

RESEARCH ARTICLE

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Receptive field properties of visual neurons in the avian nucleus lentiformis mesencephali

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Abstract The receptive field (RF) properties of visual neurons extracellularly recorded from the nucleus lentiformis mesencephali (nLM) in pigeons (*Columba livia*) were quantitatively analyzed using a workstation computer. These cells were actively spontaneous, and direction- and velocity-selective. Using spatial gratings as visual stimuli, these cells could be divided into three groups: uni- (74%), bi- (17%), and omnidirectional (9%) cells in terms of their directionality. On the basis of their velocity selectivity, they could be named slow cells (84%), preferring low velocity (0.1–11°/s), and fast cells (14%), preferring rapid motion (34–67°/s), with one cell (2%) responding maximally to an intermediate velocity of 18°/s. These two properties were correlated in the way that all unidirectionals were slow cells, omnidirectionals were fast cells, and bidirectionals were either slow or fast cells including the intermediate cell. Using small targets as visual stimuli, it was found that the majority of cells examined had RFs that each consisted of an excitatory RF (ERF) and an inhibitory RF (IRF) that overlapped. The unidirectionals were mainly of this type of RF structure, whereas the omnidirectionals apparently had ERFs alone. The direction preference of ERF was opposite to that of IRF for unidirectional cells tested, whereas they were perpendicular to each other for one bidirectional cell. The overall responses of these cells resulted from interaction between excitation and inhibition induced by directionally different motion. Under certain conditions, visual responses of a particular cells to a small target moving through its ERF were equal in responsive strength to those to whole-field gratings swept over the screen. It was suggested that optokinetic nystagmus produced by whole-field gratings results from population activity of large group(s) of neurons in some optokinetic nuclei, at least one of which is nLM.

Key words Nucleus lentiformis mesencephali · Receptive field · Optokinetic nystagmus · Directionality · Velocity selectivity · Pigeon

Introduction

Optokinetic nystagmus (OKN) is a visuomotor reflex, which stabilizes an image on the retina by compensatory movement of the eyes. It is composed of the ocular following responses (slow phase) and resetting saccades (fast phase). Extensive studies have shown that horizontal OKN (hOKN) is mediated by the nucleus lentiformis mesencephali (nLM) in lower vertebrates and by the nucleus of the optic tract (NOT) in mammals. For example, several neurobehavioral studies have indicated that destruction of these nuclei reduces or eliminates hOKN in frogs (Fite and Montgomery 1982; Lázár et al. 1983); in pigeons (Gioanni et al. 1983), in rabbits (Collewijn 1975a), and in monkeys (Kato et al. 1986, 1988, Schiff et al. 1990). On the other hand, electrical stimulation of NOT causes a strong hOKN with slow tracking to the ipsiversive side in rabbits (Collewijn 1975a) and in monkeys (Schiff et al. 1988; Mustari and Fuchs 1990). A metabolic [¹⁴C]2-deoxyglucose (2-DG) mapping method has indicated that large-field stimulation with many contrasts produces great uptake of 2-DG in the avian nLM (Chown et al. 1984; McKenna and Wallman 1981, 1985). This uptake also occurs in the amphibian nLM, the nucleus pretectalis, and pretectal gray, with high levels of 2-DG uptake being correlated with both temporal-to-nasal (T-N) and nasal-to-temporal (N-T) motion of optokinetic stimuli (Fite et al. 1992). By using pharmacological injection and search-coil recording techniques, some authors have further confirmed the mediation of nLM of frogs (Jardon and Bonaventure 1992) and of chickens (Bonaventure et al. 1992) in producing hOKN and found that cholinergic substances can significantly affect the directional asymmetry of hOKN.

