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Latency of Saccades during Smooth Pursuit Eye Movement in Man: directional asymmetries.

(ヒト滑動性眼球運動の最中の視覚誘導性サッカードの潜時変化)

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Abstracts

To examine the effects of smooth pursuit eye movements on the initiation of saccades, their latency was measured when subjects initially fixated or pursued a target. In half of the block of trials, the fixation or pursuit target was extinguished 200 ms before the saccade target was illuminated (gap trials). Reduction of the mean saccade latency in the gap trials (the 'gap effect') was evident even when the subjects were pursuing a moving target, consistent with previous observations (Krauzlis and Miles 1996). The effect of pursuit direction on saccade latency was also examined. Saccades in the same direction as the preceding pursuit (forward saccades) had shorter latencies than those in the opposite direction (backward saccades). This asymmetry was observed in both the gap and non-gap trials. Although the forward-backward asymmetry was much smaller than the 'gap effect', it was statistically significant in six of eight cases. These results suggest that the preparation of saccades is affected by smooth pursuit eye movements.

Introduction

The latency of saccadic eye movements has been used to probe processes involved in saccade initiation. Since Saslow (1967) showed that a temporal gap between the offset of a fixation point and the onset of a target reduced the latency of saccades, a large number of studies have corroborated this observation (e.g. Ross and Ross 1980; Reulen 1984; Fischer and Ramsperger 1984; Iwasaki 1990). One possible interpretation of the reduction of mean saccade latency in gap trials (the ‘gap effect’) is that the prior offset of the fixation point facilitates the termination of fixation (Kingstone and Klein 1993a; Tam and Stelmach 1993; Reuter-Lorenz 1995) and enables saccades to be initiated with shorter latencies. The termination of fixation may involve the disengagement of visual attention (Mayfrank et al. 1986; Fischer and Breitmeyer 1987; Fischer 1987; Braun and Breitmeyer 1988; Mackeben and Nakayama 1995).

Recently, it has been shown that the rostral part of the superior colliculus (SC) contains cells that discharge when monkeys fixate a stationary target and pause before saccades (Munoz and Wurtz 1993a). It has been suggested that the activity of these SC cells is related to engagement of active fixation and that the decay of their activity after fixation target offset contributes partly to the ‘gap effect’ (Dorris et al. 1995). Because the SC cells continue firing when monkeys pursue a moving target (Munoz and Wurtz 1993a, but Krauzlis et al. 1997), a temporal gap between the offset of a pursuit target and the onset of a peripheral target might be expected to reduce the latency of saccades. Indeed, Krauzlis and Miles (1996) recently demonstrated the ‘gap effect’ when human subjects pursued a moving target. They concluded that, “from the viewpoint of saccade initiation, smooth pursuit is equivalent to fixation”.

However, at least with respect to visual attention, smooth pursuit and fixation should be somewhat different. When a subject is pursuing a moving target, visual attention is mainly focused on it in order to detect and respond to changes in retinal slip, therefore, visual attention should move in space with the moving target. If visual attention does move with the target, it is possible that the attentional state becomes asymmetric in the pursuit direction. In this study, we examined whether the pursuit direction affects saccade initiation as reflected in their latency.

We have confirmed previous observations that there is a ‘gap effect’ during smooth pursuit (Krauzlis and Miles 1996) and have found an influence of pursuit direction on the latency of saccades. These results suggest that the process of saccade initiation is affected by smooth pursuit eye movements.

Methods

Subjects and recording

Four subjects (23-28 years old) participated in the experiments. Informed consent was obtained from each of them. Three were naive subjects and one was one of authors. All had normal visual acuity. None of them were taking drugs that could affect oculomotor performance.

The subjects were seated on a chair, 55 cm in front of a translucent tangent screen. Their heads were restrained by a chinrest and a head holder. The right eye of the subjects was positioned in line with the center of the screen and the left eye was patched. The experiments were carried out in the dark except for the target lights.

Horizontal eye position was recorded by an infrared reflection device (Takei Co, Eye movement monitor, DC-33 Hz, -24 dB/oct).

