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RESEARCH ARTICLE

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Presaccadic omnidirectional burst activity in the basal interstitial nucleus in the monkey cerebellum

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Abstract We recorded saccade-related neurons in the vicinity of the dentate nucleus of the cerebellum in two monkeys trained to perform visually guided saccades and memory-guided saccades. Among 76 saccade-related neurons, 38 showed presaccadic bursts in all directions. More than 80% of such burst neurons were located in the area ventral to, not inside, the dentate nucleus, which corresponded to the basal interstitial nucleus (BIN as previously described). We found that the activity of the BIN neurons was correlated with saccade duration but not with saccade amplitude or velocity. Thus, when tested with visually guided saccades, the burst started about 16 ms before saccade onset and ended about 33 ms before saccade offset, regardless of saccade amplitude. The characteristic timing of the BIN cell activity was maintained for different types of saccades (visually guided, memory-guided and spontaneous saccades), which had different dynamics. Although the number of spikes in a burst for each neuron was linearly correlated with saccade amplitude for a given type of saccade, the slope varied depending on the type of saccade. Peak burst frequency was uncorrelated with saccadic peak velocity. In contrast, burst duration was highly correlated with saccade duration regardless of the type of saccade. These results suggest that BIN neurons may carry information to determine the timing of saccades.

Key words Cerebellum · Basal interstitial nucleus · Presaccadic burst · Saccade · Monkey

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Introduction

The cerebellum is crucial in the control of saccadic eye movements. Saccadic dysmetrias and instabilities have been shown to be caused by cerebellar lesions in human patients and experimental animals (Selhorst et al. 1976; Ritchie 1976; Keller 1989). Single-unit studies have shown that there are saccade-related neurons in the cerebellar cortex and cerebellar nuclei. Prominent saccadic activities (mainly bursts) have been found in the cerebellar vermis (lobule VI and VII) (Ohtsuka and Noda 1995) and the caudal part of the fastigial nucleus (Ohtsuka and Noda 1991; Fuchs et al. 1993) to which the vermis Purkinje cells project (Noda et al. 1990). Experimental disruption of the vermal-fastigial connection led to severe saccadic dysmetrias (Sato and Noda 1992; Robinson et al. 1993), suggesting that this connection is crucial in determining saccade amplitudes.

Saccade-related activities were also found in the cerebellar hemisphere (Mano et al. 1991) and its projection areas (i.e., interpositus and dentate nuclei) (Gardner and Fuchs 1975; Hepp et al. 1982; MacKay 1988; Van Kan et al. 1993). However, their functions are still unclear; this is partly because the cell activities were variable, including both bursts and pauses, and some neurons also showed activity related to eye position.

Furthermore, the cerebellum seems more complex than was once thought. For example, Langer (1985) found a cluster of neurons outside the traditionally defined cerebellar nuclei and labeled it the "basal interstitial nucleus" (BIN). Anatomical studies have shown that the BIN is reciprocally connected with the flocculus (Langer et al. 1985a) and also projects to the pons and medulla (Gonzalo-Ruiz et al. 1988). However, the function of the BIN has not been investigated.

In this experiment, we found a group of neurons that showed a burst of spikes before a saccade irrespective of direction. Most were identified histologically to be in the BIN. Quantitative analyses showed that the presaccadic burst of BIN neurons was highly correlated with saccade duration but not with saccade amplitude or velocity.

A preliminary account of this work has been reported in abstract form (Takikawa et al. 1996; Kawagoe et al. 1996).

Materials and methods

Experimental animals

Experiments were conducted on two male Japanese monkeys (*Macaca fuscata*; monkeys B and H). The monkeys were housed in individual primate cages in an air-conditioned room and brought to the experimental room at each experimental session. Though the monkeys had free access to food in their home cages, water supply was restricted during periods of training and the experiment. Health was checked and supplementary water and fruit were provided daily. All surgical and experimental protocols were approved by the Juntendo University Animal Care and Use Committee and were in accordance with the National Institutes of Health *Guide for the Care and Use of Laboratory Animals*.

Surgical procedures

Under general anesthesia (pentobarbital sodium, i.v., 4.5–6.0 mg/kg/h), a head holder for stabilizing the head during experiments and a chamber for single-unit recording were fixed on the skull with dental acrylic resin. A search coil was implanted under the conjunctiva by the method described by Judge et al. (1980). Eye movements were recorded using the magnetic search-coil technique (Robinson 1963). The top of the recording chamber was tilted laterally by 35° from the sagittal plane and was aimed at the cerebellar dentate nucleus.

Experimental procedures

Unit activity was recorded from single neurons in the cerebellar nuclei and their surrounding areas in three conditions: (1) visually guided saccades, (2) memory-guided saccades and (3) spontaneous saccades.

The monkey sat in a primate chair in a dimly lit and sound-attenuated room with his head fixed. In front of him was a tangent screen (30 cm from his face) onto which small red spots of light (diameter 0.3°) were backprojected using two LED projectors. The first projector was used for a fixation point, the second for a target point (see Behavioral tasks below). The position of the spot was controlled by reflecting its image off two orthogonal mirror galvanometers.

