

# Stimulus features eliciting visual responses from neurons in the nucleus lentiformis mesencephali in pigeons

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## Abstract

The purpose of the present study was to find out what particular stimulus features, in addition to the direction and velocity of motion, specifically activate neurons in the nucleus lentiformis mesencephali (nLM) in pigeons. Visual responses of 60 nLM cells to a variety of computer-generated stimuli were extracellularly recorded and quantitatively analyzed. Ten recording sites were histologically verified to be localized within nLM with cobalt sulfide markings. It was shown that the pigeon nLM cells were specifically sensitive to the leading edge moving at the optimal velocity in the preferred direction through their excitatory receptive fields (ERFs). Generally speaking, nLM cells preferred black edges to white ones. However, this preference cannot be explained by OFF-responses to a light spot. The edge sharpness was also an essential factor influencing the responsive strength, with blurred edges producing little or no visual responses at all. These neurons vigorously responded to black edge orientated perpendicular to, and moved in, the preferred direction; the magnitude of visual responses was reduced with changing orientation. The spatial summation occurred in all neurons tested, characterized by the finding that neuronal firings increased as the leading edge was lengthened until saturation was reached. On the other hand, it appeared that nLM neurons could not detect any differences in the shape and area of stimuli with an identical edge. These data suggested that feature extraction characteristics of nLM neurons may be specialized for detecting optokinetic stimuli, but not for realizing pattern recognition. This seems to be at least one of the reasons why large-field gratings or random-dot patterns have been used to study visual responses of accessory optic neurons and optokinetic nystagmus, because many high-contrast edges in these stimuli can activate a neuron to periodically discharge, or groups of neurons to simultaneously fire to elicit optokinetic reflex.

**Keywords:** Optokinetic nystagmus, Nucleus lentiformis mesencephali, Receptive field, Feature detection, Pigeon

## Introduction

There have been several lines of evidence indicating that the nucleus lentiformis mesencephali (nLM) in lower vertebrates including amphibians, reptiles, and birds, and its mammalian homologue, the nucleus of the optic tract (NOT), are involved in generating optokinetic nystagmus (OKN), which stabilizes a visual image on the retina by slow tracking and rapid resetting movements of the eyes. Electrolytic or chemical lesions of the nuclei result in severe impairment of OKN in frogs (Montgomery et al., 1982; Lázár et al., 1983), in pigeons (Gioanni et al., 1983), in rabbits (Collewijn, 1975*a*), and in monkeys (Kato et al., 1986, 1988; Schiff et al., 1990). A metabolic [<sup>14</sup>C]-2-deoxyglucose (2-DG) mapping technique has been used in several species to show that neural activity occurs in nLM during optokinetic stimulation (McKenna & Wallman, 1981, 1985; Chown et al., 1984; Bodnarenko et al., 1988; Fite et al., 1992). Using drug microinjections and search-coil

recording techniques, some authors have confirmed the mediation of nLM (frogs: Jardon & Bonaventure, 1992; chickens: Bonaventure et al., 1992*a*) in producing OKN, and found that cholinergic and GABAergic substances could significantly affect the directional asymmetry of OKN. Furthermore, electrical stimulation of NOT produces nystagmic eye movements in rabbits (Collewijn, 1975*a*) and in monkeys (Schiff et al., 1988; Mustari & Fuchs, 1990).

Electrophysiological studies have provided further evidence for the involvement of nLM in OKN. Most neurons recorded from nLM of frogs (Fite et al., 1989; Li et al., 1996), turtles (Fan et al., 1995), and pigeons (Winterson & Brauth, 1985; Fu et al., 1998), and from NOT of various species of mammals including rabbits (Collewijn, 1975*b*), cats (Hoffmann & Schoppmann, 1975, 1981; Distler & Hoffmann, 1993), opossums (Volchan et al., 1989), wallabies (Ibbotson et al., 1994; Ibbotson & Mark, 1996), ferrets (Klauer et al., 1990), and monkeys (Hoffmann et al., 1988; Hoffmann & Distler, 1989; Mustari & Fuchs, 1990; Ilg & Hoffmann, 1996), are selective for the direction and velocity of stimuli moving through their receptive fields (RFs). These large-field stimuli are usually composed of random dots or checks (Collewijn, 1975*b*; Hoffmann & Schoppmann, 1975, 1981; Hoffmann et al., 1988;

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Hoffmann & Distler, 1989; Volchan et al., 1989; Klauer et al., 1990; Distler & Hoffmann, 1993; Schmidt et al., 1993; Fan et al., 1995; Ilg & Hoffmann, 1996; Li et al., 1996; Fu et al., 1998), black-and-white stripes (Collewijn, 1975*b*; Fite et al., 1989; Fu et al., 1998), or sine-wave gratings (Ibbotson et al., 1994; Ibbotson & Mark, 1996). In primates, neurons recorded from NOT and the dorsal terminal nucleus (DTN) of the accessory optic tract respond not only to large-field patterns but also to single targets (Hoffmann et al., 1988; Hoffmann & Distler, 1989; Mustari & Fuchs, 1990). Recently, we have shown that this is the case with the pigeon nLM (Fu et al., 1998). Therefore, we were wondering what particular features of stimuli used for generating OKN could be detected by optokinetic neurons. In the present study, we found some new visual feature detection properties in the pigeon nLM neurons.

