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Activity of pursuit neurons in the caudal part of the frontal eye fields during static roll-tilt

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Abstract

The smooth-pursuit system and vestibular system interact to keep the retinal target image on the fovea during head and/or whole body movements. The caudal part of the frontal eye fields (FEF) in the fundus of arcuate sulcus contains pursuit neurons and the majority of them respond to vestibular stimulation induced by whole-body rotation, that activates primarily semi-circular canals, and by whole-body translation, that activates otoliths. To examine whether coordinate frames representing FEF pursuit signals are orbital or earth-vertical, we compared preferred directions during upright and static, whole-body roll-tilt in head- and trunk-restrained monkeys. Preferred directions (re monkeys' head/trunk axis) of virtually all pursuit neurons tested (n=21) were similar during upright and static whole-body roll-tilt. The slight shift of preferred directions of the majority of neurons could be accounted for by ocular counter-rolling. The mean (±SD) differences in preferred directions between upright and 40° right ear down and between upright and 40° left ear down were 6° (± 6°) and 5° (± 5°), respectively. Visual motion preferred directions were also similar in 5 pursuit neurons tested. To examine whether FEF pursuit neurons could signal static whole-body roll-tilt, we compared mean discharge rates of 29 neurons during fixation of a stationary spot while upright and during static, whole-body roll-tilt. Virtually all neurons tested (28/29) did not exhibit a significant difference in mean discharge rates between the two conditions. These results suggest that FEF pursuit neurons do not signal static roll-tilt and that they code pursuit signals in head/trunk-centered coordinates.

Introduction

Smooth-pursuit eye movements are essential to obtain accurate visual information about a slowly moving object. In daily life, the smooth-pursuit system does not work independently but interacts with the vestibular system to keep the retinal target image on the fovea during movement of the head and/or whole-body.

The caudal part of the frontal eye fields (FEF) in the fundus of the arcuate sulcus contains pursuit neurons (e.g., MacAvoy et al. 1991; Gottlieb et al. 1993, 1994; Tanaka and Fukushima 1998). The majority of FEF pursuit neurons carry not only visual signals about target motion but also vestibular signals about whole-body rotation that activates primarily semi-circular canals (Fukushima et al. 2000, 2002a, b; Akao et al. 2005, 2006). Moreover, the majority of them also responded to otolith inputs induced by horizontal whole-body translation (Fukushima et al. 2005). These observations raise a question whether coordinate frames of pursuit signals in the caudal FEF are orbital or earth-vertical since in the head-restrained upright condition, coordinate frames cannot be differentiated. To examine this, in the present study we compared preferred directions of FEF pursuit neurons during upright and static whole-body roll-tilt in head- and trunk-restrained monkeys. Because it is well known that the gain of ocular counter-roll to static roll-tilt is very low (~0.1, see Leigh and Zee 1999 for a review; also Suzuki et al. 1997), this method allowed us to dissociate orbital from earth-vertical coordinate frames. We also asked whether FEF pursuit neurons could signal static whole-body roll-tilt during fixation of a stationary spot.

Materials and Methods

Two Japanese monkeys (H, K, Macaca fuscata, 4.6, 5.0 kg) were used. These monkeys were the same monkeys used in previous studies (Fukushima et al. 2004; Kasahara et al. 2006). All procedures were performed in strict compliance with the Guide for the Care and Use of Laboratory Animals (DHEW Publication #NIH85-23, 1985). Specific protocols were approved by the Animal Care and Use

Committee of Hokkaido University School of Medicine. Methods for animal preparation, training and recording were similar to previous studies (Fukushima et al. 2000; Kasahara et al. 2006), and therefore are summarized here only briefly. A scleral search coil was implanted on each eye (Fuchs and Robinson 1966). Monkeys' heads were stabilized in the stereotaxic plane. They were rewarded for pursuit eye movements while in an upright posture and during static whole-body roll-tilt while their trunks were restrained firmly by polystyrene foam in the primate chair. A target spot (0.2° in diameter) was presented on a 14-inch computer monitor in an otherwise dark enclosure. The computer monitor and the primate chair together with the monkey and the coil frame for detection of eye movements were tilted in the roll plane (around the interaural midpoint) to 40° or 60° from the earth vertical (either rightwards or leftwards, e.g., Fig. 1b, f), similar to previous studies (Kasahara et al. 2006).

