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Looming-sensitive responses and receptive field organization of telencephalic neurons in the pigeon

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Abstract

The tectofugal pathway in birds goes from the optic tectum to the telencephalic entopallium via the thalamic nucleus rotundus (nRt). This pathway may be homologous to the colliculo-pulvinar-cortical pathway in mammals. It is known that a population of rotundal neurons in the pigeon can signal impending collision of looming objects with the animal. Here we show by single-unit recording that there exist two groups of looming-sensitive neurons in the entopallium. A tau cell starts firing at a nearly constant time before collision whereas the response onset time of an eta cell is linearly related to the square root of the diameter/velocity ratio of looming objects. These cells are localized in the caudal entopallium. The receptive field (RF) of looming-sensitive cells was mapped on the screen plane but its inhibitory region could not suppress responses to looming objects. It appears that a population of telencephalic cells in pigeons responds to looming objects and their looming responses are not determined by the receptive field organization mapped on the screen plane.

Keywords: Receptive field; Tectofugal pathway; Telencephalon; Time-to-collision; Visual system

1. Introduction

The optic tectum in birds sends a massive output to the thalamic nucleus rotundus (nRt) that in turn projects afferents in a topographic manner to the telencephalic entopallium (formerly named the ectostriatum) [1,15,22,25,27]. This tectofugal pathway is thought to be homologous to the colliculo-pulvinar-cortical pathway in mammals [20,32]. Lesions in the entopallium impaired the visual ability of birds to discriminate brightness and shape [2,17,19,28], stimulus size [18] and avian species [37], but did not impair the ability to discriminate food and non-food, or conspecific pigeons [36]. It appears that the entopallium may be involved in stimulus identification and some visual cognitive functions [3].

Electrophysiological studies indicated that visual neurons in the pigeon nRt are able to compute different optic variables of an object approaching on a collision course towards the animal [33]. It would be attractive to ask whether telencephalic cells respond to looming objects because they receive afferents from nRt. On the other hand, visual neurons in the entopallium are selective for the direction and speed of motion and characterized by complex receptive fields (RFs) [6,13,23]. A recent study revealed a physiological separation of visual motion perception and spatial pattern perception in the pigeon [26]. It was natural to suggest that some motion sensitive cells in the entopallium may respond to looming objects.

It is known that looming sensitive neurons in the pigeon nRt and in the locust visual system, all possess a wide receptive field [11,14,29,31,33], which is naturally thought to be suitable for detecting symmetrical expansion of the edge of a looming object. However, very little is known about the RF organization of these cells in the pigeon. The RF of entopallial cells is not only large in size but also complex in organization [6,13]. We wondered whether the RF organization of entopallial cells might be related to their looming responses.

By using single-unit recoding and computer simulation techniques, the present study was carried out to reveal: (1) whether telencephalic cells respond to an object approaching on a collision course towards the animal and (2) what relationship would exist between the two-dimensional RF organization and

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response properties of looming-sensitive cells in the pigeon forebrain. For histological verification, the recording sites of some looming-sensitive cells were marked with dye.

2. Materials and methods

Forty adult pigeons (*Columba livia*) were used following the guidelines established by the Society for Neuroscience. Each pigeon was anesthetized with urethane (20%, 1 ml/100 g) and then placed in a stereotaxic apparatus. The left forebrain overlying the entopallium was exposed and the dura mater excised. The right eye was kept open and the left covered. A screen of 130° × 140° was positioned 40 cm away from and tangential to the viewing eye. The horizontal meridian of the visual field was rotated by 38° [4,5,9] to meet the pigeon's normal conditions [7].