Electrophysiological recordings have provided further evidence for the involvement of nLM in OKN. Most of

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units recorded from nLM of frogs (Fite et al. 1989; Li et al. 1996), turtles (Fan et al. 1995), pigeons (Winterson and Brauth 1985), and from NOT of various species of mammals including rabbits (Collewyn 1975b), cats (Hoffmann and Schoppmann 1975, 1981; Distler and Hoffmann 1993), opossums (Volchan et al. 1989), wallabies (Ibbotson et al. 1994; Ibbotson and Mark 1996), ferrets (Klauer et al. 1990), and monkeys (Hoffmann et al. 1988; Hoffmann and Distler 1989; Mustari and Fuchs 1990) are direction-selective, preferring temporal-to-nasal motion of visual stimulus provided to the monocular viewing eye. In some species, many units are excited by the preferred direction of motion and may be inhibited by motion in the opposite direction (Winterson and Brauth 1985; Volchan et al. 1989; Klauer et al. 1990). Recently, Ibbotson and Mark (1994) have identified nondirectional visual units in the wallaby NOT and suggested that these cells may provide inhibitory input to the directional neurons of NOT, preventing ocular following of saccade-induced visual displacements. Visual units in both nLM and in its mammalian homologue NOT are also velocity-selective. They could be classified into two groups according to their preferred velocity, slow cells preferring low velocity and fast cells preferring high velocity, in birds (Winterson and Brauth 1985) and in mammals (Ibbotson et al. 1994; Ibbotson and Mark 1996). All these properties of visual units in nLM and NOT are compatible to those needed for the generation of OKN. Moreover, there exist "jerk neurons" in the mammalian NOT and they discharge short and high-frequency bursts to fast motion of a large-patterned stimulus. These neurons might be a sensorimotor interface between visual stimuli and saccades (Schweigart and Hoffmann 1992). In primates, visual units recorded from NOT and the dorsal terminal nucleus (DTN) of the accessory optic tract respond not only to a large-field pattern but also to a single target (spots or lines; Hoffmann et al. 1988; Hoffmann and Distler 1989; Mustari and Fuchs 1990). The responsive properties of these NOT-DTN neurons to a small moving target might make a possible contribution to smooth pursuit of the eyes (Hoffmann et al. 1988). Up to now, this property has been reported neither in nonprimate mammals nor in lower vertebrates. Also, very little is known about the functional structure of receptive fields of visual units in nLM and NOT.

Compared with mammals, lower vertebrates have received little attention on electrophysiological characteristics of visual units related to optokinetic nystagmus. Therefore, we intended in the present study to use a powerful graphics computer to give a detailed description of the functional structure of receptive fields and of responsive properties of the avian nLM. It turned out that the electrophysiological properties of the avian nLM units appear to be similar to those of the mammalian NOT units.

Materials and methods

The experiments were performed on 18 adult homing pigeons (*Columba livia*), with body weights of 300–430 g, of either sex, and un-

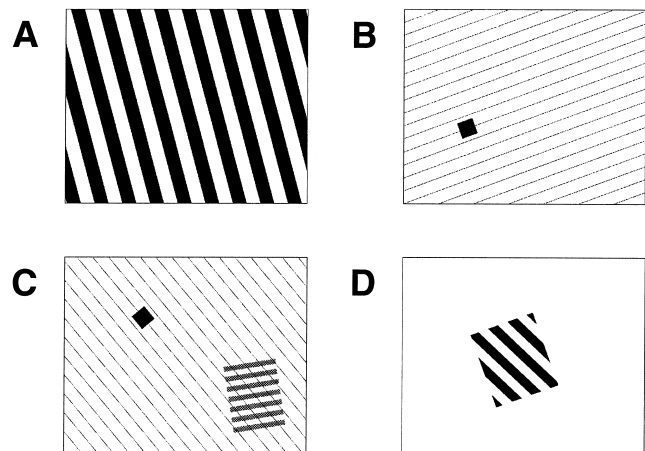


Fig. 1A–D Visual stimulation patterns used in the present study. **A** Spatial gratings of black and white stripes (0.1 cycles/deg). **B** Single small square (edges 1–20 cm) moving at random along imaginary lines used to plot the extent and the location of receptive fields. **C** Grating-square combination stimulation used to explore inhibitory responses of a weakly spontaneous cell to visual activity induced by restricted gratings moving within its excitatory receptive field. **D** Restricted stimulation applied to a circumscribed subregion of the receptive field

