

Visual Responses of Neurons in the Pretectal Nucleus lentiformis mesencephali to Moving Patterns Within and Beyond Receptive Fields in Pigeons

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Key Words

Nucleus lentiformis mesencephali · Nucleus of the optic tract · Optokinetic nystagmus · Pigeon · Receptive field · Visual system

Abstract

Large-field patterns are effective stimuli for eliciting visual responses from neurons in the pretecal nucleus lentiformis mesencephali of nonmammals. The present study shows that stimulation beyond the receptive field does not contribute to the visual responses of neurons in the nucleus lentiformis mesencephali in two respects. First, changes in the direction and velocity of motion beyond the receptive field did not affect the visual responses of the pretecal cells to motion within the receptive field. Second, time differences in the onset of stimulation within and outside the receptive field did not influence the visual responses of the pretecal cells to motion in the receptive field, implying that there may be no long-range interaction between the receptive field and its surrounding field. The present study also indicates that the pretecal cells are not only sensitive to the direction and velocity of motion, but also to the size and density of dots in a random-dot pattern moving through the receptive field. Taken together with previous studies, these results suggest that the receptive field of the pretecal cells within the nucleus lentiformis mesencephali is large in size but well defined in boundaries, and that

the pretecal cells respond to motion of visual stimuli within but not beyond their receptive fields.

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Introduction

The pretecal nucleus lentiformis mesencephali (nLM) in amphibians, reptiles, and birds, and its mammalian homologue, the nucleus of the optic tract, are thought to mediate optokinetic nystagmus, which stabilizes an object image on the retina by compensatory movement of the eyes. Lesions of these nuclei reduce horizontal nystagmus in various species of animals [Fite and Montgomery, 1982; Lázár et al., 1983; Gioanni et al., 1983; Schiff et al., 1990]. On the other hand, electrical stimulation of the nucleus of the optic tract results in horizontal nystagmus in rabbits [Collewyn, 1975] and monkeys [Mustari and Fuchs, 1990]. The involvement of these nuclei in optokinetic nystagmus has been further demonstrated by extensive electrophysiological studies. Most visual cells recorded in nLM [Winterson and Brauth, 1985; Fan et al., 1995; Li et al., 1996; Fu et al., 1998a, b] and in the nucleus of the optic tract [Klauer et al., 1990; Mustari and Fuchs, 1990; Distler and Hoffmann, 1993; Ibbotson and Mark, 1996] are direction- and velocity-selective. These properties are necessary conditions for those cells that generate optokinetic nystagmus.

Several studies have described the receptive fields of visual neurons in the reptilian and avian nLM [Winterson

and Brauth, 1985; Fan et al., 1995; Fu et al., 1998a, b], and in the mammalian nucleus of the optic tract [Hoffmann and Distler, 1989; Volchan et al., 1989]. The receptive field of visual cells in the avian nLM is composed of an excitatory receptive field (ERF) and an inhibitory receptive field (IRF), both of which have overlapping or separate extents but opposite directionality [Fu et al., 1998a]. In contrast, an ERF is surrounded by an IRF in visual cells in the mammalian nucleus of the optic tract [Hoffmann and Schoppmann, 1975]. In these studies, large-field patterns are usually used to evoke visual responses in neurons within these optokinetic nuclei. These patterns are composed of random dots or checks [Hoffmann and Distler, 1989; Volchan et al., 1989; Klauer et al., 1990; Fan et al., 1995; Li et al., 1996], stripes [Fite et al., 1989; Fu et al., 1998a, b], or sine-wave gratings [Ibbotson and Mark, 1996] that frequently cover the whole screen at which the animal looks. Therefore, we asked whether stimulation in a large region beyond the receptive field could affect the visual responsiveness of optokinetic neurons in the pigeon nLM.

Furthermore, some studies have shown that motion of a visual stimulus outside the receptive field may modify the response strength of the isthmo-optic neurons in quails [Uchiyama et al., 1998] and of the lateral geniculate cells in cats [Felisberti and Derrington, 1999]. This modification might be related to the integration field beyond the classical receptive field [Li and Li, 1994]. A large-field stimulus frequently used in studies on the visual responses of optokinetic neurons usually stimulates both the receptive field and its surrounding region. Therefore, we also asked whether long-range interaction of this kind exist between the receptive field and its large surrounding region in the nLM neurons. With these questions in mind, the present study was conducted to reveal what effects the surrounding region of a receptive field could exert on visual responses evoked by motion in the receptive field, and what features of a random-dot pattern could affect the visual responses of neurons within the pigeon nLM.

