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Receptive field organization and response properties of visual neurons in the pigeon nucleus semilunaris

Jin Yang, Xiao Li, Shu-Rong Wang*

Laboratory for Visual Information Processing, Institute of Biophysics, Chinese Academy of Sciences, 15 Datun Road, Beijing 100101, China

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Abstract

The present study provides the first electrophysiological evidence that the nucleus semilunaris is a visual center in the pigeon midbrain. The receptive field of E-type cells is either an excitatory field alone or an excitatory center with an inhibitory periphery, which in most cases is surrounded by a disinhibitory region. Cells of I-type possess only an inhibitory receptive field. Semilunar cells are selective for fast (80–160 °/s), intermediate (40 °/s) and slow (10–20 °/s) velocities of motion, with directional cells mainly preferring forward and downward motion. About 40% of cells prefer a white stimulus moving against a black background, and 60% of cells prefer a black stimulus against a white background. The physiological significance of these properties is discussed.

Keywords: Birds; Isthmic nuclei; Optic tectum; Receptive field; Tectofugal pathway; Visual system

The isthmic nuclei in the avian midbrain consist of the nucleus isthmi pars magnocellularis (Imc), the nucleus isthmi pars parvocellularis (Ipc), and the nucleus semilunaris (Slu). They have reciprocal connections with the ipsilateral tectum [7,9,11,21]. The isthmo-optic nucleus is excluded from this system because it projects centrifugally to the contralateral retina.

It has been shown that the nucleus isthmi (NI) in fish [13], amphibians [14], Imc in reptiles [15], and both Ipc and Imc in birds [20,22] are all visual centers. The nucleus in amphibians [16] and reptiles [5] exerts both excitatory and inhibitory actions on tectal cells. In birds, Imc and Ipc apply excitatory and inhibitory actions on tectal cells, respectively [1,17,18]. The Imc-tectal pathway modulates the excitatory center and the Ipc-tectal pathway modulates the inhibitory surround of the receptive field (RF) of tectal cells [19]. However, our knowledge about the physiology of Slu is still lacking although it occupies an important position in the tectofugal system [9]. The present study was, therefore, undertaken to investigate the RF organization and visual response properties of Slu neurons with single-unit recording and computer-aided mapping techniques.

Forty three pigeons *(Columba livia)* weighing 310–480 g were used following the usage of animals 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 tectum was exposed and the dura mater excised. The right eye was kept open, and the left covered. A screen of 150° (visual angle) horizontal × 130° vertical was positioned 24 cm away from the right eye. The horizontal meridian of the visual field was rotated by 38° to meet the pigeon's normal conditions [4]. The location and extent of RF of Slu cells were approximately plotted with a hand-held black square (2 × 2°). In some cases, the excitatory RF (ERF) and/or inhibitory RF (IRF) were mapped with a black or white square (6 × 6°) that was generated by a computer and projected with a projector (Electrohome ECP4101) onto the screen. The luminance of blackness and whiteness was 0.1 and 6.6 cd/m^2, respectively. The stimulus was moved along numerous parallel paths covering the screen and visual responses were fed into the computer for plotting RF [4]. A rectangle (6° wide × 6–160° long) was used for measuring IRF and a disinhibitory region beyond the classic RF. The preferred direction of a neuron was determined by moving the stimulus at 10 °/s in eight directions spaced by 45° relative to nasal 0°. Its optimal velocity was measured by moving the stimulus in the preferred direction at velocities of 5–160 °/s. Two-four sweeps were superimposed and an average firing rate was obtained. The interval between consecutive stimulations was 10 s to allow the cell to recover completely.

* Corresponding author. Tel.: +86-10-6488-9858; fax: +86-10-6486-0713.

E-mail address: wangsr@sun5.ibp.ac.cn (S.-R. Wang).

