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ORIGINAL PAPER

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Stimulus size selectivity and receptive field organization of ectostriatal neurons in the pigeon

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Abstract The avian ectostriatum is the telencephalic recipient zone of the tectofugal pathway, which may be homologous to the colliculo-pulvinar-cortical pathway in mammals. The present paper studies the visual response properties and receptive field organization of ectostriatal cells in pigeons with extracellular recording and computer mapping techniques. The results indicate that 90% of ectostriatal cells prefer forward, downward and upward motion of visual stimuli at velocities in the range of 16–128° s^{-1}. They respond optimally to small stimuli (1–4° visual angle), mostly preferring a target of 2°. Most cells (78.8%) have one excitatory receptive field that usually possesses one or two hotspots, some cells (13.5%) have two excitatory receptive fields each having one or two hotspots, and a few cells (7.7%) have one excitatory receptive field with an unresponsive region in the center. An inhibitory receptive field is not found surrounding the excitatory receptive field in the ectostriatal cells examined. These response properties and receptive field organization may reflect the possible roles of the ectostriatum in stimulus discrimination and visual cognition.

Keywords Directional selectivity · Ectostriatum · Receptive field · Size selectivity · Tectofugal pathway

Abbreviations *ERF* excitatory receptive field · *IRF* inhibitory receptive field

Introduction

The tectofugal and the thalamofugal pathways in birds convey visual information from the retina to the telencephalon. They are thought to be homologous to the colliculo-pulvinar-cortical and geniculocortical pathways in mammals, respectively (Karten 1969; Shimizu and Bowers 1999). The tectofugal pathway may play the most important role in avian vision, because retinal fibers mostly go to the optic tectum (Remy and Güntürkün 1991). The tectum sends efferents to the nucleus rotundus, which in turn projects to the ectostriatum (Benowitz and Karten 1976; Karten and Hodos 1970). The ectostriatum is composed of a central core with larger cells and a peripheral belt with smaller cells (Karten and Hodos 1970). The core receives a topographical projection from the nucleus rotundus (Benowitz and Karten 1976; Karten and Hodos 1970; Nixdorf and Bischof 1982) and sends efferents to the belt, which in turn projects to some other telencephalic areas (Husband and Shimizu 1999; Shimizu and Bowers 1999).

Behavioral studies have shown that the ability of pigeons to discriminate brightness or shape is impaired by lesions in the ectostriatum (Bessette and Hodos 1989; Hodos and Karten 1970; Hodos et al. 1988; Riley et al. 1988). Ectostriatal lesions also impair visual acuity (Hodos et al. 1984) and size-discrimination ability (Hodos et al. 1986), as well as the discrimination ability between avian species (Watanabe 1996), but not that between food and nonfood, or conspecific pigeons (Watanabe 1991, 1994). It appears that the ectostriatum in birds may be involved in stimulus identification and some visual cognitive functions (Bischof and Watanabe 1997).

However, only few electrophysiological studies (Engelage and Bischof 1996; Kimberly et al. 1971; Revzin 1970) have contributed to single-unit analysis of ectostriatal neurons in birds. It has been reported that ectostriatal neurons are characterized by large receptive fields (Revzin 1970) and by sensitivity to motion (Engelage and Bischof 1996; Kimberly et al. 1971). Surprisingly, a large number of ectostriatal cells do not respond to visual stimulation (Engelage and Bischof 1996; Revzin 1970), and the receptive field of ectostriatal cells is not well defined (Engelage and Bischof 1996). To further reveal the visual response properties and receptive field orga-

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nization of ectostriatal neurons in birds, the present study was therefore undertaken by using extracellular recording and computer mapping techniques.

