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Regional Variation in Receptive Field Properties of Tectal Neurons in Pigeons

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Key Words

Optic tectum · Pigeon · Receptive field · Retina · Topography

Abstract

The present study provides the first electrophysiological evidence for dorsoventral variation in the receptive field properties of tectal cells in pigeons. According to their receptive field organization, visual response properties and laminar locations, 95 tectal neurons recorded in the present study could be categorized into two groups: (1) Fifty-five DL-neurons were recorded in the dorsal, dorso-lateral, lateral and ventro-lateral tectum and characterized by an excitatory receptive field surrounded by an inhibitory receptive field. Most of them almost equally responded to white and black objects, but did not respond to switch-on and -off of a light spot. (2) Forty VC-neurons were recorded in the ventral tectum and characterized by an excitatory receptive field alone. Their responses to switch-on of a light spot and to a white object were significantly stronger than those to light-off and to a black object, respectively. DL-neurons preferred higher velocity, whereas VC-neurons preferred lower velocity. The recording sites of 53 of 95 cells (56%) examined were marked with pontamine sky blue, showing that DL-neurons were located in tectal layers I–IV, predominantly in layer II, whereas VC-neurons were mainly concentrated in sublayer IIc. The receptive fields of VC-neurons were located within the rostroventral visual field possibly corresponding to the red field of the pigeon retina, suggesting that they might be associated with visual food-foraging behaviors.

Introduction

The optic tectum in nonmammalian vertebrates such as birds is the principal destination of retinal ganglion cell axons. Neuroanatomical [Hamdi and Whitteridge, 1954; McGill et al., 1966; Hard, 1972; Hunt and Webster, 1975; Remy and Güntürkün, 1991] and electrophysiological [Hamdi and Whitteridge, 1954; Bilge, 1971; Clarke and Whitteridge, 1976] studies have shown that the avian retina primarily projects onto the contralateral tectum in a topographical manner. The dorsal and ventral retina project onto the ventral and dorsal tectum, respectively; and the horizontal meridian of the retina is represented in the lateral tectum. In addition to this topographical projection, there exist some dorsoventral differences between the dorsal and ventral tectum in lamination, cell number, thickness and optic terminal density [Acheson et al., 1980; Duff et al., 1981; Hayes and Webster, 1985; Theiss et al., 1998]. Glutamic acid decarboxylase-immunopositive cells are observed in the dorsolateral tectum but not in the ventral tectum [Veenman and Reiner, 1994], whereas the number of glutamate receptor-immunopositive cells dramatically increases from the dorsal tectum to the ventral tectum [Theiss et al., 1998]. These regional variations imply that the dorsal and ventral tectum

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are possibly distinct in their physiological roles in visual information processing in birds [Duff et al., 1981; Hayes and Webster, 1985; Theiss et al., 1998].

Electrophysiological studies of the response properties of visual neurons in the dorsolateral tectum, which is freely accessible to the experimenters after surgically removing the skull bone, have indicated that the receptive field of tectal cells in birds is concentrically organized, consisting of an excitatory center and an inhibitory surround [Jassik-Gerschenfeld and Guichard, 1972; Hughes and Pearlman, 1974; Jassik-Gerschenfeld and Hardy, 1979; Frost et al., 1981; Hardy et al., 1982; Leresche et al., 1984]. The extent and responsiveness of the excitatory center and inhibitory surround of tectal receptive fields can be differentially modulated by input from the magnocellular (Imc) and parvocellular (Ipc) divisions of the nucleus isthmi, respectively [unpubl. observ.]. Tectal neurons in pigeons could be categorized into two groups: motion-sensitive and direction-selective cells [Jassik-Gerschenfeld and Guichard, 1972; Hughes and Pearlman, 1974; Jassik-Gerschenfeld et al., 1975; Jassik-Gerschenfeld and Hardy, 1979; Frost et al., 1981; Sun and Frost, 1997]. There are some variations in receptive field properties including the field's size and shape from the superficial to deep layers, but no definite correlation has been observed between physiological properties of tectal cells and their locations in tectal layers [Hughes and Pearlman, 1974]. However, this observation is in disagreement with a subsequent finding by Jassik-Gerschenfeld et al. [1975] that direction-selective cells are located in tectal layer II and that motion-sensitive cells are distributed throughout all tectal layers.