### Materials and methods

The experiments were performed on 23 adult homing pigeons (*Columba livia*) of either sex, weighing 300–430 g, and under guidelines regarding the care and use of animals, established by the American Physiological Society and by the Society for Neuroscience. The animal was anesthetized with urethane (20%, 1 ml/100 g body weight, i.m.), and then placed in a stereotaxic apparatus. Its 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 overlying nLM was excised. The nictitating membrane of the right eye was removed and the eye kept open. The left eye was occluded with an opaque cover. 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 was 72 deg in these experiments, whereas it is 34 deg under the pigeon normal conditions for flying, walking, standing, and perching (Erichsen et al., 1989), the horizontal meridian was clockwise rotated by 38 deg. The pecten was plotted with an ophthalmoscope on a screen, which was positioned 40 cm distant from the viewing eye, and 24 deg 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 deg (horizontal) × 130 deg (vertical). The relationship between positions of the optic axis, horizontal meridian, vertical meridian, and pecten on the screen verified the correctness of rotation by 38 deg.

A variety of visual stimuli were generated by a graphics workstation (Silicon Graphics Indigo 2) 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 rectangles moving on white, gray, or black background, luminance of which was 6.6 cd/m<sup>2</sup>, 2.7 cd/m<sup>2</sup>, and 0.1 cd/m<sup>2</sup>, respectively. Some black rectangles had blurred leading edges, which were linearly changed in luminance by a rate of 0.65 cd/m<sup>2</sup> or 0.33 cd/m<sup>2</sup> per visual angle degree. Their length and width were usually larger than the largest extent of the cells' ERFs examined. (2) A black square, semicircle, and isosceles triangle, with an area ratio of 1.00:0.39:0.50, but with an identical leading edge. (3) A random-dot pattern possessing 250 dots/m<sup>2</sup> in density, and each dot subtended 2 deg visual angles. After isolating a nLM cell, a spot (5–13 deg) was swept over the whole screen to plot the location and extent of the cell's ERF. The dotted pattern was moved over an ERF at a series of velocities (0.2–150 deg/s) and randomly in eight directions (0 deg-nasal, 45 deg, 90 deg-dorsal, 135 deg, 180 deg-temporal, 225 deg, 270 deg-ventral, 315 deg) to find out the optimal velocity and preferred direction of the cell. Visual responses of nLM cells were then analyzed to various stimuli

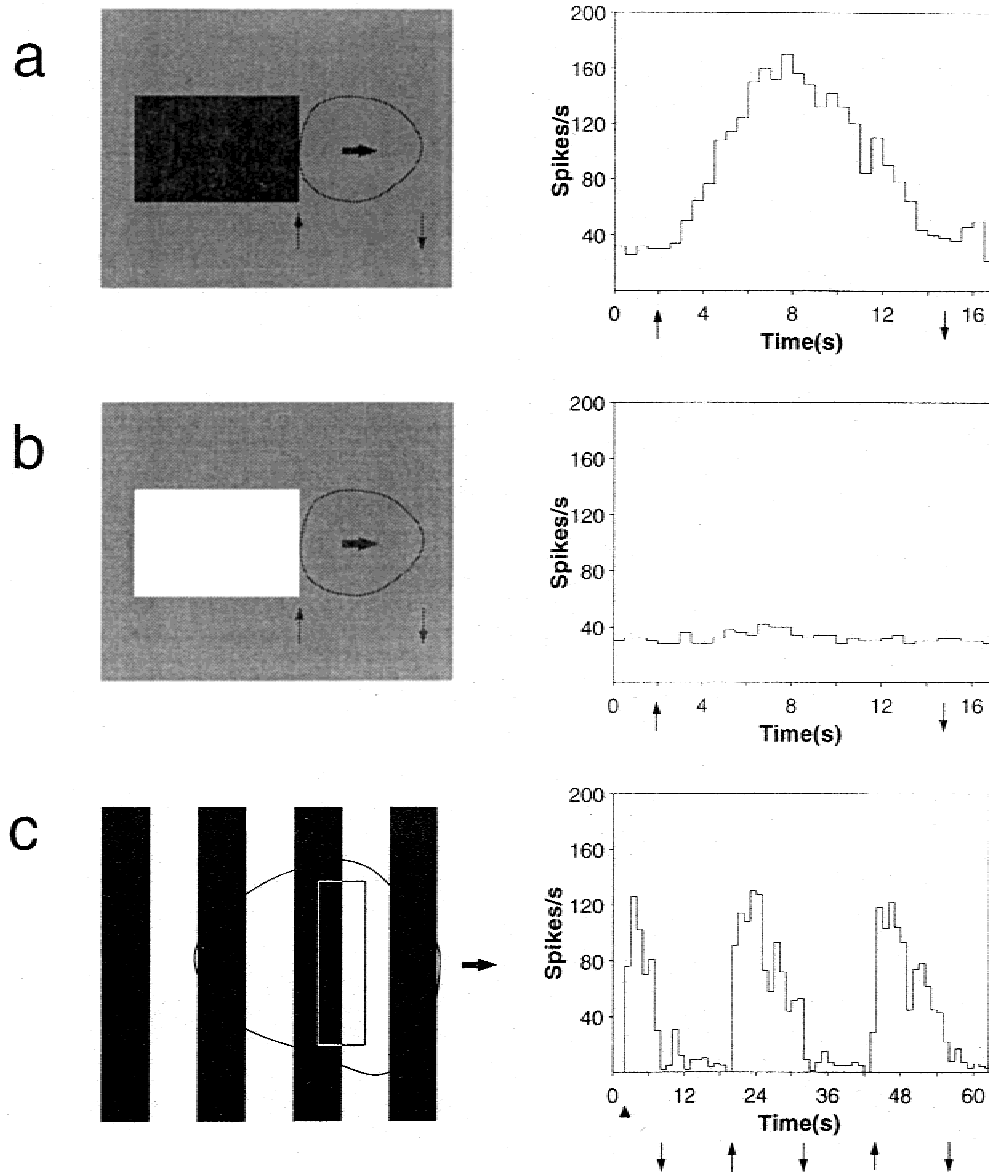
moved through their ERFs at the optimal velocities in the preferred directions. To complete all examinations on one nLM cell in this study usually took more than 5 h. Therefore, for studying a particular visual response property, we often examined a subset of 10–30 cells from a total of 60 cells recorded from nLM.

