原 著

Neural correlates of time-to-collision estimation from
visual motion in monkeys

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Most animals including humans can judge whether an approaching object will hit them, but neural correlates for time-to-collision estimation in primates are still unknown. A previous model study suggested that time-to-collision estimation could be derived in MST using optic flow. In this study, we searched for neural correlates in the dorsal MST and caudal FEF. We examined discharge of single neurons using a Julesz pattern ($20^\circ \times 20^\circ$) combined with a 0.5° single spot. For collision stimuli, a Julesz pattern of $5^\circ \times 5^\circ$ visual angles was first presented on a computer display placed 50 cm ahead of the monkeys' eyes. After 0.5–1 s, the pattern expanded to simulate its approach to the monkeys at constant velocities of 13–120 cm/s from a simulated distance of 75 cm for MST neurons (100 cm for FEF neurons) until the collision, while the monkeys fixated on a stationary spot on the screen center. We recorded 25 neurons in the dorsal MST that responded to collision stimuli. Of these, 13 neurons responded continuously during collision stimuli indicating that they simply responded to components of the optic flow (group A). The remaining 12 neurons exhibited peak discharge before the time of collision (group B). Time-to-collision of group B neurons depended on the approaching pattern velocity, whereas distance-to-collision was nearly constant, suggesting that group B neurons signaled distance-to-collision. In contrast, most caudal FEF neurons that responded to collision stimuli (8/11) exhibited peak discharge almost at the time of collision, and the peak discharge time remained constant irrespective of the approaching pattern velocity. Most of these neurons (7/8) were pursuit-related. These results suggest that dorsal MST and caudal FEF have dif-

ferent roles in estimating time-to-collision from visual motion.

Key words: Visual motion; Collision; Monkey; Smooth pursuit; MST; FEF

Introduction

Visual information is processed through two pathways in the cerebral cortex of primates; the ventral pathway specialized for the analysis of form and the dorsal pathway specialized for motion detection.¹⁾ One of the functions of the dorsal pathway is to determine when an object approaching on a direct collision course will collide. This ability is fundamental in most animals including humans for an appropriate motor response in many everyday situations.²⁾³⁾

Neural correlates for time-to-collision have been studied extensively in birds⁴⁾⁵⁾; pigeon thalamus contains neurons that code time-to-collision and distance-to-collision. In primates; however, neural substrates for time-to-collision estimation remain unknown. Many models have been proposed and most assume that the middle temporal visual area (MT) and medial superior temporal area (MST) play a major role in detecting time-to-collision.^{3)6)~8)} MST is essential in visual motion processing. MST neurons respond to optic flow,⁹⁾¹⁰⁾ and many of them also respond during smooth pursuit eye movements.¹¹⁾

In this study, we examined neural correlates for time-to-collision in the dorsal MST of monkeys. We also compared the activity of the frontal eye fields (FEF) since they receive direct projections from MST and contain neurons responding to smooth pursuit and visual motion.^{11)~14)} Some of the results have been presented in a preliminary form.¹⁵⁾¹⁶⁾

Materials and methods

General procedures

We used Japanese macaques (*Macaca fuscata*, 4.0–5.5 kg, $n = 4$). All procedures complied with the NIH guidelines for the Care and Use of Animals and the Animal Care and Use Committee of Hokkaido University School of Medicine approved our specific procedures. The general methods for animal preparation, training, eye movement recording, and data analysis were described in detail previously.¹⁷⁾¹⁸⁾ Briefly, each monkey was sedated with midazolam (0.3 mg/kg) and medetomidine (0.03 mg/kg), and then anesthetized with sodium intraperitoneal pentobarbital (25 mg/kg). Under aseptic conditions, head holders were installed to restrain the head in the primate chair. Vertical and horizontal eye movements were recorded by the search coil method. A recording chamber was stereotaxically implanted on the skull to allow single-unit recording in the MST in two monkeys^{17)~19)} and in the FEF in the remaining 2 monkeys.¹²⁾¹³⁾ Analgesics and antibiotics were administered post-surgically to reduce pain and prevent infection.