Materials and Methods

The experiments were performed on 34 adult pigeons (*Columba livia*) with body weights of 350–420 g following the Policy on the Use of Animals in Neuroscience Research approved 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 caudal forebrain was exposed and dura mater excised. The right eye was kept open and the left eye covered. A screen (120×130°) was placed 40 cm away from the viewing eye. The horizontal and vertical meridians of the visual field on the screen were rotated by 38° [Britto et al., 1990; Fu et al., 1998a] to meet the pigeon's normal conditions [Erichsen et al., 1989].

A random-dot pattern consisting of 280 black dots (2.3° in size) per 10,000 square degrees of visual angle in density was generated by a computer and rear-projected with a projector (Electrohome ECP 4101) onto the screen. It was moved at a series of velocities (1, 2, 4, 8, 16, 32, 64°/s) and randomly in 8 directions spaced by 45° (nasal was 0°) to determine the preferred direction and optimal velocity of a nLM cell. The cell's response strength was maximal when the stimulus was moved at the optimal velocity in the preferred direction. The interval between two consecutive stimulations was 8 s to allow recovery of the response. The receptive field of the nLM cell was plotted with a 2° black dot. Its ERF and IRF usually were not concentrically organized, but either partially overlapped in extent or were separated from each other without any overlap between [Fu et al., 1998a]. The remaining region outside both ERF and IRF on the screen was referred to as the surrounding field (SF). The ERF was stimulated by motion within a display window framed by it. The surrounding field was stimulated by motion outside both ERF and IRF.

A micropipette filled with 0.5 M sodium acetate and 2% pontamine-skyblue [Hellon, 1971] was stereotaxically advanced into nLM [Karten and Hodos, 1967]. Action potentials of nLM neurons were amplified, displayed on an oscilloscope and fed into another computer for data processing. The visual firing rates of nLM cells were averaged over three sweeps and their spontaneous firing rates averaged over 1.5 s before visual stimulation.

In the first series of experiments, the question of whether there exist any functional interactions between the receptive field and its SF were explored by studying the effects of motion in SF on visual responses of nLM cells to motion in the receptive field. In some trials, the direction of motion in SF and that of motion in ERF were in the same preferred or just opposite directions, whereas the velocity of motion in SF was also either identical to or different from the optimal velocity of motion in ERF of nLM cells. In other trials, the time differences between the onset of motion within the receptive field and its SF ranged from –(40, 80, 160, 200, 600, 1,200 ms) to +(40, 80, 160, 200, 600, 1,200 ms). The minus and plus signs indicated that motion in SF started either before or after the onset of motion within ERF. The second series of experiments studied the effects of the size and density of dots in a random-dot pattern on the visual responses of nLM cells. The dot size ranged from 0.3, 0.6, 1.2, and 2.3 to 4.6°, and the density of dots in a random-dot pattern ranged from 35, 70, 140, 280 and 560 to 1,120 dots per 10,000 square degrees of visual angle.

At the end of experiments, the recording sites of nLM neurons were marked with pontamine-skyblue applied by negative current pulses of 15–20 μ A 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, fixed in 2% formaldehyde and 2% paraformaldehyde, soaked in a 30% sucrose solution for 12–24 h, and then frozen-sectioned at 80 μ m thickness. The sections were counterstained with cresyl violet, dehydrated, covered, and observed with a microscope to localize the recording sites.