Three types of visual stimuli were generated by a computer with a graphics-card (Ti 4600, MicroStar) and back-projected with a projector (PG-M20X, Sharp) on the screen: (1) a black square of 1–4° (visual angle) was moved at 32–64°/s along a series of parallel paths covering the whole screen to map the excitatory RF (ERF) and inhibitory RF (IRF) of visual cells [9,35]. The ERF or IRF extents were determined by the equal-rate line whose rate was 20% higher (ERF) or lower (IRF) than the average spontaneous rate with software Adobe Photoshop (7.0, Adobe Systems Inc.), (2) twin-squares (1–4° each) one of which (control) was moved within ERF and the other (test) moved in the region outside ERF. Both stimuli were moved at the same velocity in the same direction with an increasing distance between to explore the IRF extent in the cells that were not spontaneously active [8,13,35] and (3) a soccer ball pattern (diameter = 10–80 cm) with alternating black and white panels of equal areas simulated a looming object, whose overall luminance was unchanged when it was moved towards the animal [33,34]. The luminance of black and white was 0.1 and 6.6 cd/m^2, respectively. After a looming sensitive cell was isolated in the entopallium, the simulated object loomed on a collision course towards the pigeon along a simulated 10–30 m long path at constant velocities of 3–9 m/s. It stopped moving at the moment when it reached the eye (collision) at the time = distance/velocity, and this moment was defined as the time-to-collision (Tc) and set to zero. The onset time of looming responses was calculated relative to Tc based on extracellular recordings or their superimposed histograms.

Visual cells were stereotaxically recorded from the entopallial region according to the pigeon brain atlas [21] with a micropipette (~2 μm tip diameter, ~15 MΩ impedance) filled with 2 M sodium acetate and 2% pontamine skyblue [12,16]. The object stayed on the screen for 5 s to collect spontaneous spikes as controls, and then moved on a collision course towards the viewing eye with an interval of at least 5 s between trials to allow the cell to recover from any adaptation. Neuronal spikes were analyzed by averaging firing rates accumulated in four to six repeats with the computer.

The recording sites of some neurons were marked with dye injected by negative pulses of 10–20 μA in intensity and 0.5 s in duration at 1 Hz for 10–15 min. Under deep anesthesia, the brain was removed from the skull, fixed in 4% paraformaldehyde for 6–12 h and then soaked in 30% sucrose solution in a refrigerator overnight. Frozen sections were cut at 40 μm and counterstained with cresyl violet. Sections were dehydrated and covered for subsequent microscopic observation, and the marked sites were localized.

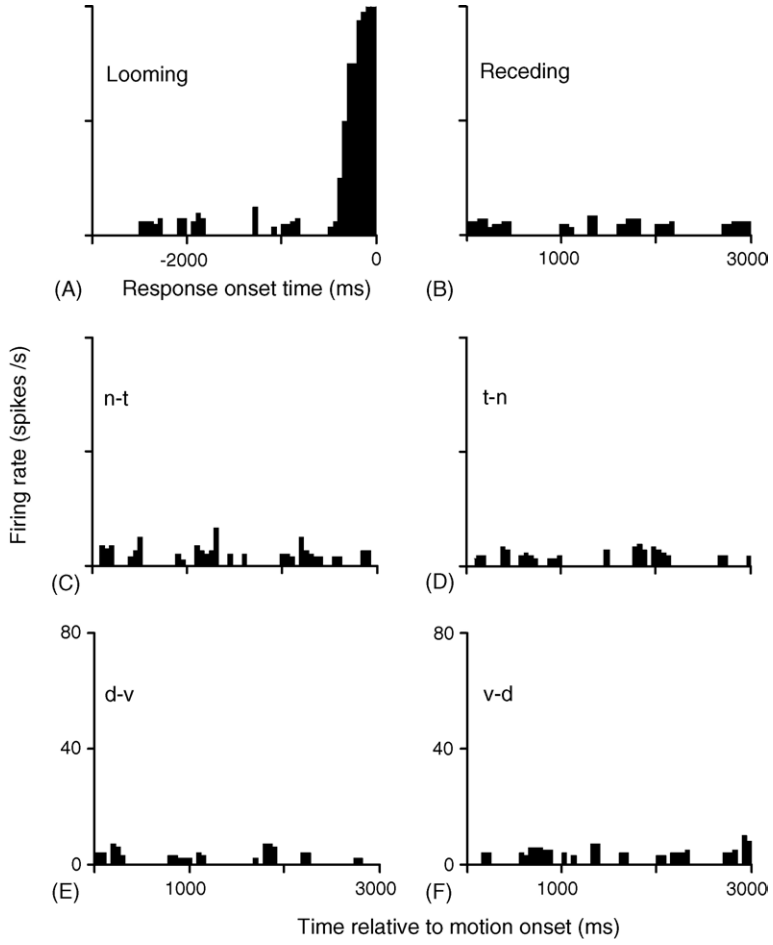

Fig. 1. Directional sensitivity of an entopallial cell to object motion. This cell discharged in a specific pattern to an object of 30 cm in diameter looming at 4 m/s towards the pigeon eye (A) but produced no or little responses to an object receding away from the eye (B) or to motion on the screen plane in the nasotemporal (C, n-t) and temporonasal (D, t-n) directions or the dorsoventral (E, d-v) and ventrodorsal (F, v-d) directions. Three repeats were superimposed and time bin = 50 ms in histograms.

