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Discharge patterns evoked by depolarizing current injection in basal optic nucleus neurons of the pigeon

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ABSTRACT: The nucleus of the basal optic root of the accessory optic system in birds is involved in optokinetic nystagmus, which stabilizes images on the retina by compensatory movements of the eyes. The present paper studies the physiological and morphological properties of basal optic neurons in the pigeon by using a brain slice preparation and intracellular recordings. Sixty-one cells examined could be categorized into six types based on their firing patterns in response to depolarizing current injection. Type I cells (54%) fire spontaneously and more spikes as current intensity is increased. Type II cells (15%) discharge regular spikes with similar interspike intervals. Type III cells (5%) show an early burst followed by tonic firing. Type IV cells (5%) fire regular bursts with similar interburst intervals. Type V cells (16%) fire a few spikes in a cluster only at onset of current application. Type VI cells (5%) produce a hump-like depolarization or a single spike depending on current intensities. Seventeen cells stained with Lucifer yellow have multipolar or piriform perikarya (15–28 μm) with two to eight primary dendrites. In some cases, an axon is observed to originate from the cell body, traveling dorsolaterally or dorsally. The physiological significance of these findings is discussed.

KEY WORDS: Accessory optic system, Brain slice, Depolarization, Fluorescent dye, Intracellular recording, Morphology.

INTRODUCTION

The nucleus of the basal optic root (nBOR) in birds is the main component of the accessory optic system, which is involved in generating optokinetic nystagmus, stabilizing images on the retina by compensatory movements of the eyes. It receives input from the retinal displaced ganglion cells [7,17,29], visual forebrain [3,31], contralateral nBOR and ipsilateral nucleus lentiformis mesencephali (nLM) [2,24,35], and projects to the contralateral nBOR, ipsilateral nLM, vestibulocerebellum and oculomotor complex [1,2,11,43,44], as well as to the hippocampal formation [42] and the inferior olive [39]. Recent studies have shown that nBOR also has neuronal connections with the nucleus rotundus in the tectofugal pathway [6,34]. Although much is known about anatomical connections of nBOR with other neuronal structures, knowledge about the morphological features of avian nBOR cells is still lacking.

Extensive physiological studies have indicated that nBOR cells in birds could be classified into several groups based on their selectivity for the direction and velocity of motion [8,23,38,40,41,45]. They are mainly categorized as cells preferring nasotemporal motion, those preferring dorsoventral motion and those preferring ventrodorsal motion, or slow-, intermediate-, and fast-velocity cells. Recent studies have found that nBOR cells in pigeons could be divided into three groups based on their responses to the orientation of stationary gratings. The first group of cells is orientation selective, the second group responds to stimuli at any orientations, and the third group is unresponsive to stationary oriented stimuli [12]. On the other hand, brain slice studies have shown that rotundal neurons and the tectal cells projecting to the nucleus rotundus discharge spikes only in two patterns in response to somatic current injection [15,20] even though there are several functional subdivisions in the nucleus rotundus and its neurons are differentiated by several distinct physiological properties [18,36,37]. We wondered whether it would be the case with basal optic cells. In view of the fact that it is very hard to make *in vivo* intracellular recordings from nBOR due to its location deep in the brain and close to the skull, the present study was, therefore, carried out in brain slices. In order to reveal (1) discharge patterns intrinsic to nBOR cells and (2) morphological features of some electrophysiologically identified neurons, intracellular recording and staining techniques were used.