Extracellular recordings were made in the left peri-arcuate sulcus region at Ant. 20-26 and Lat. 10-17 stereotaxic coordinates as previously described (Tanaka and Fukushima 1998; Fukushima et al. 2000; Akao et al. 2005). Target motion was applied sinusoidally. Single neurons responding to smooth-pursuit were located and pursuit responses were tested in 4 directions (vertical, horizontal and two oblique directions at 45° and 135° polar angle) at 0.5 Hz (±10°) to determine the preferred direction for pursuit activation of each neuron. We selected pursuit neurons with clear directional responses. Preferred activation directions (re monkeys' head/trunk axis) of pursuit neurons were compared during upright posture and during static whole-body roll-tilt while the target was moved along different directions. Typically, we tested upright first, followed by the right ear down, and finally the left ear down. To examine response variability, we repeated the whole procedure two or three times in five neurons.

To examine whether FEF pursuit neurons could signal static whole-body roll-tilt, the monkeys fixated a stationary spot straight ahead of the monkeys' eyes during upright and during static

whole-body roll-tilt for 2-3 s. In some neurons, visual responses of pursuit neurons were also

examined by requiring the monkeys to fixate the stationary spot (fixation spot, 0.2° in diameter) while

a second spot (0.6° in diameter) was moved sinusoidally along one of the 4 directions at 1.0 Hz (±10°)

and compared to the effect of static whole-body roll-tilt. Smooth-pursuit gains of the two monkeys

during upright posture and static roll-tilt were similar to those described previously (Kasahara et al.

2006).

Eye and target position signals and their derivatives were digitized at 500 Hz. Neural discharge was

discriminated and stored in temporal register with analog signals. Cycle histograms were constructed by

averaging the discharge of each neuron over 10–30 cycles. Sinusoids were least-squares fitted to neuron

and eye movement responses. Signal-to-noise ratio (S/N) of the response was defined as the ratio of

amplitude of the fitted fundamental frequency component to the root mean square amplitude of the 3rd

through 8th harmonics. Harmonic distortion (HD) was defined as the ratio of the amplitude of the 2nd

harmonic to that of the fundamental (Wilson et al. 1984). Responses with $HD > 50\%$ or $S/N < 1.0$ were

discarded. Each neuron's sensitivity during pursuit was calculated by dividing amplitude of the

fundamental component of discharge modulation by peak target velocity. Phase shifts were measured

between the peak of the fundamental component of the response and the peak target velocity. The

preferred activation direction of each neuron was estimated by the method of Krauzlis and Lisberger

(1996) using a Gaussian function:

$$y = A0 + A*\exp[-0.5*((x-x0)/s)^2] \qquad\qquad (1)$$

where A0 is the resting rate, A is the maximal discharge modulation at the preferred direction, x0 is the

preferred direction, and s characterizes the width of the Gaussian (Krauzlis and Lisberger 1996; Tanaka

and Fukushima 1998).

Responses to 8 polar directions were examined. For simplicity, we estimated the Gaussian fit by

plotting sensitivity (re target velocity) as described previously (Fukushima et al. 2000). Sensitivity

values were plotted as positive for the increasing discharge, and as negative for the direction toward which discharge rate decreased (e.g., Fig. 1a).

To analyze retinal image-motion response, all traces were aligned on the second spot cycles. Traces that contained saccades or slow eye movement were removed since they were indicative of the monkeys' failure to fixate the stationary target, and only those traces with eye position changes of less than 1° during each cycle were analyzed as described previously (Fukushima et al. 2000, 2002a; Akao et al. 2005).

