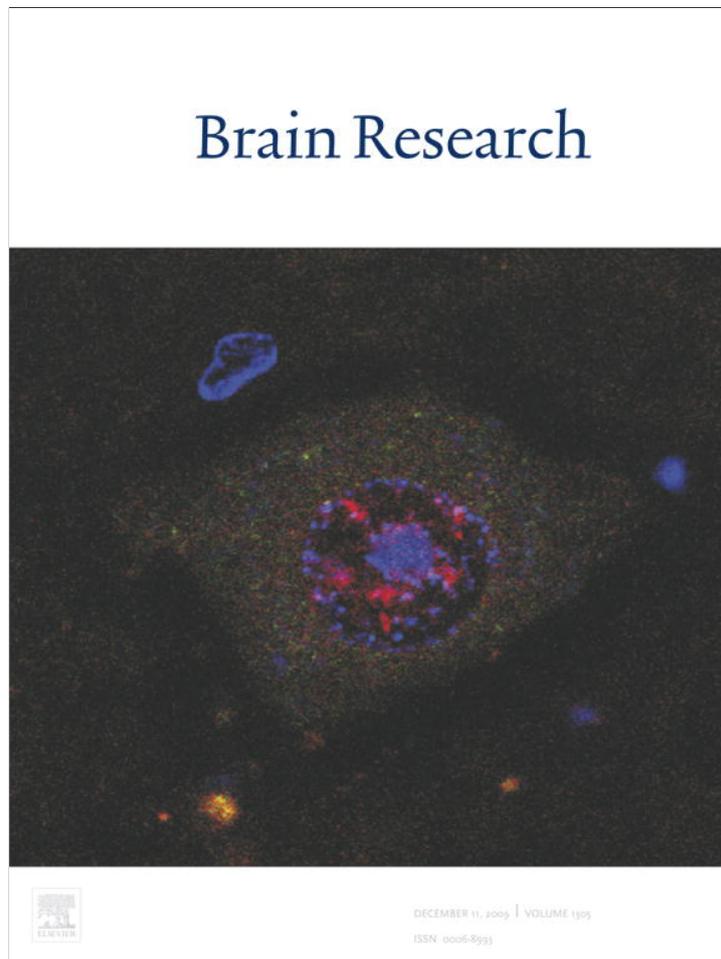


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Research Report

Looming responses of telencephalic neurons in the pigeon are modulated by optic flow

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ABSTRACT

The movement of animals through space filled with various objects requires the interaction between neuronal mechanisms specialized for processing local object motion and those specialized for processing optic flow generated by self-motion of the animal. In the avian brain, visual nuclei in the tectofugal pathway are primarily involved in the detection of object motion. By contrast, the nucleus of the basal optic root (nBOR) and the pretectal nucleus lentiformis mesencephali (nLM) are dedicated to the analysis of optic flow. But little is known about how these two systems interact. Using single-unit recording in the entopallium of the tectofugal pathway, we show that some neurons appeared to be integrating visual information of looming objects and whole-field motion simulating optic flow. They specifically responded to looming objects, but their looming responses were modulated by optic flow. Optic flow in the nasotemporal direction, typically produced by the forward movement of the bird, only mildly inhibited the looming responses. Furthermore, these neurons started firing later than when the looming object was presented against a stationary background. However, optic flow in other directions, especially the temporonasal direction, strongly inhibited their looming responses. Previous studies have implicated looming-sensitive neurons in predator avoidance behavior and these results suggest that a bird in motion may need less time to initiate an avoidance response to an approaching object.

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1. Introduction

Information about time-to-collision (TTC) has important consequences for the survival of countless species and for their interactions with both inanimate and animate objects in the natural environment. When animals move through space filled with various objects, their abilities to detect objects approaching directly toward them are critical for avoiding predatory attacks or achieving desirable interceptions. Previously, we have argued that there may be two populations of looming neurons that compute TTC (Frost and Sun, 2004). One set of neurons computes TTC with approaching objects and

precipitates an avoidance or capture response. Another set of neurons computes TTC with stationary objects and initiates a steering action relative to these objects. Consequently, one might expect an interaction between visual mechanisms specialized for processing object motion where this motion is a feature of the object itself, and those for processing optic flow produced by the animal's own locomotion.