Though electrophysiological studies have been extensively performed on the dorsolateral tectum, nothing is known about the receptive field properties of visual neurons in the ventral tectum due to its location deep in the brain and on the skull floor. Anatomical and electrophysiological mappings [Bilge, 1971; Clarke and Whitteridge, 1976; Remy and Güntürkün, 1991; Karten et al., 1997] have indicated that the ventral tectum is the projection region of the dorsal retina with the red field, which corresponds to the pecking field in pigeons [Goodale, 1983; Nalbach et al., 1990]. The isthmo-optic nucleus, a major component of the centrifugal system in birds, mainly receives input from the ventral tectum [Woodson et al., 1995]. The tectum topographically projects to the nucleus rotundus [Karten et al., 1997; Hellmann and Güntürkün, 1999], with the ventral tectum sending significantly more projections to the nucleus rotundus than the dorsal tectum [Hellmann and Güntürkün, 1999]. In view of the physiological significance of the ventral tectum, the present study was therefore undertaken to reveal the receptive field properties of ventral neurons and compare them with those of neurons in the dorsal, dorso-lateral, lateral and ventro-lateral tectum in pigeons.

Materials and Methods

The experiments were performed on 38 adult pigeons *(Columba livia)* of either sex, weighing 300–420 g, and under guidelines regarding the use of animals in neuroscience research approved by the Society for Neuroscience. The pigeon was anesthetized with urethane (20%, 1 ml/100 g body weight), and then placed in a stereotaxic apparatus. Its body temperature was maintained at 41 °C by a heating pad. The left tectum was surgically exposed, and the overlying dura mater was excised. The dorsal, dorso-lateral, and lateral tectum were seen and therefore freely accessible to an electrode. However, the ventro-lateral tectum is protected by bone and the ventral tectum is deep in the brain and on the skull floor. Therefore, these regions are difficult to search with an electrode. The nictitating membrane of the right eye was removed and the eye kept open, and the left eye was occluded with an opaque cover. A screen of 180 cm in height and 220 cm in width was positioned 40 cm distant from the viewing eye, and 24° to the mid-sagittal plane of the pigeon. As described in our previous studies [Fu et al., 1998; Zhang et al., 1999], the horizontal meridian of the stereotaxically fixed pigeon visual field was rotated clockwise by 38° to meet the pigeon's normal conditions for flying, walking, standing and perching [Erichsen et al., 1989]. In some cases, the screen was moved 20 cm closer to the viewing eye in order to wholly plot receptive fields, which would be otherwise plotted on both the screen and the ground.

Three types of visual stimuli were generated by a graphics workstation (Indigo 2, Silicon Graphics, Inc., Mt. View, Calif., USA) and rear-projected by a three-color projector (Electrohome ECP4101, Electrohome Limited, Kitchener, Ontario, Canada) onto the screen: (1) a white or black square (2.8°) moved against a black or white background with luminance of 0.1 cd/m^2 and 6.6 cd/m^2, respectively, for plotting the excitatory receptive field (ERF) [Fu et al., 1998; Zhang et al., 1999] and examining visual responses to an edge defined by luminance contrast; (2) white twin-squares for plotting the inhibitory receptive field (IRF) in such a way that while one square was moved within the ERF to excite a cell the other was moved outside the ERF to plot the cell's IRF; and (3) a spot of light (2.8×2.8°) for examining ON-OFF responses of tectal cells to its switch-on and -off.