Materials and methods

Forty-nine pigeons *(Columba livia)* of 310–430 g body weight were used. Each pigeon was anesthetized with urethane (20%, 1 ml/100 g) and then placed in a stereotaxic apparatus. The left forebrain was surgically exposed and the dura mater overlying the ectostriatum excised according to the pigeon brain atlas (Karten and Hodos 1967). The right eye was kept open, and the left eye covered. A screen of 130° vertical×140° horizontal was positioned 40 cm away from the right eye. The horizontal meridian of the visual field was rotated clockwise by 38° from the experimenter's point of view (Britto et al. 1990; Fu et al. 1998) to meet the pigeon's normal conditions (Erichsen et al. 1989). The receptive field of ectostriatal neurons was approximately plotted with a hand-held target and then examined for visual response properties. Three types of visual stimuli were generated by a workstation (Silicon Graphics Indigo 2) and back-projected onto the screen with a projector (Electrohome ECP4). They were all black and moved against white background, whose luminance was 0.1 cd m^{-2} and 6.6 cd m^{-2}, respectively. The first type of stimulus was a single square (2–4°), which was used to determine the directional selectivity of ectostriatal cells by moving it in eight orthogonal directions relative to nasal 0°, spaced by 45°, at velocities of 32–128° s^{-1}, and to measure the optimal velocity by motion in the preferred direction at velocities of 4–256° s^{-1}. It was also used to explore effects of the stimulus size (1–32°) on visual responsiveness of ectostriatal cells when it was moved in the preferred direction at the optimal velocity, and to map the receptive field organization by motion in the preferred direction at the optimal velocity along a series of parallel paths covering the whole screen. The second type of stimulus was twin-squares, with the test stimulus moving within the excitatory receptive field (ERF) and the second stimulus moving in the region surrounding ERF. The second stimulus was above or below the test stimulus (horizontal motion), or left or right to the test stimulus (vertical motion). The stimuli were moved at the same velocity in the same direction with an increasing distance between both stimuli to map the inhibitory receptive field (IRF) (Frost et al. 1981; Wang et al. 2000). The third type of stimulus was a random-dot pattern consisting of 2° dots with densities of 100–1000 dots over the screen (130°×140° = 18200°^{2}), which was used for examining effects of the dot density on visual responsiveness of ectostriatal cells. Each of the examinations was repeated for three trials and an average firing rate was obtained. Ectostriatal cells were strongly habituated and thus complete recovery usually took 15–30 s according to the data obtained with five cells. Therefore, the inter-stimulus interval used in the present study was 30 s.

Action potentials of ectostriatal neurons were extracellularly recorded with a micropipette (1–3 μm tip diameter) filled with 2 mol l^{-1} sodium acetate and 2% pontamine-skyblue (Hellon 1971). Neuronal spikes were amplified and displayed on an oscilloscope, as well as fed into the workstation for on-line analysis. By the end of some experiments, the recording sites were marked with dye applied 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 and fixed in 4% paraformaldehyde for 6–12 h, soaked in 30% sucrose solution in a refrigerator overnight. Frozen sections were cut at 100 μm thickness and then conventionally processed for subsequent microscopic observation.

Results

One hundred and eight neurons were recorded and divided into several groups for various examination purposes. Some cells were used for a few kinds of examination. The recording sites of 13 cells were marked and all within the ectostriatal complex, with 12 being in the core and 1 in the belt. It implied that all 108 cells recorded in the present study were, if not exclusively, ectostriatal neurons. Of these, 72 cells were spontaneously firing at rates of 0.1–19 spikes s^{-1} and 36 others were silent, which were isolated by their visual responses.

Thirty-one ectostriatal cells were examined for the selectivity for direction of motion. They preferred forward (38.7%), downward (38.7%), upward (16.1%), and backward (6.5%) motion. Altogether, about 90% of ectostriatal cells preferred forward, downward and upward motion of visual stimuli (Fig. 1a). The selectivity for velocity was examined on 26 cells by moving the stimulus in the preferred direction at velocities in the range 4–256° s^{-1}. The measurements showed that 4 cells preferred 16° s^{-1}, 7 cells preferred 32° s^{-1}, 12 cells preferred 64° s^{-1} and 3 cells preferred 128° s^{-1}. Their average optimal velocity was 55.4 ± 32.1° s^{-1} (mean ± SD, $n = 26$). Figure 1b shows the velocity tuning curves of some cells, indicating that their firing rates were reduced dramatically as velocities of motion were deviated from the optimal values.

Forty-nine cells were examined for the dependence of firing rates on the stimulus size (Fig. 1c). The size-variable stimuli were black squares and moved at the optimal velocity in the preferred direction. Of these, 47 cells responded optimally to small stimuli, including 3 cells responding maximally to stimulus of 1° in size, 28 cells to 2°, 12 cells to 4°, 3 cells preferred stimuli ranging from 2° to 4°, and 1 cell preferred stimuli of 2–16° in size. Therefore, they could be grouped into sharply tuned cells and broadly tuned cells. In the first group of cells, firing rates were decreased dramatically as the stimulus size was deviated from the optimal value, whereas firing rates in the second group of cells were changed slowly as the stimulus size was changed. The remaining 2 cells did not change their firing rates as the stimulus was changed in size.