The perception of looming objects and optic flow are processed separately by different nuclei in the avian brain (Fig. 1). Electrophysiological experiments have indicated that the nucleus of the basal optic root (nBOR) of the accessory optic system and the nucleus lentiformis mesencephali (nLM)

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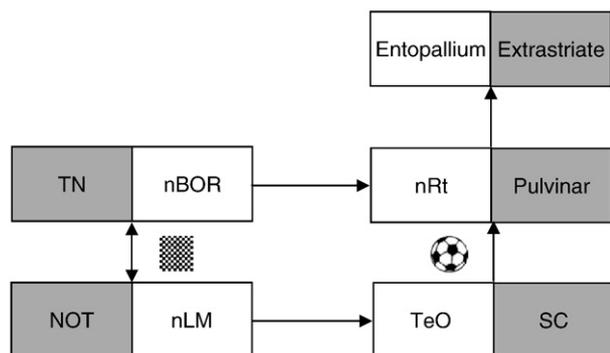


Fig. 1 – Visual structures and pathway are comparable in birds and mammals. Paired squares represent similar structures in birds (white) and mammals (gray). Arrows symbolize neural projections between different nuclei. In birds, the tectofugal pathway goes from the optic tectum (TeO) to the nucleus rotundus (nRt) and then to the telencephalic entopallium. These structures might be homologous to the superior colliculus (SC), the pulvinar and the extrastriate cortex in mammals. The nBOR and nLM are comparable to the terminal nuclei (TN) of the accessory optic tract and the nucleus of the optic tract (NOT) in mammals. Stimulus patterns described in the text are also shown (soccer ball and whole-field motion).

primarily process optic flow (Fu et al., 1998; Wylie and Frost, 1999; Frost and Wylie, 2000). Nuclei of the tectofugal pathway are specialized for the analysis of object motion (Frost et al., 1990). The optic tectum (TeO) projects to the thalamic nucleus rotundus (nRt) where there is a topographic segregation of function (Wang et al., 1993). In turn, nRt projects to the telencephalic entopallium (formerly called ectostriatum) where this segregation is preserved (Karten and Hodos, 1970; Benowitz and Karten, 1976; Hellmann and Güntürkün, 2001; Laverghetta and Shimizu, 2003). It has been suggested that this ascending visual pathway is homologous to the colliculo-pulvinar-cortical pathway in mammals (Shimizu and Bowers, 1999). In the avian brain, looming-sensitive neurons specifically responding to an object approaching toward the viewing eye on a direct collision course have been found only in the tectofugal pathway (TeO: Wu et al., 2005; nRt: Wang and Frost, 1992; Sun and Frost, 1998; entopallium: Xiao et al., 2006).

However, anatomical and physiological studies have revealed that some visual neurons detecting optic flow project onto the telencephalic entopallium indirectly via other brain regions. In the avian brain, the entopallium appears to be the only thalamic recipient area in contrast to multiple thalamic recipient areas of the extrastriate cortex in mammals. Many anatomical experiments indicate that the caudal part of entopallium is the putative avian equivalent of the medial temporal area/the medial superior temporal area (MT/MST) in mammals (Karten and Shimizu, 1989; Shimizu and Karten 1991, 1993; Butler and Hodos, 1996; Shimizu and Bowers, 1999). Visual pathways by which the information of optic flow might reach the entopallium are diverse. It could arise from the projection from nLM to TeO (Gamlin and Cohen, 1988), and

TeO might send this information to nRt and thence to the entopallium. Another possible indirect route to the entopallium is a projection from nBOR to nRt (Wang et al., 2000; Diekamp et al., 2001) although this pathway is controversial (Brecha et al., 1980).