In the task conditions (visually guided saccades or memory-guided saccades), saccades were controlled by the light targets presented on the screen and the monkey performed these saccades to obtain a reward. Horizontal and vertical eye movements together with single-cell activities were recorded continuously for a block of trials, on-line digitizing. Recordings were repeated with different target eccentricities (see below for details of the tasks).

In the spontaneous saccade condition, no light target was presented on the screen and the monkey was free to move his eyes while obtaining no reward. Eye movements together with single-cell activities were recorded during a 3-min period.

For single-unit recordings, tungsten or Elgiloy electrodes with a resistance of 0.5–2 MΩ at 500 Hz were used. The electrode was inserted into the cerebellum directly through the dura and, in some cases, through a guide tube that was implanted chronically. After recording, small electrolytic lesions (5 μA, 200 s, electrode positive) were placed at recording sites of the saccade-related neurons.

Behavioral tasks

The monkeys were trained to perform visually guided saccades and memory-guided saccades (Hikosaka and Wurtz 1983; Hikosaka et al. 1989). In either of the saccade tasks, a small spot of red light (fixation point) came on at the center of the screen (see below) automatically. The monkey was required to fixate on the fixation point during the period starting 0.7 s after the onset of the fixation point until it went off. If the monkey failed to do so, the trial was aborted, and a new trial started after an intertrial interval. The fixation was judged to be correct if the eye position recorded with the search-coil method (see below) was maintained within a window around the position of the fixation point (usually ±2°).

In the visually guided saccade task, the fixation point went off after a random period (1.5–2.5 s) and at the same time another red spot of light (target point) appeared at a random position, to which the monkey was required to make a saccade. The target point dimmed after 0.5 s. If the monkey's gaze was directed at the target point (within a position window, usually ±3°) when the target dimmed, the monkey received a small amount of water as a reward. Successive trials were separated by an intertrial interval of 1.7–2.2 s (randomized).

In the memory-guided saccade task, 1 s after the fixation point appeared, another spot of light was presented for a short period (50 ms) to indicate the future location of the target point (subsequently called the target cue). The monkey was required to remember the location of the target cue, but had to continue to fixate on the fixation point. The fixation point went off after a random period of time (2–3 s), and the monkey had to make a saccade to the remembered location of the target cue. The actual target point came on after a time gap (0.4 s) and dimmed immediately (after 0.1 s). The monkey received a water reward if his gaze was directed at the target point when it dimmed, as in the visually guided saccade task. If the monkey waited for the appearance of the target point before making a saccade, he could not obtain the reward because the gaze could not reach the target within the short duration of the target point.

In a block of trials, the target point was presented randomly at one of eight target points (separated by 45° with the same eccentricity) (Fig. 1A). The target eccentricity was either 5°, 10°, 20°, or 30°. A block consisted of 32 or 64 trials (4–8 trials for each of the eight target points).

Data analysis

The main purpose of the off-line analyses was to determine the relationship between the characteristics of saccades and single-cell activities of BIN neurons.

We first determined the time of saccade. Parameters used for the determination were eye velocity, acceleration and duration (Kato et al. 1995). We judged that a saccade started if both velocity and acceleration exceeded threshold values (30°/s and 90°/s^2 respectively). The end of the saccade was defined as the time at which the velocity fell below 40°/s. For each saccade thus determined, we calculated its amplitude, peak velocity and duration.

To characterize the burst activities of a BIN neuron, we first made a histogram and cumulative histogram containing 32–64 trials with bin width of 2 ms that was aligned at either saccade onset or saccade offset. The onset and offset of the burst activities were determined by the start and end of an upward inflection of the cumulative time histogram (Robinson et al. 1978). The time of burst peak was determined by the position of bin with the largest value in the histogram. When more than two consecutive bins had the same maximum value, the mean value of the two bins was adopted as the time of burst peak.

We did not attempt to determine burst onset, offset or peak for each saccade, as the number of spikes in burst could be fairly small, so that the presaccadic activity was obvious only when unit activities in several trials were summed.

We used one-way ANOVA for statistical analysis, unless otherwise stated.

Histological procedure

At the end of the experiments monkey B was given an overdose of Nembutal sodium and was perfused with normal saline followed by

4% paraformaldehyde and 0.5% glutaraldehyde. Coronal serial frozen sections (50 μm thick) through the cerebellum were stained with cresyl violet. By comparing the pattern of electrode tracts and electrolytic lesions with the description of the penetration at the time of the experiments, we identified the locations of neurons at or near the electrolytic lesions. Monkey H is still being used and the recording sites were estimated based on the description of the discharge pattern at the time of the experiments.

Results

Discharge pattern and location of omnidirectional burst neurons

We recorded 76 saccade-related neurons in the dentate nucleus and its vicinity of the cerebellum in the two monkeys. Among them, 55 neurons (72%) showed presaccadic bursts; 14 neurons (18%) showed saccade-related pauses before or after the saccade onset; and 7 neurons (9%) showed a long burst activity that outlasted the saccade.