Ectostriatal cells were also selective for the density of dots in random-dot patterns. The dot density used here was 100–1000 dots (2°) over the screen (18200°^{2}). Of 35 cells examined, 34 cells responded optimally to dot patterns at low densities (100–200 dots/screen), and their firing rates were reduced dramatically as the density of dots was increased. For example, 90% of the cells reduced their visual firing rates to the spontaneous levels when the densities were increased to 1000 dots or 2000 dots over the screen (Fig. 1d). The remaining cell did not change its firing rate as the density of dots was increased from 100 dots/screen to 1000 dots/screen. Reduction in firing rate by increasing the density of dots might stem from the interactions of dots, because two dots spaced by 3–10° may decrease visual responses as stated below.

The location and organization of ERF in 52 ectostriatal cells were mapped with a 2° black square moved at 32° s^{-1} in the preferred direction randomly

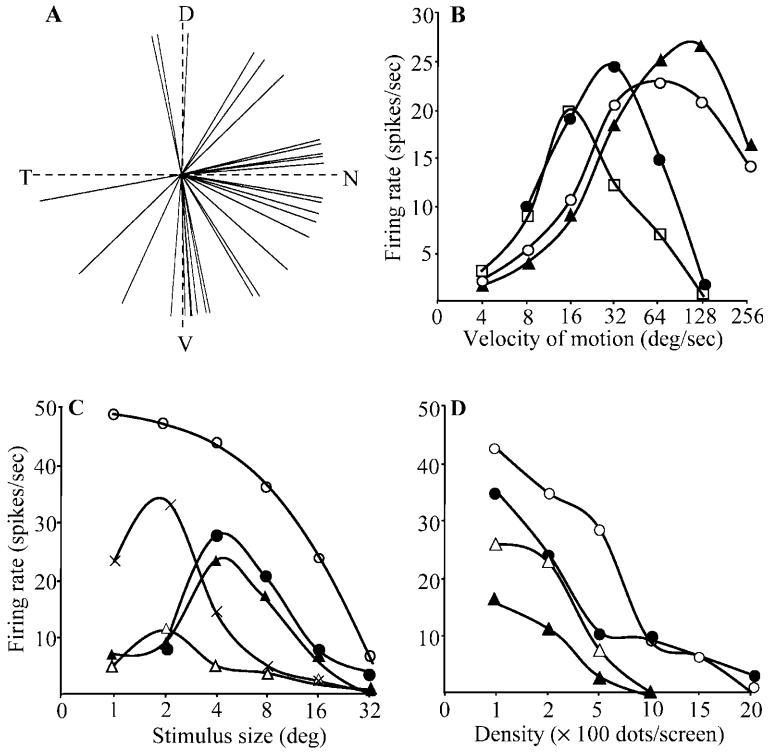

Fig. 1. Total distribution of directionalities of 31 ectostriatal cells that was obtained by Gaussian fitting based on the directional response data from measurements in eight directions (**a**). It shows that most ectostriatal cells prefer motion in forward, downward and upward directions. *D*, *N*, *T*, and *V* represent dorsal, nasal, temporal, and ventral sides of the visual field, respectively. Tuning curves of ectostriatal cells showing the dependence of firing rates on the velocity of motion (**b**), as well as on the size of stimulus (**c**) and on the density of dots in random-dot patterns (**d**). **b** Ectostriatal cells prefer velocities in the range 16–128° s^{-1}. **c** Ectostriatal cells prefer black squares of 2–4°, which were moved in the preferred direction at the optimal velocities. **d** Firing rates of ectostriatal cells dramatically reduce as the density of dots (2°) in random-dot patterns increases, which were moved at 32° s^{-1} in the preferred direction. The firing rates are averaged for three sweeps for each cell

along a series of parallel paths covering the whole screen. The ERF of ectostriatal cells was usually large and frequently extended beyond the screen. According to 19 cells whose ERF was wholly plotted on the screen, the ERF was elliptic or round in shape and had an average size of 77 ± 34° ranging from 20° to 130° (longest diameter)×50 ± 27° ranging from 10° to 110° (shortest diameter). Most cells (41 cells, 78.8%) had one ERF that was round, elliptic or irregular in shape, with one (30 cells; Fig. 2, cell A), two (4 cells) or no hotspots (7 cells). Seven cells (13.5%) had two ERFs each having one or two hotspots (Fig. 2, cell B). A hotspot here indicated the best responsive region in the receptive field (Kimberly et al. 1971; Engelage and Bischof 1996). The fact that spikes produced by motion separately through each of the two ERFs or hotspots were of identical amplitude and waveform indicated that the two ERFs or hotspots belonged to the same cell. The possibility could be excluded that two hotspots in the same ERF were produced by the two edges of a stimulus, because the stimulus used for mapping an ERF was 2° in size and moved randomly, and the inter-hotspot distance was usually larger than the stimulus size. Two ERFs of the same cell were arranged vertically or nasotemporally, and this arrangement was not always aligned along the preferred direction (Fig. 2, cell B). Most hotspots were located in the vicinity of the horizontal meridian, and only six hotspots in the foveal area. The remaining 4 cells (7.7%) had an ERF with an unresponsive region in the center, which was about 10° in diameter (Fig. 2, cell C). These regions were located within the foveal area in 3 cells and in the lower visual field in 1 cell.