Most entopallium neurons are direction-selective neurons which specifically respond to local motion in the preferred direction but not to whole-field motion (Frost et al., 1990; Bischof and Watanabe, 1997; Gu et al., 2002). Looming-sensitive neurons are all located in the caudal part of the entopallium (Xiao et al., 2006). They receive a topographical projection from the caudal part of nRt (Benowitz and Karten, 1976; Laverghetta and Shimizu, 2003), where looming responses were first described (Wang and Frost, 1992). It is known that looming-sensitive neurons in the entopallium consist of two distinct groups: tau neurons and eta neurons. The response onset time of tau neurons is approximately constant, but for eta neurons, it varies with the diameter and velocity of looming objects (Wang and Frost, 1992; Sun and Frost, 1998; Wu et al., 2005; Xiao et al., 2006).

Electrophysiological studies have shown that entopallium neurons do not respond in an excitatory manner to whole-field motion (Gu et al., 2002; Xiao et al., 2006). However, it is possible that the whole-field motion could modulate in some way looming responses of entopallium neurons. By using single-unit recording and computer simulation techniques, the present study was carried out to determine whether looming-sensitive neurons in the entopallium were modulated by different directions of optic flow.

2. Results

A total of 258 entopallium neurons were isolated based on their visual responses to provided stimuli. Most of them (79%) responded only to the two-dimensional motion of a small stimulus (1° – 4°) moving in different directions on the tangent screen plane, but not to the motion of looming object in depth. Therefore, these neurons were omitted from the further analysis. Fifty-four neurons (21%) responded with a specific firing pattern to the soccer ball simulating an object approaching toward the viewing eye on a collision course. But no responses were recorded when the soccer ball receded away from the viewing eye or moved in different directions on the screen plane. According to the physiological criteria used for identifying different classes of looming-sensitive neurons, these entopallium neurons were classified into tau neurons (17/54) and eta neurons (37/54). No rho neurons were found in this sample.

2.1. Effects of optic flow on looming responses of tau neurons

Neural responses of a typical tau neuron were shown in Fig. 2A–L. In response to a looming object against a stationary background, the response onset time of this neuron was approximately constant (0.48 s before collision) irrespective of the diameter and velocity of looming object (Fig. 2A–D). When the background moved on the screen plane in eight directions with 45° apart, no visual responses were recorded to the