Training procedures and recording procedures

Each monkey was seated in a primate chair in darkness facing a 22-inch computer display (Mitsubishi, 120 Hz) placed 50 cm away from the eyes. The head was firmly restrained in the stereotaxic plane. A target spot (0.5° visual angle in diameter) moved sinusoidally at 0.3 Hz ($\pm 10^\circ$ visual angle) in vertical, horizontal or 2 oblique directions (45° – 225° , 135° – 315°). When it stayed stationary, the monkeys were trained to fixate on it for juice reward. After this initial training, a Julesz pattern ($20^\circ \times 20^\circ$ visual angles in diameter) was presented. The pattern was moved in 8 cardinal directions separated by 45° (horizontal, vertical and oblique directions) and contraction or ex-

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pansion while the monkeys fixated a 0.5° stationary spot at the screen center. During contraction or expansion, the Julesz pattern decreased or expanded, respectively, to simulate pattern movement away from or towards the monkey.

For our search task, the spot moved sinusoidally along oblique trajectories across the stationary background pattern in order to locate neurons whose activity was related to smooth pursuit and/or visual motion. To examine the preferred directions for optic flow, a smaller Julesz pattern ($10^\circ \times 10^\circ$ visual angles in diameter) was used while the monkeys fixated a 0.5° stationary spot at the screen center. A further smaller visual pattern ($2.5^\circ \times 2.5^\circ$ or $5^\circ \times 5^\circ$ visual angles) was also used to examine roughly the receptive field size and whether the receptive field included the ipsilateral hemifield.

To examine how individual neurons responded to collision stimuli, typically 50 repetitions were tested for each stimulus velocity. For this, monkeys first fixated a stationary red spot and then a stationary Julesz pattern ($5^\circ \times 5^\circ$) was presented (Fig. 1 A). After 0.5–1 s, it started expanding to simulate its approach to the monkeys at constant velocities of 13–120 cm/s from a simulated distance of 75 cm for MST neurons and 100 cm for FEF neurons while the monkeys fixated the stationary spot on the screen center (Fig. 1 B) until the simulated pattern collided to their eyes (Fig. 1 C). After the collision, it disappeared for 2–3 s.

Previous studies have shown that MT/MST and FEF neurons respond during smooth pursuit eye movements.^{(12)–(14)(18)(19)} To examine whether responsive neurons in our search stimulus responded to smooth pursuit, the 0.5° spot was moved sinusoidally without presenting the background pattern.

Data analysis

Data were analyzed off-line as previously described.⁽¹⁷⁾⁽¹⁸⁾ Eye-position and Julesz pattern-position signals were digitized at 500 Hz using a 16-bit A/D board on a personal computer. Neuronal discharge was detected at 100 kHz clock rate,

Fig. 1. Collision stimuli. Monkeys fixated a 0.5° stationary red spot at the center of the monitor screen. A stationary Julesz pattern ($5^\circ \times 5^\circ$ visual angles) was presented (A). After 0.5–1 s, it started expanding to simulate its approach to the monkeys at constant velocities of 13–120 cm/s while the monkeys fixated the stationary spot on the screen center (B) until the approaching pattern collided to their eyes (C). For further explanation, see text.

and was discriminated with a dual time-amplitude-window discriminator and digitized together with other analog signals at 500 Hz. Saccades were marked with a cursor on eye velocity traces and removed using an interactive computer program as described previously.⁽¹⁷⁾⁽²⁰⁾ To examine discharge modulation to pattern/spot motion, we first aligned typically 50 trials on the stimulus onset. A spike density function was constructed from spike trains of individual neurons as the sum of Gaussian functions (unit area, 17.6 ms sigma) centered on the individual spike events.⁽²¹⁾⁽²²⁾ Traces in which saccades and/or blinks appearing within 1 s of the time of collision were omitted.