Target presentations

Two kinds of targets were used. One was a red laser spot (0.1° diameter) back-projected on the screen, which was used to maintain fixation and to elicit smooth pursuit. The position of this target was controlled using a pair of mirror galvanometers. Two other targets (0.3° green light-emitting diodes, LEDs) were used to induce saccades. They were placed at 10° right and left of the screen center. All stimulus parameters were updated every millisecond by a Macintosh computer using an A/D board (National Instruments, NB-MIO-16X).

Before and after each experiment, eye and target position signals were recorded for calibration by asking the subjects to fixate the red spot at known visual angles (± 5 , 10 and 15°).

Fig. 1 shows a schematic diagram of the pursuit paradigm and fixation paradigm. In all trials, the subjects were asked to follow the red laser spot and move their eyes to the green LED immediately after its onset. In the pursuit paradigm (Fig. 1A), after a random 1000-1500 ms fixation period the red target jumped 10° either to the left or right and moved in the opposite direction at a constant speed ($10^\circ/\text{sec}$). After 800 ms, the red pursuit target disappeared and one of the saccade targets was turned on. Because the saccadic reaction time positioned the eye approximately in the straight ahead position, the magnitude of saccades in the same direction as the preceding pursuit (forward saccades) and that in the opposite direction (backward saccades) were roughly the same. The directions of both pursuit and saccades were interleaved randomly. In the fixation paradigm (Fig. 1B), the red target appeared at the center of the screen for a duration random between 1000 to 1500 ms. After extinction of the red target, one of the saccade targets was illuminated. In half the trials, the saccade target was illuminated 200 ms after the offset of the red target (gap trials). The intertrial interval was always 1000 ms.

To reduce anticipatory saccades and anticipatory decreases in pursuit velocity, we also interleaved 10 to 20 % catch trials in which the saccade targets were not illuminated and the red target remained on. In the pursuit paradigms, the target continued to move at a constant speed ($10^\circ/\text{s}$) for additional 1200 ms (Fig. 1A, broken line). In the fixation paradigm, the target stayed at the center of screen for additional 1200 ms.