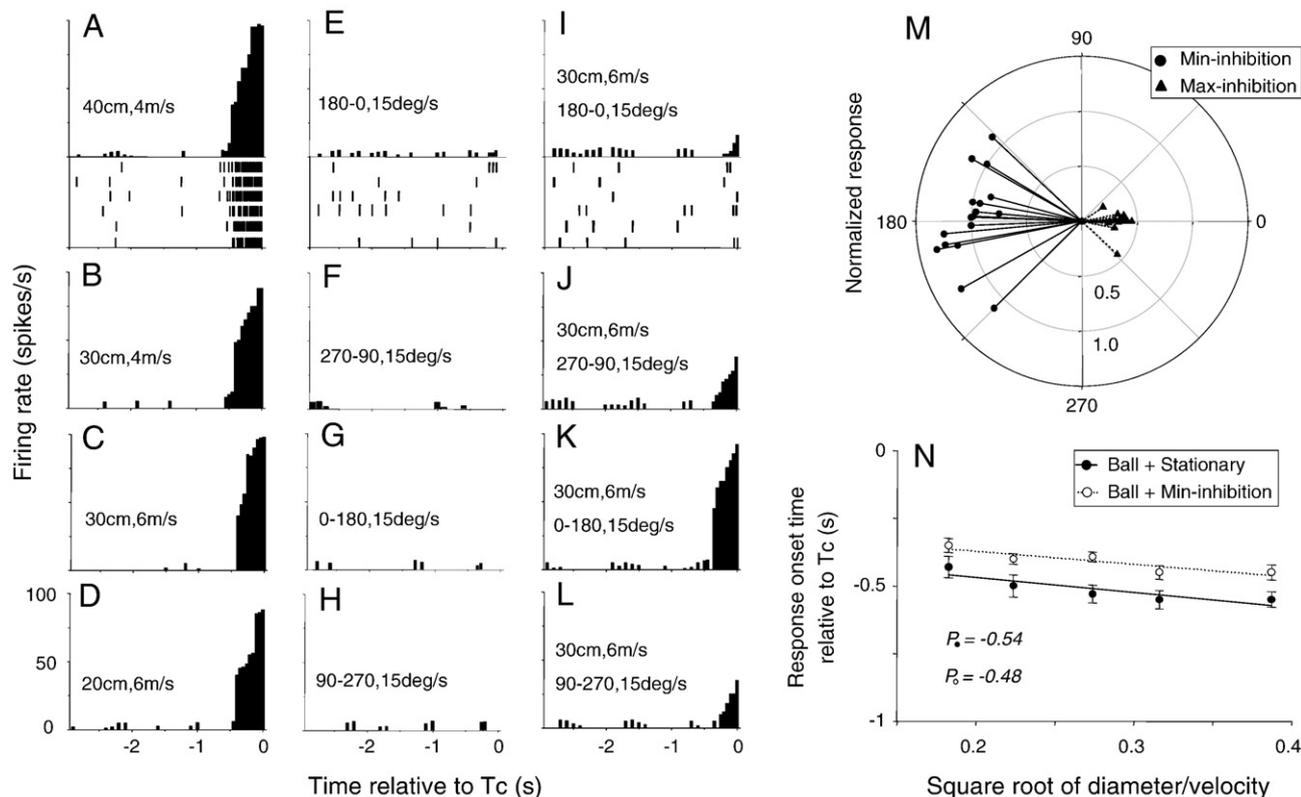


Fig. 2 – Effects of optic flow on tau neurons. Neural responses of a typical tau neuron are shown in panels A–L. This neuron started firing 0.48 s before collision (collision time: $T_c=0$) regardless of the diameter (10–60 cm) or velocity (2–7.5m/s) of looming object against a stationary background (A–D). No neural responses were recorded when the background was presented alone and moved in any two-dimensional direction (E–H). Its looming responses were modulated by different directions of background motion (I–L). Histograms A, E and I were superimposed by displayed spike rasters. The maximal/minimal inhibitory direction and strength of 17 tau neurons were represented by the orientation and length of a solid/dotted line in polar coordinates (M). Response patterns of tau neurons to looming objects were preserved when the background moved in the minimal inhibitory direction (N). Slopes (p) of fitted lines were shown. The average onset time was changed from 0.51 ± 0.05 s (mean \pm S.D., $n = 17$) against a stationary background to 0.41 ± 0.04 s (mean \pm S.D., $n = 17$) when the background moved in the minimal inhibitory direction. Negative values indicate the time before collision. Time bin was 0.05 s. Error bars represent \pm S.E.M.

whole-field background motion simulating different directions of optic flow (Fig. 2E–H). But if the background also moved when the object was approaching toward the viewing eye, looming responses of this neuron were differentially modulated by the direction of background motion (Fig. 2I–L). It appeared that looming responses were mildly inhibited by the background motion in the nasotemporal direction (0° – 180° , Fig. 2K). When the background moved in the opposite direction (180° – 0° , Fig. 2I), looming responses of this neuron were almost completely inhibited.

Looming responses of 17 tau neurons significantly depended on the direction of whole-field motion ($F_{8, 128}=21.01$, $p < 0.0001$, one-way ANOVA). The maximal and minimal inhibitory direction and strength for looming responses of all tau neurons were plotted in polar coordinates (Fig. 2M). In general, the minimal inhibitory direction for tau neurons ranged between 135° and 225° . When the background moved in this direction, it minimally reduced peak responses of each neuron to looming objects and the overall response patterns were still preserved (Fig. 2N). Their average response onset time shifted 0.1 s toward the collision time compared to that

produced by a single looming object presented against a stationary background.

2.2. Effects of optic flow on looming responses of eta neurons

Neural responses of a typical eta neuron were shown in Fig. 3A–L. In response to the single looming object against a stationary background, the response onset time of this neuron varied with the diameter and velocity of looming object (Fig. 3A–D). It had no responses to any whole-field background motion in different directions on the screen plane (Fig. 3E–H). Looming responses of this neuron were also less inhibited when the background moved in the nasotemporal direction (0° – 180° , Fig. 3K) compared to other directions. However, the background motion in the temporonasal direction (180° – 0° , Fig. 3I) mostly inhibited its looming responses.