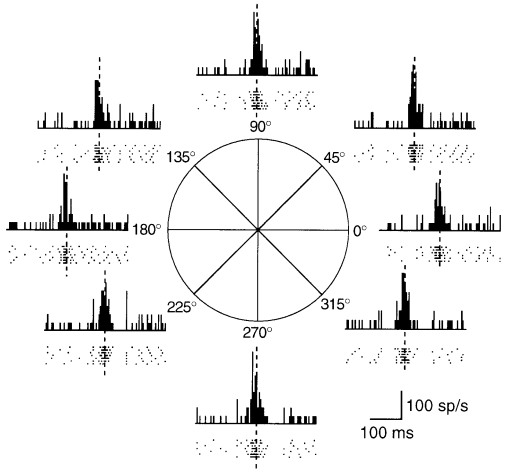

Fig. 1 Omnidirectional bursts of a neuron in the basal interstitial nucleus (BIN). Activity associated with visually guided saccades in one of eight directions is aligned at saccade onset (*vertical dashed line*). The eccentricity of the targets was 30°. The targets were presented randomly from the eight directions. Each histogram (bin width: 5 ms) is the average of the seven trials shown in the associated raster displays

In this report we focus on neurons that showed presaccadic bursts in all directions (omnidirectional burst neurons) because they appeared to form an anatomical-functional group of neurons. We designated a neuron to be omnidirectional if the discharge rates for the eight directions were not statistically different ($P>0.1$). Among the 55 presaccadic burst neurons, 38 (69%) showed omnidirectional presaccadic bursts. A typical example is shown in Fig. 1. This neuron showed a burst of spikes before the onset of a visually guided saccade for each of the eight different directions; otherwise it fired sporadically. The sporadic firing of the neuron did not change with eye position, and the burst was also present with centripetal saccades. These features were common to all the omnidirectional burst neurons. The background discharge rate of the omnidirectional burst neurons was 9.4±6.0 (SD) spikes/s (n=38). We did not test the effect of vestibular or optokinetic stimulation.

Another feature common to the ominidirectional burst neurons was that they showed bursts for memory-guided saccades and spontaneous saccades as well (Fig. 2), which we will analyze further in the next section.

We encountered the omnidirectional burst neurons usually at about 500 μm after the cessation of neuronal activity in the presumed dentate nucleus. The neuronal density around the omnidirectional burst neurons appeared to be lower than in the dentate nucleus. This observation was confirmed by the histological examination. In Fig. 3A, a lesion made at the location of one of the burst neurons is indicated by an arrow. It was just ventral to the dentate nucleus and was among a cluster of neurons facing the roof of the fourth ventricle. This group of neurons probably corresponds to the basal interstitial nucleus (BIN) described by Langer (1985).

Figure 3B illustrates the recording sites of 33 omnidirectional burst neurons in one monkey that were determined with reference to the electrolytic lesions together with the description at the time of the experiments. Among them, 28 (85%) were judged to be in BIN, 27 lay ventral to the dentate nucleus and one was at the hilus of the flocculus.

Among 17 neurons that were not classified as omnidirectional, only one neuron was found to be in the BIN.

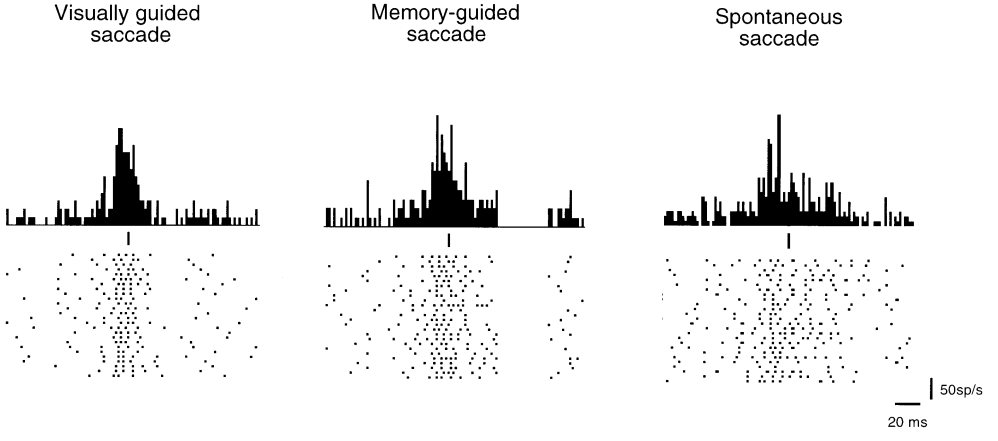

Fig. 2 Activity of a BIN neuron in visually guided, memory-guided and spontaneous saccades, aligned at saccade onset. The eccentricity of the targets was 20° in visually guided and memory-guided saccades. In spontaneous saccades, saccades whose amplitudes ranged from 15° to 20° were selected. Histogram bin width: 2 ms

