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VISUAL RESPONSES OF NEURONS IN THE AVIAN NUCLEUS ISTHMI

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Electrophysiological responses of neurons to visual and auditory stimulation are extracellularly recorded from the pigeon isthmic area. Cobalt sulfide markings show that only visual units are localized within the nucleus isthmi pars parvocellularis (Ipc) and pars magnocellularis (Imc), while visual–auditory bimodal units are localized outside. Visual units respond to black or white targets moving through their receptive fields (RFs). The RF centers are mainly distributed in the contralaterally lower visual field. The rostral Ipc and Imc receive information from the nasal visual field, and the caudal part of the Ipc and Imc corresponds to the temporal field. Therefore, both Ipc and Imc are visual centers instead of auditory centers as described before.

Our previous studies have shown that the amphibian nucleus isthmi and the nucleus isthmi pars magnocellularis in reptiles are visual nuclei in the midbrain of these species [14–16], while the nucleus isthmi of submammals has long been proposed to be homologous to the parabigeminal nucleus of mammals [10], which is also closely related to visual information processing [12]. However, until now, there have been only some conflicting electrophysiological results suggesting that the two subdivisions of the avian nucleus isthmi, the parvocellular part (Ipc) and magnocellular part (Imc), could be either important mesencephalic representatives of the auditory system [2, 5] or implicated in the control of pupillary size in the pigeon [13].

It is known that in pigeons a reciprocal topography exists between the optic tectum and the Ipc [6], and the Imc receives its tectal afferent [7], which may also be topographic [18]. More recently, we used diisopropylfluorophosphate pretreatment and acetylcholinesterase (AChE) histochemical techniques to indicate that cells in both the Ipc and the Imc of pigeons contain high concentrations of AChE [11], histochemically resembling the amphibian nucleus isthmi and the reptilian Imc as visual centers [17]. From a comparative viewpoint, it was necessary to carry out an electrophysiological study to reveal the functional significance of the avian nucleus isthmi.

The experiments were performed on pigeons (*Columba livia*) weighing 250–400 g. The animals were anesthetized with 2% pentobarbital sodium (initial dose 0.18 ml/100 g body wt.), paralyzed with gallamine triethiodide (1%, initial dose 0.02–0.05 ml/

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100 g body wt.), artificially ventilated using a unidirectional airflow of an O₂-CO₂ mixture [1], and the body temperature was maintained at 41°C using a heating pad. The left optic tectum was exposed, the dura opened. The center of a perimeter was aimed at the middle point of the interocular line. Visual and auditory stimulation were presented as described previously [15]. Extracellular recordings of spikes were made from the Ipc and Imc with a micropipette (3–4 μm tip diameter) filled with a solution containing 2.5 M NaCl and 100 mM CoCl₂, which was stereotaxically advanced to the targets [8]. At the end of some of the experiments, cobalt ions were ejected iontophoretically to reconstruct the recording sites [14–16].

A total of 75 units, including 73 visual units and two visual-auditory bimodal units, were extracellularly recorded, of which 30 units were histologically localized with cobalt sulfide. Among 28 visual units marked, 15 units were localized within the Ipc, 7 in the Imc and 6 in an area surrounding the Ipc. Two bimodal units were marked 400–700 μm far from the dorsal rim of the Ipc. It appears that both Ipc and Imc in birds are visual centers, whose surroundings also have something to do with vision.

These Ipc units were recorded at an average depth of 3800 μm from the tectal surface. The majority of units produced a weaker spontaneous activity (1.5–5.0 spikes/s). Their receptive fields (RFs) were round or oval in shape, measuring from 15° to 70° with an average size of 46°. All Ipc units responded to black or white discs moving through their RFs, and most of them gave ON-OFF responses to a stationary spot of light. About half of the units were directionally selective, mostly preferring the temporonasal movement (Fig. 1). The Imc units were recorded from a region 3200–4700 μm deep, averaging 4100 μm. In comparison with Ipc units, relatively

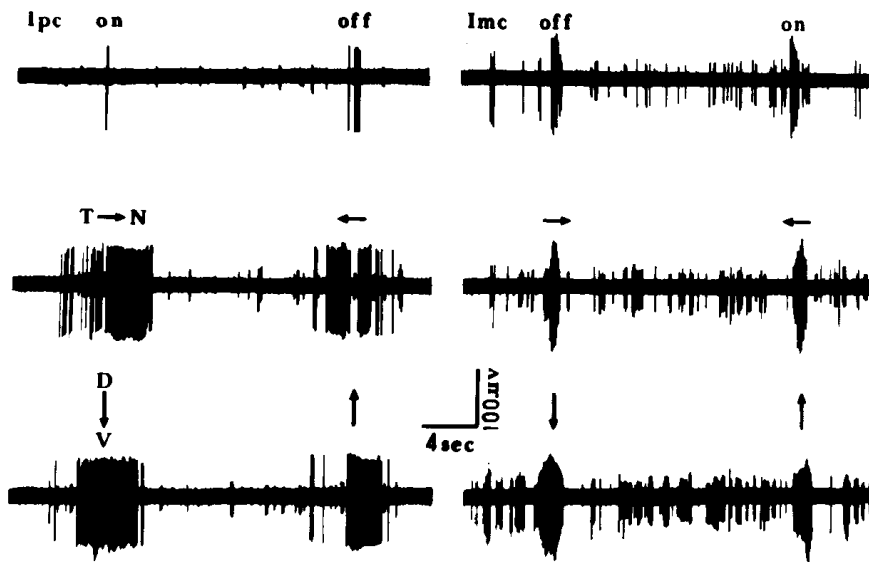


Fig. 1. Discharge patterns of an Ipc unit (left) and an Imc unit (right), responding to on- and offset of a 2° stationary spot of light and to a 7° black disc moving through their RFs in the temporonasal (T-N) and dorsoventral (D-V) or opposite directions. These units correspond to unit 2 and unit d in Fig. 2, respectively.