An IRF was not found surrounding ERF in 12 cells examined. The firing rate produced by motion of the test stimulus in the central ERF was not significantly reduced by simultaneous motion of the second stimulus in a region surrounding ERF ($t = 0.172$, $n = 12$, $P > 0.01$). However, the visual responses of ectostriatal cells to motion in the peripheral ERF were significantly decreased by simultaneous motion in a region surrounding ERF ($t = 8.88$, $n = 12$, $P < 0.01$). The effective distance between the test stimulus in ERF and the second stimulus in the presumptive IRF was in a range of 3–10°. On the other hand, simultaneous motion of both stimuli along parallel paths spaced 3–10° in the central ERF also significantly reduced visual responses to motion of the test stimulus alone. Taken together, it seemed that reduction in firing rate was due to interactions between the two stimuli but not to inhibitory surround. Further experiments were done on 16 additional cells to test whether there existed an IRF sur-

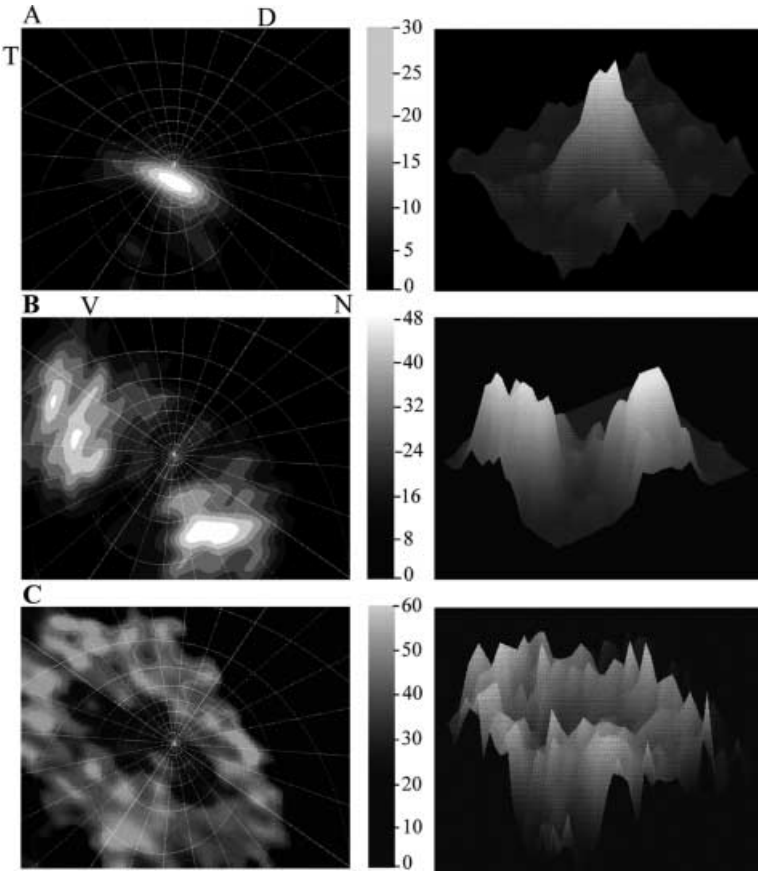

Fig. 2. Topographic maps of the excitatory receptive fields (*left column*) and their three-dimensional profiles (*right column*) of three ectostriatal cells (*A*, *B*, *C*). They were mapped with a 2° black square that was moved in the preferred direction at a velocity of 32° s^{-1} along a series of parallel paths covering the whole screen. Cell A preferring forward motion had one ERF with one hotspot in the foveal area. Cell B preferring upward motion had two ERFs each having one or two hotspots. Cell C preferring forward motion had an ERF with an unresponsive region in the center. The firing rates (spikes s^{-1}) were measured in the gray scales shown between the left and right columns. The spontaneous firing rate of these cells was about 2 spikes s^{-1}, 0.1 spikes s^{-1}, and 2 spikes s^{-1}, respectively. The horizontal meridian of the visual field was rotated clockwise by 38° from the experimenter's point of view to meet the pigeon's normal conditions. *D*, *N*, *T*, and *V* represent dorsal, nasal, temporal, and ventral sides of the visual field, respectively

rounding an ERF. A 2° black square was moved in the preferred direction of a cell within ERF framed by the restricted window to elicit visual responses, while a large-field pattern consisting of dots (2°) at density of 100 dots/screen was moved outside the window in the directions that were the same, opposite or orthogonal to the preferred direction. All experiments showed that motion outside ERF did not change visual responses elicited by motion within ERF (same direction: $t = 1.086$; opposite direction: $t = 0.281$; orthogonal direction: 0.410; $n = 16$, $P > 0.01$).