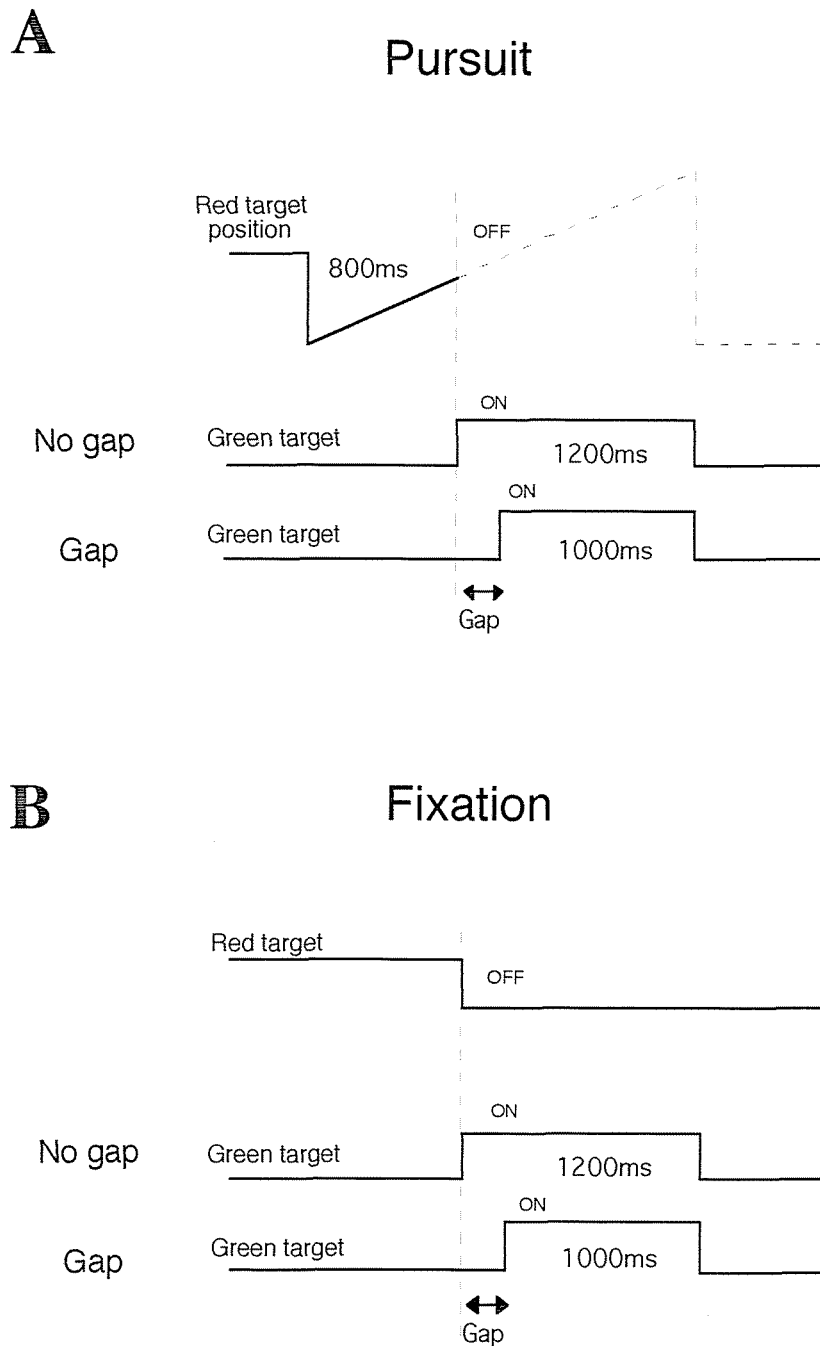


Figure 1

Experimental design. The offset of a red target was followed by the onset of one of two saccade targets. In the fixation paradigm the red target stayed on for 1000 to 1500 ms at the center of the screen (A). In the pursuit paradigm the red target jumped 10° and moved back at a constant speed ($10^\circ/\text{s}$) (B). In half of the block of trials the 200 ms gap period was introduced.

The subjects rested for several minutes in the lit room between blocks that usually consisted of 100 trials. The experiments were discontinued when the subjects showed signs of fatigue.

Data acquisition and analysis

Eye position and all stimulus events were stored on analog tapes. Data were digitized off-line at 303 Hz. Eye position was calibrated by using the files that were recorded before and after the experiments. To obtain eye velocity, we calculated an eye position slope with a “sliding box car” method (Rabner and Gould 1975; Fukushima et al. 1996) using a least squared fit for every consecutive 7 data points of eye position. Because the slope of each regression line was defined as eye velocity at the time of the fourth point (i.e. the center of the 7 consecutive points), the velocity trace was advanced ~10 ms with respect to the eye position trace.

Eye position and eye velocity traces were aligned on the onset of the saccade target. Saccade latency was defined as the time between the saccade target onset and saccade onset. To minimize the effects of pursuit velocity on the estimation of the latency, eye acceleration was calculated using a linear regression fitted for 5 consecutive points of eye velocity data, and the first point that exceeded 2000 °/s/s (i.e. a velocity change greater than 32 °/s for 16 ms) was defined as saccade onset. Because the eyes slowly decelerate after pursuit target offset, a large acceleration value was used to avoid the effects of deceleration on the estimation of latency.

Data were combined for individual subjects. Saccades shorter than 75 ms and longer than 350 ms were eliminated from statistical analysis. In the pursuit paradigm, the differences in saccade latencies in the four task conditions (with/without gap and same/opposite direction of preceding pursuit) were evaluated by the two-way factorial ANOVA for the mean of all subjects and the Kolmogorov-Smirnov test for the mean of each subject.

Results

Two to four days were required for each subject to complete the whole recording sessions. Four thousand one hundred eighty one of 4500 non-catch trials (> 90 %) were examined and 4166 saccades were used to calculate the mean latencies. The proportion of catch trials was 17 % of all trials.