MATERIALS AND METHODS

The experiments were performed on brain slices of 26 pigeons (*Columba livia*) with body weight of 280–380 g, following the policy on the use of animals in neuroscience research approved by the Society for Neuroscience. Each pigeon was anesthetized with ketamine hydrochloride (40 mg/100 g) and then decapitated. Its brain was immediately removed from the skull, and washed in ice-cold Krebs–Ringer solution containing (in mM) NaCl, 124; KCl, 5; $CaCl_2$, 2; $MgSO_4$, 2; KH_2PO_4, 1.25; $NaHCO_3$, 26; glucose 10 [13], oxygenated with a mixture of 95% O_2 and 5% CO_2. A brain block containing nBOR was glued on the stage of Vibroslice (Campden Instruments Ltd., 752M, LE12 7IZ, UK). Slices were coronally sectioned at 400 μm in thickness, and then transferred from a storage container into the recording chamber (BSC-HT, Medical System Corp., Greenvale, NY, USA) perfused with Krebs–Ringer solution

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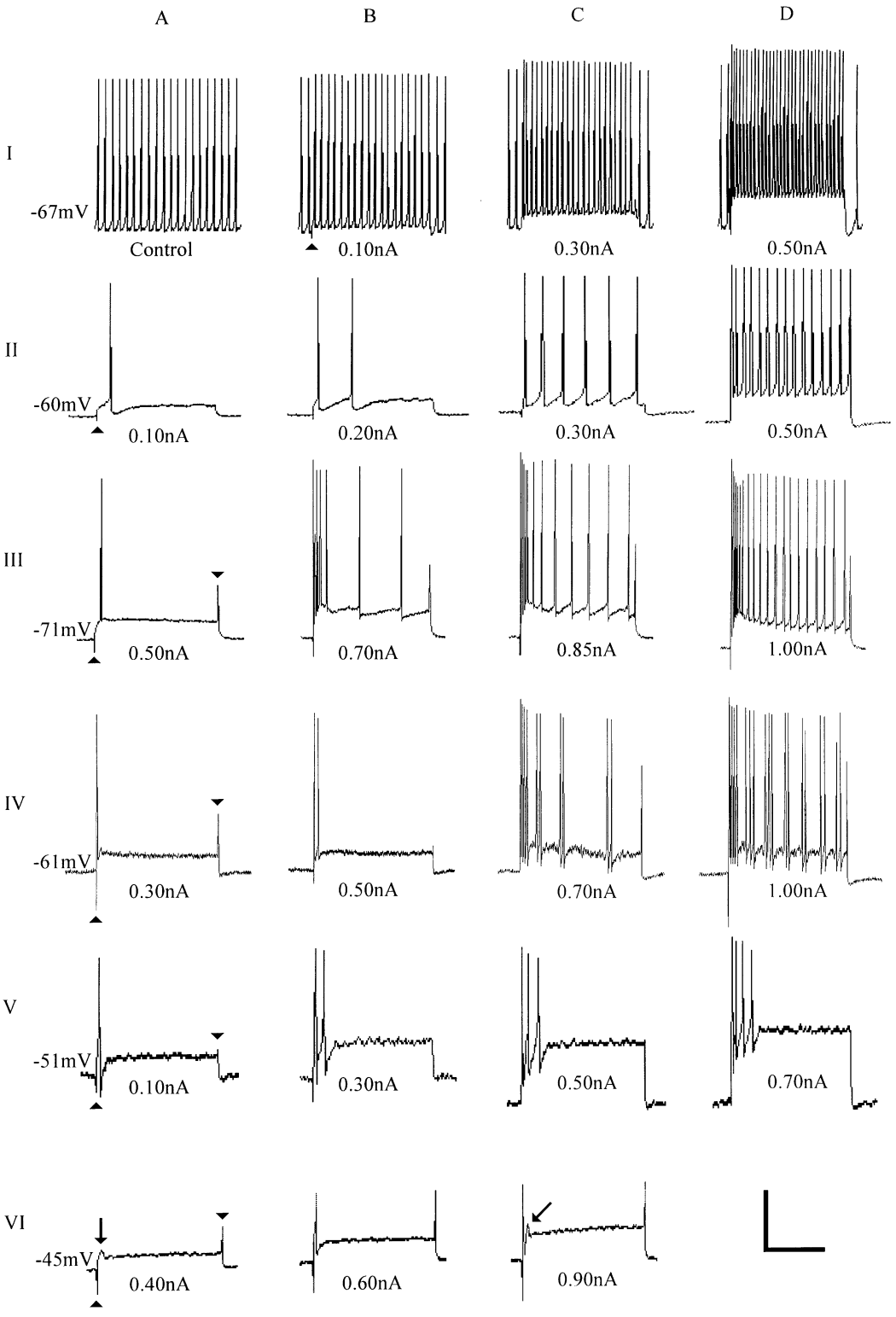