For extracellular recording of action potentials and marking the recording sites of tectal cells, a micropipette (1–3 μm tip diameter) filled with a solution containing 0.5 *M* sodium acetate and 2% pontamine sky blue [Hellon, 1971] was used in the present experiments. According to the pigeon's brain atlas [Karten and Hodos, 1967], the electrode was advanced normal to the tectal surface to isolate visual cells in the dorsal, dorso-lateral and lateral tectum. The ventral and ventro-lateral tectum was searched with a vertically advanced electrode for visual cells. In some cases, visual responses found in the Ipc or the Imc were taken as a reference for further advancement of an electrode to find visual cells in the ventral tectum. During electrode advancement, additional visual (gratings, random-dots, single circle and triangle) and other sensory stimuli, including auditory (whistle, hand-claps, bell-rings), tactile (brushing pigeon's back, flanks, and face) were also applied. Generally speaking, a single-unit spike with a large amplitude and high signal/noise ratio was considered to be firing from a cell in the present study. These spikes were recorded, amplified,

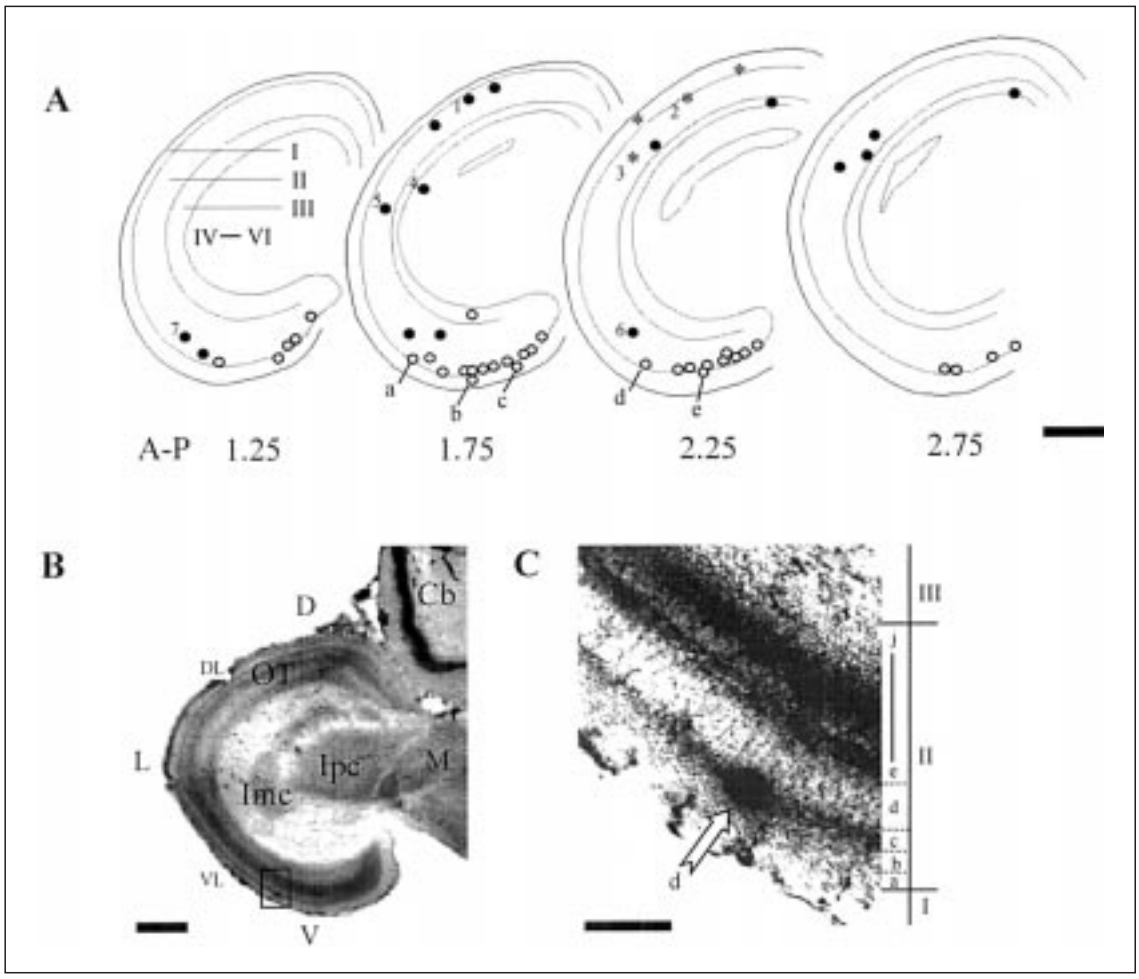

Fig. 1. Serial cross-sections (**A**) and microphotographs (**B**, **C**) of the pigeon tectum showing distribution of dye-marked recording sites of 53 tectal neurons. **A** Filled circles, asterisks and empty circles represent the recording sites of DL_1-, DL_2- and VC-neurons, respectively. Receptive fields of some tectal cells are shown in figure 2, with corresponding numerals or letters. **B** A cross-section of tectum showing a dye-marked spot in tectal