Results

Thirty-four nLM cells were recorded, and almost all were spontaneously discharging at an average firing rate of 12.8 ± 11.4 spikes/s (mean \pm SD, $n = 33$). The receptive field of nLM cells were composed of an ERF and an IRF, both of which partially overlapped in extent or were sepa-

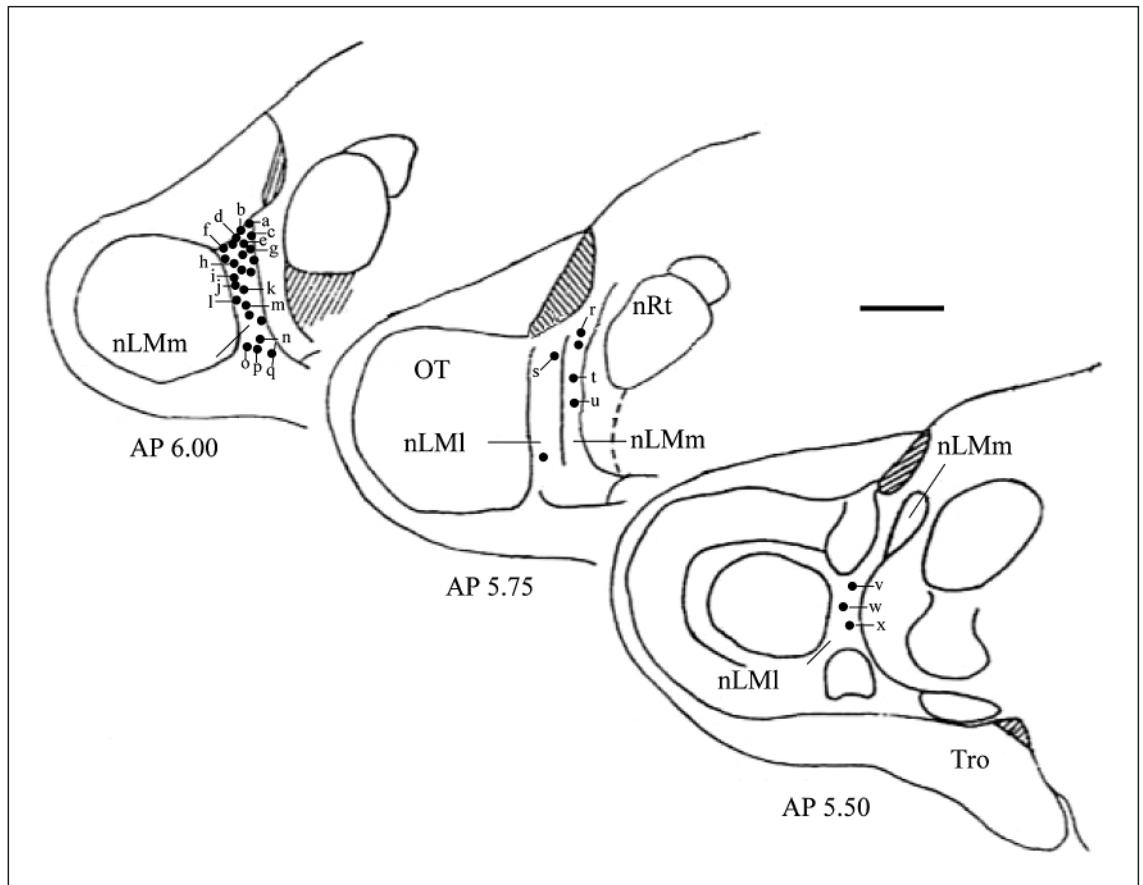


Fig. 1. Topographic distribution of dye-marked recording sites (filled circles) of 34 neurons within the nucleus lentiformis mesencephali pars medialis (nLMm) and pars lateralis (nLMI) [Gamlin and Cohen, 1988] shown on three cross-sections of the pigeon's brain. Pretectal cells labeled with letters correspond to those with identical letters in subsequent figures. AP = Anterior-posterior levels according to the pigeon brain atlas by Karten and Hodós [1967]. Other abbreviations: OT = Optic tectum; nRt = nucleus rotundus; Tro = optic tract. Scale: 1 mm.

rated from each other without any overlap between. Roughly speaking, both ERF and IRF were elliptic in shape. The mean size of ERF was $80 \pm 16^\circ$ in length and $55 \pm 13^\circ$ in width ($n = 19$), whereas that of IRF was $69 \pm 13^\circ$ in length and $48 \pm 12^\circ$ in width. The identified cells included 30 directional and 4 non-directional cells. Among the directional cells, 23 cells preferred horizontal motion and 7 vertical motion. The recording sites of 34 cells were marked with dye within nLM. Twenty-nine sites were located in the medial part and 5 in the lateral part of the nucleus lentiformis mesencephali [Gamlin and Cohen, 1988] (fig. 1), which are equivalent topographically to the nucleus lentiformis mesencephali, pars magnocellularis and the nucleus lentiformis mesencephali, pars parvocellularis, respectively. No obvious differences in the visual response properties of

nLM cells examined in the present study were observed in the two subdivisions of this pretectal nucleus.