Electrodes for extracellular recordings were micropipettes filled with a solution containing 2 M NaCl and 100 mM CoCl<sub>2</sub>, and their tip diameter was 1–3 μm, with an impedance of 5–15 MΩ. The micropipette was stereotaxically advanced into nLM, guided by the pigeon brain atlas of Karten and Hodos (1967). Neuronal responses to various visual stimuli were conventionally preamplified and fed into the workstation for on-line processing. In some experiments, cobalt ions were ejected by positive current (3–5 μA, 0.5 s in duration, 1 Hz in frequency, 5–10 min) to mark the recording sites. The pigeon was killed by overdose of the anesthetic, and the brain was removed from the skull, and then immersed in a saline solution containing 10% sulfide ammonium for 30–45 min to form CoS black precipitate (Wang et al., 1981). The brain was fixed in 10% formalin for 48 h, and then trimmed and frozen cut at 60 μm in thickness. The sections were counterstained with cresyl violet, dehydrated, covered, and observed with a microscope to histologically verify the recording sites.

### Results

The recording sites of ten cells marked with cobalt-sulfide stainings were all localized within nLM, indicating the reliability of stereotaxically locating this nucleus in the present study. A total of 60 cells were extracellularly recorded, and they had an average spontaneous rate of 15 spikes/s (14.6 ± 13.1, mean ± s.d., *n* = 60). Their ERFs were mainly distributed along the horizontal meridian in the superior visual field, and had an average size of about 50 deg in width and 60 deg in length, elongated primarily in the horizontal or vertical directions. About 40% of the plotted ERFs included the foveal region, and the others were located in the extrafoveal region. As we indicated in a previous study (Fu et al., 1998), the visual responsiveness of nLM cell ERFs was nonhomogeneous, with visual stimulation inducing the maximal effect in the field center and this effect gradually decreasing while the stimulus was moving away from the center. According to their directional selectivity, they contained 49 unidirectional cells (81%) that responded maximally to motion in particular directions, seven bidirectional cells (12%) that produced stronger responses to objects moving in two opposite directions, and four omnidirectional cells (7%) that were characterized by their nondirectionality, almost responding equally to all directions (Fu et al., 1998). The unidirectional cells preferred motion mainly in the temporonasal direction (41%) and nasotemporal direction (47%), and motion in vertical direction (12%) as well, while the bidirectional cells usually responded to both temporonasal and nasotemporal directions. All these cells were velocity selective, with optimal velocities of 0.7–67 deg/s.

We examined the effect of several parameters of stimuli moved at the optimal velocity in the preferred direction on visual responses of nLM cells. Most of 25 cells examined for contrast sensitivity produced stronger responses to a black edge than a white one (Figs. 1a and 1b). This contrast preference could be described by contrast sensitivity ratio (*R*) defined as  $R = (f_b - f_s)/(f_w - f_s)$ , where  $f_b$  and  $f_w$  were maximum discharge rates to moving black and white edges, respectively, and  $f_s$  was spontaneous firing rate. The *R* values were 1.00–1.19 in seven cells (28%), 1.20–1.99 in nine cells (36%), 2.00–4.99 in three cells (12%), and >5.00 in six cells (24%). It appeared that most nLM cells preferred black edges. A white-edge preference