Effect of a temporal gap on the saccade latency

A temporal gap clearly reduced saccade latency when the subjects were pursuing a moving target. Fig. 2A shows the distribution of latencies from all subjects in the pursuit

paradigm with (above) and without (below) a temporal gap. The latency distribution in gap trials did not show a distinct cluster of short-latency express saccades (Fig. 2A, lower panel). However, many saccades fall into the ‘express range’ (e.g. <150 ms; Kalesnykas and Hallett 1987, Braun and Breitmeyer 1990), and the distribution is skewed toward the shorter latencies. In contrast, the histogram of the non-gap trials is quite symmetric (Fig. 2A, upper panel).

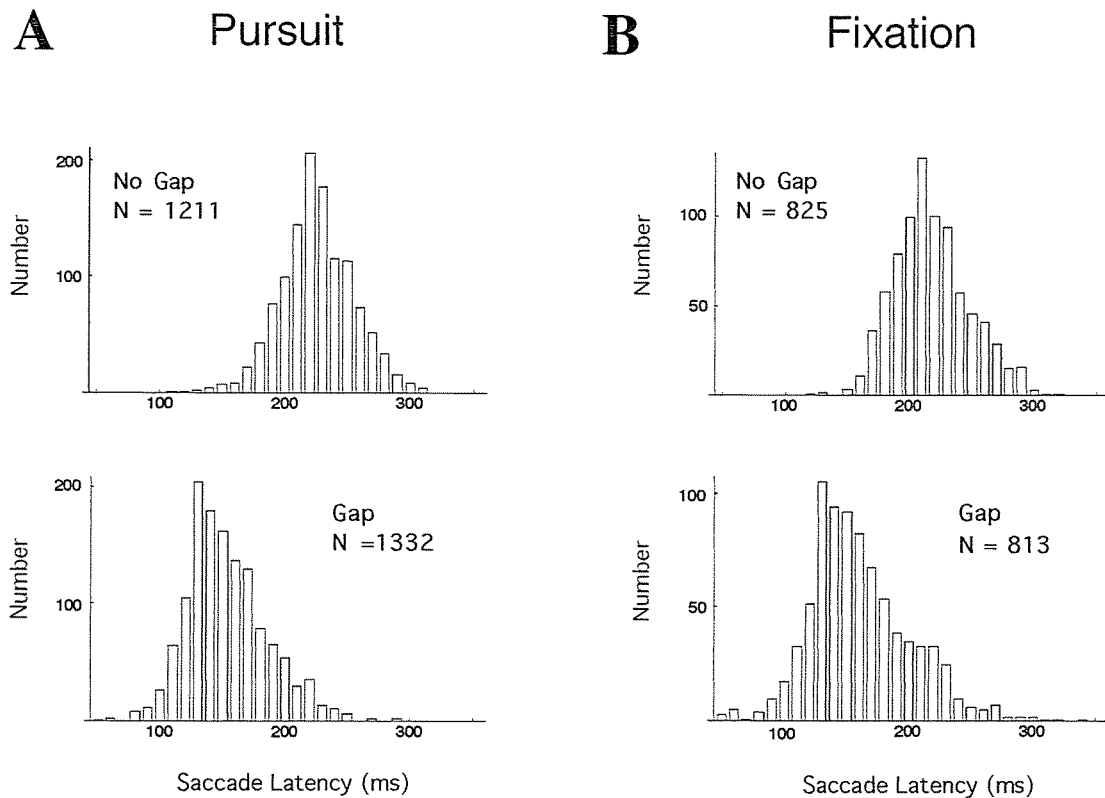


Figure 2

The latency distributions of all subjects. A: fixation paradigm. B: pursuit paradigm. The upper histograms are for non-gap trials, the lower are for 200 ms gap trials.

Fig. 2B shows latency distribution of saccades when the subjects were fixating a stationary target. The change of the latency distribution caused by a gap period in the fixation paradigm was similar to that in the pursuit paradigm. Again, the histogram for the gap trials is skewed toward shorter latencies (Fig. 2B, lower panel), compared to that of the non-gap trials (Fig. 2B, upper panel). The reduction of latency in gap trials was comparable to that in the fixation paradigm. The mean differences of latencies between in the gap and the non-gap trials (gap effect) were 56 ms for pursuit and 71 ms for fixation paradigm, respectively.

