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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.

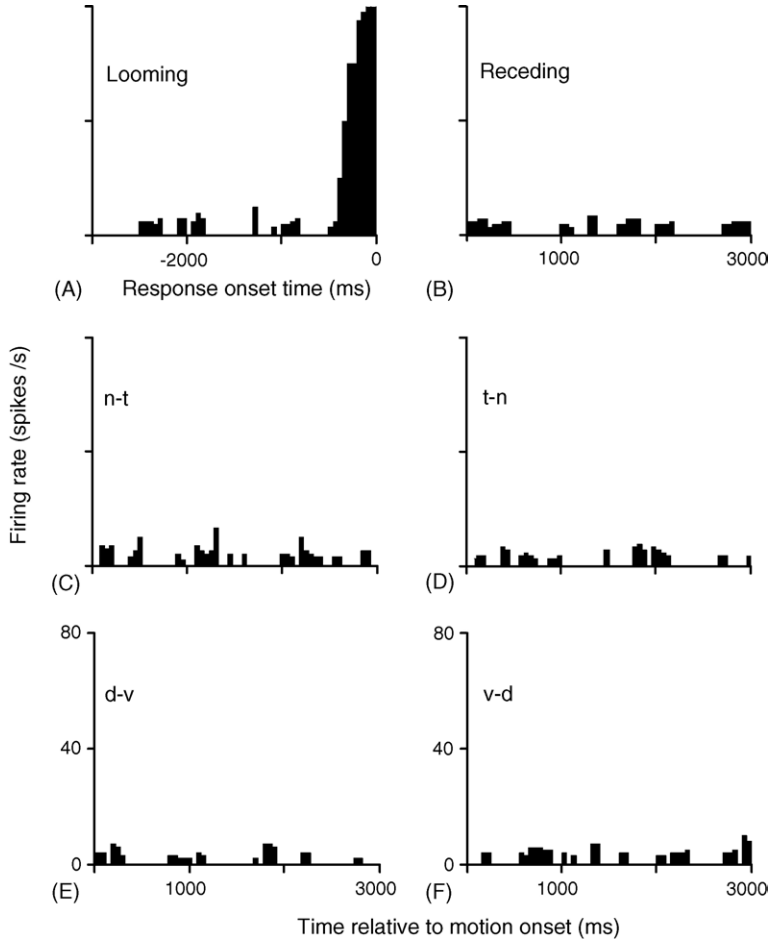


Fig. 1. Directional sensitivity of an entopallial cell to object motion. This cell discharged in a specific pattern to an object of 30 cm in diameter looming at 4 m/s towards the pigeon eye (A) but produced no or little responses to an object receding away from the eye (B) or to motion on the screen 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.