on other species. Nevertheless, it appears that the lobula giant movement detector (LGMD), the descending contralateral movement detector (DCMD) and the late DCMD (LDCMD) in the locust respond to looming stimuli in a pattern very similar to that of eta cells [Rind and Simmons, 1992; Gabbiani et al., 1999, 2001; Gray et al., 2001, 2010] (but in some cases, the detectors may respond in a more rho-like manner, see Rind and Simmons, 1997, 1999). The looming responses observed in *Drosophila* [Fotowat et al., 2009], the moth [Wicklein and Strausfeld, 2000], the mantis [Yamawaki and Toh, 2009], the crab [Medan et al., 2007; Oliva et al., 2007], fish [Gallagher and Northmore, 2006] and the frog [Ishikane et al., 2005; Kang and Li, 2010; Nakagawa and Hongjian, 2010] are, more or less, analogous to those of LGMD and DCMD. Normally, the neuronal firing rates increase as an object is approaching towards the animal, with or without a drop-off before collision. It has been proposed that, in accordance with their response patterns, rho cells signal the absolute rate of image expansion (i.e. angular velocity) of looming objects [Sun and Frost, 1998] and LGMD/DCMD neurons (and eta cells as well) perform a multiplication of the angular velocity of expansion and an exponential function of the angular size of the image [Hatsopoulos et al., 1995; Gabbiani et al., 1999, 2004]. Remarkably, Gabbiani et al. [2002] described the biophysical implementation of the multiplicative operation in the locust. However, little is known about how the complicated variables, such as those mentioned above, might be computed in the brain of other species.

Besides the overall response patterns, rho and eta cells in the SC were also similar to their counterparts in the pigeon tectofugal pathway in the relationship between the timing of responses and physical parameters of looming stimuli [Sun and Frost, 1998; Wu et al., 2005; Xiao et al., 2006]. For both classes of cells, the response onset time was linearly correlated to the square root of the D/V ratio of looming objects, whereas for eta cells, the response peak time was linearly correlated to the D/V ratio. The linear relationship between the response peak time and the D/V ratio has also been observed in the locust LGMD/DCMD neurons [Gabbiani et al., 1999, 2001, 2004], the collision-sensitive neurons in the frog optic tectum [Kang and Li, 2010; Nakagawa and Hongjian, 2010] and the looming-evoked activity in the nerve cord of *Drosophila* [Fotowat et al., 2009], but no analysis on the response onset time is available in the literature. The linear relationship with the square root of D/V may approximately indicate an angular velocity threshold for re-

sponse onset, and the linear relationship with D/V an angular size threshold for peak response [Sun and Frost, 1998; Gabbiani et al., 1999, 2001, 2004]. Although many questions still remain to be answered, rho and eta cells are thought to signal an early warning of impending collision [Sun and Frost, 1998; Rind and Simmons, 1999; Wu et al., 2005]. Sun and Frost [1998] proposed that rho cells might serve as building blocks for other neurons (including eta cells) to calculate more complicated optical variables. However, data obtained from both the pigeon [Sun and Frost, 1998; Wu et al., 2005] and the cat (fig. 4) showed that the responses of eta cells to looming stimuli were generally earlier than those of other cells, casting doubt on the division of labor among different neurons. Presumably, specialized cells may carry out several different computations in parallel to analyze signals from an approaching object.

A third class of looming-sensitive neurons, tau cells, have been recorded in the pigeon tectofugal pathway [Wang and Frost, 1992; Sun and Frost, 1998; Wu et al., 2005; Xiao et al., 2006]. They start tonic firing at an approximately constant time before collision, and therefore are considered as capable to provide precise 'time-to-collision' information. This type of cell was absent in the present study and, to our knowledge, is yet to be found in other species. The reason could be one or a combination of the following: (1) species specialization; (2) differences in experimental protocols, including the level of alertness and anesthesia and the construction of looming stimuli; (3) limits of neurons and nuclei being studied. The present study was conducted in a very similar way to that applied on the pigeon [Sun and Frost, 1998; Wu et al., 2005; Xiao et al., 2006], in particular the looming stimuli were almost identical. Since a large number of cells have been surveyed in the full range of the SC from the outermost layer SZ to deep layers SAI and SGP, the nucleus is unlikely to contain a substantial number of tau cells. Although the tau operation appears simple and accurate in signaling impending collision, the practicality of this strategy is a controversial issue in the literature [Tresilian, 1999; Regan and Gray, 2000; Frost, 2010]. Anyway, considering the complexity of the mammalian brain, the present study would not exclude the possibility of encountering tau-like cells in other structures in the visual system, for example, the pulvinar and the extra-striate cortex in the colliculo-pulvinar-cortical pathway, which are homologues of the nucleus rotundus and the telencephalic entopallium in the pigeon tectofugal pathway, respectively [Shimizu and Bowers, 1999].