der guidelines regarding the care and use of animals, established by the American Physiological Society and by the Society for Neuroscience. The pigeon was anesthetized with urethane (20%, 1 ml/100 g i.m.), and then placed in a stereotaxic apparatus. The body temperature was maintained at 41° C by a heating pad. The caudal forebrain on the left side was surgically exposed and the dura mater overlaying the nLM was opened. The nictitating membrane of the right eye was removed and the left eye covered with an occluder to prevent viewing. Under our experimental conditions, the stereotaxic coordinates of the magnocellular nLM (LMmc; Karten and Hodós 1967) were modified, using cobalt sulfide markings (Wang et al. 1981), to be AP 5.85–6.10, ML 3.90–4.20, and DV 8.20–10.90 mm. Ten markings showed that all those units were localized throughout LMmc, which were isolated from this stereotaxically defined area and had visual responses to a large-field stimulation. In view of the fact that the angle between the horizontal meridian of the visual field and the eye center-bill tip line of the stereotaxically fixed pigeon is 72°, while it is about 34° under the pigeon's normal conditions for flying, walking, standing, and perching (Erichsen et al. 1989), the horizontal meridian was rotated by about 38°. The pecten was plotted with an ophthalmoscope on the screen. The relative positions of the optic axis, horizontal meridian, vertical meridian, and pecten on the screen verified the correctness of this modification (see Fig. 4). The coordinates in Figs. 2 and 3 were also corrected. The screen was positioned 40 cm distant from the viewing eye and 24° to the midsagittal plane of the pigeon, and measured 180 cm in height and 220 cm in width. The area being visually stimulated was about 140° (horizontal angle) × 130° (vertical angle).

A variety of visual stimuli were generated by a graphics workstation (SiliconGraphics Indigo2) and rear-projected by a three-color projector (Electrohome ECP 4101) onto the screen. Visual stimuli used here were the following: (1) black-and-white stripe gratings oriented perpendicular to their motion direction (Fig. 1A); (2) black or white squares moving on white, black, or random-dotted background (Fig. 1B). The small squares were used not only for examining visual responses of nLM neurons recorded but also for plotting the location and the extent of the receptive fields by moving them randomly along numerous parallel paths covering the whole screen (for example, oblique lines in Fig. 1B). If a neuron under test was very weakly spontaneous, a grating was restricted to and moved over its excitatory receptive field (ERF) and a square was used to examine inhibitory responses of this cell (Fig. 1C). This restricted stimu-

lation was also used to examine the effects of the stimulated region of the visual field on the neuronal firings (Fig. 1D). In the present experiments, spatial frequency of gratings was 0.05–1.0 (usually 0.1) cycles/deg and contrast between black and white stripes was 0.97, defined as $(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$. The square's dimension was 1–20 cm. These stimuli were moved randomly in eight directions ($0^\circ, 45^\circ, 90^\circ, 135^\circ, 180^\circ, 225^\circ, 270^\circ, 315^\circ$) at a series of velocities (0.125, 0.25, 0.5, 1, 2, 4, ..., 128, 256 cm/s). Angular velocities in the present paper are mean values calculated from the linear velocity under certain stimulation conditions. The interval between two stimulations was more than 10 s for complete recovery. Generally speaking, nLM cells produced the strongest responses during the first 0.5 s after onset of grating stimulation, and then the discharge gradually became steady. The mean firing frequency calculated in the first 5 s was considered to be response strength under certain circumstances (direction and velocity).

Electrodes for extracellular recordings were micropipettes filled with a solution containing 2 M NaCl and 100mM CoCl₂, and their tip diameter was 1–3 μm , with an impedance of 5–15 M Ω . Neuronal action potentials were preamplified and fed into the workstation for on-line processing of the data. By the end of the experiments, cobalt ions were ejected by positive current (3–5 μA , 0.5 s in duration, 1 Hz in frequency, 5–10 min) into the recording sites. The animals was killed by overdose of anesthetic and its brain removed from the skull. The brain block was immersed in 10% ammonium sulfide in saline for 30–45 min to form black cobalt sulfide. It was postfixed in 10% formalin for 48 h and frozen-cut at 60 μm thickness. The sections were conventionally processed for histological verification of the recording sites.