3. Results

A total of 381 entopallial neurons were isolated by their visual responses. Most of them (86%) responded only to motion of a small stimulus (1–4°) on the screen plane but not to looming motion in depth and were thus omitted from further analysis. Fifty-five others (14%) responded with a specific firing pattern to an object approaching on a collision course towards the viewing eye (Fig. 1A). However, they produced no or little responses to an object receding away from the eye or to motion on the screen plane (Fig. 1(B–F)). According to the physiological criteria used for identifying different classes of looming-sensitive cells in the pigeon nRt [33], these entopallial cells were classified into tau cells (13/55 = 24%) and eta cells (42/55 = 76%).

Visual firing in entopallial tau cells began at an approximately constant time before collision and grew exponentially during approach of a simulated object towards the eye, and finally peaked at the moment when collision of the object with the animal occurred (Fig. 2(A–C)). This firing pattern could be described by a formula $\tau(t) = \theta(t)/\theta'(t)$, where $\theta(t)$ is the angle subtended by the approaching object and $\theta'(t)$ is the rate at which the angle expands at a given time t. It appears that the response onset time of tau cells is independent of the size and velocity of looming objects. The response onset time of tau cells averaged 475 ± 160 ms (mean $\pm$ S.D., $n = 13$) (Fig. 3A).

In response to a looming object, the firing rate of an eta cell increased to a peak and then dropped off until collision occurred. The onset time of their responses and peaked firing was earlier for larger or slower-looming objects (Fig. 2(D–F)). This firing pattern could be described by a formula $\eta(t) = C \times \theta'(t)/e^{\alpha\theta(t)}$, where $\theta(t)$ is the angular size of the approaching object and $\theta'(t)$ is the change rate of $\theta(t)$, and C and α are constants for a given neuron. The response onset time of eta cells was linearly related to the square root of the diameter/velocity ratio of looming objects (Fig. 3B).

It appears that looming sensitive cells in the entopallium were distributed in two distinct groups, because the response onset time in a tau cell was approximately constant whereas in an eta cell it varied depending on the diameter and velocity of looming objects, and because firing rate in tau cells peaked at the