Effect of pursuit direction on the saccade latency

To examine the effect of pursuit direction on latency, the latency of saccades in the same direction as the preceding pursuit (forward) and in the opposite direction (backward) was compared.

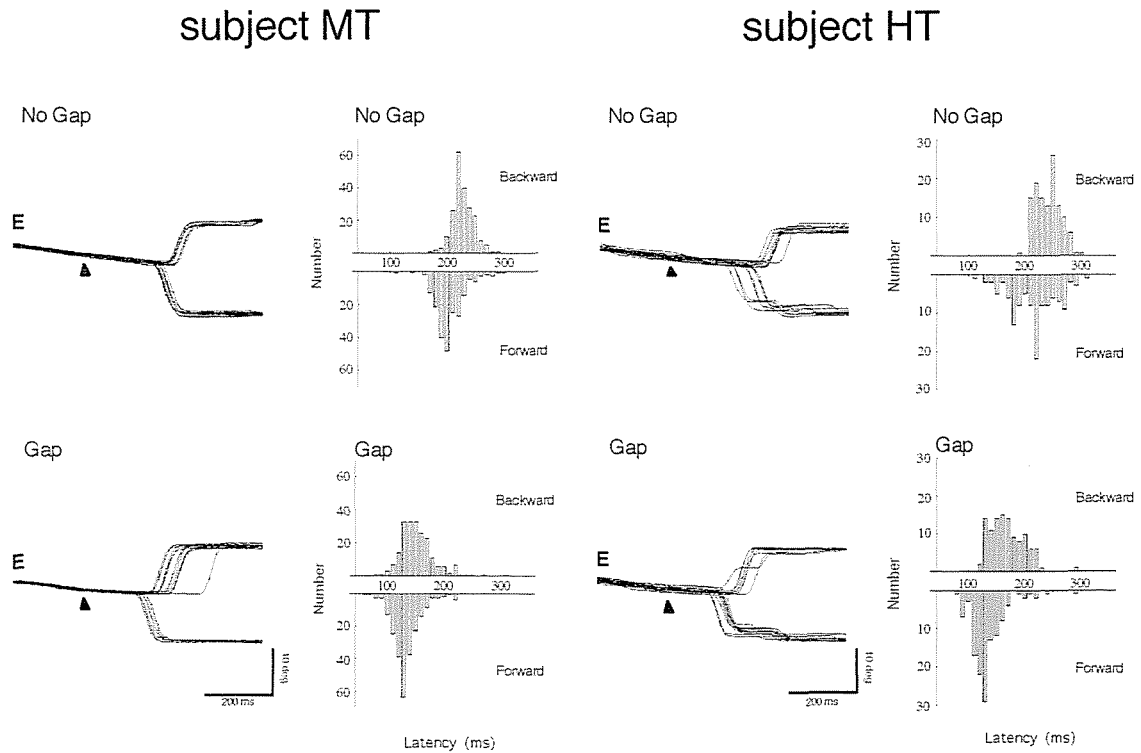


Figure 3

Records of two subjects in the pursuit paradigm. *left*: horizontal eye position obtained from consecutive leftward pursuit trials. Triangles indicate onsets of the saccade target. *right*: distribution of saccade latencies. Histograms separated by two factors; gap and non-gap trials and forward-backward saccades.

Fig. 3 shows records from two subjects (MT; *left* and HT; *right*) in the pursuit paradigm. In the left columns, eye position traces of 20 consecutive trials in which the target moved smoothly to the left are aligned on saccade target onset (upward triangles). The upper row shows the data from non-gap trials and the lower from gap trials. Right columns show the latency distributions of forward and backward saccades obtained from both the rightward and leftward pursuit trials. The latencies of forward saccades (lower histogram of each panel) tended to be shorter than those of backward saccades (upper histogram of each panel) in both subjects.