sublayer IIc framed by a box, which is enlarged in **C**. Empty arrow d in **C** points to the recording site of cell d in **A**. I–VI are tectal layers according to Cowan et al. [1961]. A–P indicates anterior-posterior levels of the pigeon's brain atlas by Karten and Hodos [1967]. Abbreviations: Cb = cerebellum; OT = optic tectum; Imc = nucleus isthmi pars magnocellularis; Ipc = nucleus isthmi pars parvocellularis. D, DL, L, VL, V and M represent dorsal, dorso-lateral, lateral, ventro-lateral, ventral and medial, respectively. Scale bars = 1 mm in **A** and **B**; 200 μm in **C**.

and displayed on an oscilloscope, as well as fed into the workstation computer for on-line analysis. The data were usually collected for the first 400–600 ms following stimulation to show the total number of spikes accumulated by superimposing 3–5 sweeps.

For histological verification of the recording sites of some tectal cells which were found in the dorsal, dorso-lateral, lateral or ventro-lateral tectum and of all tectal cells recorded in the ventral tectum, the dye was ejected by negative current pulses of 10–20 μA in intensity, 0.5 s in duration at 1 Hz frequency, for 10–15 min. Under deep anesthesia, the brain was removed from the skull 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 in thickness and counterstained with cresyl violet. Sections were dehydrated and covered for microscopic observation of the recording sites marked by dye.

Results

Ninety-five visual neurons were extracellularly recorded from the optic tectum, and examined for their response characteristics. The recording sites of 53 (56%) of these cells were marked with pontamine sky blue (fig. 1), showing a