Results

Fifty-four cells were isolated from the nLM area, and they were usually discharging spontaneously, with a mean firing rate of 14.3 spikes/s. The recording sites of 10 out of 54 cells were marked with cobalt sulfide and all histologically verified to be localized throughout the magnocellular nLM, showing the reliability of our finding nLM cells by a combination of their stereotaxic coordinates and visual responses. They vigorously responded to motion not only of a whole-field stimulus but also of a small target ($5\text{--}13^\circ$ in diameter) through their receptive fields, especially in the horizontal direction.

Direction and velocity selectivities

Visual responses of 54 nLM cells were measured to motion of black-and-white stripe gratings moving through their RFs in eight directions and represented by direction-selectivity diagrams (Fig. 2). According to these diagrams, the cells fell into 3 groups. Unidirectional cells included 40 cells (74%) that had unidirectionally tuning diagrams (Fig. 2A). Motion in a particular direction (usually, horizontal) induced the maximal responses of the cell, other directions of motion produced weaker or no responses, and movement in the direction opposite to this preferred direction depressed the cell's responses (non-preferred or null direction). Spontaneous activity in most of cells (93%) was reduced by more than 50% by motion in the null direction. Nine (17%) bidirectional cells had more or less symmetrical tuning diagrams. They produced stronger responses in two opposite directions. Some of

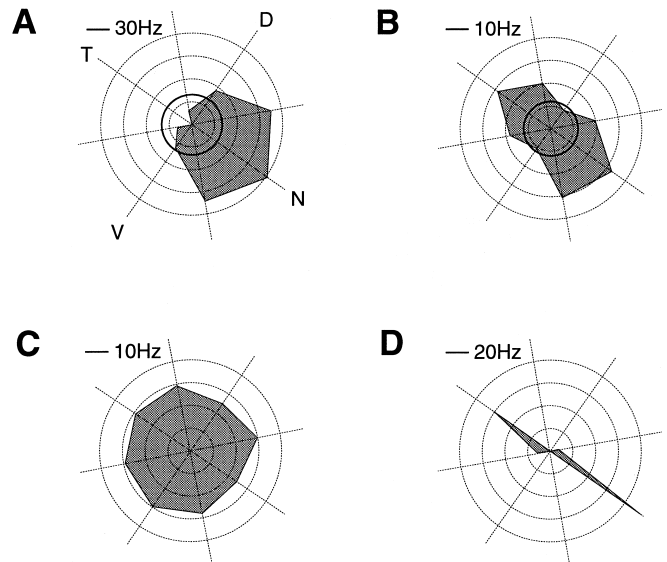


Fig. 2A–D Directional tuning diagrams of four nucleus lentiformis mesencephali cells as examples. **A** Unidirectional cell preferring temporonasal motion was depressed by nasotemporal motion. Note that spontaneous activity was abolished (*notch*). **B** Bidirectional cell was broadly tuned for both temporonasal and nasotemporal motion and slightly depressed by upward motion; whereas the cell in **D** was sharply tuned for horizontal motion and did not respond to any other directions of motion. **C** Omnidirectional or nondirectional cell almost equally responding to all directions of motion. No inhibition was observed in any direction. Equal firing-rate circles are spaced by 10–30 Hz, as indicated by *calibration bars*. *Boldfaced circles* represent spontaneous activity level and cells in **C** and **D** had no spontaneity (*N, T, D, V* nasal, temporal, dorsal, ventral)

them were broadly tuned (Fig. 2B) and others sharply tuned (Fig. 2D). In these cells, their non-preferred direction was perpendicular to the preferred direction. However, lower percentages of the bidirectionals were depressed and this perpendicular depression was weaker (usually by less than 50%). Some cells as shown in Fig. 2D were strongly direction-selective. Slight deviation from the preferred direction sharply reduced firing frequencies. In the omnidirectional (nondirectional) group were five cells (9%), which were characterized by their nondirectionality, almost responding equally to all directions (Fig. 2C). Of 40 unidirectionals, 16 (40%) cells preferred temporal-to-nasal motion ($0^\circ, 45^\circ, 315^\circ$) mainly along the horizontal direction (0°), 18 (45%) cells preferred nasal-to-temporal motion in a sector formed between 135° and 225° , and 6 (15%) cells preferred vertical direction mainly upward.