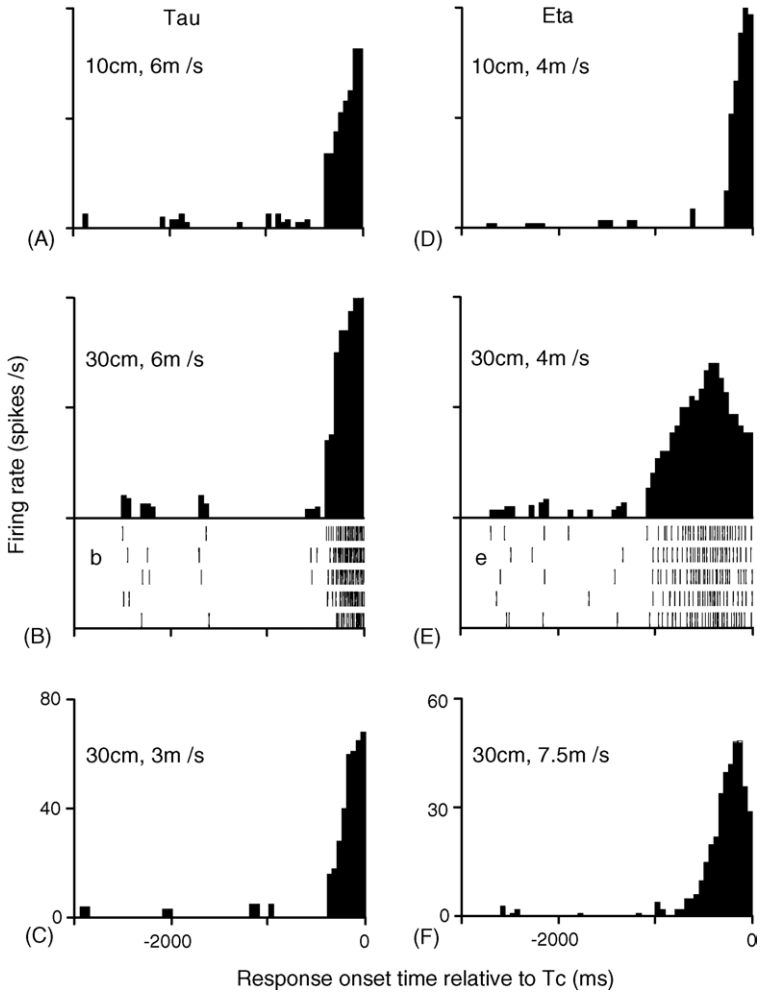

Fig. 2. Response histograms of two entopallial cells to looming objects. The tau cell (A–C) started firing at an approximately constant time before collision (time-to-collision, Tc = 0) regardless of the size (10–30 cm in diameter) and velocity (3–6 m/s) of looming objects, and the eta cell (D–F) started earlier firing in response to larger and/or slower-moving objects. As examples, histograms B and E were superimposed from firing spikes that were distributed in rasters b and e, respectively. Five repeats were superimposed, time bin = 50 ms.

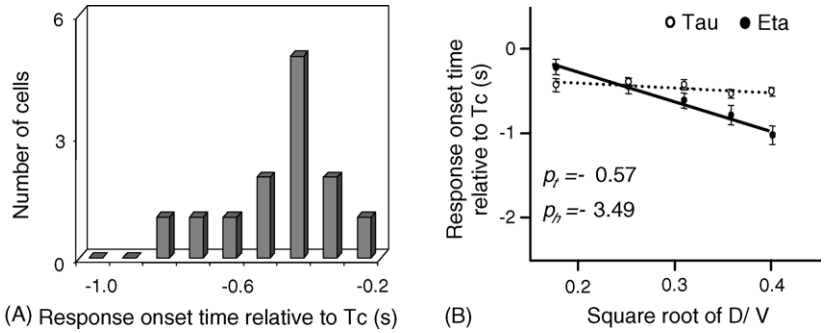

Fig. 3. Statistics of the response onset time in looming-sensitive cells. Tau cells initiated firing at averaged 480 ms before collision (A, B, $n = 13$). The response onset time of eta cells is linearly related to the square root of the diameter/velocity ratio of looming objects (B). The slopes (p) of the linearly fitted lines are shown with suffixes for tau (τ) and eta (η) cells. Five diameter/velocity ratios were examined for each of five cells whose response onset time was averaged in five repeats. Negative values indicate the time before collision (time-to-collision, Tc = 0). Error bars represent ±S.E.M.

time-to-collision whereas in eta cells it grew to a peak and then dropped off until collision. Their firing behaviors were examined with objects that were 20 and 40 cm in diameter and moved at 2 and 4 m/s on a collision course towards the animal. The standard deviation of the response onset time was calculated for each individual cell. Meanwhile, percentage of drop-off in firing rate was calculated by a formula $(f_p - f_{tc})/(f_p - f_s)$ where f_p, f_{tc} and f_s are the peak rate, firing rate at the time-to-collision and spontaneous rate, respectively. Fig. 4 shows two distinct groups of looming sensitive cells (13 tau and 42 eta cells).