To examine whether FEF pursuit neurons could signal static whole-body roll-tilt, mean discharge rate and coefficient of variation (CV) of the mean rate were calculated during fixation of a stationary spot straight ahead of the monkeys' eyes for 2 s epochs during upright posture and during static whole-body roll-tilt. The CV was calculated by dividing the SD by the mean discharge rate in order to examine the variability of discharge rate during fixation.

Recording locations were histologically confirmed to be within the fundus of the arcuate sulcus by making electrolytic lesions through the recording electrodes as previously described (Tanaka and Fukushima 1998; Fukushima et al. 2000, 2002a, b; J Fukushima et al. 2004).

Results

We tested the effects of static whole-body roll-tilt on a total of 29 pursuit neurons in the caudal FEF. Of these, pursuit preferred directions were compared in 21 neurons, visual motion preferred directions were compared in 5 neurons, and resting discharge rates during fixation were compared in all 29 neurons. The number of neurons tested varied between tasks due to the occasional degradation or loss of neural recordings. Figure 1 shows discharge of a representative neuron as the animal pursued in the neuron's preferred pursuit direction (i.e., downward) while upright (c) or during static whole-body roll-tilt (a, e). This neuron discharged similarly during the three task conditions (Fig. 1a, c, e). The preferred direction estimated using a Gaussian fit was 266° during upright posture (Fig. 1d).

If preferred directions of FEF pursuit neurons are coded in the earth-vertical coordinates, the expected preferred direction during 40° static roll-tilt would be the same (i.e., downward) irrespective of the monkey's whole-body roll-tilt. Expected preferred directions of this neuron during the 40° right ear down (266+40=306°) and 40° left ear down (266-40=226°) are indicated in Fig. 1b and f (grey and dashed lines, respectively). Actual preferred directions (relative to monkey's head/trunk axis) were 271° during the right ear down condition (solid line in Fig. 1b) and 263° during the left ear down condition (solid line in Fig. 1f), and were clearly different from the directions expected from the earth-vertical coordinates (dashed lines in Fig. 1b, f, bottom).

Figure 2a summarizes preferred directions for a total of 21 FEF pursuit neurons during upright and 40° static whole-body roll-tilt. For virtually all neurons tested, preferred directions during upright and static whole-body roll-tilt were similar. The differences were small, and the shift of preferred direction for the majority of neurons tested was consistent with expected ocular counter-rolling. Figure 2b summarizes the difference in preferred direction between upright and right ear down (RED). Fifteen of 18 neurons tested shifted preferred directions towards the counter-clockwise direction, and one neuron did not show any difference (Fig. 2b). Only 3 neurons shifted preferred directions towards the clockwise direction. The mean difference between clockwise and counterclockwise preferred direction shifts for all neurons tested was 3° counter-clockwise. The mean absolute difference in preferred directions between upright posture and 40° right ear down was 6° (± 6° SD, range 0-13°).

During the left ear down condition (Fig. 2a, LED), 7 of 11 neurons tested shifted preferred directions towards the clockwise direction (Fig. 2c), consistent with the expected ocular counter-rolling (e.g., Fig. 1f). The mean difference between clockwise and counterclockwise preferred direction shifts for all neurons tested was 2° clockwise (Fig. 2c). The mean absolute difference in preferred directions between upright and 40° left ear down was 5° (± 5° SD, range 1-11°). In 9 neurons we further compared preferred directions during static roll-tilt at 60°. The mean

absolute difference in preferred directions between the two conditions was still 5° (range 3-7°).

To examine response variability, in 5 neurons we repeated preferred direction testing (see Materials and Methods). The estimated preferred directions were very consistent with differences of $\leq 2°$ in 4 neurons and 4° in one neuron. We also compared s values (Equation 1) that indicate the width of the Gaussian for each neuron (see Materials and Methods)(Krazulis and Lisberger 1996; Tanaka and Fukushima 1998). s values in Fig. 1b, d, and f were 80°, 80° and 85°, respectively. s values were similar between the three conditions for each neuron tested.