Discussion

The present study not only confirms that ectostriatal cells are selective for the direction and velocity of motion (Engelage and Bischof 1996; Kimberly et al. 1971), but also shows the visual response properties and receptive field organization of ectostriatal cells. Their optimal velocity is averaged to be 55.4° s^{-1}, much higher than that of tectal cells in pigeons (Gu et al. 2000). About 90% of the cells prefer downward, upward and forward motion, in disagreement with the finding that most ectostriatal cells prefer forward and upward motion (Kimberly et al. 1971). This might be due to different samplings, and/or our rotation of the visual field to meet the pigeon's normal conditions (Erichsen et al. 1989). The directional preference for forward and downward motion has also been shown in tectal cells (Frost and Di Franco 1976).

The present study indicates that ectostriatal cells examined all vigorously respond to visual stimulation, in disagreement with the finding that a large number of ectostriatal units are not visually responsive (Engelage and Bischof 1996; Revzin 1970). This discrepancy might be due to different types of visual stimuli used. Ectostriatal cells prefer motion of a black stimulus against white background, but those authors used light or white patterns on black background to activate ectostriatal cells (Engelage and Bischof 1996; Revzin 1970). Another possibility may be that large stimuli are not adequate for ectostriatal cells, because they respond optimally to small black stimuli (1–4°) against white background, mostly preferring a moving target of 2° in size. It appears that ectostriatal cells in pigeons optimally respond to small fast-moving targets within large receptive fields. The cellular mechanism underlying this property has been recently hypothesized in tectal cells in birds (Luksch et al. 1998, 2001; Troje and Frost 1998).

The ERF of ectostriatal cells is well defined and heterogeneous in excitability, with a hotspot or unresponsive region in it. Only a few hotspots are in the foveal area, and this distribution is different from that obtained on the zebra finch (Engelage and Bischof 1996). Differences in avian species and/or methodologies used may cause this discrepancy. Due to the presence of interactions between both eyes in the zebra finch ecto-

striatum (Engelage and Bischof 1988, 1989), it may imply that the unresponsive region of the receptive field shown in Fig. 2, cell C might correspond to an area activated by the ipsilateral eye. Another possibility could not be excluded that this cell's receptive field is characterized by a complex structure, whose central region is inhibited and peripheral region excited by motion of the stimulus used for mapping the receptive field, because ectostriatal cells could respond with inhibition (Engelage and Bischof 1996).

The ectostriatum receives a topographical projection from the nucleus rotundus (Benowitz and Karten 1976; Karten and Hodos 1970; Nixdorf and Bischof 1982), whose cells cluster in several physiological domains according to their responses to luminance, color, motion and looming (Wang and Frost 1992; Wang et al. 1993). Although the rotundo-ectostriatal projection is topographic, and the ectostriatal subdivisions are demonstrated with anatomical (Benowitz and Karten 1976; Karten and Hodos 1970; Nixdorf and Bischof 1982) and histochemical (Hellmann et al. 1995) approaches, physiological domains in the avian ectostriatum are still not revealed (Engelage and Bischof 1996). It is probable that some functional segregation, if any, needs to be demonstrated by using specific visual stimuli other than simple stimuli used to date. Alternatively, there might exist a transformation between the nucleus rotundus and the ectostriatum, so that physiological domains shown in the nucleus rotundus are more or less lost at the ectostriatal level. For example, looming detection neurons are present in the ectostriatum, but they do not cluster together (Engelage and Bischof 1996). It is reminiscent of the tectorotundal projection, where each point of the tectal surface projects onto the entire nucleus rotundus, topographic place coding in the tectum is more or less lost in the nucleus (Hellmann and Güntürkün 2001).

It has been suggested that the ectostriatum may pay important roles in brightness, size, and shape discrimination (Bessette and Hodos 1989; Hodos et al. 1986, 1988; Riley et al. 1988), visual conditioning and cognition (Wall et al. 1985; Watanabe 1991, 1994, 1996). The stimulus size preference and object interactions, as well as the receptive field organization of ectostriatal cells in pigeons may favor these suggestions.

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