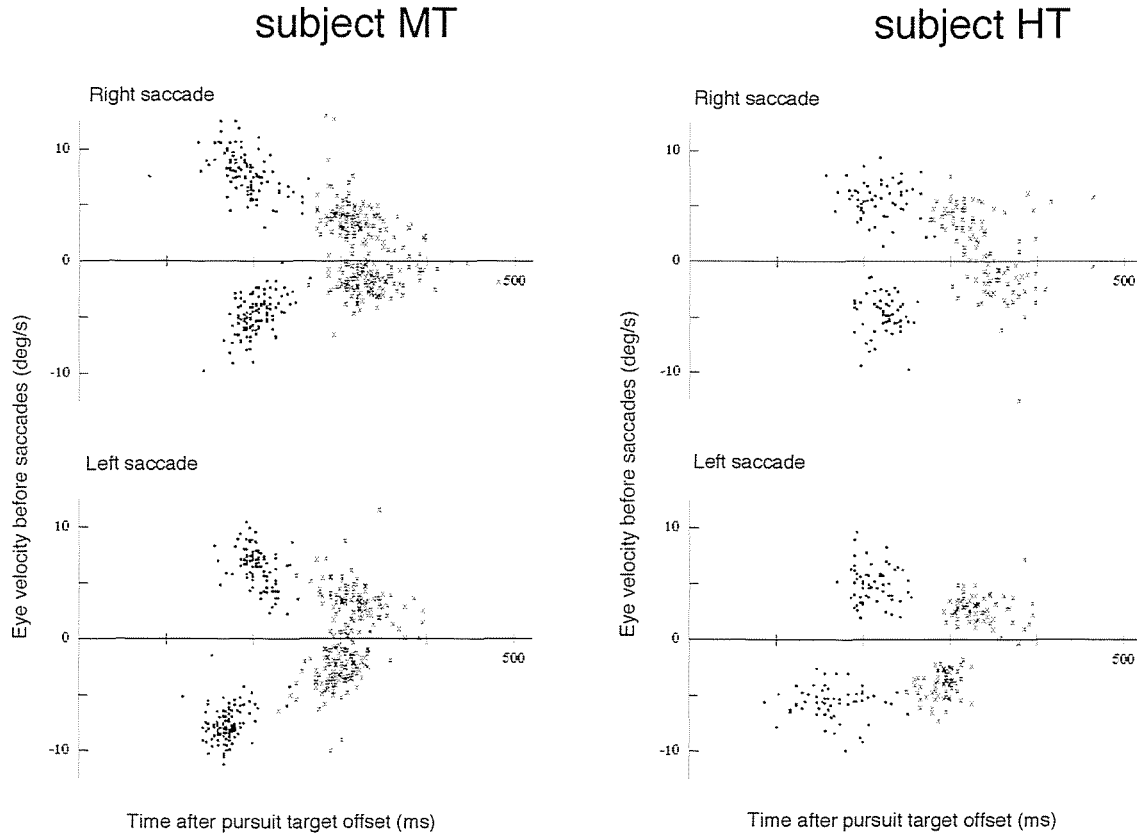


Figure 4

Decay of eye velocity after offset of the pursuit target in the same subjects as in Fig. 3. Eye velocity 30 ms before saccades are plotted against the time after pursuit target offset. Dots indicate eye velocity in non-gap trials, crosses those in the gap trials. Positive value of ordinate indicates rightward eye velocity, negative value the leftward.

As shown in Fig. 3, the effects of pursuit direction were observed in both the gap and the non-gap trials. However, pursuit velocities before saccades in the gap trials were smaller than those in the non-gap trials, because eye velocity decreased during the gap interval. To show the decay of pursuit velocity after target offset, eye velocity immediately before saccade onset in the pursuit paradigm was plotted. Fig. 4 shows the data obtained from the same two subjects shown in Fig. 3. The mean eye velocity from 30 ms to 23 ms (3 points) before saccade onset was calculated for individual trials. These values are plotted against the time after pursuit target offset. To emphasize the asymmetry of saccade latency, data are plotted separately for the right and left saccade trials. Dots show eye velocities in non-gap trials, crosses those in the gap trials. The pursuit velocity immediately before saccade in the gap trials is lower than those in the non-gap trials. This indicates that the asymmetry of saccade latency is not simply due to the orbital mechanics such as the inertia of eye ball and viscoelastic elements (see Discussion).