Histological procedures

Towards the end of the recordings, some of the recording sites were marked by passing current ($50 \mu\text{A}$ for 30 s) through the iron-plated tip of a tungsten electrode. After recording was com-

Fig. 2. Discharge of representative MST neurons during collision stimuli and their response properties. A and B, discharge of group A and B neurons, respectively. In A and B, discharge modulation of each neuron during collision stimuli are shown at different velocities as indicated. At each velocity, three traces are shown; a trajectory of visual stimuli and discharge modulation (raster and histogram) of neuronal discharge. C and E, distance-to-collision and time-to-collision of individual group B neurons plotted against approaching pattern velocity. D and F, mean $\pm$ SD. For further explanation, see text.

pleted, the monkeys were deeply anesthetized with pentobarbital sodium (50 mg/kg, i.p.) and perfused with 3.5% formalin. After histological fixation, coronal sections were cut at 100 μ m thickness on a freezing microtome. These sections were stained using the Nissl method and the recording sites were verified microscopically as previously described.¹³⁾¹⁷⁾¹⁸⁾

Results

MST neurons

We recorded 61 neurons that responded during smooth pursuit across a stationary visual pattern in the dorsal MST. Of these, 25 responded to collision stimuli. If the activity of these neurons was related to time-to-collision, they should exhibit peak discharge at a particular time with respect to the time of collision irrespective of the velocity of the approaching pattern. If their activity was not related to time-to-collision, they should respond

Fig. 3. Discharge characteristics of a representative MST group B neuron. A, preferred direction testing by applying optic flow along different directions. B, receptive field size testing. C, smooth pursuit. Discharge modulation (raster and histogram) is shown for each stimulus presentation. Arrows in A and B indicate the direction of optic flow in the fronto-parallel plane at the screen distance. These stimuli were applied sinusoidally as indicated. During contraction or expansion in A, the Julesz pattern decreased or expanded, respectively, to simulate pattern movement away from or towards the monkey. The stimulus trajectory (third trace from bottom of A) indicates the actual signal to give sinusoidally moving pattern motion in depth for the monkey's point of view. During B, optic flow stimuli were applied along the preferred direction with the pattern size as indicated. During A–B, the monkey fixated a stationary spot at the screen center as schematically illustrated (dot) in B. This neuron had a large receptive field in the contralateral and downward visual field (B). In C, stimulus trajectory is not shown, since the monkey pursued the spot motion nearly perfectly as indicated in the horizontal eye position trace. D, data for Fig. 2 B were re-analyzed by aligning them on the onset of blinks as indicated by vertical eye position traces. Pos indicates position. Ipsi and contra indicate ipsilateral and contralateral, respectively, to the recording side. For further explanation, see text.

simply to the pattern motion but should not exhibit peak discharge near the collision time. Thirteen of the 25 neurons exhibited the latter response pattern (group A), meaning that they were simply responding to optic flow. The remaining 12 neurons exhibited peak discharge before the collision time (group B).

Group A neurons

Figure 2 A illustrates discharge modulation of a representative group A neuron during collision

stimuli at different velocities while the monkey fixated a stationary spot at the screen center. This neuron discharged nearly continuously during collision stimuli at different pattern velocities (Fig. 2 A). To examine the nature of the responses during collision stimuli, preferred direction and receptive field size were tested during optic flow (see Materials and methods). All 13 group A neurons exhibited strong modulation to optic flow, consistent with previous reports.^{9)10)17)~19)} Dis-

Fig. 4. Discharge of representative caudal FEF neurons that responded during collision stimuli and their response properties. A and B, discharge of 2 neurons; note in B that resting discharge during pattern off was suppressed during pattern presentation. In A and B, discharge modulation of each neuron during collision stimuli are shown at different velocities as indicated. At each velocity, three traces are shown; a trajectory of visual stimuli and discharge modulation (raster and histogram) of neuronal discharge. C and E, distance-to-collision and time-to-collision of individual neurons, respectively, are plotted against approaching pattern velocity. D and F plot mean $\pm$ SD. Filled symbols in D and F are mean $\pm$ SD of MST group B neurons.