Eighteen nLM cells were examined for the effect of peripheral patterns moved within the cells' SF on the visual responses of these cells to motion of central patterns through ERF in the preferred direction. These included: 11 cells preferring horizontal motion, 5 vertical motion and 2 equally responding to motion in all directions examined. In control cases where the central pattern was moved through ERF, the firing rates of these cells averaged 56.4 ± 26.6 spikes/s ($n = 18$). The average firing rates produced by simultaneous motion within both ERF and SF in the same or opposite directions were 55.0 ± 25.4 and 55.5 ± 25.0 spikes/s, respectively. These firing rates were not significantly different from the control values (same direction: $t = 2.12$, $n = 18$, $p > 0.01$;

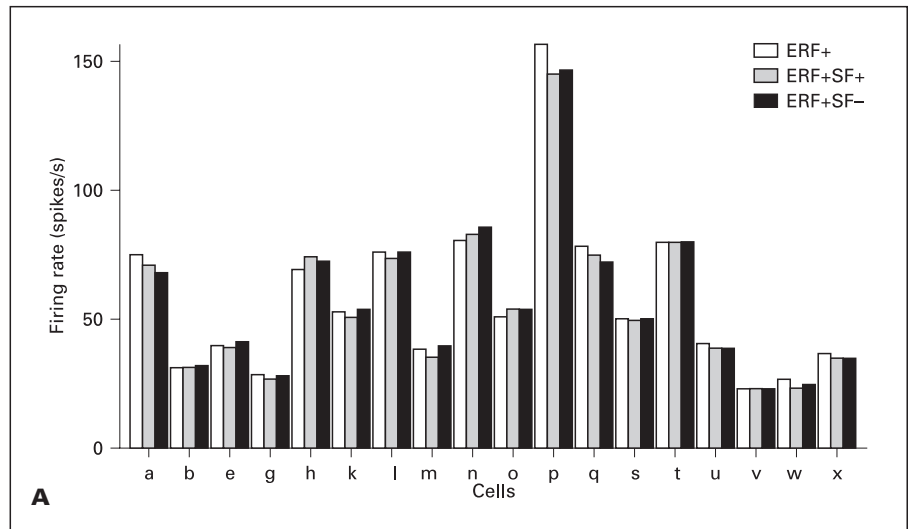
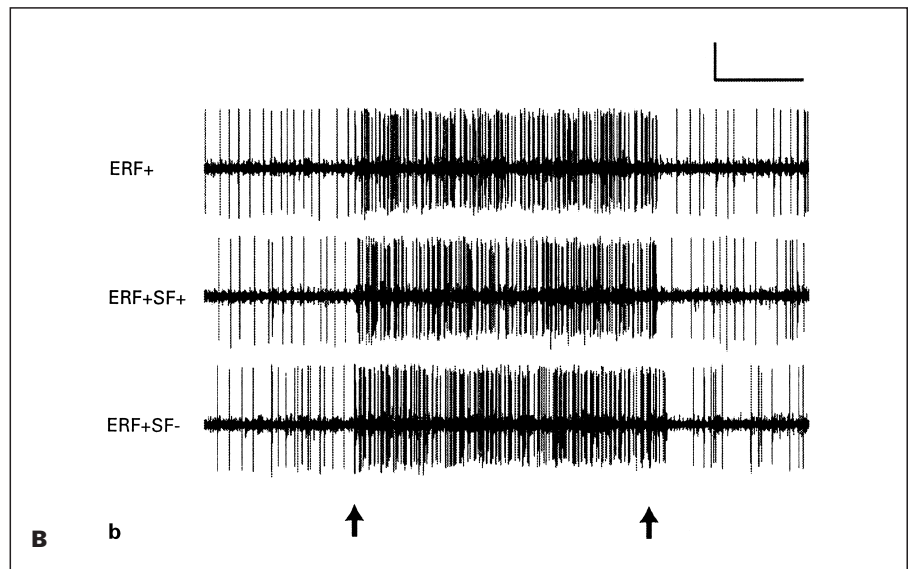