more units were more spontaneously active (about 10 spikes/s) and less units directionally selective. Regarding the other parameters measured, Imc units were unlikely to be significantly different from Ipc units (Fig. 1). Non-isthmic units marked outside the Ipc and Imc possessed larger RFs (60° average size), temporonasal preference and usually weaker spontaneity. In the other 45 visual units whose recording sites were not marked, the recording depth averaging $3800\ \mu\text{m}$, discharge patterns of responses to visual stimulation and spontaneous activity were similar to those found in Ipc units, while an average RF size of 38° was the same as that of Imc units. It is certain that this group consists of mostly Ipc units, partly Imc units and some non-isthmic units as well.

The RF centers of the visual units recorded were mainly distributed in the contralateral lower visual field, with 13% of RF centers localized in the upper field (Fig. 2B). From the correlation between localization of the recording sites marked in the isthmic nuclei and that of the RF centers plotted in the visual field, it can be seen that the contralateral hemifield was topographically projected on both the Ipc and Imc (Fig. 2A). Roughly speaking, the rostral part of the Ipc receives information from the nasal area of the visual field, whereas the caudal Ipc corresponds to the temporal field. This topography held true for the Imc.

To sum up, the Ipc and Imc are visual nuclei in the avian midbrain. This is compatible with the preceding reports on the amphibian nucleus isthmi [14, 15] and reptilian

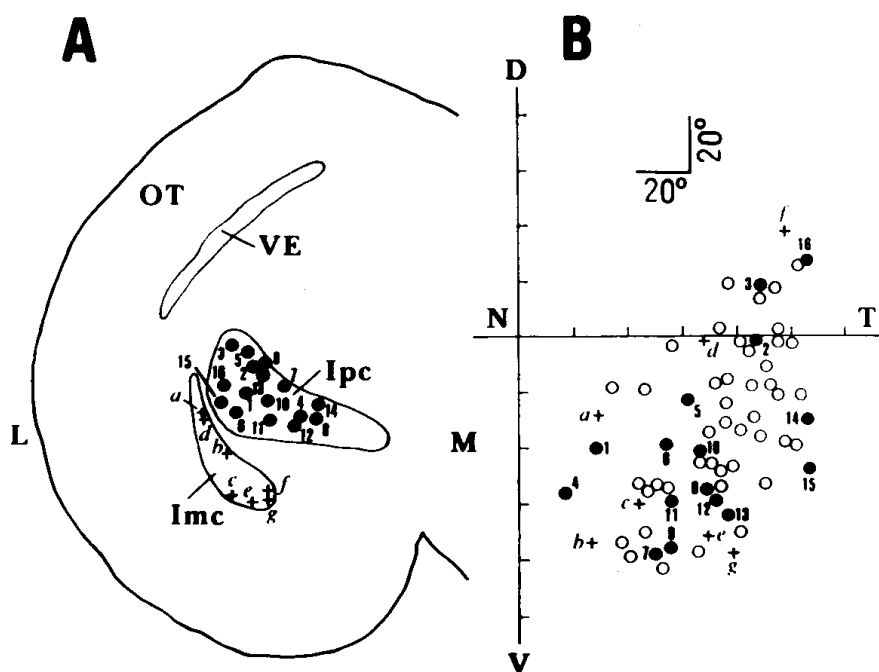


Fig. 2. Correlation between localization of units marked in the Ipc (solid circles, location of unit 2 is inferred from that of a consecutively recorded unit marked) and in the Imc (crosses) (A) and distribution of the RF centers of these units in the visual field (B). Symbols, Arabic numerals and letters in A correspond to those in B. The order of numerals or letters represents arrangement of units in the rostro-caudal direction. Empty circles represent the RF centers of visual units unmarked. D, dorsal; L, lateral; M, medial; N, nasal; T, temporal; V, ventral sides; OT, optic tectum (caudal tectum faces the observer); VE, tectal ventricle.

Imc [16]; however, in reptiles the Imc and Ipc are structurally and functionally independent nuclei [11, 16]. In this study, electrophysiologically mapped, visual field topography in the avian Ipc and Imc could obtain some support from neuroanatomical studies [6, 7, 18]. Auditory responses recorded from the isthmus nuclei [2, 5] may result from the misplacement of electrodes, which were inserted in the adjoining tegmentum or among the lemniscal fibers passing by these nuclei. The participation of the avian nucleus isthmi in the hippus [13] is not easy to explain, although it is known that the area preectalis and Edinger–Westphal nucleus are mediated in the pupillary light reflex of pigeons [3].

Some visual units marked outside the Ipc and Imc suggest that these nuclei may be not so well-bordered functionally as the amphibian nucleus isthmi [14, 15] and the reptilian Imc [16], even though the AChE-stained Ipc and Imc are well-defined [6, 11]. A possible explanation for this difference could be proposed by the suggestion that the avian Ipc and Imc and their adjacent tegmentum form a satellite system of the optic tectum, as in other species [4, 9], which may be a visual complex. The present study also shows that marking microelectrode tip positions is essential for identifying the electrophysiological characteristics of units in a small nucleus deep in the brain.

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