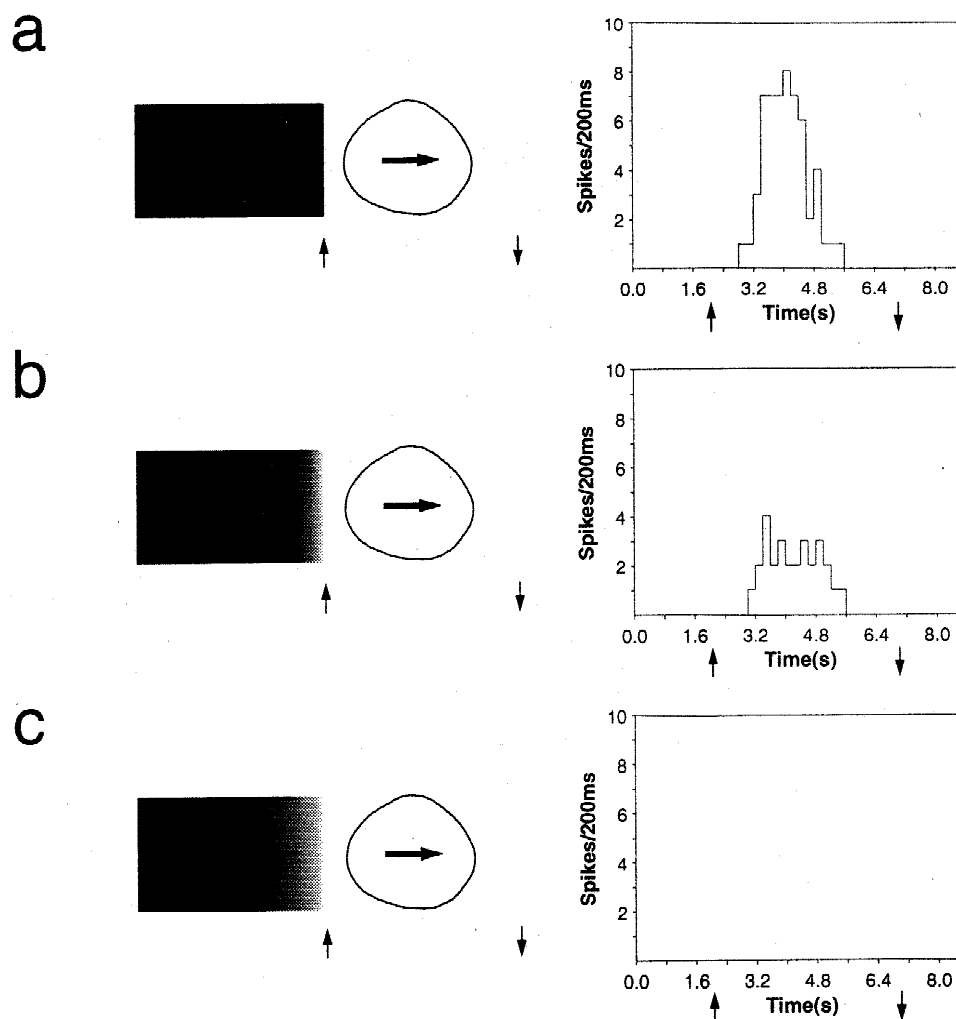
**Fig. 1.** Visual responses of a nLM cell to black (a) and white (b) edges, which were orientated perpendicular to and moved at 5.0 deg/s in the preferred direction (thick arrows) through its ERF (elongated circles, 55 × 65 deg in size). Spontaneous firing rate of the cell was 33 spikes/s. Three sweeps were averaged. In (c) were visual responses of a nLM to spatial gratings (0.04 cycles/deg) moved at 1.1 deg/s in the preferred direction (thick arrow) through a display window (rectangle, 13 × 46 deg) over its ERF (elongated circle, 60 × 70 deg). Triangle near the 0 value denotes when the black edge stayed in the window started to move. Thin arrows denote the entry (upward) and exit (downward) of the leading edges (a, b) or black edges (c) into and from ERF (a, b) or the window (c).

was never observed in this study. The contrast sensitivity of nLM neurons was also clearly demonstrated by their burst-like responses to black–white stripe gratings (Fig. 1c). In this situation, each black edge evoked vigorous firings, but white edges did not.

Visual responses were examined in ten nLM cells to the onset (ON) and offset (OFF) of a light spot, whose diameter was equal to the extent of ERFs. Light stimulation produced no ON–OFF responses in four cells, ON responses in four cells, ON–OFF responses in one cell, and OFF responses in one cell. All these cells vigorously responded to black rectangles, whose leading edges were also equal to the ERF extents, orientated perpendicular to the preferred directions and moved at the optimal velocities. The number of spikes produced in the ON and/or OFF cells by light stim-

ulation was about 60% ( $59.3 \pm 18.3\%$ , mean  $\pm$  s.d.  $n = 6$ ) of that by motion of a black edge in the first 200 ms. It appeared that visual preference of nLM neurons to black edges could not be explained by their responses to OFF stimulation.

Edge sharpness was also an essential factor affecting the responsive strength of all ten nLM cells examined. It was defined here as the spatial rate of change in luminance at the edge region. As shown in Fig. 2, a sharp edge moved at 9.8 deg/s in the preferred direction through a cell's ERF (50 × 55 deg) evoked obvious responses, while decreases in luminance from 6.6 cd/m<sup>2</sup> (white) to 0.1 cd/m<sup>2</sup> (black) linearly by a rate of 0.65 cd/m<sup>2</sup>/deg resulted in significant reduction of its responsive strength, and a blurred edge formed by a rate of 0.33 cd/m<sup>2</sup>/deg produced no



**Fig. 2.** Edge contrast sharpness was an essential factor affecting responsive strength of a nLM cell. A sharp edge (a) evoked stronger responses than a blurred edge (b), whose luminance at the border region was linearly changed at a spatial rate of  $0.65 \text{ cd/m}^2/\text{deg}$ . Visual responses of this cell disappeared when luminance at the border region was changed at a rate of  $0.33 \text{ cd/m}^2/\text{deg}$  (c). Thick arrows denote the preferred direction of the cell and motion direction of the edges. Thin arrows represent the start and end of movement ( $9.8 \text{ deg/s}$ ) of the leading edges. Ellipses symbol the cell's ERF ( $50 \times 55 \text{ deg}$ ). This cell was spontaneously silent. Three sweeps were averaged.