The receptive field of these cells was mapped on the screen plane and grouped into three types. Nine of the 13 tau cells (69%) possessed a single ERF (type I) that averaged $80^\circ \times 120^\circ$ in size (Fig. 5A) and four others (31%) had juxtaposed ERF and IRF (type II), which averaged $60^\circ \times 100^\circ$ and $30^\circ \times 60^\circ$, respectively (Fig. 5E). The receptive field in all 42 eta cells examined had a concentrically organized IRF ($30^\circ \times 50^\circ$) and ERF ($110^\circ \times 150^\circ$) (type III) (Fig. 5I). For comparison, the RF in some cells unresponsive to looming objects was mapped and

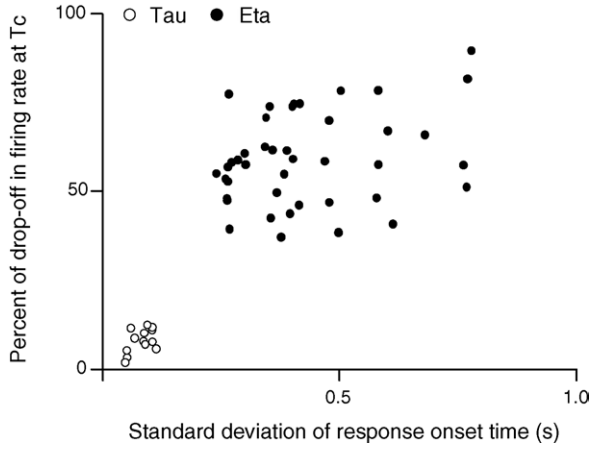

Fig. 4. Looming-sensitive cells are distributed in two distinct groups (13 tau and 42 eta cells). Ordinate represents percent of drop-off in firing rate calculated by a formula $(f_p - f_{tc})/(f_p - f_s)$ where f_p, f_{tc} and f_s are respectively the peak rate, rate at the time-to-collision (Tc) and spontaneous rate, and abscissa standard deviation of the response onset time relative to Tc, which was calculated from the responses to objects of 20 and 40 cm in diameter and moving at 2 and 4 m/s in four repeats.

it consisted of two separate ERFs as reported in a previous study [13]. In the looming sensitive cells, motion of a small stimulus (1–4°) on the screen plane evoked sustained excitatory responses in ERF and inhibitory responses in IRF. However, an object approaching on a collision course towards the viewing eye elicited a specific firing pattern before collision. For example, when a small or large object was looming at 6 m/s towards the animal, the cell shown in Fig. 5(E–H) produced identical responses even though the large object expanded across the IRF. In both cases, the response onset time and peak rate of this cell were 400 ms and 40 spikes/s, respectively; the average rate was 35.3 spikes/s for the small object and 35.4 spikes/s for the large object. However, motion of a small object in the IRF on the screen suppressed visual responses of this cell to motion in the ERF. Similarly, visual responses of an eta cell were inhibited by planar motion in the IRF, but this IRF did not influence the response patterns of the cell to small and large looming objects (Fig. 5(I–L)).

The recording sites of 4 tau cells and 16 eta cells were marked with dye and they were all localized in the entopallial region consisting of the entopallium and the perientopallium (formerly known as the periectostriatal belt) (Fig. 6). Because the anterior–posterior levels of the entopallium ranged from AP11.25 to AP8.25 according to the pigeon brain atlas [21], the marked sites localized at AP9.25–8.75 were in the caudal entopallium. Our recordings were within the entopallial region as verified histologically.

4. Discussion

The main finding of the present study is that a population of visual neurons in the pigeon's forebrain responds to an object approaching on a collision course towards the animal. These looming sensitive cells are classified into tau and eta cells according to their different response properties to looming objects. It appears that their visual responses are evoked by symmetrical expansion of a looming object but not by apparently lateral motion of the edge of the looming object on the screen plane for three reasons. First, all neurons respond to movements of small objects in the screen plane [13] but not to larger edges, whereas only 14% of them respond to motion of a looming object towards