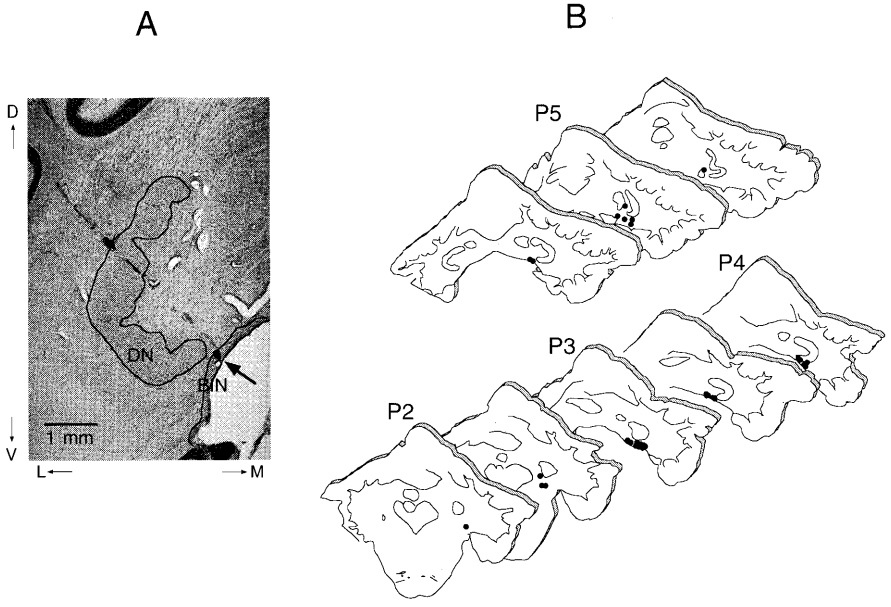

Fig. 3A, B Anatomical locations of omnidirectional burst neurons. **A** Photomicrograph of a coronal section through the cerebellar nuclei illustrating a microelectrode penetration. An electrolytic lesion indicated by *arrow* was made at the recording site of one of the omnidirectional burst neurons. The dentate nucleus (*DN*) and *BIN* are indicated by lines. **B** Locations of 33 omnidirectional burst neurons reconstructed with reference to the electrolytic lesions together with the description at the time of the experiments. They are plotted on one side on equally spaced coronal sections from P2 to P5.5

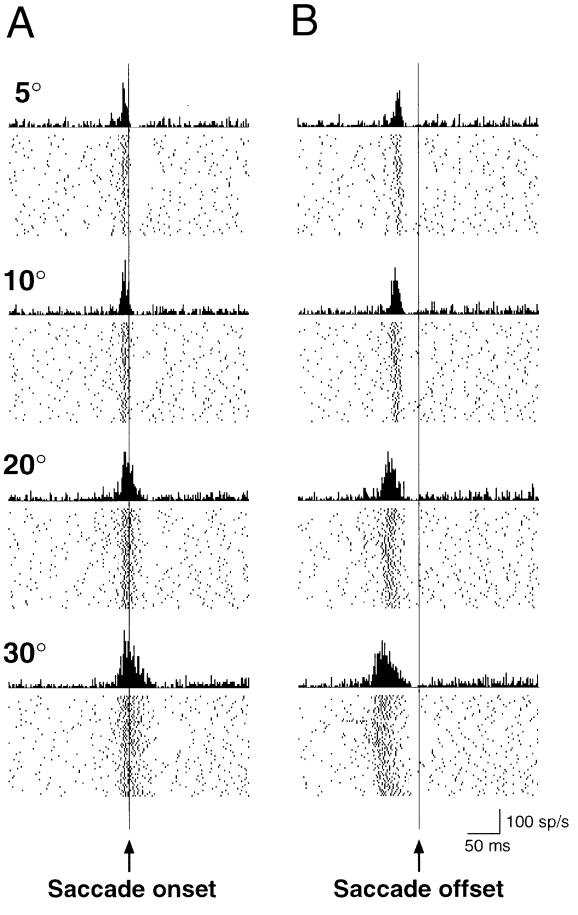

Fig. 4A, B Activity of a BIN neuron during visually guided saccades of four different amplitudes, which were aligned at saccade onset (**A**) and saccade offset (**B**). Each raster-histogram is the average of 56 trials during saccades in eight directions. Histogram bin width: 2 ms

Characteristics of omnidirectional bursts of BIN neurons

Saccade-related burst neurons have been found in various brain regions. Is there anything unique about the burst neurons in the BIN? We attempt to answer this question in the following sections.

We first changed the eccentricity of the saccade target, as shown in Fig. 4. Burst onset clearly preceded saccade onset (Fig. 4A), while burst offset preceded saccade offset (Fig. 4B). These characteristics were common to the 38 omnidirectional burst neurons. This BIN neuron showed a pause of activity after the burst; however, this phenomenon was not consistent (observed in 15 of 38 neurons) and therefore was not examined in detail. In addition, the magnitude of the burst, in terms of its duration and the number of spikes, appeared to be correlated with saccade amplitude.

These observations suggested that the burst of BIN neurons reflects both the timing (or duration) and amplitude of saccades. However, we still could not determine which of the saccade parameters (e.g., amplitude, velocity, duration) the BIN neurons specifically encoded, because these parameters are closely related to each other (Robinson 1964). One way to disentangle the relationships would be to examine different types of saccades in which the parametric relationships vary. For example, it has been shown that, for a saccade of a given amplitude, velocity is slower (and consequently duration is longer) for memory-guided saccades than for visually guided saccades (Hikosaka and Wurtz 1985).