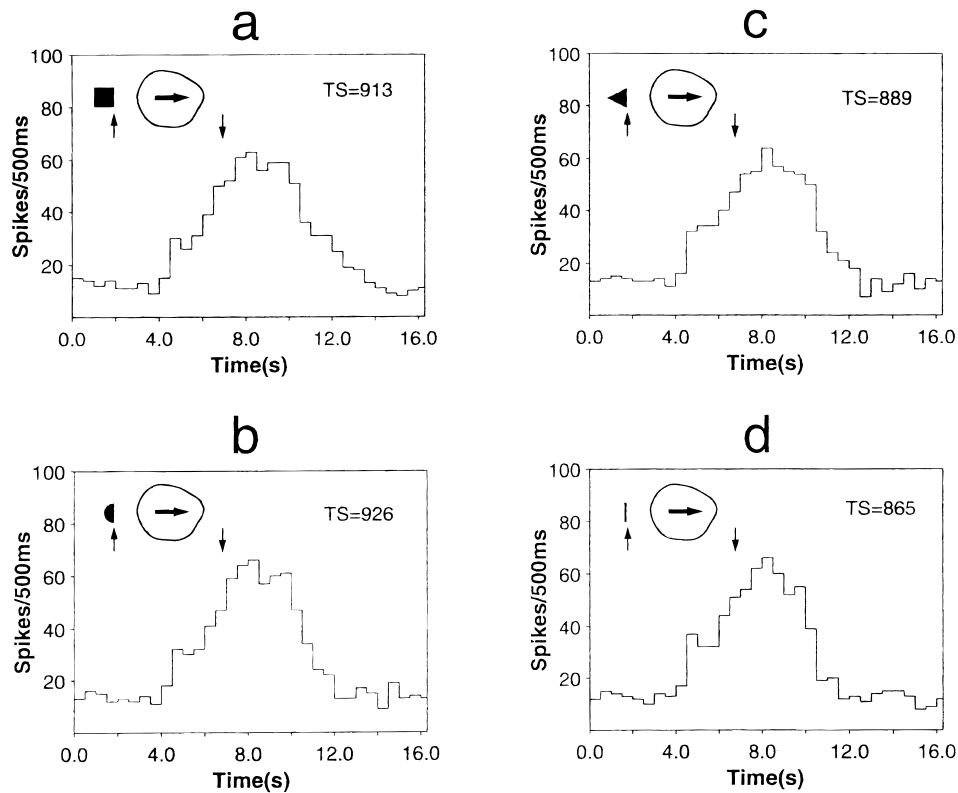
responses at all. All of these ten cells, like this one, vigorously responded to sharp-contrast edges and produced either weak or no responses to the blurred edges.

Eighteen cells were examined for their visual responsiveness to stimuli possessing various shapes and areas, but with an identical leading edge. Though a black square, semicircle, and isosceles triangle were quite different in shape and area with an area ratio of 1:0.39:0.50, they elicited almost the same responses in terms of total number of spikes, whose ratio was 1:1.01:0.97 correspondingly (Figs. 3a–3c). If the black square was significantly reduced to one-tenth of its area but the edge was still identical, this slim rectangle could generate 95% of spikes produced by motion of the square (Fig. 3d). Sixteen of 18 cells behaved in this fashion, and two others appeared to somewhat respond in a shape- and/or area-dependent way. For example, their responsiveness to the triangle was about 80% of that to the square.

Spatial summation processing was found in all 11 nLM neurons examined. In the cases that the leading edge of a moving black

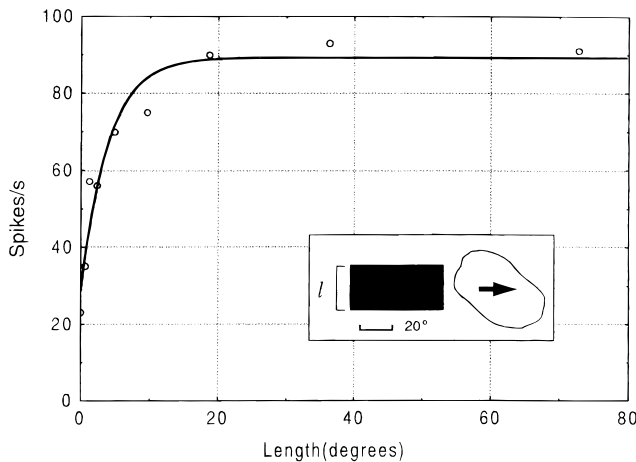
object was orientated perpendicular to the preferred direction, the magnitude of visual responses in these cells increased as the leading edge was lengthened up to a certain value. Lengthening beyond that value did not cause any further increases in their responsiveness. It was shown in Fig. 4 that the central region of a cell's ERF was much more sensitive than the peripheral region. For example, motion of a 10-deg black edge over the cell's central ERF produced 90% of the maximal firing rate. Further increases in edge length only resulted in a negligible increase in firing rate, reaching a plateau at 20 deg in the length-tuning curve, though the ERF size was  $45 \times 55 \text{ deg}$ . Most neurons reached their saturation levels at the edge lengths of 30–50 deg. No correlation was found between the length-tuning curves and the locations and extents of ERFs of nLM cells tested.