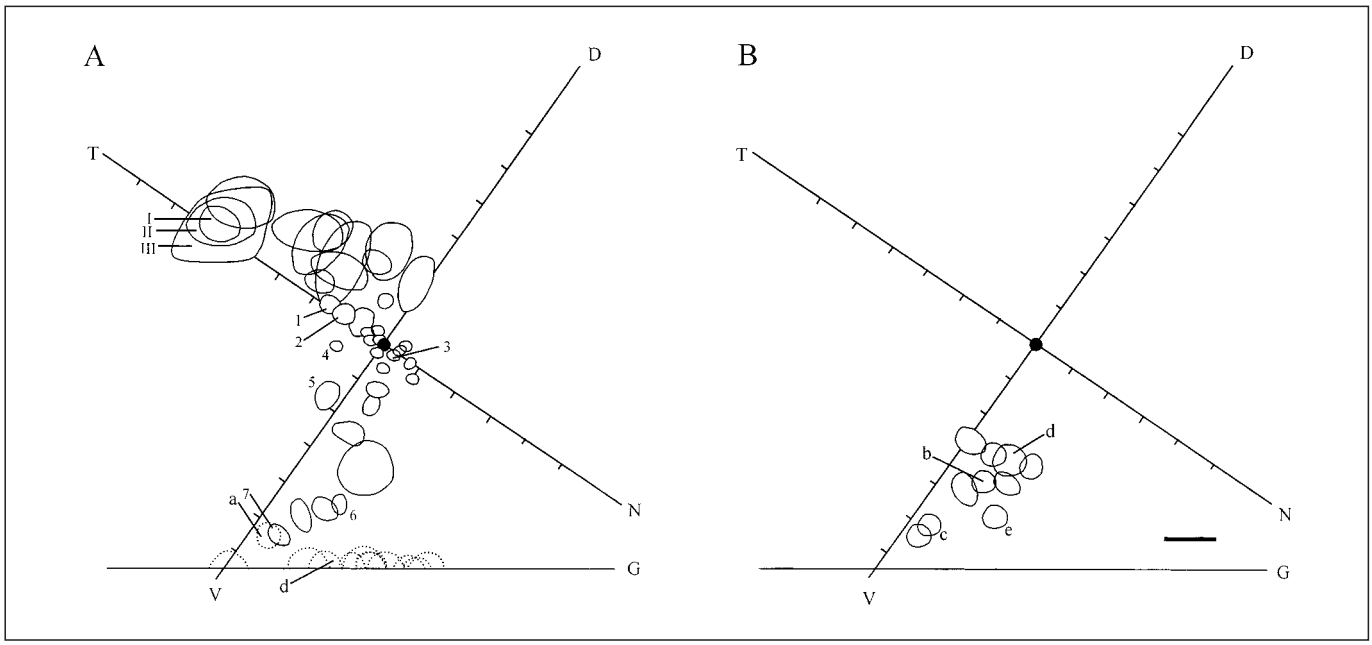

Fig. 2. Shape, size and distribution of receptive fields of tectal cells in the visual field. **A** Receptive fields of DL- (solid-line circles) and VC-neurons (dashed-line circle or semicircles), which were plotted on a screen 40 cm distant from the viewing eye. Note that receptive fields of VC-neurons recorded in the ventral tectum were truncated by the ground (G). When the screen was moved 20 cm closer to the eye, receptive fields of VC-cells were completely plotted as shown in **B**. As an example, receptive field of cell d was truncated in **A** but not in **B**. Receptive fields numbered with Roman numerals I, II and III (**A**) were plotted for three cells recorded in the same penetration, but with recording depths of 350, 600 and 1,200 μm respectively. The visual field was rotated by 38° to meet the pigeon normal conditions. N, D, T and V represent nasal, dorsal, temporal and ventral, respectively. Note that ordinate (D–V) and abscissa (T–N) have the same scale of 20 cm, and the cell d's RF has different coordinates but the same size in visual angle degrees in **A** and **B**. Small filled circle represents the optic axis. Numerals and letters labeling receptive fields of tectal cells correspond to those in figure 1. Scale bar = 20°.

correlation of their visual response properties with locations within the tectum. According to their receptive field organization and visual response properties, these cells were categorized into two types: DL- and VC-neurons.

Fifty-five DL-neurons were recorded in the dorsal, dorsolateral, lateral, and ventro-lateral tectum, and 20 recording sites of these cells were marked with dye (fig. 1). Most marked sites (75%) were located in tectal layer II and others in layers I (10%), III (10%) and IV (5%). The sites marked in layer II were scattered in sublayers a–e, g, i, j (fig. 1). Their receptive fields (RFs) were mainly distributed in the dorsotemporal and ventronasal quadrants of the visual field (fig. 2A). Among them, 54 cells had RFs characterized by a concentric organization consisting of an excitatory receptive field (ERF) surrounded by an inhibitory receptive field (IRF) (fig. 3), with the exception of one cell that only had an ERF. The tectal location and receptive field of this cell (no. 3) are shown in figures 1 and 2. Generally speaking, tectal fields were enlarged in size as the recording depths increased from superficial to deep layers. Figure 2A shows an example indicating that ERFs of tectal cells recorded in the same penetration at depths of 350, 600 and 1,200 μm were gradually increased in size and arranged in a concentric fashion. Based on the field size, ERFs of DL-neurons could be divided into two groups: small and large fields. Small fields were usually located within the central 20° around the optic axis, having an average ERF size of 6.0 ± 0.7° by 5.7 ± 0.4° (mean ± S.D., n = 16). Their recording sites corresponded to the lateral tectum (fig. 1, 2). Large fields had a mean size of 19.4 ± 11.3° by 13.2 ± 6.9° (n = 26). Both ERFs and surrounding IRFs were oval in shape (fig. 2, 3). The longest dimension of IRFs in the central visual field was 31.9 ± 4.0° (n = 6), whereas their shortest axis was 21.1 ± 5.0°. These parameters for IRFs of the other DL-cells were 20 ± 6.8° and 14.6 ± 5.9° (n =16), respectively. These tectal cells had an average optimal velocity