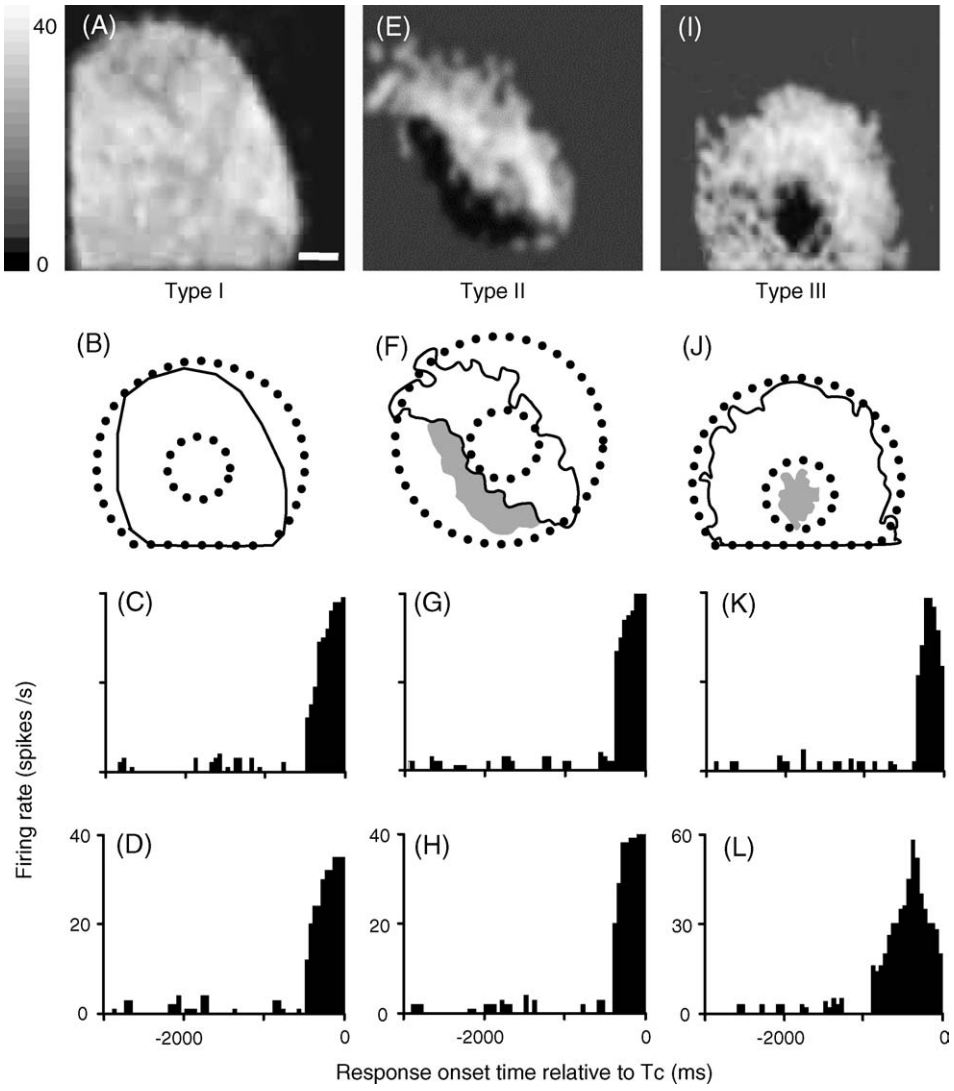

Fig. 5. Receptive field organization mapped with computer and firing patterns in two classes of looming-sensitive neurons. A single ERF (A, type I) and juxtaposed ERF and IRF (E, type II) were computer-mapped based on firing activity in two tau cells, and concentric IRF and ERF (I, type III) in an eta cell. Their contours are respectively depicted in the second row (B, F and J) showing the locations of the edges (dotted circles) of small and large looming objects at the time-to-collision (Tc = 0). Histograms of firing rates evoked by the small and large objects are shown in the third (C, G and K) and fourth (D, H and L) rows, respectively. Horizontal dotted lines (B and J) denote the limits of large objects by the screen bottom edge. Gray scale: 0–40 spikes/s. Scale bar: 20° in A and E, 30° in I. Four repeats were superimposed and time bin = 50 ms in histograms.

the animal. It is clear that expansion but not apparently lateral motion of the edge of a looming object evokes visual responses in looming sensitive cells. Second, the IRF of a looming sensitive cell shows inhibitory responses to motion of an object on the screen but not to motion of a looming object in depth. Third, firing of the looming sensitive cells to motion of an object on the screen is sustained whereas that evoked by a looming object is characterized by a specific firing pattern in which firing rate steadily increases and peaks approximately at collision. Neuronal mechanisms underlying directional selectivity to motion in depth have been extensively studied in the locust visual system, and it is found that looming detection is implemented by integration computation of excitatory and inhibitory inputs to looming sensitive cells [10,24,30,31].