In five FEF pursuit neurons, we tested whether their visual motion preferred directions were affected by static whole-body roll-tilt (right ear down at 40°). The difference in preferred direction is plotted in Fig. 2d for the 5 neurons. Visual motion preferred directions were similar for the two conditions; the mean absolute difference was 6° (range 1-12°).

To examine whether FEF pursuit neurons could signal static whole-body roll-tilt, Fig. 2e plots mean discharge rates of 29 neurons during fixation of a stationary spot straight ahead of the monkeys' eyes while upright and during the 40° right ear down (RED) and 40° left ear down (LED) (see Materials and Methods). Although some neurons exhibited a difference, in the majority of neurons the difference was small. Mean ($\pm$ SD) discharge rates during upright and right ear down and left ear down conditions were 14 ($\pm$7), 15 ($\pm$7), and 15 ($\pm$8) spikes/s. These mean discharge rates were virtually identical for the three task conditions (Fig. 2e, open squares connected by thick lines).

To examine variability of discharge rates during fixation while upright and during static roll-tilt, we calculated CV of the mean discharge rate for each neuron (see Materials and Methods). The CVs ranged from 0.33 to 1.19 and were similar in each neuron during each condition. The overall mean CVs during upright, 40° right ear down and 40° left ear down were 0.58, 0.52 and 0.60, respectively, and the mean for all points was 0.56. In Fig. 2f, we plotted the difference in discharge rate between upright and right ear down (+) and between upright and left ear down (open circles) for each neuron

against the mean discharge rate during fixation while upright. The differences in discharge rates of

individual neurons ranged from 0 to 10 spikes/s. The mean differences between upright and RED was

2 spikes/s and the mean difference between upright and LED was zero. The mean for all points was 1

spike/s. The oblique dashed lines in Fig. 2f indicate the expected mean error ranges that were

estimated from the mean CV (slope ±0.56). Virtually all neurons tested except for one (arrow) were

within the error ranges of the discharge rates, suggesting that virtually all tested neurons

(28/29=97 %) did not exhibit a significant difference in discharge rate between upright and

whole-body roll-tilt.

Discussion

It is well known that the gain of ocular counter-rolling to static roll-tilt is very low (~0.1, see Leigh

and Zee 1999 for a review). Our laboratory has also confirmed that gains of ocular counter-rolling in

Japanese macaques are very low (0.09-0.13)(Suzuki et al. 1997). The present results indicate that the

preferred directions (re monkeys' head/trunk axis) of virtually all FEF pursuit neurons in Japanese

macaques tested were similar during upright and static whole-body roll-tilt and that the slight shift of

preferred directions of the majority of neurons could be accounted for by expected ocular

counter-rolling. Thus, these results indicate that FEF neurons do not code pursuit signals in

earth-vertical coordinates. To the best of our knowledge, this is the first study that examined preferred

directions of pursuit neurons in the cerebral cortex during upright and static whole-body roll-tilt.

Pursuit preferred directions are sorted in horizontal and vertical directions in cerebellar floccular

Purkinje cells (e.g., Krauzlis and Lisberger 1996). Preferred directions of vertical Purkinje cells (re

monkeys' head/trunk axis) remained vertical when squirrel monkeys were tested on their side (e.g.,

Zhang et al. 1995).

Using unanesthetized, paralyzed cats, Tomko et al. (1981) examined the effects of 45°

whole-body tilt on receptive field properties of simple (Hubel and Wiesel 1959, 1962) visual cortical

neurons. The receptive field orientation of 73 % of the cells examined remained unaltered relative to the head axis after tilt, whereas in the remaining 27 %, receptive field orientations either over- or under-shot the retinal tilt by more than 15° (Tomko et al. 1981; see however, Schwartzkroin 1972 using 30° tilt). In the present study, although the number of tested neurons was small, none of the FEF pursuit neurons tested exhibited shifts of visual motion preferred directions or pursuit preferred directions more than 14° during 40° static roll-tilt (Fig. 2b-d) or even during 60° static roll-tilt. These results suggest that FEF pursuit signals are represented in head-centered and/or trunk-centered coordinates. The present study was unable to distinguish between the two.