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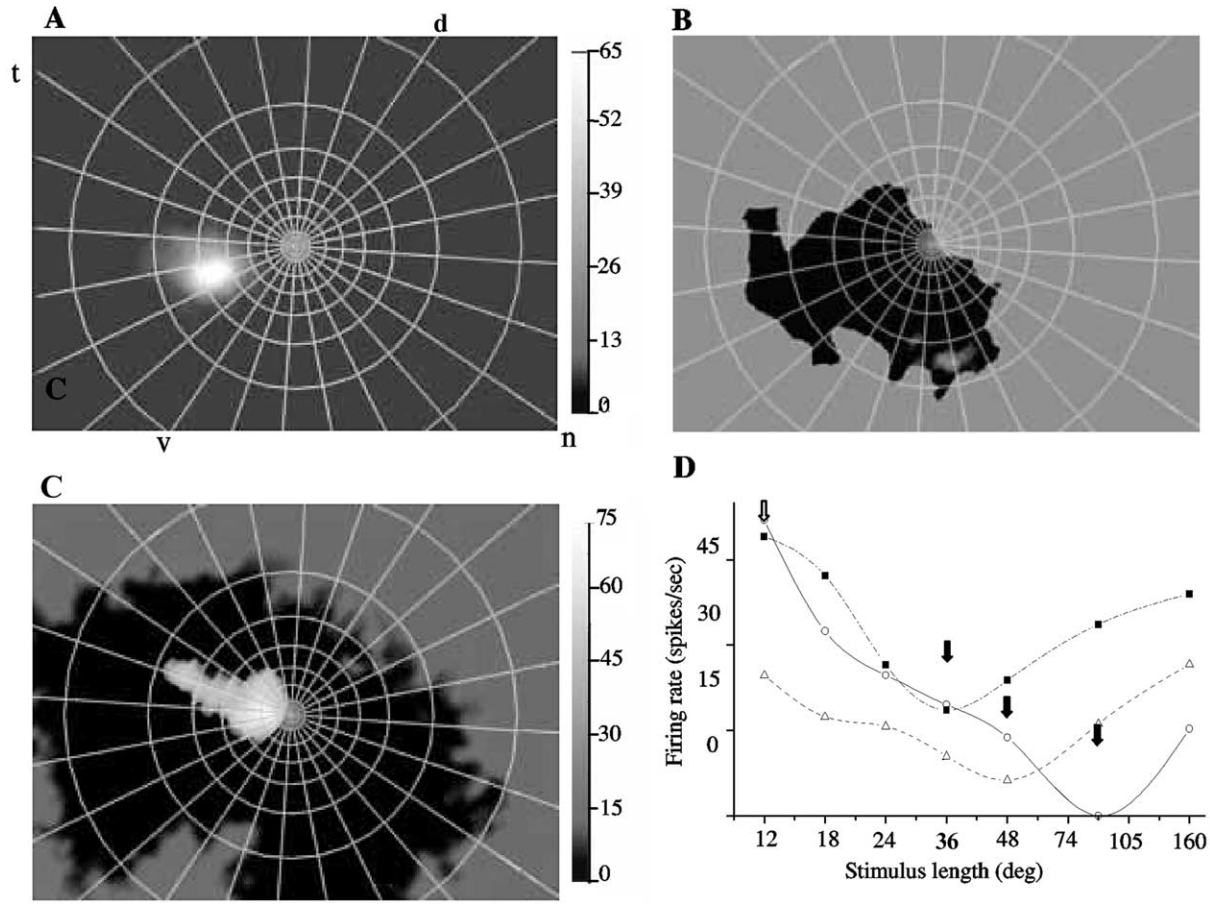

Fig. 1. Topography of receptive fields of three semilunar neurons (A–C) that was mapped by equal firing rate (gray) as indicated by the rate scales shown between A and B as well as on the right to C, and stimulus-length tuning curves of some cells showing the existence of a disinhibitory region surrounding an IRF (D). Cell A has an ERF (white) alone, cell B has an IRF (black) alone, and cell C has an ERF surrounded by an IRF. In most cells, the classic RF is surrounded by a disinhibitory region, which can be demonstrated by lengthening stimulus (D). Empty and solid arrows point to the inner borders of IRF and disinhibitory region, respectively. Abbreviations: d, n, v, and t represent dorsal, nasal, ventral, and temporal sides of the visual field, which is rotated by 38° to meet the pigeon's normal conditions.

Visual cells were stereotaxically recorded from Slu [12] with a micropipette (2–3 μm tip diameter) filled with 2 M sodium acetate and 2% pontamine-skyblue. Spikes were amplified, displayed and fed into the computer for off-line analysis. In some experiments, the recording sites of Slu cells were marked with dye applied by negative current 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 and histologically processed for microscopic observation [6].