Fig. 2. Histograms (**A**) and original recordings (**B**) of visual responses of nLM cells, showing that firing rates produced by motion of the random-dot pattern (2.3° dot, 280 dots per 10,000 square degrees) in the preferred direction at the optimal velocity through the excitatory receptive field (ERF) are not affected by motion within the surrounding field (SF). Visual responses in each of 18 nLM cells are superimposed for three sweeps. Original recordings (**B**) were made from a nLM cell, which responded to motion of a pattern (0.3° dot, 1,120 dots/10,000 square degrees) at a velocity of $2^\circ/s$. Their histograms are drawn in **A** (cell i). Plus and minus signs postfixed to ERF and SF signify motion through ERF and SF in the preferred and anti-preferred directions, respectively. The recording sites of these cells are shown in figure 1 with corresponding letters. Arrows point to the start and end of visual stimulations. Scales: 100 μV , 1 s.



opposite direction: $t = 0.59$, $n = 18$, $p > 0.01$; fig. 2). Within this group, 10 nLM cells were spontaneously discharging at an average rate of 12.1 ± 5.7 spikes/s and fired at 5.8 ± 5.2 spikes/s when their IRF was stimulated alone. Their firing rates, produced by simultaneous motion within both IRF and SF in the same or opposite directions, were 6.1 ± 5.2 and 6.4 ± 5.1 spikes/s, respectively. This indicated that motion within SF did not affect inhibition produced by motion in IRF (same direction: $t = 1.38$, $n = 10$, $p > 0.01$; opposite direction: $t = 2.63$, $n = 10$, $p > 0.01$).

The effect of the velocity of peripheral motion on the visual responses of 6 nLM cells to central motion was examined in 3 horizontal- and 3 vertical-preferring cells.

Their visual responses to motion through ERF at the optimal velocity in the preferred direction were 41.2 ± 18.1 spikes/s. Motion in SF at one-third or three times the optimal velocity in ERF produced firing rates of 40.3 ± 17.1 and 39.3 ± 15.9 spikes/s, respectively. Paired t tests showed that the velocity of motion within SF did not exert significant effects on visual responses evoked by the central motion (one-third: $t = 1.33$, $n = 6$, $p > 0.01$; three-fold: $t = 2.52$, $n = 6$, $p > 0.01$).

A possible long-range action was examined in an additional 10 nLM cells including 6 preferring horizontal motion, 2 vertical motion and 2 responding equally to motion in all directions. The firing rates in 9 of these cells

Fig. 3. Visual response curves of 10 nLM cells showing that firing rates of these cells are not dependent on motion beyond the receptive field. Abscissa represents the onset time differences between the start of motion in the SF and that of motion in the receptive field, with negative and positive values indicating the onset time (ms) of peripheral motion prior to and after central motion, respectively. Firing rates are averaged over three sweeps. Broken lines represent data not obtained. Letters at the right ends of lines correspond to those labeling the recording sites of these nLM cells in figure 1.