Looming-sensitive neurons in invertebrates and lower vertebrates usually possess a wide receptive field which may cover a whole visual hemifield or even up to the entire visual space [Wicklein and Strausfeld, 2000; Gallagher and Northmore, 2006; Medan et al., 2007; Oliva et al., 2007; Yamawaki and Toh, 2009; Rogers et al., 2010]. Their counterparts in the pigeon, except for part of the tectal cells, have an ERF of at least 30° [Sun and Frost, 1998; Wu et al., 2005; Xiao et al., 2006]. By comparison, the receptive field is smaller ($18.5 \pm 3.8^\circ$) in the collision-sensitive neurons in the frog optic tectum [Kang and Li, 2010]. In the present study, the ERF size was moderate (8–20°) for both rho and eta cells, though it seemed somewhat larger than that of ordinary collicular neurons in the superficial layers [Wurtz and Albano, 1980; Stein and Meredith, 1991; Waleszczyk et al., 1999; Hashemi-Nezhad et al., 2003]. It is naturally thought that a wide receptive field is suitable for detecting symmetrical expansion of a looming object. However, the looming-sensitive neurons in the SC were featured by a receptive field consisting of a moderate excitatory center and a much larger suppressive surround. Similar to that of the pigeon tectal cells [Wu et al., 2005], the surround was often incapable of suppressing the neuronal responses to looming stimuli. On the other hand, although rho and eta cells exhibited distinct response patterns, little difference was found between them in receptive-field structure and size. Together with the other data shown in figures 5 and 6, these results suggest that looming responses were independent of the receptive-field organization of collicular cells.

In the present study, most of the looming-sensitive neurons were recorded in the lower part of the superficial layers (SGSl and SO) of SC, a smaller proportion in the upper sublaminae, SGSu, but none in the outermost layer, SZ. This distribution might be relevant to the fact that collicular cells near the surface tend to have small central activating regions and that receptive-field size tends to increase with depth in the superficial layers [Wurtz and Albano, 1980; Stein and Meredith, 1991]. Previous studies on the SC have shown that the cells in the superficial layers are primarily visually driven whereas the cells in the deep layers discharge mostly in relation to eye and head movements or multimodal stimuli [Wurtz and Albano, 1980; Stein and Meredith, 1991; May, 2005]; thus, the probability is relatively low to evoke tonic responses of deep cells with solely visual stimuli. Nevertheless, both rho and eta cells were observed in the deep layers and, on the whole, the proportion of looming-sensitive neurons was close to that in the superficial layers.

Although looming-sensitive neurons have been studied in a number of vertebrates, it remains to be clarified how the looming responses are evolved and modulated in the central visual system and how the sensory signals are converted into motor commands to trigger collision avoidance reactions. Previous studies suggest that synchronized oscillations in the frog retina are likely to encode essential information for escape behavior [Ishikane et al., 2005] and that a type of approach-sensitive ganglion cells in the mouse retina may serve as elementary building blocks to feed useful information to downstream detectors [Münch et al., 2009]. These findings raise the possibility that the looming responses in the SC originate from the direct inputs of the retina, though the activities of collicular cells are probably modulated by afferent projections from the visual cortex and other brain nuclei and connections within the SC [Wurtz and Albano, 1980; Stein and Meredith, 1991; May, 2005]. On the other hand, looming-sensitive tectal cells may provide the principal inputs to elicit looming responses in the nucleus rotundus and in turn the telencephalic entopallium in the pigeon tectofugal pathway [Wu et al., 2005; Xiao et al., 2006], and homologically, their counterparts in the SC may perform a similar task to convey the necessary signals to the colliculo-pulvinar-cortical pathway in mammals for comprehensive processing of looming information. Concerning visuomotor coordination, part of the looming-sensitive tectal cells project to premotor regions in the tectopontine system and thereby may initiate behavioral responses to impending collision [Wu et al., 2005]. Among the extensive efferent connections of the SC, the ipsilateral descending projections to the brainstem are implicated in the defensive behaviors of animals. In particular, the collicular outputs to the periaqueductal gray and cuneiform nucleus are thought to play an important role in the mediation of avoidance reactions [Dean et al., 1989; Westby et al., 1990; Brandão et al., 1994; Schenberg et al., 2005]. However, direct evidence is still too limited to understand the process of sensorimotor transformation. More thorough investigations to elucidate the neural circuits and mechanisms underlying the visually elicited escape behaviors are awaited.

In summary, the present study has identified two classes of looming-sensitive neurons, rho and eta cells, in the SC of the cat. Despite some differences in cell type and receptive-field organization, these collicular cells are very similar to their counterparts in the pigeon tectofugal pathway and specific movement detector neurons in the locust optic lobe in the response patterns to looming

stimuli and the timing of responses. These results indicate that the collicular neurons are probably involved in signaling impending collision and that the neural computation of optical variables in a collision course might be, at least partly, conservative across species from insects to mammals.

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