Among 96 Slu cells examined, 84 cells (88%) responded to visual stimuli in an excitatory fashion (E-type). They fired spontaneously at an average rate of 2.2 spikes/s and responded at 29.6 spikes/s ($n = 72$) to motion in the preferred or temporonasal directions. Twelve others (12%) responded in an inhibitory fashion (I-type). Their average spontaneous rate was 8.0 spikes/s, which was dropped to zero in response to motion in any direction. The ERF of E-type cells was elliptic or irregular in shape, ranging from 3.4 to 33.9° in size. Some E-type cells (7.9%) were characterized by an ERF alone (Fig. 1A), but most E-type cells (92.1%) had an ERF surrounded by an IRF (Fig. 1C). The width of the IRF rings ranged from 4 to 97° with an average of 25.9°. In 65% of these cells, there existed a disinhibitory region surrounding IRF. It was shown by changes in responsiveness to lengthening the rectangle perpendicularly to its direction of motion. For example, 13 cells examined fired spontaneously at 3.1 spikes/s and responded at 31.8 spikes/s to motion of the rectangle equal in length to the maximal ERF extent. When the stimulus was lengthened to completely cover both ERF and IRF, the firing rate was reduced to 4.0 spike/s. The rectangle was further increased in length to cover the screen, the response to motion reached an average rate of 14.4 spikes/s. The saddle-shaped curves of changes in firing rates strongly implied the existence of a disinhibitory region beyond IRF (Fig. 1D). This region was quite large and extended outside of the screen. On the other hand, I-type cells only had an IRF without other observable substructures (Fig. 1B). These IRFs were irregular in shape and large in size ranging

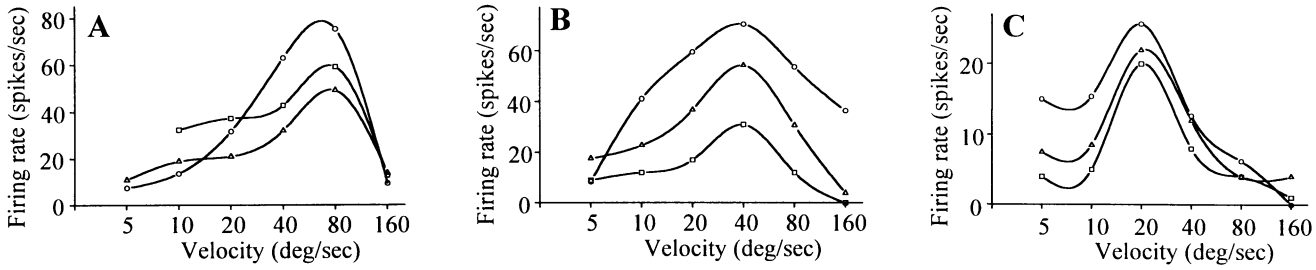

Fig. 2. Velocity-tuning curves of some semilunar neurons showing that these cells could be categorized into fast cells preferring velocity of 80 °/s (A), intermediate cells preferring 40 °/s (B), and slow cells preferring 20 °/s (C).

from 81.2 to 124.1° with an average value of 99.2°. They produced inhibitory responses to motion in any directions.

Fifty-three cells were examined for directional selectivity, which could be described by the directional index (DI) defined as $1 - (f_{min} - f_{spont})/(f_{max} - f_{spont})$ where f_{max} and f_{min} are the maximum and minimum rate, respectively, and f_{spont} is the spontaneous rate. Among 53 cells examined, 19 cells (35.8%) had an average DI value of 0.81 (>0.50) and thus were directional. They mainly preferred forward and downward motion. Thirty-four others (64.2%) were not directional, with an average DI value of 0.26 (<0.50). Thirty-four of 42 cells (81%) examined were selective for the velocity of motion. They included 14 fast cells preferring velocities of 80–160 °/s, 12 intermediate cells preferring 40 °/s, and six slow cells preferring 10–20 °/s (Fig. 2). Two others responded almost equally to motion at wide ranges of velocities. Fifteen of 39 cells (38.5%) examined for contrast sensitivity responded more vigorously to the white stimulus than the black one, with a firing ratio of 1.9:1. Twenty-four others (61.5%) had preferences for black over white stimuli and firing ratio was 2.1:1. The RF centers of white-preferring cells were located in the ventral visual field, whereas those of black-preferring cells were located around the horizontal meridian.