We thus re-examined the difference between visually guided saccades and memory-guided saccades, together with spontaneous saccades, and found indeed that these types of saccade had different dynamics, as shown in Fig. 5. For each type of saccade, the duration increased with amplitude (Fig. 5A). However, for a given amplitude, the duration appeared shortest for visually guided

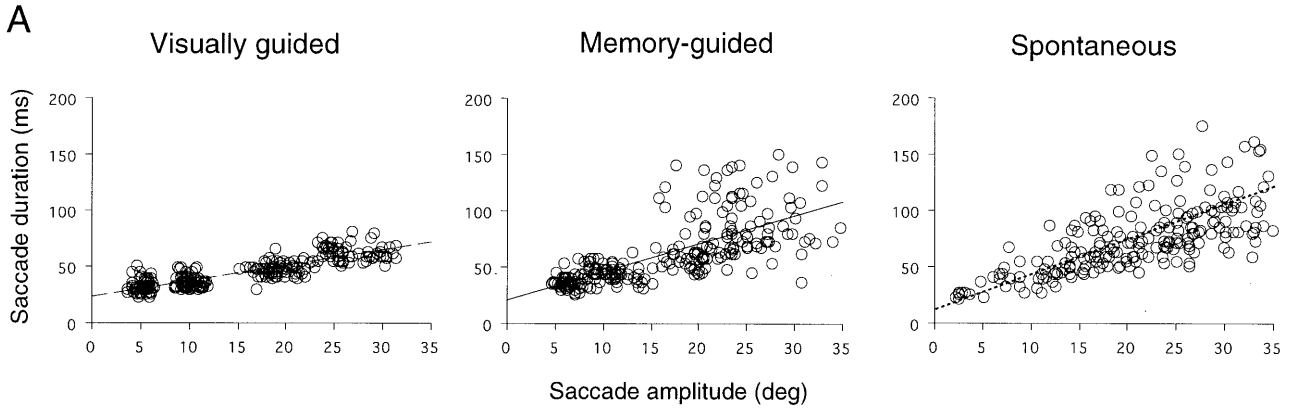

Fig. 5A, B Relationship of saccade duration versus saccade amplitude for three types of saccade. **A** Data obtained in a single experimental session for visually guided saccades (*left*, n=256), memory-guided saccades (*center*, n=256) and spontaneous saccades (*right*, n=204), each *data point* indicating a single saccade. For visually guided saccades and memory-guided saccades, the target was presented from eight different directions randomly with eccentricities of 5°, 10°, 20° or 30°. Spontaneous saccades (whose amplitudes were below 35°) were recorded during a 3-min period while the monkey was not performing a task. **B** Summary data for four different experimental sessions, for visually guided (*dashed line*), memory-guided (*continuous line*) and spontaneous saccades (*dotted line*), each line representing the regression line obtained in a single session

saccades and longest for spontaneous saccades. This tendency was consistent across different experimental sessions (Fig. 5B). The mean slope values of linear regression lines for visually guided, memory-guided and spontaneous saccades were 1.43±0.06, 2.50±0.19 and 2.91±0.14 (n=4), respectively. The slope values that were grouped into three types of saccades were significantly different ($P<0.05$).

The parametric differences between the three types of saccades should allow us to determine whether the BIN cell activity was correlated uniquely with the specific parameter.

We first asked whether the timing of the BIN burst was correlated with the timing of a saccade. Figure 6 shows the mean data for 7 of 38 omnidirectional burst neurons in which we could obtain a complete set of data for three types of saccade and four different target eccentricities. As shown in Fig. 6A, the onset of the burst preceded saccade onset with fairly constant lead times for each type of saccades regardless of their amplitudes ($P>0.5$), although the lead times were different between the different types of saccade ($P<0.01$). The average lead times of burst onset for visually guided, memory-guided and spontaneous saccades were 16.3±2.3, 22.0±5.4 and 24.9±5.5 ms, respectively. The average lead times of the burst peak were 7.6±1.8, 7.9±2.4 and 12.0±3.7 ms, respectively. In contrast, burst offset followed saccade onset and increased with saccade amplitude.

The same data are replotted in Fig. 6B, now aligned on saccade offset. Burst offset preceded saccade offset with fairly constant lead times for each type of saccade regardless of amplitude ($P>0.5$), although the lead times were different between the different types of saccade ($P<0.01$). The average lead times of burst offset for visually guided, memory-guided and spontaneous saccades were 32.5±3.6, 30.9±5.4 and 28.3±4.7 ms, respectively.

These features were common to the other BIN burst neurons in which we obtained an incomplete set of data; they were within the range of the standard deviation shown in Fig. 6.

It should be noted, however, that the data shown in Fig. 6 were obtained from the summed histograms for each neuron. That is, the activity of BIN neurons appeared quite variable from saccade to saccade, unlike the activity of premotor burst neurons (Hepp et al. 1989).