FIG. 1. Six firing patterns of nBOR neurons in response to depolarizing current injections, which were recorded from steadily spontaneous cells (I), regular-spiking cells (II), early-bursting cells (III), regular-bursting cells (IV), frequency-adaptation cells (V), and spiking-inactivation cells (VI), respectively. Upward and downward arrowheads in the first column of recording traces obtained at current thresholds point to artifacts produced by the start and end of current injection, whose intensities are shown in increasing magnitude (nA) from A to D. Artifacts in other recording traces are not labeled for clarity. Arrows in VI signify a hump-like depolarization. Scales: 150 ms, 20 mV.

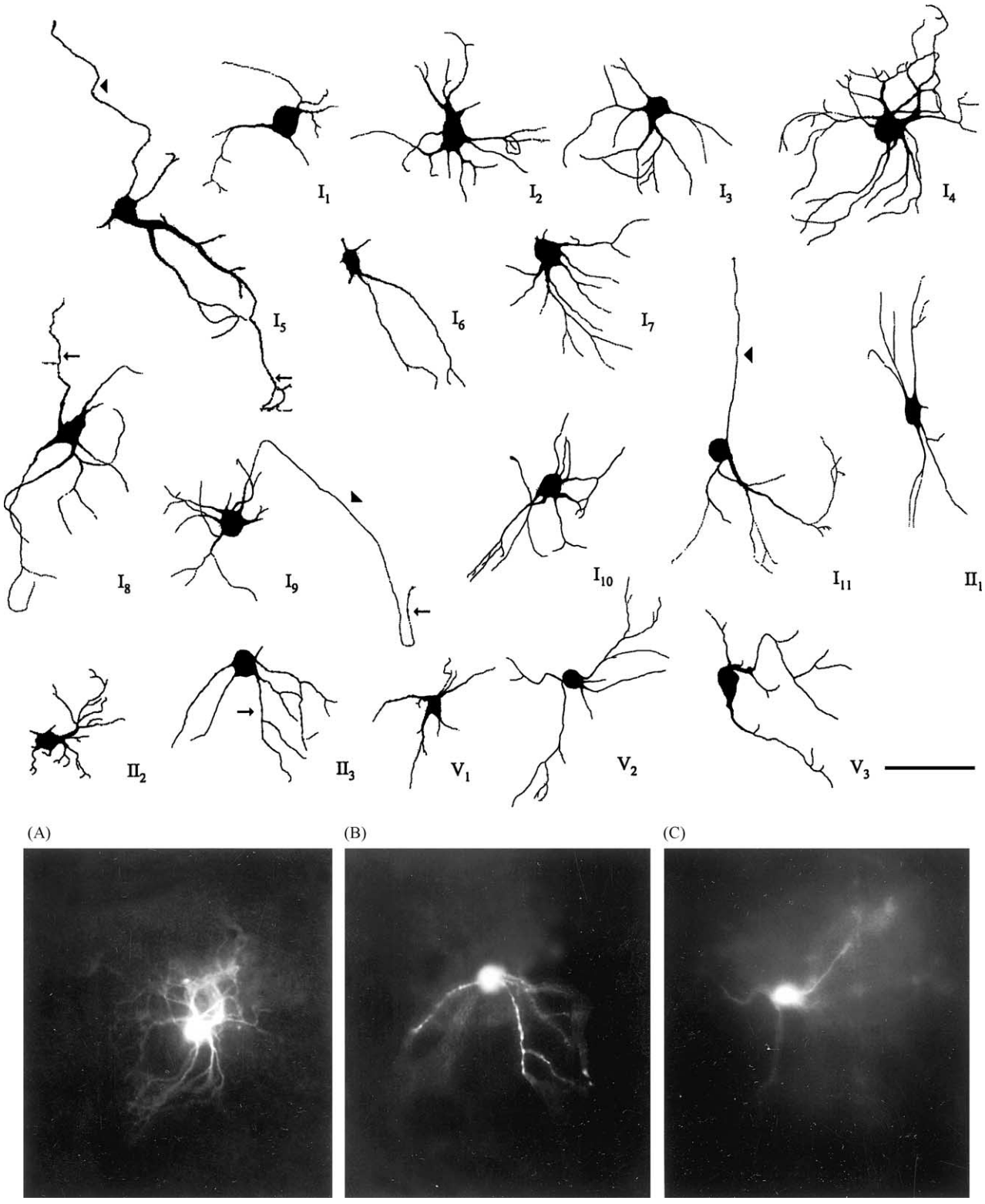

FIG. 2. Computer-aided reconstruction drawings of morphological features (top) and microphotographs (bottom) of nBOR cells stained with Lucifer yellow. Cells $I_{1–11}$, $II_{1–3}$, and $V_{1–3}$ are physiologically identified as cells of I, II, and V types, respectively. Microphotographs of cells I_4, II_3, and V_2 are shown in A, B, and C, respectively. The orientations of morphological structures in the drawings and photos are the same as in cross-sections of the nucleus. Dorsal is up, and lateral is to the left. Arrowheads point to axons. Arrows point to varicosities on dendrites or axons. Scale bar: 100 μm.

bubbled with 95% O_2 and 5% CO_2 at a rate of 2 ml/min. The slices were incubated at $35 \pm 1^{\circ}C$ for 60 min before being recorded.