The recording sites of 21 cells including 17 E-type cells and four I-type cells were marked in the nucleus with dye. The E-type cells were located in the dorsal and middle regions whereas the I-type cells mainly in the ventral region of Slu (Fig. 3). Generally speaking, cells with ERF-IRF were located dorsally, those with IRF alone in the ventral part, and those with ERF alone distributed between.

The present study provides the first electrophysiological evidence that avian Slu is a visual center. Its response properties are similar to those recorded from Imc and Ipc in that (i) the RF of isthmic cells is composed of an excitatory center surrounded by an inhibitory periphery [20]; (ii) isthmic neurons are selective for the direction of motion [20,22]. Furthermore, Slu cells are characterized by some additional visual properties. First, some Slu cells have an ERF or IRF alone. Second, Slu cells could be grouped into fast-, intermediate- and slow cells depending on their optimal velocities. It is conceivable that some response properties of Slu cells may stem at least partly from the tectum due to the connections between both structures [9]. For example, tectal [2] and semilunar cells prefer forward and downward motion. Receptive fields in tectal [3,6] and semilunar cells are characterized by an antagonistic organization. However, there exists a disinhibitory region beyond the classic RF in

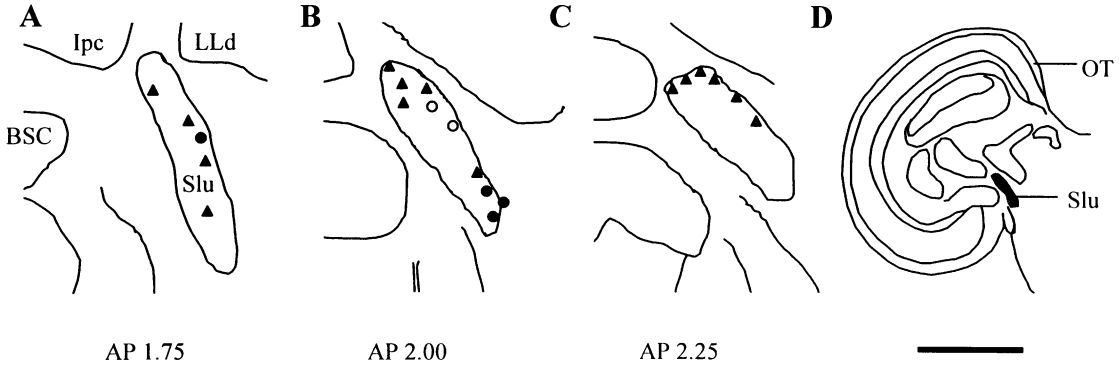

Fig. 3. Distribution of the recording sites of 21 semilunar neurons in cross-sections of the pigeon midbrain at the nucleus semilunaris (Slu) level (A–C). The location of Slu is shown in black in D. AP values are anterior–posterior levels according to the pigeon brain atlas [12]. Solid triangles, circles and empty circles represent neurons whose receptive field is composed of an excitatory receptive field surrounded by an inhibitory receptive field, an inhibitory receptive field alone and an excitatory receptive field alone, respectively. Other abbreviations: BSC, brachium colliculi superioris; Ipc, nucleus isthmi pars parvocellularis; LLd, nucleus lemnisci lateralis pars dorsalis; OT, optic tectum. Scale bar: 600 μm in A–C, and 2 mm in D.

most Slu cells. Some Slu cells and neurons in the ventral tectum only possess an ERF [6]. To our knowledge, 'pure' IRF is only found in I-type of Slu cells. They respond to motion independent of direction, probably signaling the appearance of a moving target.

Imc and Ipc have reciprocal connections with the tectum [7,9,11,21], and send excitatory and inhibitory signals to tectum and thereby modulate ERF and IRF of tectal neurons, respectively [1,17–19]. However, Slu not only has reciprocal connections with the tectum, but also projects to the nucleus rotundus and the lateral spiriform nucleus, which sends output to tectum [9]. Therefore, Slu may modulate tectal activity through both direct and indirect ways. The transformation of retinotopic coding at tectal level into functionotopic coding within the nucleus rotundus [8] may be fulfilled through a direct tectorotundal pathway and two indirect pathways via the pretectal nuclei and Slu [9,10].

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