Though it is known that there exist three types of RF organization in the pigeon entopallium [13], the present study is the first to map the RF organization of looming sensitive cells. An additional type of RF organization is found in the current study, which is similar to the side-by-side arrangement of ERF and IRF in simple cells in the mammalian cortex. It is generally thought that looming sensitive neurons possess a wide RF so that they are able to detect symmetrical expansion of a looming object. We mapped the RF organization of looming sensitive cells with a small object and found that a tau cell is characterized by a single ERF or juxtaposed ERF and IRF, and an eta cell by concentric IRF and ERF. It appears that classic RF is defined only for stimulation on the *X–Y* plane but not for stimulation in the *Z*-direction. In particular, looming sensitive cells in the entopallium generally respond to a small object moving on the screen plane as shown in a previous study [13], and they specifically respond to looming objects of small and large sizes. It is quite puzzling that looming responses do not depend on the classic

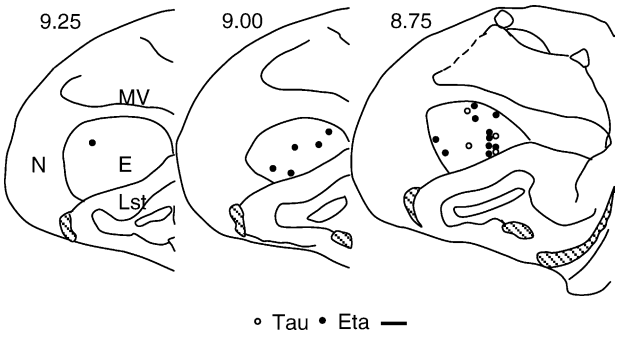

Fig. 6. Topological distribution of the recording sites of 4 tau cells and 16 eta cells marked with dye in the entopallial region. This region consists of the entopallium and perientopallium both of which are indistinguishable from each other in cresyl violet stained sections. Tau and eta cells are localized in the caudal entopallium (E). Other abbreviations: Lst, lateral striatum; MV, mesopallium ventrale; N, nidopallium. Numerals at the top represent the anterior–posterior levels of the pigeon brain atlas. Bar = 1 mm.

RF organization on one hand but the RF organization seems somehow related to the classification of looming-sensitive cells on the other hand. Under natural conditions, looming sensitive cells detect a real stimulus moving along the *Z*-axis and their receptive fields would occupy a three-dimensional space in the visual field. It is likely that two-dimensional RF organization might be related to three-dimensional RF organization in some way that could not be mapped in the present study.

Anatomical studies indicated that the rostral nRt projects to the rostral entopallium whereas the caudal nRt to the caudal entopallium [1,25]. Looming-sensitive cells were found in the dorsal and caudal nRt [33,34] and they may send axons to the caudal entopallium. A recent study revealed a physiological separation of visual motion perception in the caudal entopallium and spatial pattern perception in the rostral entopallium in the pigeon [26]. The recording sites marked in the present study show that they are all localized in the caudal entopallium. It suggests that entopallial tau and eta cells may receive inputs from tau and eta cells in the nRt, respectively. Rho cells were found in the nRt but not the entopallium, probably because this computation is already executed in tau and eta cells. In fact, the best known looming sensitive neurons in the locust visual system only execute eta computation and they start firing when impending collision is 200–400 ms away [31]. This response onset time approximates that of entopallial tau cells (480 ms). The fact that the response onset time of entopallial tau cells is smaller than that of rotundal tau cells [33,34] is conceivable because looming information is transferred from the nRt to entopallium.

The present study provides electrophysiological evidence that entopallial neurons in the pigeon can signal impending collision of a looming object with the animal. It appears that these visual cells may execute dual functions: one is to detect a small target moving on the *X*–*Y* plane and the other is to signal impending collision of an object looming in the *Z*-direction. This is the case with the locust looming sensitive cells that are highly sensitive to an object approaching towards the animal [11,14,29,31] but also respond to small objects moving in their receptive fields [14]. In view of the fact that the telencephalic entopallium in birds may be homologous to the extrastriate cortex in mammals, it would be interesting and attractive to find out whether some cortical neurons also respond to looming stimuli.

Acknowledgments

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