We were unable to record torsional eye movements in this study. However, our results showing that FEF neurons do not code pursuit signals in earth-vertical coordinates (Figs. 1, 2a-d) are consistent with the results that virtually all tested neurons (28/29=97 %) did not exhibit a significant difference in discharge rate during upright and static whole-body roll-tilt (Fig. 2f). We, therefore, think that FEF pursuit neurons do not signal static roll-tilt.

Because the majority of FEF pursuit neurons receive otolith inputs induced by horizontal whole-body translation (Fukushima et al. 2005), and because roll-tilt also induces linear acceleration towards the tilted direction (e.g., Angelaki et al. 2004), we expected that FEF neurons should also respond to roll-tilt. A possible explanation for our negative result is that, during static whole-body roll-tilt, sensitivity of FEF pursuit neurons to linear acceleration is reduced. This possibility needs to be tested. Task dependent activity is a well-known feature of cortical neurons including eye movement related neurons in the frontal cortex (e.g., Tanji 1996; Fukushima et al. 2006). Although static roll-tilt induces ocular counter-rolling and it may affect the subjective vertical, it does not require smooth-pursuit (see Leigh and Zee 1999 for a review). The present results suggest that caudal FEF neurons contribute to pursuit eye movements specifically in head/trunk-centered coordinates.

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Legends for figures

Fig. 1. Discharge and preferred direction of a representative FEF pursuit neuron while upright or

during static whole-body roll-tilt. **a** and **b**, 40° static whole-body roll-tilt towards right. **c** and **d,**

upright. **e** and **f**, 40° static whole-body roll-tilt towards left. The three traces in **a, c** and **e** are target

velocity, superimposed de-saccaded vertical eye (VE) velocity and raster and histograms of neuron

discharge. **b, d** and **f** (top) illustrate computer monitor and target motion directions from the monkey's

view for the three different task conditions. Actual preferred directions are indicated by black arrows.

Expected preferred directions in the earth-vertical coordinates are indicated by grey arrows in **b** and **f**.

b, d and **f** (bottom) illustrate directional tuning and Gaussian fits for actual responses for each

condition. Solid and dashed lines are actual and expected preferred directions, respectively. Dots indicate actual sensitivity values.