The above data suggest that the BIN neurons encode the timing of saccades. This conclusion is supported by the graphs in Fig. 7, in which the relationships between BIN burst activity and saccade parameters are shown for one representative neuron (a) and for seven neurons grouped together (b). The data indicate that burst duration increased linearly with saccade duration and, more importantly, the relationship was similar between the three types of saccade (Fig. 7A). The mean correlation coefficients for the seven neurons for visually guided, memory-guided and spontaneous saccades were 0.96±0.03, 0.93±0.10 and 0.90±0.08, respectively. The mean slope values of the regression lines were 0.78±0.15, 0.88±0.20 and 0.94±0.19 (n=7), respectively. There were no significant differences in the slope values between the three types of saccade (nonparametric Friedman's test, $P>0.2$).

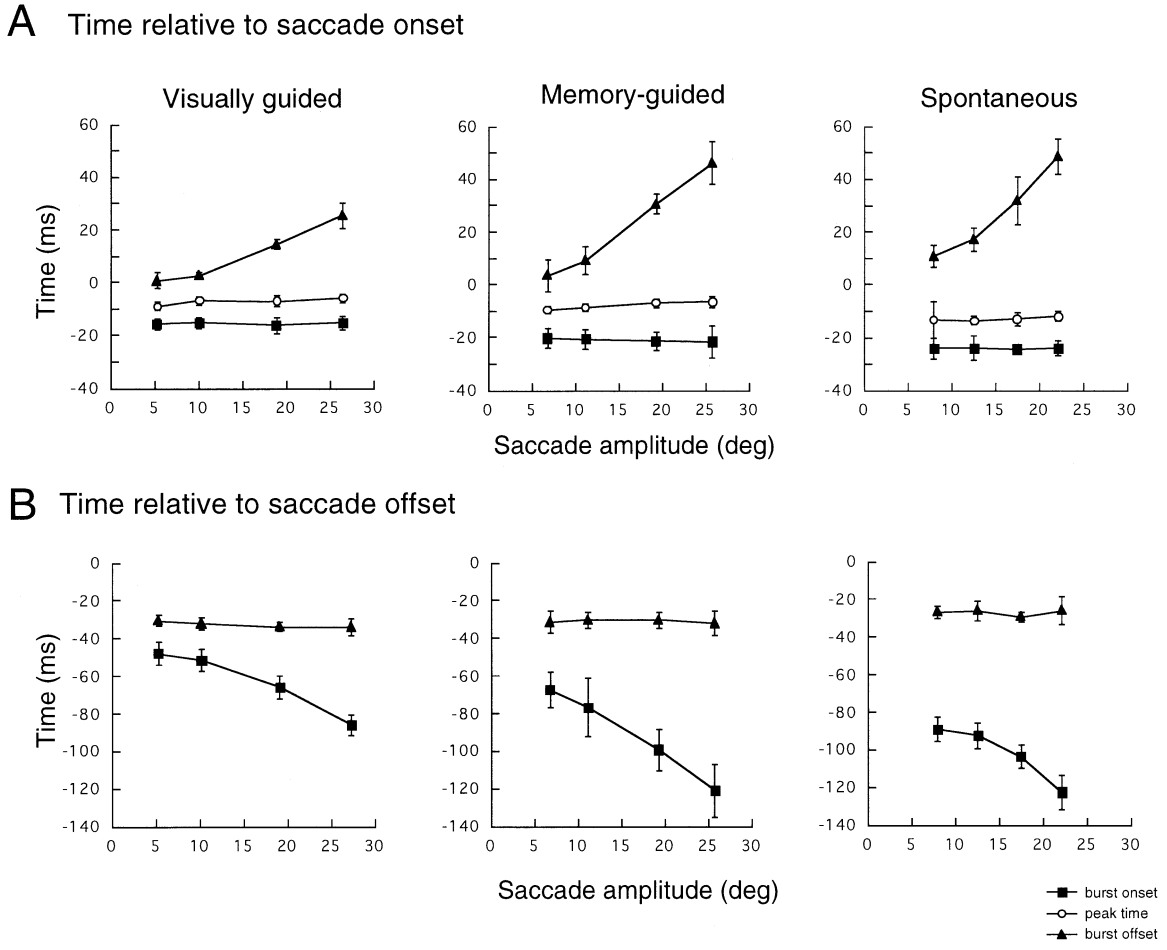

Fig. 6 Temporal characteristics of BIN burst neurons: burst onset, peak and offset relative to saccade onset (**A**) and offset (**B**). The data are shown separately for three types of saccade: visually guided, memory-guided, and spontaneous saccades. Time 0 indicates saccade onset (**A**) and saccade offset (**B**); a negative (positive) value indicates that the event (e.g., burst onset) preceded (followed) saccade onset (**A**) or saccade offset (**B**). For visually guided saccades and memory-guided saccades, the target was presented from eight different directions randomly with eccentricities of 5°, 10°, 20° or 30°. *Abscissa* shows the mean amplitude of actual saccades that were made for a given target eccentricity. Spontaneous saccades were recorded during a 3-min period while the monkey was not performing a task; the saccades were grouped into four amplitude ranges (5–10°, 10–15°, 15–20° and 20–25°) according to the amplitude of actual saccades and the mean amplitude for each group was used as the saccade amplitude, respectively. Each *data point* represents the mean value for seven BIN neurons; *vertical bar* represents the standard deviation

Such a unique relationship was not observed for saccade amplitude (Fig. 7B) or peak velocity (Fig. 7C). Although the number of spikes per burst increased linearly with saccade amplitude for each type of saccade, the slope values of the linear regression lines were different. The mean correlation coefficients for visually guided, memory-guided and spontaneous saccades were 0.95±0.07, 0.97±0.03 and 0.97±0.04 (n=7). The mean slope values were 0.11±0.03, 0.22±0.06 and 0.17±0.04 (n=7); they were significantly different (nonparametric Friedman's test, $P<0.01$).