Looming responses of 37 eta neurons significantly depended on the direction of whole-field motion ($F_{8, 288}=15.3$, $p < 0.0001$, one-way ANOVA). The maximal and minimal

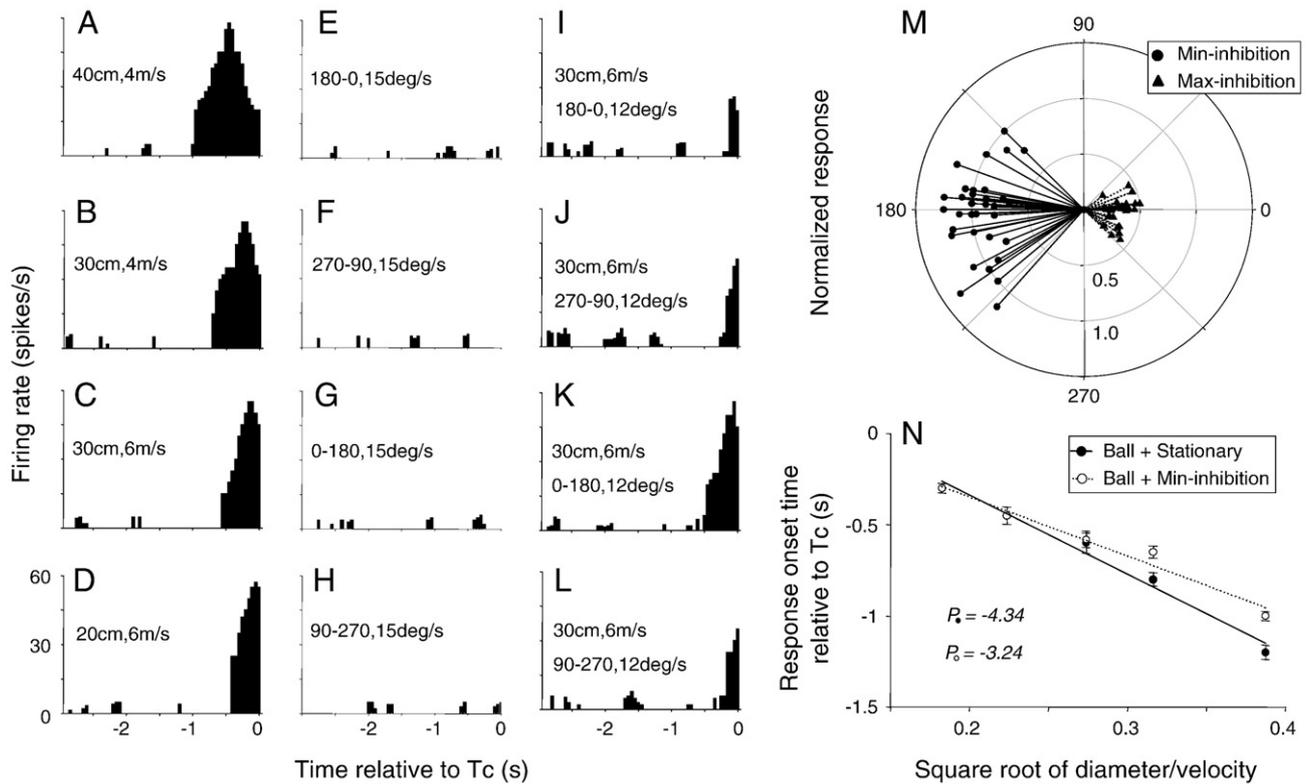


Fig. 3 – Effects of optic flow on eta neurons. Neural responses of a typical eta neuron are shown in panels A–L. The response onset time of this neuron depended on the diameter and velocity of looming object presented against a stationary background (A–D). No neuronal responses were recorded when the background was presented alone and moved in any two-dimensional direction (E–H). Looming responses of this neuron were less inhibited when the background moved in the nasotemporal direction (K: 0°–180°). The maximal/minimal inhibitory direction and strength of 37 eta neurons were represented by the orientation and length of a solid/dotted line in polar coordinates (M). The response onset time of eta neurons was linearly related to the square root of diameter/velocity of looming object and response patterns were preserved when the background moved in the minimal inhibitory direction (N). Slopes (p) of fitted lines were shown. Negative values indicate the time before collision. The time bin was 0.05 s. Error bars represent \pm S.E.M. Collision time: Tc=0.