Fig. 2. Comparison of smooth-pursuit preferred directions, visual motion preferred directions and mean discharge rate of FEF pursuit neurons during fixation while upright or tilted. **a** plots pursuit preferred directions for a total of 21 neurons while upright and during 40° right ear down (RED) or left ear down (LED) tilt. Preferred directions of the same neurons are connected by lines. **b** plots difference in preferred directions between upright and right ear down for each neuron tested. **c** plots difference in preferred directions between upright and left ear down for each neuron tested. **d** plots difference in visual motion preferred directions of 5 pursuit neurons during upright and right ear down. During visual motion testing, the monkeys fixated a stationary spot straight ahead of the monkeys' eyes. **e** compares mean discharge rates during fixation of a stationary spot straight ahead of the monkeys' eyes while upright and during 40° RED or LED. Discharge rates of the same neurons are connected by lines. Open squares connected by thick lines indicate overall mean discharge rates for all neurons tested in each condition. **f** plots difference in discharge rate between upright and 40° RED (+) and between upright and LED (open circles) against mean discharge rate of each neuron during upright. Oblique dashed lines indicate the expected error ranges that were estimated from the mean CV. Horizontal dashed line indicates zero difference. Discharge rate difference of only one neuron (arrow) was outside the expected error ranges.
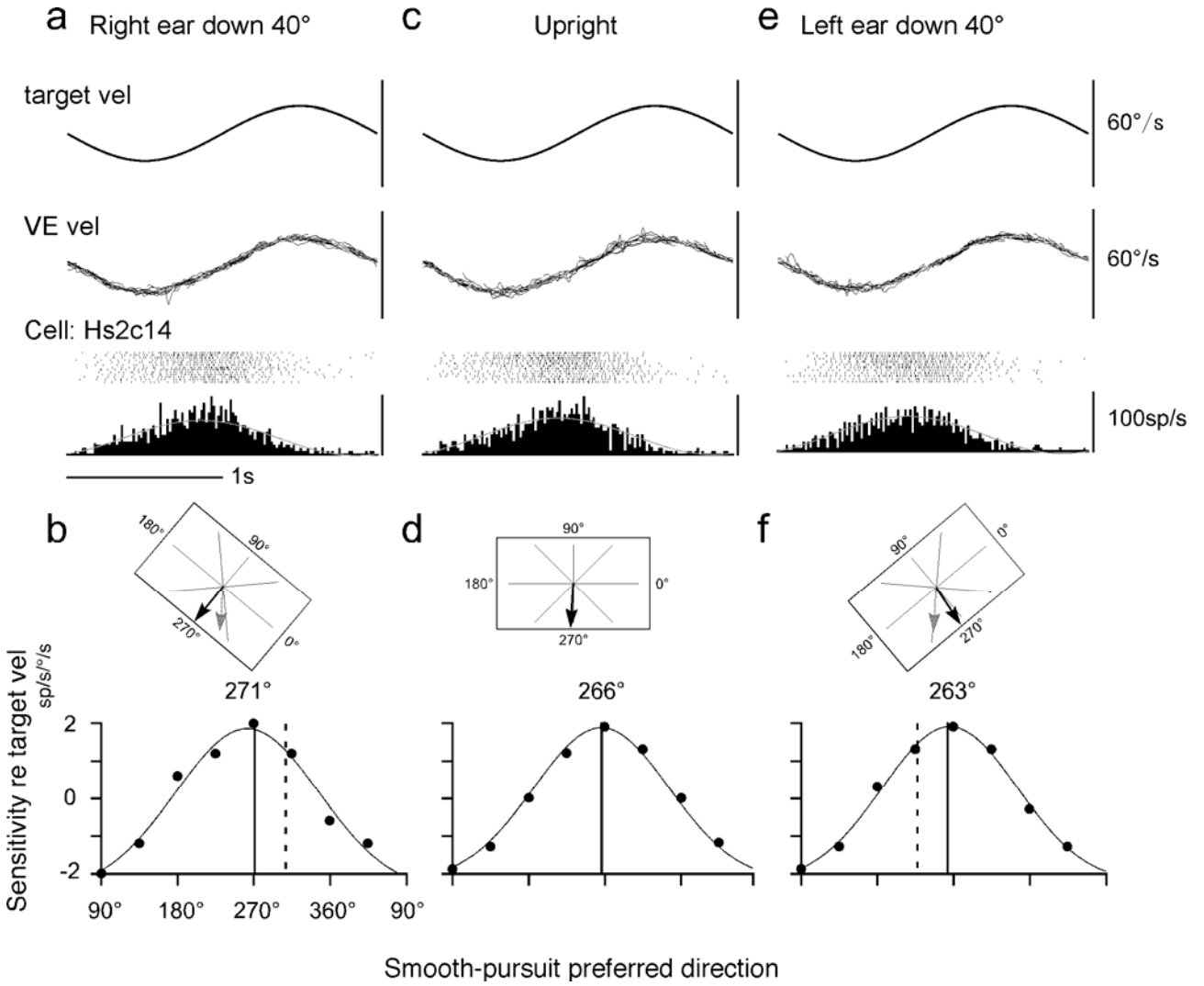
Figure 1

Figure 2