For intracellular recording and staining, a micropipette (0.5–1 μm tip diameter) filled with either 3 M potassium acetate (impedance = 25–75 MΩ) or a solution of 3% Lucifer yellow (dilithium salt, Sigma Chemical Co., St. Louis, MO, USA) plus 0.1 M LiCl [25] (impedance = 95–250 MΩ) was advanced into nBOR in slices under microscopic control. Neurons were impaled by applying brief positive current pulses (4 nA in intensity, 0.3 s in duration) and intracellular impalement was signaled by a sudden d.c. drop of 30–75 mV. The firing responses of nBOR cells were examined by injecting depolarizing current pulses of 0.05–1.0 nA in several intensity steps and 200–400 ms in each injection duration. During current injections, intracellular recordings were made in bridge mode because the electrodes had high impedance. Intracellular potentials or spikes were amplified with a preamplifier (WPI Intra 767, Sarasota, FL, USA), displayed on a digital oscilloscope (VC-7104, Hitachi Denshi Ltd., Tokyo) and stored on magnetic tapes (TEAC RD-135T Data Recorder, TEAC Corp., Tokyo), and then off-line analyzed with a computer.

In some experiments, electrophysiologically identified nBOR cells were injected with dye by passing a negative current of 2–4 nA for 2–20 min, with one injection in one slice in most cases. After 0.5–2 h survival, slices were removed from the recording chamber, fixed in 4% paraformaldehyde and kept in a refrigerator overnight. They were rinsed with physiological saline and then placed in 100% dimethylsulfoxide (DMSO) for 20 min [9]. The slices containing dye-marked cells were coverslipped and photographed at different depths of focus with a fluorescence microscope (Nikon Microphot FXA, BV filter). The morphology of nBOR cells was then scanned with a scanner (StudioStar, AGFA, Hong Kong) into a computer and reconstructed with software tools of Adobe Photoshop 5.0.