Fig. 5. Discharge characteristics of a representative caudal FEF neuron. A, preferred direction testing by applying optic flow along different directions. B, receptive field size testing. C, smooth pursuit. Arrows in A and B indicate the direction of optic flow (A and B) in the fronto-parallel plane at the screen distance with the stimulus motion trajectory as indicated. During A-B, the monkey fixated a stationary spot at the screen center as schematically illustrated (dot) in B. During B, optic flow stimuli were applied along the preferred direction with the pattern size as indicated. In C, stimulus trajectory is not shown, since the monkey pursued the spot motion nearly perfectly as indicated in the horizontal eye position trace. D, data for Fig. 4 A were re-analyzed by aligning them on the onset of blinks as indicated by vertical eye position traces. Abbreviations as indicated in Fig. 2. For further explanation, see text.

charge of six of 13 neurons was unrelated to smooth pursuit, but was related in the remaining 7.

Group B neurons

Figure 2 B illustrates discharge modulation of a representative group B neuron during collision stimuli at different velocities while the monkey fixated a stationary spot at the screen center. In contrast to group A neurons (Fig. 2 A), group B neurons exhibited clear peak discharge before the collision time (Fig. 2 B).

To evaluate the peak discharge, we defined 2 parameters: time-to-collision and distance-to-collision. As indicated in Fig. 2 B, time-to-collision equals the time difference between the peak discharge time and the time the approaching pattern collided with the monkey (thick horizontal bars), whereas distance-to-collision is the distance between the pattern and the monkeys' eyes when the neuron exhibited peak discharge (thick verti-

cal bars). Figure 2 C-F plots distance-to-collision (C) and time-to-collision (E) of 12 group B neurons and their mean $\pm$ SD (D, F) against approaching pattern velocities. Distance-to-collision remained nearly constant (Fig. 2 C, D), whereas time-to-collision depended on the approaching pattern velocity (Fig. 2 E, F), suggesting that MST group B neurons signaled distance-to-collision (Fig. 2 D).

Figure 3 (A-C) illustrates discharge characteristics of the group B neuron illustrated in Fig. 2 B during optic flow along different directions (Fig. 3 A) and smaller optic field stimuli (Fig. 3 B) and smooth pursuit (Fig. 3 C). Similar to group A neurons, this neuron exhibited strong modulation to optic flow with the preferred direction contralateral to the recording side (Fig. 3 A) and had a large receptive field in the contralateral visual field (Fig. 3 B). Thus, visual motion responses of this neuron during collision stimuli reflected dis-

charge in response to components of optic flow (Fig. 2 B). Most group B neurons (10/12) were pursuit-related (Fig. 3 C), and all ($n = 12$) responded to optic flow.

Caudal FEF neurons

We recorded 20 neurons that responded during smooth pursuit across a stationary visual pattern in the caudal FEF. Of these, 11 responded during collision stimuli. Their responses were mixed. Of the 11, 8 exhibited peak discharge near the time of collision irrespective of the approaching pattern velocity. Of these 8, 5 also responded to visual motion, while 3 others rarely exhibited visual motion response during collision stimuli. Discharge of representative neurons is shown in Fig. 4 (A, B) for the above described 2 types of responses. Both neurons showed peak discharge near the time of collision (Fig. 4 A, B, arrows).