The responsive strength of nLM cells depended on orientation of the leading edge of visual stimuli. In all three unidirectional cells examined in the present study, any deviation of the leading edge from its orientation perpendicular to the preferred direction



**Fig. 3.** A nLM neuron responded to the black leading edges but not to the shape and area of a square (a), semicircle (b), isosceles triangle (c), and line (d). These leading edges were identical in length (12 deg) and orientated perpendicular to, and moved (3.8 deg/s) in, the preferred direction (thick arrows) through the cell's ERF (ellipses, 35 × 40 deg). In the inset, thin arrows represent the start (upward arrow,  $t = 0$ ) and end (downward arrow,  $t = 16$  s) of motion. TS: total number of spikes averaged from three sweeps.

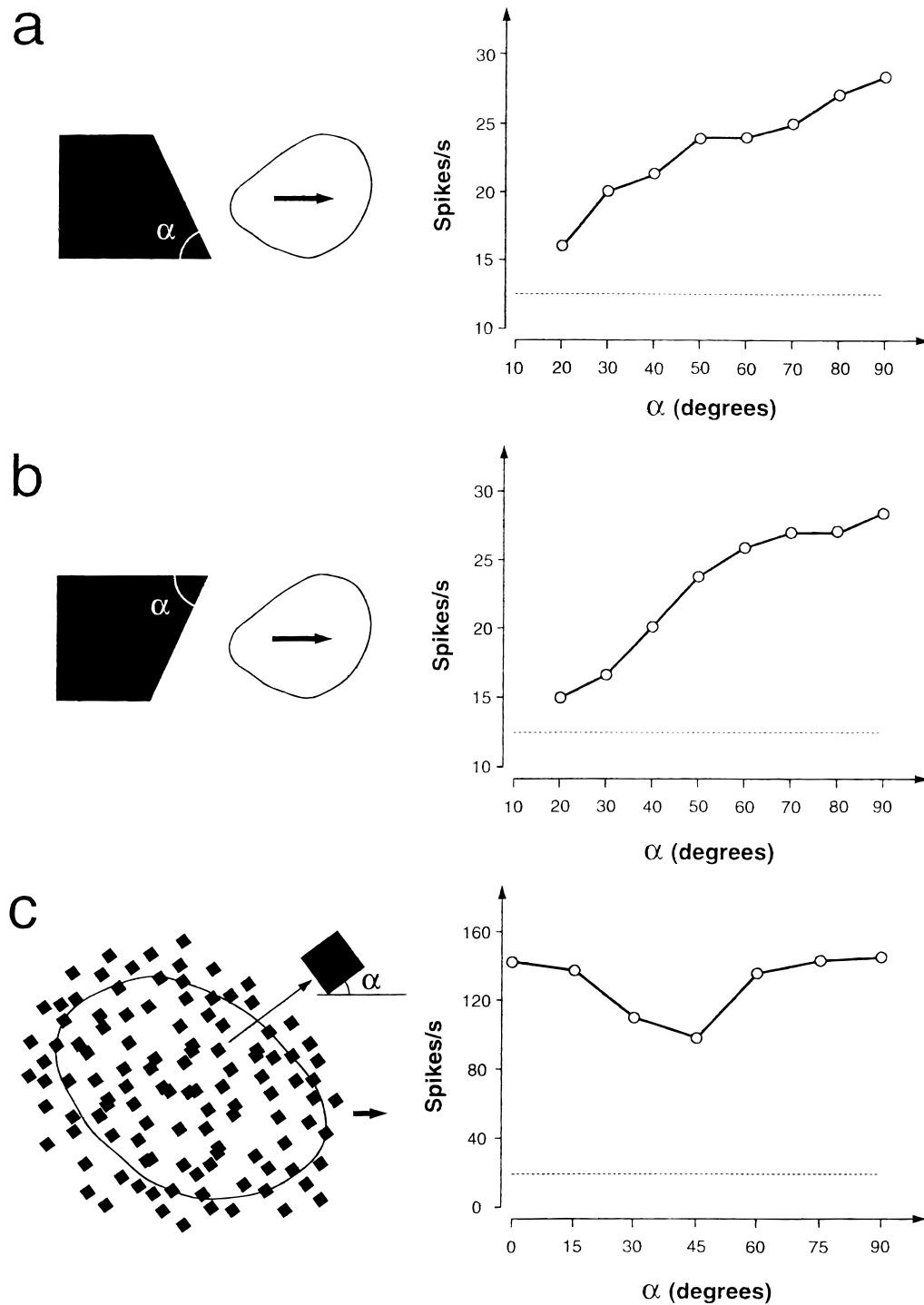
would decrease firing rates of these cells. The more the edge was inclined, the weaker the cell's responses was (Figs. 5a and 5b). It was interesting to note that visual responses in nLM cells evoked by a random pattern consisting of black squares (2 deg in size, 250