inhibitory direction and strength for looming responses of each neuron were all plotted in polar coordinates (Fig. 3M). The response onset time of eta neurons was linearly related to the square root of the diameter/velocity of looming object. When the background moved in the minimal inhibitory direction, looming response patterns of eta neurons were preserved (Fig. 3N).

Looming responses of 54 neurons were modulated more or less by whole-field motion. Furthermore, their looming responses were significantly correlated with the direction of optic flow simulated by the whole-field background motion in the present experiment. A minimal effect was recorded when the background moved in the nasotemporal direction (0°–180°), which would result from the animal translating forward in the natural environment (Figs. 2M and 3M). In this direction, response patterns of these neurons were preserved (Figs. 2N and 3N).

2.3. Recording location

Recording sites of 5 tau neurons and 8 eta neurons were marked with the dye and they were all localized in the entopallium. According to the pigeon brain atlas, the anterior-

posterior level of the entopallium ranged from A11.25 to A8.25. Marked sites were all located at A9.25–A8.25 in the caudal part of the entopallium (Fig. 4).

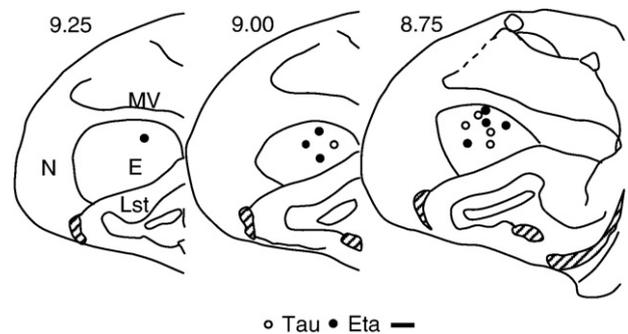


Fig. 4 – Topological distribution of recording sites of 5 tau neurons and 8 eta neurons marked with dye in the telencephalic entopallium. Tau and eta neurons were all located in the caudal entopallium. Lst, the lateral striatum; MV, the mesopallium ventrale; N, the nidopallium. Numbers at the top represent the anterior–posterior levels of the pigeon brain atlas. Scale bar=1 mm.

3. Discussion

The present study provides the electrophysiological evidence that looming responses of entopallium neurons are modulated by optic flow produced by the movement of bird through its visual environment. In addition, their looming responses are significantly correlated with the direction of optic flow. In the natural environment, pigeons always walk and fly forward. Therefore, images of stationary objects would always move in the nasotemporal direction across the visual field of animals. We found that looming responses of entopallium neurons were only mildly inhibited by the optic flow moving in this direction. However, under this condition, these neurons started firing later than when a single looming object was presented against a stationary patterned background. Response patterns of these neurons were also preserved. By contrast, optic flow moving in the opposite direction (temporo-nasal direction) dramatically inhibited their looming responses. Thus, these two types of visual information appear to be integrated at the level of the caudal entopallium, and then are subsequently sent to the nidopallium caudolaterale (NCL) and the nidopallium intermedium laterale (NIL). Many researchers have suggested that this pathway (tectal layer 13 - caudal nRt - caudal telencephalic entopallium - NIL and NCL) is comparable to the dorsal stream in mammals which is proposed to be involved in the guidance of actions and recognizing where objects are in space (Shimizu and Bowers, 1999). The combined information about the looming object and optic flow would facilitate the animal's detection and analysis for the movement of approaching objects in the natural environment and possibly also be involved in selecting the appropriate action.