RESULTS

Sixty-one nBOR cells were intracellularly recorded at depths ranging from 26 to 290 μm to the surface, and examined for their firing responses to depolarizing current injection. Their resting membrane potential ranged from −30 to −75 mV, with an average value of -56 ± 10 mV (mean ± SD, $n = 61$).

On the basis of their firing behavior in response to depolarizing current injection, these cells could be categorized into six types. Type I contained 33 steadily spontaneous cells (54%), whose firing rate ranged from 40 to 90 spikes/s with an average rate of 67 ± 17 spikes/s and firing lasted up to 1 h. Their threshold current was in the range of 0.05–0.15 nA, and firing rates increased as current intensities were increased. Their tonic firing lasted steadily during the current injection. For example, the cell shown in Fig. 1I spontaneously discharged at a rate of 57 spikes/s, whereas current intensities of 0.10, 0.30, and 0.50 nA could elicit firing rates at 60, 76, and 103 spikes/s, respectively. Type II included 9 regular-spiking cells (15%) (Fig. 1II). They fired a single spike in response to the threshold current pulses (0.10–0.20 nA). Higher current intensities (0.20–0.50 nA) induced higher repetitive firing rates (6–47 spikes/s). It should be noted that the second values of lower intensities usually overlapped (for example, 0.20 nA) the first values of higher intensities because these data were obtained from a group of cells. Further increases in current intensities up to 1.0 nA could produce firing rates of up to 100 spikes/s. The interspike intervals were not obviously altered.

In type III were three early-bursting cells (5%) (Fig. 1III). They fired a single spike in response to the threshold current pulses (0.30–0.70 nA). An increase in current intensities (0.50–0.80 nA) evoked a burst consisting of 2–3 spikes, which was followed by solitary spikes (13–25 spikes/s). Further increases in intensities (0.70–1.0 nA) produced a high-frequency burst (190–300 spikes/s), which was followed by tonic firing (56–100 spikes/s), with similar interspike intervals. In type IV were three regular-bursting cells (5%) (Fig. 1IV). They fired a single spike at the threshold current intensities (0.30–0.50 nA). Higher intensities of current (0.50–0.70 nA) evoked a single burst consisting of 2–3 spikes. Further increase in intensities (0.70–1.0 nA) produced a series of bursts with similar interburst intervals. A burst consisted of 2–8 spikes and intraburst frequencies were 102–213 spikes/s.

Ten frequency-adaptation cells (16%) were of type V (Fig. 1V). They fired a single spike at the threshold intensities (0.10–0.20 nA). Higher intensities of current (0.30–0.50 nA) produced 2–3 spikes with frequencies of 60–90 spikes/s. Further increases in current intensities (0.70–1.0 nA) elicited 4–5 spikes with frequencies of 90–210 spikes/s. In these cases, all spikes were clustered in a short spiking phase, which was followed by adaptation phase where no spikes were produced. Three spiking-inactivation cells (5%) were of type VI (Fig. 1VI). At the threshold levels (0.20–0.50 nA), current injection could induce a hump-like depolarization. Higher intensities of current (0.50–0.80 nA) fired a single spike from this hump-like depolarization. Further increases in current intensities (0.70–1.0 nA) produced a spike followed by a hump-like depolarization. Two of these cells were examined on the same slice preparations, where type I cells were also examined.

Of the recorded cells, 17 were intracellularly stained with dye, including 11 type I cells (Fig. $2I_{1–11}$), 3 type II cells (Fig. $2II_{1–3}$), and 3 type V cells (Fig. $2V_{1–3}$). Cells in types III, IV, and VI were not successfully stained. As shown in Fig. 2, type I cells were morphologically diverse, but they could be generally divided into two groups. The first group of cells (I_5 and I_{11}) had piriform perikarya (23–25 μm), which issued an apical and 1–2 thin primary