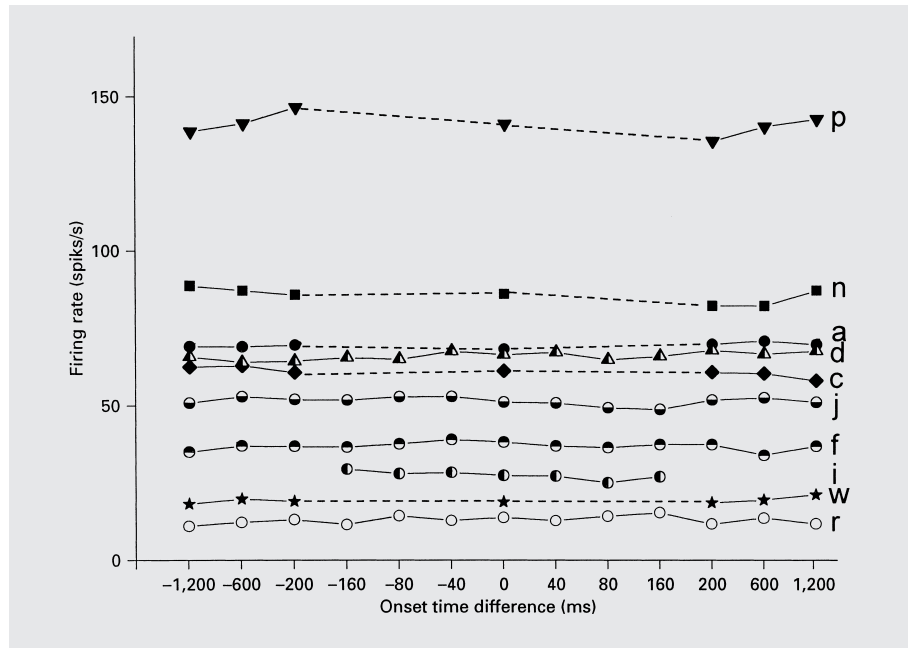
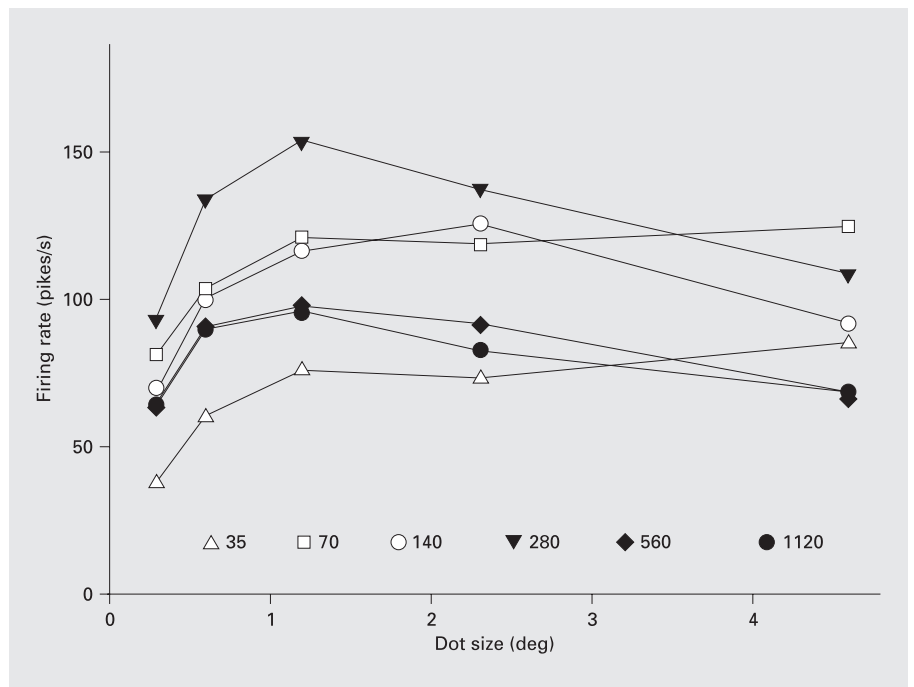


Fig. 4. Tuning curves showing the dependency of firing rate in a nLM cell on the size and density of dots in random-dotted pattern. Symbols represent various densities of dots in a range of 35–1,120 dots per 10,000 square degrees. This cell preferred dots subtended to 1.2° of visual angle and density of 280 dots per 10,000 square degrees. Its recording site is labeled in figure 1 with letter p.



produced by motion of a random-dot pattern through both ERF and SF was 59.2 ± 31.6 spikes/s. When the pattern started to move in SF at 200, 600 and 1,200 ms prior to the onset of motion in ERF, the firing rates produced by both stimulations were 59.2 ± 32.8 , 59.1 ± 31.9 , and 58.3 ± 32.3 spikes/s, respectively. In the cases where SF stimulation

started 200, 600 and 1,200 ms after the onset of ERF stimulation, these rates were 58.3 ± 30.7 , 58.7 ± 31.4 and 59.3 ± 32.3 spikes/s. Paired t tests show no significant differences between the control and experimental values in these trials ($p > 0.01$). Similarly, the effect of onset time differences of 40, 80 and 160 ms on visual responses was examined in 5 of

the 10 cells. The visual responses of the nLM cells were not significantly changed by motion within SF, which started earlier or later than the onset of motion in ERF ($p > 0.01$; fig. 3).