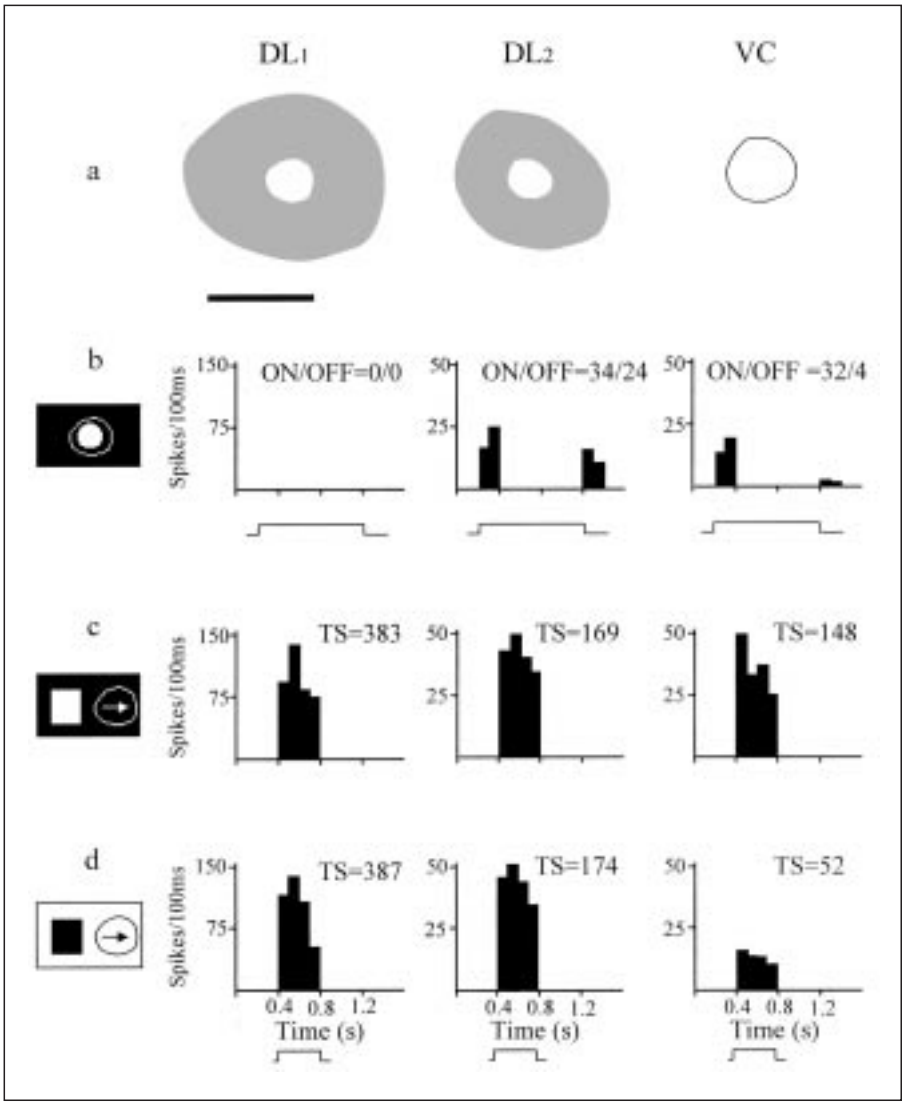

Fig. 3. Differences between DL- (DL_1, DL_2) and VC-neurons in their receptive field organization (**a**) and visual responses to switch-on and -off of a light spot (**b**), as well as responses to motion of white (**c**) and black (**d**) objects. Lower traces signify visual stimulation: upward deflection represents switch-on of a light spot (**b**) or entry of a luminance-contrast object into the receptive field (**c**, **d**), and downward light-off (**b**) or exit of the object out of the field. Tectal locations and receptive fields of cells DL_1, DL_2 and V correspond to 1, 2 and d in figure 1 and figure 2A, respectively. **a** White and gray regions are excitatory and inhibitory receptive fields, respectively. **b** ON/OFF, total number of spikes produced by switch-on and -off of a light spot. **c**–**d** TS, total number of spikes counted for three sweeps. Scale bar = 20°.