Neurons recorded from nLM were also characterized by their velocity selectivity. Forty-four cells tested could be classified into two groups, i.e., 37 slow cells (84%), preferring motion velocities of 0.10–11°/s, and 6 fast cells (14%), preferring 34–67°/s, with 1 intermediate cell (2%) producing its maximal responses to motion at velocity of 18°/s.

A comparison of the direction selectivity with the velocity selectivity of these nLM cells showed the existence of correlation between these two characteristics. General-

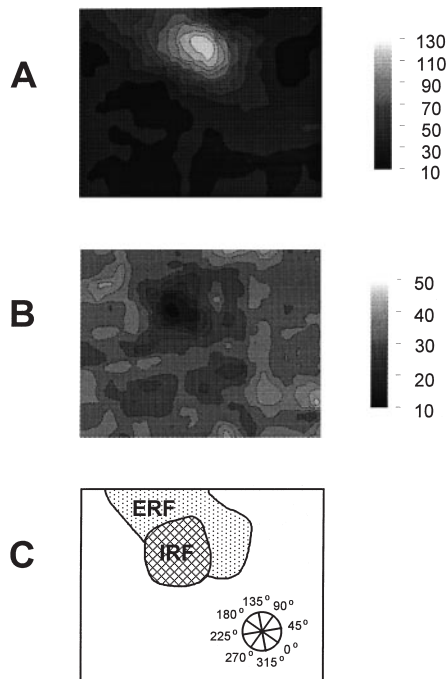


Fig. 3 Topography of excitatory receptive field (ERF) (A) and inhibitory receptive field (IRF) (B) of a nucleus lentiformis mesencephali cell was mapped by equal firing-rate lines as indicated by frequency scales on the right side. The ERF was measured with a square moving in 225° (roughly nasotemporal) direction, whereas the IRF was measured by the opposite direction motion. This cell had a high level of spontaneous activity (about 30 spikes/s) and therefore showed a clear inhibition (B) by 45° motion. The location and the extent of its ERF and IRF were plotted on the screen and overlapping of these subregions was shown in C

ly speaking, all the unidirectionals were slow cells, the omnidirectionals preferred fast motion, and the bidirectionals were either slow or fast, as well as intermediate cells. Nevertheless, the unidirectionals included two groups that had different velocity preferences, with temporonasal cells preferring a mean velocity of 2.5°/s, being slower than nasotemporal cells, preferring a velocity averaging 4.1°/s.

Receptive field properties

Our experiments showed that nLM cells responded not only to whole-field stimuli needed to induce OKN but also to small targets, which usually evoke smooth-pursuit motion of the eyes in mammals. By using the whole-screen test (Fig. 1B) on 30 nLM cells, it was found that they all had ERFs, with each having 1 ERF in 26 cells (87%), including 22 unidirectionals, 1 bidirectional, and 3 omnidirectionals, and 2 ERFs in 4 unidirectional cells (13%). The majority of unidirectionals (24 cells, 92%) also each had one inhibitory receptive field (IRF). This was the case with the bidirectional cell examined. However, no IRFs were observed in all 3 omnidirectionals. These ERFs and IRFs were not completely separated, but overlapped (Fig. 3). Roughly speaking, both ERFs and IRFs