Twenty-three nLM cells were examined for the effects of the size and density of dots in a random-dot pattern on their visual responses. They included: 14 cells preferring horizontal motion, 6 vertical motion and 3 equally responding to motion in all directions examined. The preferred density (dots per 10,000 square degrees of visual angle) of nLM cells and their percentage were 70 dots (18%), 140 dots (4%), 280 dots (39%), 560 dots (none) and 1,120 dots (39%). The preferred size of dots of nLM cells and their percentage were 0.3° (4%), 0.6° (31%), 1.2° (17%), 2.3° (35%) and 4.6° (13%). These data show that 78% of the cells preferred densities of greater than 280 dots per 10,000 square degrees and 96% of the cells preferred dots of larger than 0.6° in a random-dot pattern. Generally speaking, in a range of lower densities the firing rates of nLM cells were increased as the dot size was enlarged; whereas in a range of higher densities, the firing rates were increased and then decreased as the dot size was increased (fig. 4). In all the experiments reported here, any differences in the general properties examined for the peripheral effect and the effect of the size and density of dots in a random-dot pattern were not observed between the horizontally- and vertically-tuned nLM cells.

Discussion

Traditionally, large-field stimuli such as random-dots or checks [Hoffmann and Distler, 1989; Volchan et al., 1989; Klauer et al., 1990; Fan et al., 1995; Li et al., 1996], stripes [Fite et al., 1989; Fu et al., 1998a, b], or gratings [Ibbotson and Mark, 1996] have been used to study the visual response properties of optokinetic neurons in various species of animals. The present study provides electrophysiological evidence that motion of a random-dot pattern outside the receptive field does not exert any obvious influence on the visual responses of pigeon nLM cells, regardless of the direction, velocity, and onset time of motion over a large region surrounding the receptive field. It appears that there exist no long-range interactions between the receptive field and its SF of the type shown in the quail isthmo-optic nucleus [Uchiyama et al., 1998] and in the cat lateral geniculate nucleus [Felisberti and Derrington, 1999]. This difference in long-range interactions might be due to various visual systems (centrifugal system, optokinetic system, or thalamofugal system) or species of animals. The present and

previous [Fu et al., 1998a, b] studies indicate that nLM cells possess large but well-defined receptive fields which are composed of spatially overlapping or separate ERF and IRF. Therefore, large-field stimuli covering the whole screen is not needed for activating single nLM cells in birds. However, large-field stimulation is needed for both repeatedly stimulating a single cell and simultaneously stimulating an assembly of optokinetic cells. Thus, the direction and magnitude of optokinetic nystagmus could be coded by activity patterns of groups of optokinetic cells [Lee et al., 1988; Fite et al., 1989; Fu et al., 1998a].

A random-dot pattern is useful for determining the directional selectivity of optokinetic cells because they do not contain much information regarding the orientation of visual stimuli. However, the size and density of dots in a pattern can influence the magnitude of visual responses of nLM cells. It appears that most nLM cells prefer a random-dot pattern with dots of larger than 0.6° in size and densities of higher than 280 dots per 10,000 square degrees of visual angle. Generally speaking, the firing rate of nLM cells is increased as the dot size is enlarged at lower densities, and it is increased and then decreased as the dot size is increased at higher densities. This phenomenon might be explained by one or two possibilities. First, each nLM neuron might prefer a particular dot size in a random-dot pattern. For example, it appears that the cell shown in figure 4 may prefer a dot size of 1.2° . Second, the visual responses of nLM cells might depend on the magnitude of black leading edges [Fu et al., 1998b] in a random-dot pattern. When the density of dots is higher, larger dots could overlap each other thus reducing the magnitude of black leading edges. Further increase in dot size would result in extensive overlapping of dots which could reverse the stimulus pattern (black) vs. background (white). A white stimulus is not effective to evoke visual responses from nLM cells [Fu et al., 1998b].

In conclusion, the present study indicates that the receptive field of optokinetic cells is large but well defined. These cells are sensitive to motion of visual stimuli within but not beyond their receptive fields. They are also selective to the size and density of dots in a random-dot pattern, in addition to the direction and velocity of motion.

Acknowledgments

This work was supported by the National Natural Science Foundation of China and by the Chinese Academy of Sciences.

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