of 32 ± 11.6°/s (n = 23). Thirty-five of 48 (72.9%) DL-cells (DL_1-neurons) did not respond to switch-on and -off of a light spot, whereas 13 others (DL_2-neurons, 27.1%) produced significantly stronger ON-responses than OFF-responses (t test: $t = 2.70$, $n = 13$, $p < 0.01$). The recording sites of DL_1-neurons mixed with those of DL_2-neurons in the dorsal, dorso-lateral, lateral and ventro-lateral tectum. Both groups of cells almost equally ($t = 1.18$, $n = 53$, $p > 0.01$) responded to motion of black and white squares of identical size. Visual responses of DL_2-neurons to light on-off were about 10–20% of those to motion of single black or white objects.

Forty VC-neurons were recorded in the ventral tectum, and their ERFs were located in the rostroventral visual field. No IRFs were found surrounding ERFs in any VC-neurons examined (fig. 3). Of these, 30 cells had their ERFs partially on the screen and partially on the ground (fig. 2A) when the screen was 40 cm distant from the viewing eye. Their fields seemed to be oval-shaped. Ten other cells' receptive fields were wholly plotted on the screen that was moved 20 cm closer to the viewing eye (fig. 2B). The fields had an average size of 9.3 ± 2.5° by 7.4 ± 1.5° (n = 10). These cells had an average optimal velocity of 24.5 ± 11.7°/s (n = 7). All VC-neurons responded to switch-on and -off of a light spot, with ON-responses being significantly stronger than OFF-responses ($t = 2.96$, $n = 10$, $p < 0.01$). On an average, visual responses of VC-neurons to switch-off were 67% of those to switch-on of a light spot. VC-neurons responded more vig-

orously to a white object than to a black one ($t = 5.40$, $n = 10$, $p < 0.01$), with black responses averaging 43% of white responses. The recording sites of 33 of 40 VC-neurons were successfully marked in the ventral tectum, 24 of which (73%) were concentrated in sublayer IIc and others in sublayers IIb (2 cells) and IId (2 cells) as well as in tectal layers I (4 cells) and III (1 cell) (fig. 1A). Systematic recordings made in 2 pigeons showed that VC-neurons were found in a ventral region at coordinates of AP 1.00–3.00, ML 3.50–6.00, and DV 5.7–7.2 according to the pigeon's brain atlas by Karten and Hodos [1967].

Discussion

The present study provides the first electrophysiological evidence that visual neurons in the dorsal, dorso-lateral, lateral and ventro-lateral tectum are different from those in the ventral tectum in their receptive field organization, visual responses and laminar locations. Thus, tectal neurons electrophysiologically recorded in the present study could be divided into two groups: DL- and VC-neurons. However, it should be stressed that our recordings were only made from a relatively limited area of the tectum, because the rostral tectum and a large part of the ventro-lateral tectum could not be reached by an electrode due to the overlying forebrain or the ventro-lateral skull protection. Though 95 cells were recorded in the present study, this number is still negligible in comparison with the total number of tectal cells. Also, there exist a variety of electrophysiologically identified morphological types of tectal cells [Hardy et al., 1985]. Therefore, there might be other physiological types of tectal neurons yet to be found.

The receptive field of DL-neurons is composed of an ERF surrounded by an IRF in a concentric fashion, in agreement with the tectal field organization reported previously [Jassik-Gerschenfeld and Guichard, 1972; Hughes and Pearlman, 1974; Jassik-Gerschenfeld and Hardy, 1979; Frost et al., 1981; Leresche et al., 1984; Sun and Frost, 1997]. Our recent study indicates that ERF and IRF of visual cells in the dorsolateral tectum are differentially modulated by the Imc and the Ipc, respectively [unpubl. observ.]. The isthmotectal modulation by the Imc takes action via both glutamatergic and cholinergic pathways, whereas the modulation by the Ipc is mainly through a GABAergic pathway [Felix et al., 1994; Gao et al., 1995; Wang et al., 1995]. In contrast, the receptive field of VC-neurons is characterized by an ERF alone. This is to some extent supported by the finding that glutamic acid decarboxylase-immunopositive cells are observed in the dorsolateral, but not in the ventral, tectum [Veenman and Reiner, 1994], whereas the number of glutamate receptor-immunopositive cells dramatically increases from the dorsal to ventral tectum [Theiss et al., 1998].