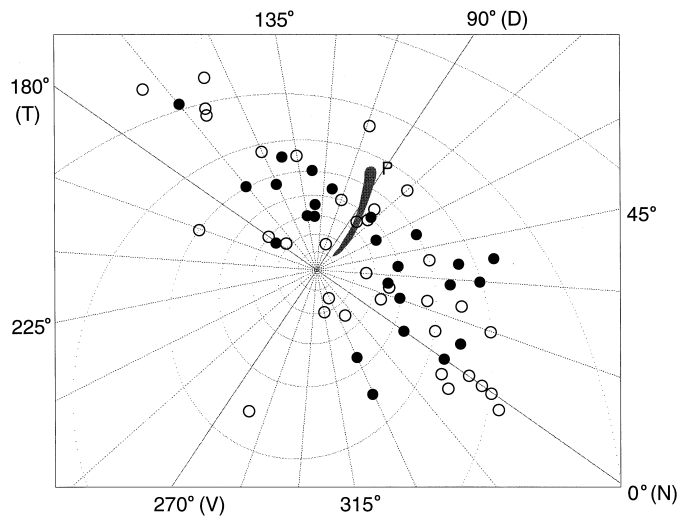


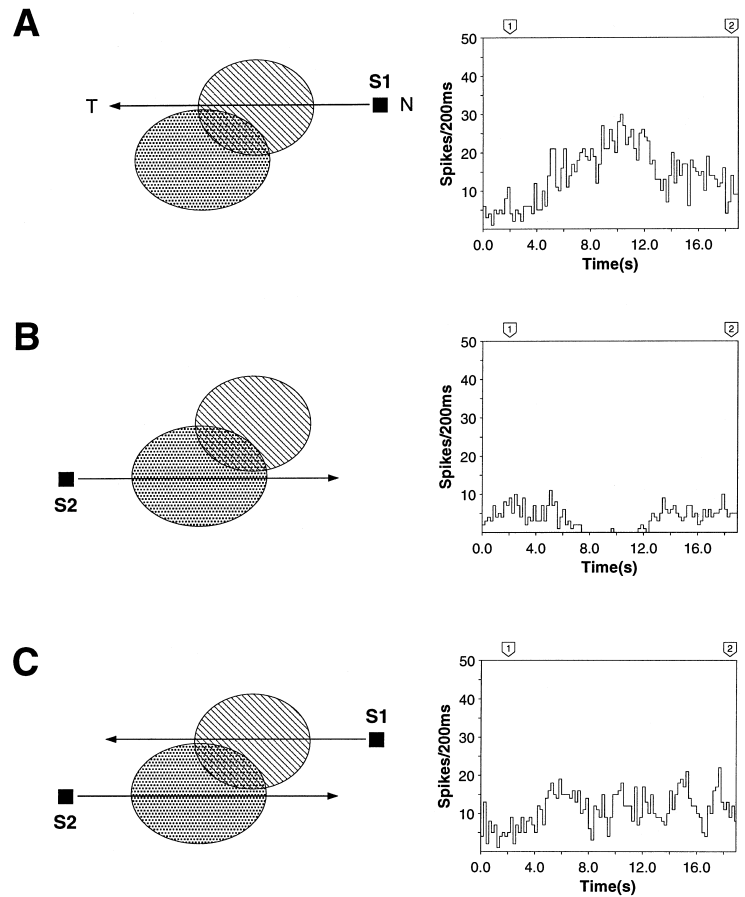
Fig. 4 Distribution of ERF centers (empty circles) and IRF centers (solid circles) of 30 nucleus lentiformis mesencephali cells in the visual field. The origin of the coordinates is the visual axis. Concentric circles are spaced by 10° visual angles (P pecten, N, T, D, V nasal, temporal, dorsal, ventral)

were elliptic in shape. The mean size of ERFs was 61° degrees (mean±SD 60.8±21.5, $n=34$) in length and 47° (mean±SD 47.4±18.0, $n=34$) in width, while that of IRFs was 60° (mean±SD 60.4±19.2, $n=24$) in length and 48° (mean±SD 47.8±15.6, $n=24$) in width. ERFs were similar to IRFs in that the responsivity of the fields was nonhomogeneous, evidenced by the fact that visual stimulation induced the maximal effect in the field center, and this effect gradually decreased while the stimulus was moving away from the center, and in that the majority of ERFs and all IRFs were direction-selective. The excitation was maximally evoked by visual stimuli moving in the preferred direction, deviation from which produced weaker or no responses. Similarly, the inhibition was also the maximal, while the visual stimuli were moving in the inhibition-preferred direction. A weaker or no-inhibition effect was observed along other directions. The preferred directions of ERFs and IRFs were opposite in the unidirectionals and perpendicular to each other in the bidirectionals; while the omnidirectionals had isotropic ERFs, which were not antagonized by IRFs. As shown in Fig. 4, ERFs and IRFs of the recorded nLM cells had similar distributions in the visual field, in that they were mainly located along the horizontal meridian in the superior field. IRFs tended to lie on the preferred direction side of ERFs.