It is unknown whether this integration of visual information of looming objects and optic flow occurs in the entopallium itself or is fully or partially accomplished in TeO or nRt. Electrophysiological experiments suggest that TeO may play an important role in signaling incoming collision, and initiate avoidance responses through the tectopontine system (Wu et al., 2005). Since there is a weak projection from nLM to TeO (Gamlin and Cohen, 1988), it is possible that tectal looming-sensitive neurons are also modulated by whole-field motion. Further electrophysiological research is required to see whether the modulation by whole-field motion is accomplished either in TeO or nRt before being transmitted to the entopallium.

Although there are no direct projections from nBOR and nLM to the entopallium, indirect connections via nRt and TeO may convey optic flow information to these looming-sensitive neurons. Alternatively, it could be argued that the nucleus isthmi pars magnocellularis (Imc) could send optic flow information to the looming detecting system because Imc receives input from TeO and makes diffuse projections back to TeO (Wang et al., 2004; Marin et al., 2007). However, electrophysiological experiments clearly indicate that Imc neurons do not respond to whole-field motion, which makes this an unlikely possibility (Wang and Frost 1991; Li et al., 2007).

It is known that the detection of collision time would be a valuable strategy for the animal's survival because it provides accurate predictions of an approaching object with unknown

size and velocity. Two types of looming-sensitive neurons were recorded in the entopallium: tau neurons and eta neurons. It is noteworthy that no rho neurons were recorded in the present study which confirms a previous report (Xiao et al., 2006). It suggests that the computations of both tau and eta functions must have been done by this stage because both have rho as a term in their equations (Sun and Frost, 1998). When optic flow in the nasotemporal direction was presented, looming response patterns of tau neurons were preserved. It means that tau neurons still detect TTC and could trigger a motor action for impending collision (Fig. 2N). However, the average response onset time of tau neurons shifted closer toward the collision time than when a looming object was presented against a stationary background. This could mean that birds in motion need less time to initiate suitable motor responses to avoid approaching objects. Indeed, this could be advantageous for them because it would leave less time for the predator to counter-respond to the evasive maneuver of birds. For eta neurons, one of their key features is that the response onset time is linearly related to the square root of diameter/velocity of looming object. For different sized objects moving at the same speed, larger objects would make these neurons fire earlier. This feature might have certain evolutionary benefits for prey like pigeons because larger objects often represent a greater danger or reflect a higher probability that this looming object is a predator. When optic flow in the nasotemporal direction was presented, response patterns of eta neurons were preserved (Fig. 3N). This could mean that an earlier urgent signal might be sent out by eta neurons to elicit quick defensive actions when large objects are approaching toward the bird in motion. Therefore, the combination of the earlier warning signal from eta neurons and the accurate avoidance behavior triggered by tau neurons might achieve successful survival in the natural environment. Recent studies on monkeys also show the multisensory integration of auditory and visual looming signals in the cortex (Maier et al., 2004, 2008). It seems that different animals use similar strategies to combine different modalities of sensory information to successfully avoid some incoming dangerous objects on a collision course.

Although looming responses of entopallium neurons depended on the direction of optic flow, no excitatory responses were recorded when the looming object was combined with a looming background and moved toward the viewing eye. It seems that looming responses of entopallium neurons were completely inhibited by this configuration of stimuli which simulates the self-motion of bird toward stationary objects, rather than moving objects approaching the bird. Similar responses are also found for looming-sensitive neurons in nRt (Sun and Frost, 1998). Frost and Sun (2004) suggested that, in the natural environment, the former stimuli are produced by self-motion of birds toward stationary surfaces, which will produce approaching, steering and landing behavior of birds. By contrast, a single looming object against a stationary background would be produced by an approaching object and trigger an avoidance response since it might represent a potential predator. Recent electrophysiological experiment (Liu et al., 2008) shows that some neurons in the nucleus opticus principalis thalami (nOPT) of the thalamofugal pathway in the pigeon do not discharge response

spikes until a large approaching surface reaches a threshold distance from the viewing eye. These distance-to-collision neurons seem to be specifically involved in this self-motion expansion pattern produced by a bird approaching toward a large surface on a direct collision course. However, no such distance-to-collision neurons are found in nuclei of the tectofugal pathway in the pigeon. It suggests that the visual information of looming objects appears to be only processed in the tectofugal pathway and the thalamofugal pathway is involved in detecting the self-motion of animals toward large surfaces.