**Fig. 4.** Edge-length tuning curve showing the relationship between responsive strength produced by an edge and its length ( $l$ ) when it was perpendicular to and moved (6.0 deg/s) in the preferred direction (thick arrow) through the cell's ERF (ellipse, 45 × 55 deg) (Inset, scale = 20 deg). Small circles were experimental data.

squares/m<sup>2</sup> in density) also depended on orientation of the square edges. When the leading edge was orientated perpendicular to the preferred direction and moved at the optimal velocity, 11 of 12 nLM cells produced the maximal responses. Any deviation of the leading edge from the optimal orientation would result in decreases in the cells' firing rates, reaching their minimum at 45-deg inclination (Fig. 5c). The other did not show a clear dependence of visual responses on orientation of the leading edge. It appeared that there was no correlation between this orientation-detecting property and the location of these cells' ERFs in the visual field. Furthermore, in nine cells tested, whether stimuli moving in the nonpreferred directions could elicit visual responses from nLM cells depended on if there existed a component of stimuli that was apparently moved in the preferred direction. As shown in Fig. 6, a black square did not produce obvious responses, because it had no component apparently moving in the preferred direction, while a circle and triangle could elicit stronger visual responses, due to the apparent motion of some components of these objects in the preferred direction. This so-called "aperture" phenomenon and Fig. 5c indicated that visual analysis by nLM cells seemed very local.

Taken together, the present study indicated that visual responses of nLM cells to moving objects were determined by, in addition to the direction and velocity of motion, some physical properties of objects, including contrast, sharpness, length, and orientation of their leading edges, but not by their shapes and areas. It was instructive to note that sharp-contrast black edges orientated perpendicular to their motion direction would be suited for further studies on visual properties of the accessory optic cells in birds.

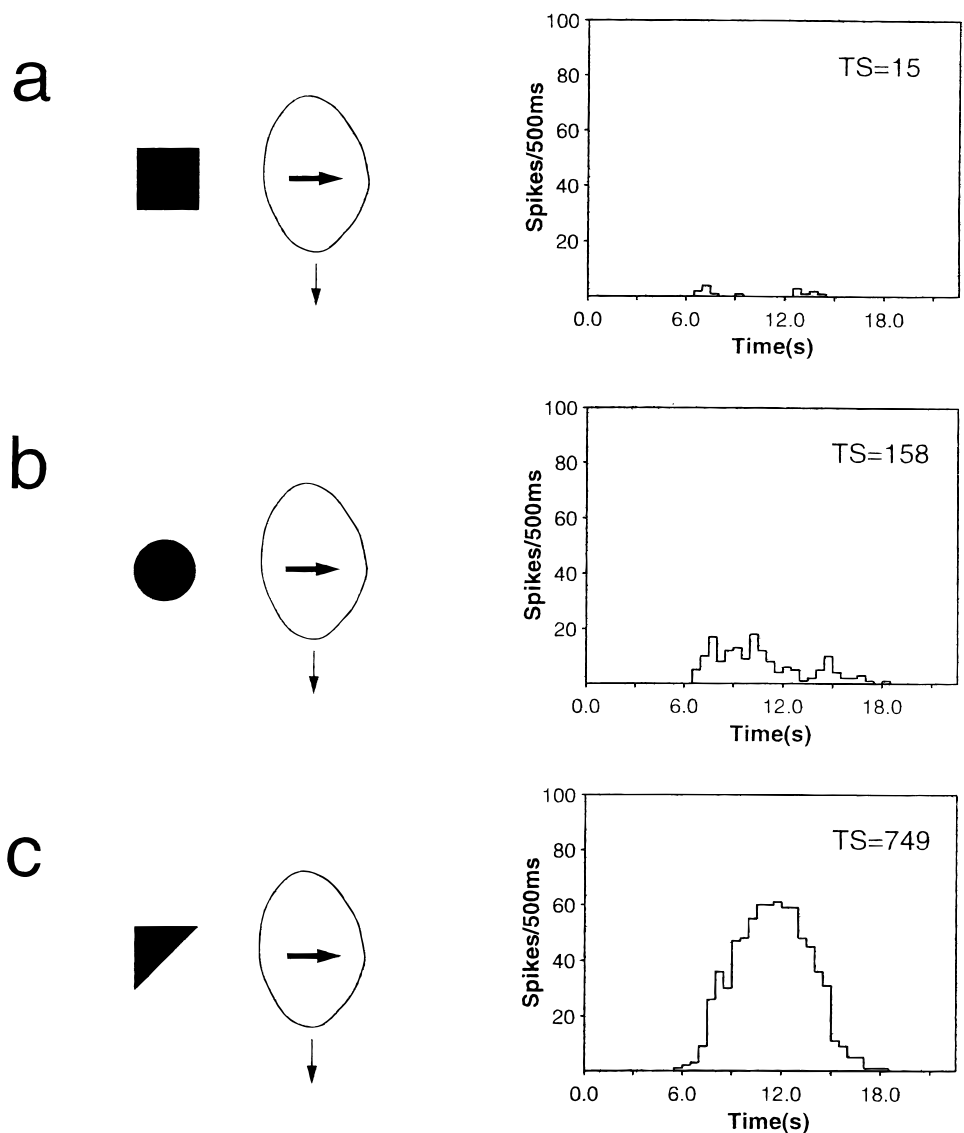


**Fig. 5.** Orientation tuning curves showing that visual responses of a nLM cell were related to orientation of the leading edges relative to the cell's preferred direction (thick arrows). Ordinates (spikes/s) represent firing rates evoked by the edges when their middle points were passing (3.0 deg/s) through the ERF (ellipses, 50 × 60 deg) center. Abscissas represent inclination angles ( $\alpha$ , degrees). Note that the firing rates reached maximum when the inclination angle was 90 deg (a, b). In (c) were responses of a nLM to a random-dot pattern (2 × 2 deg in size, 250 dots/m<sup>2</sup> in density) moved at 4.2 deg/s. Symbols were the same as in (a) and (b).