Peak burst frequency showed no significant correlation with saccadic peak velocity (Fig. 7C); mean correlation coefficients for seven neurons for visually guided, memory-guided and spontaneous saccades were 0.63±0.28, 0.57±0.26 and 0.31±0.35, respectively.

Discussion

We found a group of presaccadic burst neurons just beneath the dentate nucleus. Their discharge patterns were very similar to each other in that the burst was present for saccades in any direction and amplitude and for any type of saccade (i.e., visually guided, memory-guided or spontaneous). The burst uniquely represented the timing of saccades, but no other parameters (i.e., amplitude or velocity). BIN burst neurons depended on the saccade amplitude, but the relation did not hold constant across different types of saccades; for example, they emit more spikes for a memory-guided saccade than for a visually guided saccade with the same amplitude.

The BIN is the interstitial populations of neurons just ventral to the cerebellar nuclei and has reciprocal connections with the flocculus (Langer et al. 1985a,b). Furthermore, Gonzalo-Ruiz et al. (1988) showed that many neurons in the BIN were labeled retrogradely from the medial

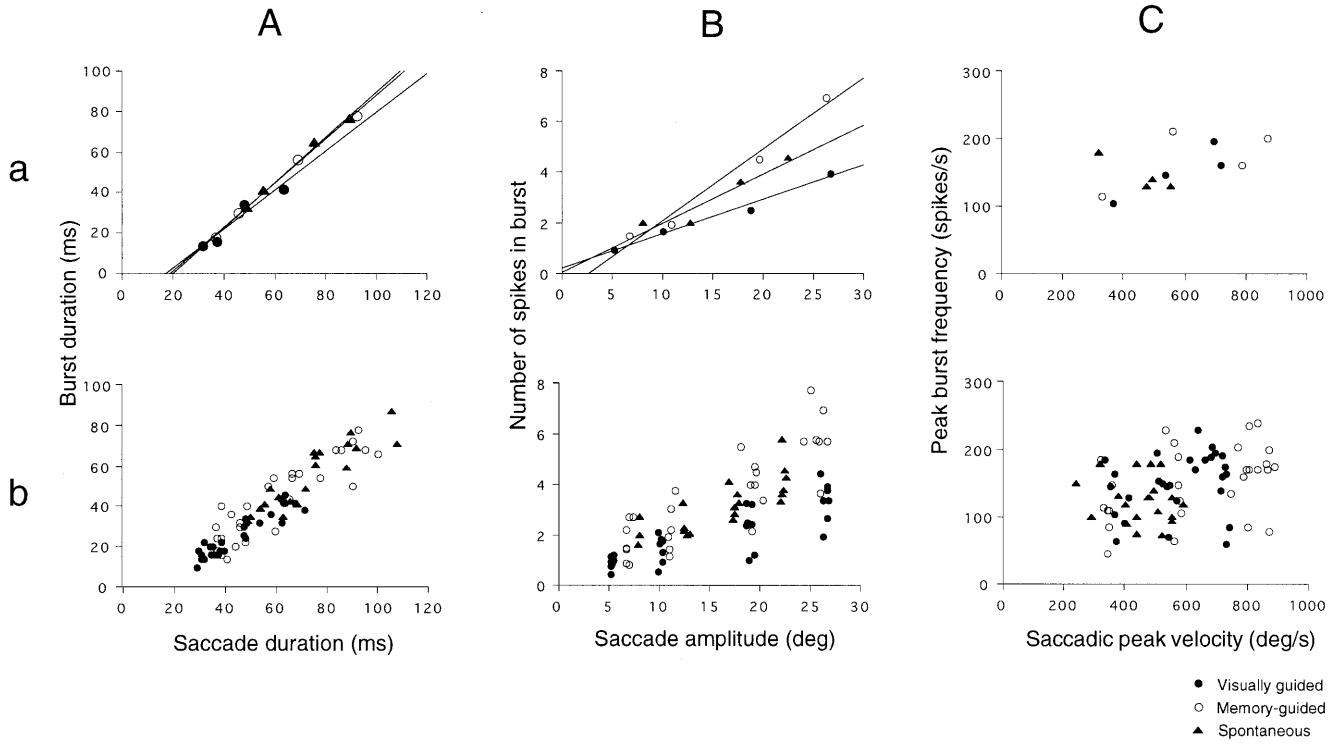

Fig. 7 Relationship between the BIN burst discharge and saccade parameters: burst duration versus saccade duration (**A**), the number of spikes in a burst versus saccade amplitude (**B**), and peak burst frequency versus saccadic peak velocity (**C**). Each *data point* represents the mean value for a single BIN neuron for visually guided saccades (*filled circles*), memory-guided saccades (*open circles*) and spontaneous saccades (*filled triangles*). **a** Data for one BIN neuron; **b** pooled data for seven neurons (the same neurons as those used for Fig. 6). In **Aa**, the regression lines for visually guided, memory-guided and spontaneous saccades were y=0.96x–16.84 (r=0.94), y=1.08x–20.23 (r=1.00) and y=1.11x–21.98 (r=0.99), respectively. In **Ba**, the regression lines were y=0.14x+0.21 (r=0.99), y=0.28x–0.76 (r=0.98) and y=0.19x+0.04 (r=0.91), respectively

pontine tegmentum, which perhaps included omnipause neurons (OPNs).