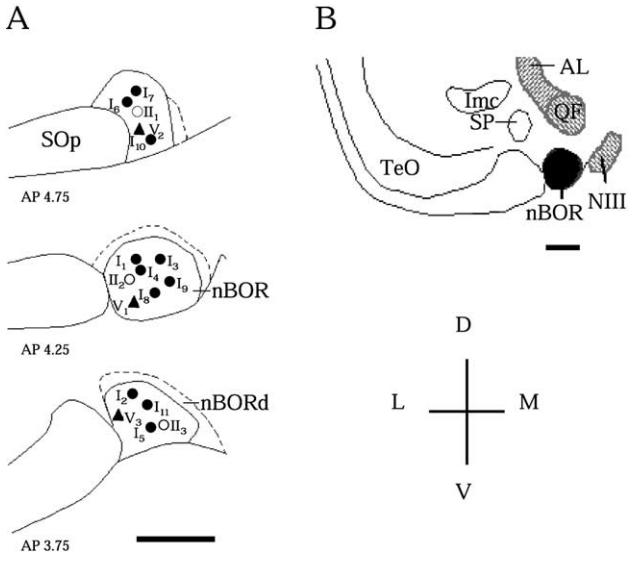

FIG. 3. Distribution of intracellularly stained cells in the nucleus of the basal optic root (nBOR) (A), whose location is shown in a cross-section of the pigeon brain (B). Solid and empty circles, and solid triangles represent cells of types I, II, and V, respectively. Morphologies of these cells are depicted in Fig. 2 with corresponding labelings. AP, anterior–posterior levels in the pigeon brain atlas [16]. D, L, V, and M represent dorsal, lateral, ventral, and medial, respectively. Other abbreviations: nBORd, nBOR dorsalis; SOp, stratum opticum; SP, nucleus subpretectalis; Imc, nucleus isthmi pars magnocellularis; AL, ansa lenticularis; QF, tractus quintofrontalis; NIII, nervus oculomotoris; TeO, tectum opticum. Scale bars: 1 mm.

dendrites, as well as an axon traveling dorsally or dorsolaterally. The primary dendrites gave off a few branches, some of which bore varicosities. Cells in the second group were characterized by multipolar perikarya (17–28 μm), which radiated 4–8 primary dendrites with no or few branches. Some dendrites in these cells bore varicosities. One cell (I_9) issued from its soma a tortuous axon, which traveled dorsomedially and then turned ventromedially, and turned again dorsally after forming a pin-like loop. This axon bore some varicosities in the pin-like loop. Cells in type II had multipolar perikarya (16–25 μm), which radiated 4–5 primary dendrites with no or some branches. Cell II_3 bore numerous varicosities in its dendrites. Type V cells were characterized by multipolar or piriform perikarya (15–26 μm), which issued 2–4 primary dendrites giving rise to no or few branches. A few dendrites or branches bore varicosities. Axons in type II and V cells were not observed. Generally speaking, these cells could be grouped into large (26–28 μm), medium (23–25 μm), and small (15–20 μm) cells according to their perikaryal size. Perikarya in large cells ($I_{1,2,4,7,10}$, II_3, V_3) were multipolar or piriform in shape, those in medium cells ($I_{3,5,8,9,11}$, II_2) were multipolar or round shaped, and those in small cells (I_6, II_1, $V_{1,2}$) were round or fusiform except cell V_1 whose cell body was multipolar. It appears that most physiological type I cells belong to large- and medium-sized ones (Fig. 2). Distribution of their recording sites is shown in Fig. 3, demonstrating no observable correlation between the locations and discharge patterns of the recorded cells in response to depolarizing current injection in such a small sample of cells.