Figure 4 C–F plots distance-to-collision (C) and time-to-collision (E) of the 8 neurons and their mean $\pm$ SD (D, F, open squares) against approaching pattern velocities. Unlike MST group B neurons, distance-to-collision of caudal FEF neurons varied during different pattern velocities (Fig. 4 C), whereas time-to-collision remained relatively constant (Fig. 4 E, F). For comparison, Fig. 4 D and F (filled squares) plot mean $\pm$ SD of MST group B neurons. Although, we were unable to examine MST neurons at higher approaching pattern velocities (vs. Fig. 2 C–F), differences in responses between MST group B and caudal FEF neurons are clear (Fig. 4 D, F), suggesting that some caudal FEF neurons signaled time-to-collision (Fig. 4 F)

Figure 5 (A–D) illustrates discharge of the caudal FEF neuron shown in Fig. 4 A during optic flow along different directions (Fig. 5 A). This neuron exhibited strong modulation to optic flow with the preferred direction ipsilateral/upward to the recording side (Fig. 5 A) with a large receptive field (Fig 5 B). Caudal FEF neurons that discharged specifically near the time of collision (e.g., Fig. 4 B) exhibited suppression of resting discharge rate during optic flow. All 8 neurons that

exhibited peak discharge near the time of collision had a large receptive field including both ipsilateral and contralateral visual fields and modulation was stronger when pattern motion was applied near the fovea using a smaller pattern as illustrated in Fig. 5 B. Virtually all of them (7/8) were pursuit neurons (Fig. 5 C).

Of the remaining 3 (of the 11) caudal FEF neurons that responded during collision stimuli, discharge of 2 neurons was similar to that of MST group A neurons, and one was similar to MST group B neurons.

Discharge during blink

Collision-related discharge peaks of MST and caudal FEF neurons (Figs. 2 B, 4 A, 4 B) might have been induced by blinks, although clear blinks that appeared within 1 s of the time of collision were deleted in our analysis (see Data analysis). To examine this possibility, we re-analyzed data by aligning discharge on blink onset. Results are shown in Fig. 3 D and 5 D for the same neurons. Although there was a brisk blink-related discharge (Fig. 3 D, 5 D), it hardly explains collision related discharge of the same neurons (Figs. 2 B, 4 A, 4 B). None of group B MST neurons or caudal FEF neurons exhibited blink-related discharge comparable to that during collision stimuli. These results indicate that collision-related discharge was not the result of blink-related discharge.

Recording locations

Recording locations of 2 of the 4 monkeys were shown previously (MST: Fig. 10 of ref 18; FEF: Fig. 11 of ref 13). In MST, most of the tracks passed through the rostral bank of the superior temporal sulcus, consistent with MSTd. In the caudal FEF, recordings tracks were confirmed to be within the fundus of the arcuate sulcus (e.g. ref 13). Recording sites of the remaining 2 monkeys were similarly confirmed histologically.

Discussion

Neurons coding time-to-collision and distance-to-collision are present in pigeon thalamus.^{4/5} Although the number of tested neurons was small in our study, group B MST neurons signaled

distance-to-collision (Fig. 2 D), and time-to-collision signals are found in the caudal FEF (Fig. 4 F). We were unable to detect MST neurons coding time-to-collision. However, we do not exclude the possibility that MST contains a subset of neurons that are specifically involved in detecting time-to-collision. These results are consistent with the MST model study that predicts distance-to-collision and time-to-collision estimation by integrating optic flow in MT.³⁾

Functional MRI studies in humans reported collision judgment-related brain activation in the inferior parietal cortex.²³⁾ Consistent with this finding is the representation of time in monkey posterior parietal cortex including the lateral intraparietal area (LIP).²⁴⁾²⁵⁾ MST projects not only to the LIP but to the FEF.¹¹⁾ Our results showing that neurons signaling time-to-collision were present in the caudal FEF suggest that time-to-collision estimation requires further processing of distance-to-collision signals carried by MST neurons. How this conversion is done remains unknown. However, since most collision-related FEF neurons were pursuit neurons, there may be a common mechanism for collision time detection and smooth pursuit, such as prediction to compensate for inherent delays in responses to target motion during pursuit.¹¹⁾¹⁴⁾ Our results suggest that MST and caudal FEF in monkeys have different roles in estimating time-to-collision from visual motion.

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