Possible relation of BIN neurons with omnipause neurons

The anatomical data raise the possibility that the burst of BIN neurons contributes to the pause of OPNs. Both the burst of BIN neurons and the pause of OPNs are omnidirectional (Keller 1974). For visually guided saccades, the burst of a BIN neuron starts about 16 ms before saccade onset (present study), while the pause of an OPN starts 12–25 ms before saccade onset (Keller 1974); for spontaneous saccades, the burst of a BIN neuron starts about 25 ms before saccade onset (present study), while the pause of an OPN starts 15–35 ms before saccade onset (Strassman et al. 1987).

These data are consistent with the idea that BIN neurons determine the onset of the pause of OPNs, either directly or indirectly through inhibitory interneurons. However, the discharge of BIN neurons started decreasing before saccade started and stopped discharging way before saccade ended (Figs. 4, 6), while OPNs remain largely silent during a saccade (Keller 1974; Evinger et al. 1982). It is therefore unlikely that BIN neurons determine the end of the pause of OPNs or the end of a saccade.

Inputs to BIN neurons

The burst of BIN neurons must be generated by pulse-like inputs that start more than 16 ms before the onset of a saccade. Earlier studies (Sparks and Travis 1971; Luschei and Fuchs 1972; Cohen and Henn 1972) described the presence of omnidirectional burst neurons in the brainstem. However, later studies have shown that such burst neurons generally have direction selectivity in that the burst for the preferred direction is stronger and/or starts earlier compared with the burst for the non-preferred direction (for a review see Hepp et al. 1989).

Short-lead burst neurons, which provide extraocular motoneurons with excitatory or inhibitory inputs, are unlikely to be the source of the inputs to BIN neurons because they start discharging about 5–10 ms before a saccade (i.e., after the BIN neurons start discharging) (Yoshida et al. 1982; Strassman et al. 1986a,b). One candidate for the inputs to BIN neurons is long-lead burst neurons in the brainstem, whose bursts usually start more than 15 ms before a saccade (Scudder et al. 1988).

Burst neurons in the superior colliculus could also provide BIN neurons with excitatory inputs, but again their bursts are direction-selective (Sparks and Hartwich-Young 1989; Munoz and Wurtz 1995). They start firing

20–30 ms before saccade onset, peak at saccade onset, and end just before saccade offset, the timing of discharge being similar to the burst of BIN neurons.

These comparisons raise the possibility that burst neurons in the superior colliculus or long-lead burst neurons in the brainstem might contribute to the bursts of BIN neurons, although there is no anatomical evidence to support this hypothesis.

Omnidirectional burst activity in other cerebellar neurons

Saccade-related burst neurons are also found in the interpositus and dentate nuclei. Their activities are both directional and nondirectional (Gardner and Fuchs 1975; MacKay 1988; Van Kan et al. 1993). In the neurons of the dentate nucleus especially, the burst started before saccade onset and their activities were usually omnidirectional, though the time of the end of the burst was unclear (Gardner and Fuchs 1975; MacKay 1988).

In the flocculus (Noda and Suzuki 1979a,b) and dorsal paraflocculus (Noda and Mikami 1986) are found saccade-related neurons (Purkinje cells) that either burst or pause with saccades. Most pause neurons in the flocculus or paraflocculus stopped firing in all directions. In addition, a linear relationship was present between pause duration and saccade duration. The pause in activity preceded saccades by an average of 9.6 ms, with a maximum lead time of 30 ms. These features were very similar to that of BIN neurons, though the polarity of cell activity is opposite.

The flocculus has connections with the BIN (Langer et al. 1985a,b) and ventral portions of the dentate nucleus (Haines 1977). Therefore, inhibitory output of Purkinje cells in the flocculus might contribute to the omnidirectional bursts of BIN neurons.

Possible function of BIN burst neurons

The bursts are omnidirectional and thus, convey no information on saccade direction. The dependence of the BIN burst on saccade amplitude is inconsistent across different types of saccades, and therefore cannot be used to determine saccade amplitude per se. Instead, the burst of BIN neurons clearly precedes the saccade, and therefore could be used to determine the timing of the saccade.

There are two crucial questions in this regard. First, do BIN neurons really contribute to determining the timing of a saccade, and if so, how? An interesting possibility is that BIN neurons send information to brainstem pause neurons that also carry the timing information, not others. Second, how do BIN neurons obtain the information on the timing of a saccade? One totally speculative possibility is that long-lead burst neurons in the superior colliculus or the brainstem might converge onto BIN neurons to create the omnidirectional burst. BIN neurons would play an important role in determining the timing of a saccade and consequently other saccade parameters.

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