For a particular cell, its visual responses resulted from the interaction between ERF and IRF of this cell. Figure 5A, B showed visual responses induced by a square moving in the preferred directions through the ERF and IRF, respectively. The stimulation of the two regions by two spatially separated spots produced a resultant response, which appeared to be a summation of the excitatory and inhibitory responses (Fig. 5C). Spatial gratings moved only in the restricted region (Fig. 1D) formed by the cell's ERF were as effective as whole-field gratings in producing identical visual responses from this cell, with respect

Fig. 5 Interaction between excitation and inhibition induced by a single square moving in the preferred directions through ERF (A) and IRF (B), respectively. Note that ERF and IRF have just opposite preferred directions (arrows). When the two targets were simultaneously moved so that they were passing through the centers of ERF and IRF at the same time, the resultant responses of this cell were the summation of excitatory and inhibitory responses (C).

Hatched area and stippled area represent ERF and IRF, respectively. Histograms of neuronal responses are shown on the right. Arrowheads denote start (1) and termination (2) of stimulation (N nasal, T temporal, S1, S2 visual stimuli)



not only to direction selectivity but also to response strength. If these gratings were moving beyond the restricted region, the cell did not respond at all. Similarly, an IRF was the sole region where inhibition by whole-field gratings took place. Therefore, for a particular nLM neuron, whole-field stimulation was in effect equivalent to a whole receptive field one in producing its visual responses. Under physiological conditions, a whole-field pattern induced a large amount of neurons to fire, thereby optokinetic responses happened. These data maybe give some support to the population-coding hypothesis (Lee et al. 1988; Fite et al. 1989).

Discussion

The results of the present study are generally similar to those obtained by Winterson and Brauth (1985) in that nLM cells in pigeons are direction- and velocity-selective. However, they are particularly different in the following two ways. First, there exist three classes of cells in nLM, i.e., unidirectional, bidirectional, and omnidirectional cells, not only unidirectional or directional cells. Eighty-five percent (85%) of the unidirectionals preferred either temporonasal or nasotemporal motion and 15% preferred vertical motion, implying that avian nLM is not only responsible for horizontal OKN, but also involved in vertical OKN. This vertical selectivity may be

related to afferents from the nucleus of the basal optic root (nBOR; Brecha et al. 1980), which could modulate neuronal activity in nLM (Fite et al. 1979; Baldo and Britto 1990). The bidirectionals have not been reported in nLM in other species studied so far, except directionally asymmetric units in amphibians (Fite et al. 1989). The omnidirectionals or nondirectional units are also recently reported in the mammalian NOT, and it has been suggested they provide an inhibitory input to the retinal slip neurons (thought to be involved in generating OKN) and therefore suppress ocular following responses to visual displacement caused by saccades (Ibbotson and Mark 1994). Secondly, cells in the avian nLM (Winterson and Brauth 1985) and in the mammalian NOT (Ibbotson et al. 1994) are categorized into slow and fast cells according to the optimal velocity at which they produce the maximal responses and these velocity selectivities have a similar broader range (Winterson and Brauth 1985; pigeon, 0.2–80°/s; Ibbotson et al. 1994: wallaby, 0.3–60°/s). However, these velocity ranges are quite different from those found in rabbits (Maekawa et al. 1984; 5–150°/s) and monkeys (Mustari and Fuchs 1990: 4–180°/s) although our categories of slow and fast cells are similar to those reported by Winterson and Brauth (1985) in pigeons, but they have different velocity-preferences (0.1–11°/s compared with less than 1.0°/s; 34–67°/s compared with more than 3.3°/s), and different locations. Our study indicates the existence of both slow and fast cells in LMmc, whereas

Winterson and Brauth (1985) reported that slow units tend to be in LMmc and fast units in the parvocellular nLM (LMpc). These differences in the optimum velocities may be due to different spatial characteristics of the stimuli used by the authors (Ibbotson et al. 1994). It is interesting to note that there exists a correlation between direction-preference and velocity-preference in the pigeon nLM cells in that all unidirectionals are slow cells, all omnidirectionals are fast cells, and bidirectionals are either slow or fast cells. Therefore, the spatiotemporal properties of the optokinetic cells need to be further studied.