DISCUSSION

We found very variable responses of nBOR neurons to intrasomatic current injection in our slice study. There are at least six physiological types of neurons within the pigeon nBOR. In agreement with *in vivo* extracellular recordings [6,35,45], most nBOR neurons in brain slices are spontaneously active, demonstrating that spontaneous activity is likely to be generated by ionic mechanisms intrinsic to nBOR cells. These cells and type II cells all respond to depolarizing current injection in tonic mode, i.e., their firing frequency increases as current strength is increased. This firing mode is most frequently observed in excitatory responses both on *in vitro* and on *in vivo* preparations because it affords linear summation [33]. The discharge pattern in type III cells may represent a transition from bursting mode to tonic mode. It has been reported in the rat superior colliculus [32], and in the visual cortex of cats [10] and turtles [21]. The firing pattern of the regular-bursting cells (type IV) is similar to that of chattering cells in the visual cortex [10,21] and in the avian tectum [13,20]. It is interesting to note that a group of nBOR cells fire regular bursts in response to stationary objects within their receptive fields [12]. Burst firing provides better signal detection, perhaps acts as a “wake-up call”, signaling something changed in the environment [33]. It may also mediate synchronous firing in assemblies of neurons [10], as well as synaptic plasticity [14,19]. The frequency-adaptation pattern has been described in tectal cells [13,32]. The spike-inactivation has been observed in rats [32] and pigeons [15]. It is unlikely that these responses are pathological due to the deterioration of neuronal vitality, because some of them are recorded in slices where other types of cells are also examined. The transient nature of these patterns may suggest that these cells could provide a starting or warning signal reporting that something comes into or starts to move in the receptive field of the cell. Although the threshold of current intensity for eliciting discharges varies from cell to cell, it appears that the threshold values of I, II and V types are lower than other types of cells. This difference in thresholds may be attributed to intrinsic properties of the cells, but its real physiological significance is unclear.

Intracellular stainings show that nBOR neurons possess diverse morphologies and are characterized by multipolar, piriform, or fusiform perikarya, which give rise to several primary dendrites with or without branches. They could be grouped into large, medium, and small cells. These results are generally in accordance with those by other authors. Rio [30] revealed three morphological types of nBOR neurons in the pigeon: large multipolar neurons, medium fusiform neurons, and small round neurons. Brecha et al. [2] also described three types of neurons in the pigeon nBOR: large stellate, medium ovoid, and small fusiform neurons. The classification criteria used in the present study and the previous studies are similar in somatic size measurements but different in shape description. This difference in morphological description might be due to a sampling bias. Although the neuron number in the pigeon nBOR is not reported to date, the number of nBOR neurons in the chick is about 8240 [26]. There is no doubt that, for example, the present study only describes few thousandths of total number of nBOR neurons. However, it seems likely that nBOR neurons may have some morphological differences between various species. There exist four types of nBOR cells in chicks: large multipolar neurons, medium fusiform neurons with many dendritic branches, medium fusiform neurons with few dendritic branches, and small round neurons [27]. It has been proposed that there may be some corresponding relationship between morphological types of nBOR neurons in pigeons and chicks [22,27]. Small neurons may be intrinsic interneurons [27,30], while large and medium-sized neurons are projecting neurons [30]. In the present study, axons are seldom observed probably due to the incompleteness of the dye filling and/or visualization of the cells. In these circumstances, thin dendritic processes may be not completely observed, either. To facilitate the observation of fine processes, either confocal microscopy or re-cut sections of the slices should be used. An axon in cell I_5 travels dorsolaterally and apparently goes to nLM or the dorsolateral thalamus, and axons in cells I_9 and I_{11} travel dorsally and probably go to the contralateral nBOR [44]. These cells of type I are all spontaneously active and discharge regularly in response to depolarizing current injection, but they are characterized by different morphologies as shown in Fig. 3. It appears that discharge patterns and morphological features of nBOR neurons might not be related. The correlation of physiological properties with morphological features of neurons has been revealed in the visual cortex [4,5] and the optic tectum [20], but not in the suprachiasmatic nucleus [28] and the nucleus rotundus [15]. Failure to revealing morphological correlates, if any, of physiological types might be due to a small sample of neurons examined.

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