4. Experimental procedures

Seventeen adult pigeons (*Columba livia*) were used following the guidelines established by Canadian Council on Animal Care and Queen's University Animal Care Committee.

4.1. Surgery and extracellular recording

Each pigeon was anesthetized with urethane (20%, 1 ml/100 g) and then placed in a stereotaxic apparatus. Its body temperature was maintained at 41 °C. The left forebrain overlying the entopallium was exposed and the dura mater excised. The right eye was kept open and the left one covered. A tangent screen 110° × 100° was positioned 40 cm away from the viewing eye. Since the stereotaxic apparatus rotated the horizontal meridian of the visual field clockwise from the pigeon's natural view by 38°, the directions of all two-dimensional stimuli were also likewise rotated by the same amount to match the animal's natural condition (Erichsen et al., 1989; Britto et al., 1990; Wang and Frost, 1991; Li et al., 2007). A micropipette (~2 µm tip diameter, ~15 MΩ impedance) filled with 2 M sodium acetate and 2% pontamine skyblue was used for recording neuronal activity and marking electrode tip sites. The extracellular signal was amplified, filtered and displayed on an oscilloscope and fed into a window discriminator. TTL pulses representing single spikes were analyzed using Cambridge Electronic Designs (CED) Micro1401 and peri-stimulus time histograms (PSTHs) were constructed with Spike2 software (CED).

4.2. Visual stimulus and data analysis

After a single neuron was isolated in the entopallium, three types of visual stimuli were generated by the custom software written in Matlab (Mathworks Inc.) and rear-projected onto the screen by a projector (Mitsubishi LVP-X300). (1) A soccer ball (diameter: 10–80 cm) with alternating black and white panels of equal areas expanded symmetrically to simulate an approaching object. The space-averaged mean luminance of the soccer ball was unchanged. The whole background was covered with the same checkerboard pattern as the soccer ball. The luminance of black and white was 0.1 and 6.6 cd/m², respectively. The simulated object (soccer ball) approached toward the viewing eye on a direct collision course along a simulated 10–30 m long path at constant velocities of 2–9 m/s. It stopped moving when it reached the viewing eye. (2) Optic flow was simulated by the movement of whole-field back-

ground pattern. The background moved on the screen plane at 10–30°/s in eight directions with 45° apart to simulate the bird translating in different directions. (3) An object (soccer ball) moved toward the viewing eye while the background randomly moved in one of eight two-dimensional directions.

The stationary stimulus was presented on the screen for 5 s to collect spontaneous spikes as control. An interval of at least 5 s between trials was applied to allow the neuron to recover from any adaptation. Neuronal spikes were analyzed by averaging firing rates accumulated in four to six repeats with Spike2 software (Cambridge Electronic Design Limited). For all visual stimuli, the time when the looming object reached the viewing eye was defined as the collision time and set to zero. Histograms were timed back from this event. The onset time of neural responses was calculated relative to the collision time based on their superimposed histograms.

In order to quantify the sensitivity of looming responses of each neuron to the direction of whole-field background motion, two independent analyses were used in the experiment. First, one-way ANOVA was used to determine whether the neuron's peak responses to looming objects were modulated by the direction of background motion in a statistically significant way. Second, the neuron's peak responses to looming objects against the moving background were normalized with respect to that produced by the looming object presented against a stationary background. Values were plotted in polar coordinates based on the direction of background motion. B-spline interpolation was used to fit these points. The maximal or minimal inhibitory direction was the point of fitted line at which looming responses of this neuron were maximally or minimally inhibited by the background motion in this direction.

4.3. Histology

Recording sites of some neurons were marked with the dye injected by negative pulses of 10–20 µA 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 the cresyl violet. Sections were dehydrated and covered for subsequent microscopic observation, and the marked sites were localized.

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