**Discussion**

Large-field stimuli have been conventionally used for studying OKN and visual response properties of neurons in nLM of lower

vertebrates and in NOT-DTN of mammals. Several studies have reported that optokinetic neurons also respond to single targets as well (Hoffmann et al., 1988; Hoffmann & Distler, 1989; Mustari & Fuchs, 1990; Fu et al., 1998). The present study not only provides



**Fig. 6.** Histograms showing visual responses of a nLM cell to components in the cell's preferred direction (thin arrows) of a square (a), circle (b), and triangle (c) that were moved (thick arrows) perpendicularly to the preferred direction at 4.0 deg/s through the cell's ERF (ellipses, 40 × 60 deg ). TS: total number of spikes averaged from three sweeps. Note that the square with no moving component in the preferred direction did not elicit visual responses, whereas the triangle had a larger component than the circle, so that the former produced stronger responses than the latter.

further evidence for nLM neurons responding both to large-field stimuli and to single targets, but also is the first paper to describe some particular features, in addition to the direction and velocity of motion, of single targets that effectively activate visual neurons in the pigeon nLM.

Our electrophysiological data show that these cells prefer black edges to white ones, in accordance with direction-selective units in the rabbit NOT (Collewyn, 1975*b*). However, this black-edge preference cannot be explained by OFF responses, because the majority of the black-edge preferring nLM cells do not show visual responses to offset light stimulation. On the other hand, the blurred edge created by gradually reducing luminance at the boundary region failed to elicit visual responses from nLM neurons. This contrast response property is similar to that of the wallaby NOT-DTN neurons, which decrease latency and increase responsiveness

as stimulus contrast increases (Ibbotson et al., 1994). It may be deduced that square-wave gratings appear to be stronger than sine-wave gratings in eliciting visual responses from nLM neurons and optokinetic nystagmus as well, if the other parameters of both stimuli are identical, because black stripes in the former possess sharp-contrast edges. The leading-edge orientation is also a stimulus feature affecting responsiveness of nLM cells. Their selectivities for orientation of the leading edges and for the direction of motion probably originate in part from the retinal ganglion cells, because retinofugal fibers with direction selectivity may converge on NOT cells to create directionality in this nucleus (Collewyn, 1975*b*; Hoffmann & Schoppmann, 1975) and there exist several types of ganglion cells in the pigeon retina that respond selectively to orientated edges moving in some particular directions (Maturana & Frenk, 1963; Maturana, 1963). The pigeon nLM also can

be modulated by the nucleus of the basal optic root (nBOR) (Fite et al., 1979; Wylie et al., 1997), by the isthmo-optic nucleus (ION) through the retina (Woodson et al., 1995), and by the optic tectum as well (Hunt & Künzle, 1976).

The sizable ERFs of nLM neurons imply that they receive inputs from many precursor neurons with smaller receptive fields, and therefore they can spatially summate converging signals (Ibbotson et al., 1994), characterized by the fact that neuronal firings increase as stimulus area is enlarged (Ibbotson et al., 1994), or with increasing stimulus edge. The ERFs of nLM neurons are mainly distributed around the horizontal meridian in the superior visual field (Fu et al., 1998). About 40% of ERFs include the foveal region, differing from the primate NOT in that the receptive fields of most NOT neurons in monkeys include the foveal region, whereby they are activated by the foveal and parafoveal region (Hoffmann & Distler, 1989); while most nLM neurons in pigeons can respond to stimuli presented to the extrafoveal region. It has been suggested that the primate NOT seems to be specialized for analyzing perifoveal motion and full-field stimulus velocities (Mustari & Fuchs, 1990). The avian nLM neurons also can analyze the direction and velocity of visual motion not only in the perifoveal region but also in the extrafoveal region. The ERF center was maximally responsive (Fu et al., 1998), similar to the "hot spot" in the pigeon nBOR cells (Wylie & Frost, 1990) and in ectostriatal neurons of the zebra finch (Engelage & Bischof, 1996). This might be a reason why nLM cells are very sensitive to changes in a small part of their ERFs. The present study shows for the first time that pigeon nLM cells can detect contrast, orientation, and length of the leading edges, but not the shape and area of visual objects. It is conceivable that these feature-extraction characteristics are specialized for detecting optokinetic stimuli, but not for realizing pattern recognition. This might be at least one of the reasons why large-field gratings or random-dot patterns have been used to study visual responses of the accessory optic neurons and optokinetic nystagmus as well, because many high-contrast edges in these stimuli can activate a neuron to periodically discharge (Fig. 1C), or groups of neurons to simultaneously fire to elicit optokinetic reflex.

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