One of our findings is that cells in the pigeon LMmc almost equally respond both to whole-field stimulation and to single small targets. Until now, this response property of some cells in NOT and in the DTN of the accessory optic tract has only been reported in the studies of primates (Hoffmann et al. 1988; Hoffmann and Distler 1989; Mustari and Fuchs 1990), but not in other species. These cells usually have small perifoveal receptive fields, and therefore are suggested to provide a visual signal that evokes smooth-pursuit eye movements, or, alternatively, to be involved in the generation of optokinetic responses to small visual stimuli (Mustari and Fuchs 1990). It may be attributed to the neuronal projection from specialized motion analyzing areas in the primate cortex to NOT and DTN (Hoffmann and Distler 1989). Similarly, the pigeon nLM also receives a large projection from the visual Wulst (Miceli et al. 1979). It seems likely that selectivity of the pigeon nLM cells to single small objects may be also involved in generating optokinetic responses.

Though several studies have reported the extent and the location of receptive fields of neurons in nLM (Winterson and Brauth 1985; Fan et al. 1995) and in NOT-DTN (Hoffmann and Schoppmann 1975, 1981; Hoffmann and Distler 1989; Volchan et al. 1989); only one paper mentioned an ERF surrounded by an IRF (Hoffmann and Schoppmann 1975). Our studies show that the majority of the unidirectionals (92%) have IRFs, which are usually overlapped by ERFs. The preferred direction of an ERF is just opposite to that of an IRF. This opposite direction inhibition has been also reported in the studies of amphibians (Fite et al. 1989), birds (Winterson and Brauth 1985), and mammals (Volchan et al. 1989; Klauer et al. 1990). Its functional significance has been suggested to increase activity in one nLM or NOT and decrease activity in the other nucleus, thereby producing a signal for controlling slow-phase eye velocity (Klauer et al. 1990). In one bidirectional cell tested, the preferred direction of IRF is perpendicular to that of ERF. It is plausible that this vertical inhibition property may result from afferents from nBOR (Brecha et al. 1980), most cells of which prefer upward or downward motion (Frost et al. 1990). On the other hand, vertical preference of some nLM cells may also be influenced by nBOR, because nBOR can modulate activity of nLM cells (Fite et al. 1979; Baldo and Britto 1990). Whereas the omnidirectionals or nondirectional cells do not have IRFs, and they are suggested to suppress some ocular following response (Ibbotson and Mark 1994). Generally speaking, ERFs and

IRFs of the nLM neurons are elongated in shape and mainly distributed along the horizontal meridian of the visual field. This distribution is in agreement with anatomical findings that retinal ganglion cells labeled after an injection of horseradish peroxidase (HRP) into the pigeon nLM are localized in a horizontal belt along the retinal equator (Bodnarenko et al. 1988), approximately corresponding to the visual streak in the pigeon retina (Erichsen et al. 1989).

Our study shows that every cell has at least one ERF, through which single objects moving in the preferred direction produce the same strength of responses as induced by whole-field stimulation. This whole-field stimulation is generally accepted to be needed for producing OKN in various species of animals so far studied. Therefore, it is reasonable to suggest that the direction and magnitude of OKN are coded by activity patterns of a population of broadly tuned and narrowly tuned cells. In fact, several lines of evidence for the population-coding hypothesis have been obtained by Lee et al. (1988) on saccadic eye movement control in the primate superior colliculus, and by Fite et al. (1989) on directional selectivity of the amphibian nLM. The present study may also give some support to this notion.

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