Visual cells in the dorsal, dorso-lateral, lateral, and ventro-lateral tectum are also different from those in the ventral tectum in their visual response properties. Most DL-cells are unresponsive to light stimulation. Only about one-third of the cells respond to switch-on and -off of a light spot, with ON-responses larger than OFF-responses. However, both light-unresponsive and light-responsive cells almost equally respond to a moving white and black object. It appears that their luminance-contrast responses are not dependent on ON-OFF responses. In contrast, all the ventral cells produce stronger ON-responses than OFF-responses. They fire many more spikes to a white object than to a black one. It suggests that these cells prefer white or luminous objects. In this regard, VC-neurons are just the opposite of pretectal and accessory optic neurons, which prefer black edges [Fu et al., 1998; Wang et al., 2000]. This might reflect a functional segregation in which pretectal and accessory optic cells can detect luminance-contrast edges for generating optokinetic nystagmus, whereas ventral cells in the pigeon tectum search for food and discriminate grains from grits on the ground. Furthermore, DL-neurons prefer higher velocity movements whereas VC-neurons prefer lower velocity, implying that the dorsal and central fields are mediated by neurons detecting fast-moving objects and the ventral field by neurons responding to static or slow-moving objects [Maldonado et al., 1988].

It is difficult to differentiate between recording from a cell and that from a fiber, because (i) not every large spike means that one is recording from a cell [Gruberg and Lettvin, 1980], and (ii) a postsynaptic and fiber unit spike can not be identified by the number of phases in its waveform [Fite, 1969]. However, the distribution of the recording sites marked with dye implies that our recordings are primarily, if not exclusively, made from tectal cells. DL-cells are scattered in layers I–IV, predominantly throughout sublayers of tectal layer II, whereas 73% of VC-cells are concentrated in the cellular sublayer IIc. This concentration results from successful markings of all recording sites in the ventral tectum, and thus is not a sampling bias. It is interesting to note that though the Ipc projects onto the ventral tectum [Güntürkün and Remy, 1990], it projects mainly upon the superficial sublayers IIb and IId but not IIc [Hunt et al., 1977]. This might be one of the reasons why ventral cells in this sublayer only have an ERF without an inhibitory surround. One puzzle is that visual responses in the ventral tectum are restricted to a very narrow band beyond which it is hard to

find visual units. This phenomenon could be explained by the following possibilities: (1) some specific visual stimulus properties are needed to excite visual neurons in other tectal layers or sublayers; and/or (2) numerous ventral neurons might respond to sensory stimuli other than vision. We tried a variety of visual stimuli and other sensory stimulations, but failed to find a successful combination.

Taken together with previously reported dorsoventral differences between the dorsal and ventral tectum in lamination, cell number and optic terminal density [Hayes and Webster, 1985; Theiss et al., 1998], as well as in the distribution of some important neuroactive substances [Veenman and Reiner, 1994; Theiss et al., 1998], our results suggest a regional variation in visual information processing in the retinotectal system [Duff et al., 1981; Hayes and Webster, 1985; Theiss et al., 1998]. The ERF locations of VC-neurons in the visual field indicate that these cells might receive information from the red field of the retina [Nalbach et al., 1990; Hahmann and Güntürkün, 1993; Karten et al., 1997]. When pecking a grain, the pigeon's eyes make convergent movement so that the red field looks deeply into the binocular field and the area dorsalis within the red field gazes onto the bill tip [Nalbach et al., 1990; Hahmann and Güntürkün, 1993]. The receptive field properties of ventral neurons could thus be suited for finding grains and distinguishing them from grits on the ground.

Acknowledgments

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