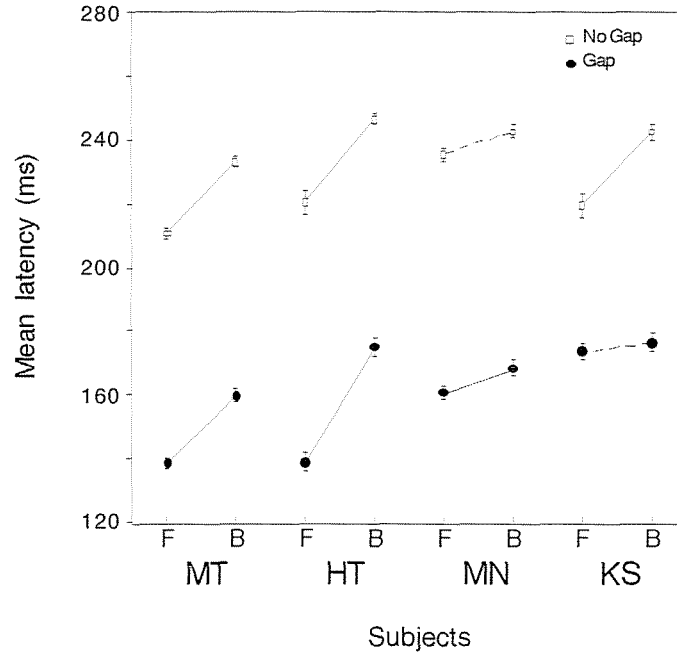


Figure 5

Mean saccade latencies for all subjects. F: forward saccades. B: backward saccades. Error bars indicate ± 1 SE. The forward-backward pairs which showed significant difference by the Kolmogorov-Smirnov test ($p < .05$) are connected by solid lines.

Fig. 5 summarizes mean saccade latencies for each subject in the pursuit paradigm. The error bars indicate ± 1 SE. The means of all subjects in the 4 cases (forward/backward, gap/non-gap) were analyzed by two-way ANOVA. Both the factors of direction ($F_{(1,3)}=8.5$, $p < 0.05$) and gap ($F_{(1,3)}=166.1$, $p < 0.0001$) were significant. There was no significant interaction effect ($F_{(1,3)}=0.37$, $p > 0.5$).

The latency in each condition for individual subjects was also compared by the Kolmogorov-Smirnov test. Although the gap effects were significant for all four subjects ($p < 0.001$), two of 8 pairs of forward vs. backward saccades did not show significant differences (non-gap trials of subject MN, gap trials of KS, $p > 0.05$; connected by broken lines in Fig. 5).

Because the pursuit target was extinguished 200 ms before it reached the center of the screen and because its offset was immediately followed by the onset of saccade target in the non-gap trials (see Fig. 1A), it is possible that the effect of pursuit direction on the latency was caused by the difference in retinal eccentricity of saccade targets. To exclude this possibility, we examined saccade latencies of two subjects (MT and HT) in trials in which the pursuit target was extinguished at the center of the screen and was immediately followed by the onset

of saccade target (i.e. the pursuit target moved smoothly for 1000 ms, cf. Fig. 1A). The mean ($\pm$ SE) latencies of forward and backward saccades were 199 ms ($\pm$ 1.7 ms) and 222 ms ($\pm$ 1.7 ms) for subject MT, and 210 ms ($\pm$ 2.5 ms) and 231 ms ($\pm$ 4.1 ms) for subject HT. These values were significantly different for both subjects ($p < 0.05$, Kolmogorov-Smirnov).

Discussion

Reduction of saccade latency in gap trials

The latency of saccades when subjects fixate a stationary target is affected greatly by the experimental conditions. One well known factor is the prior offset of the fixation point which reduces the latency of saccades directed to a peripheral target (e.g. Saslow 1967; Ross and Ross 1980; Reulen 1984; Fischer 1987; Braun and Breitmeyer 1988; Iwasaki 1990; Kingstone and Klein 1993a,b; Tam and Stelmach 1993; Tam and Ono 1994; Reuter-Lorenz et al. 1995; Weber et al. 1995). This reduction of saccade latency was also observed in the present study (Fig. 2B). Furthermore, it was evident that a temporal gap before the target onset was effective in reducing the latency even when the subjects were pursuing a moving target (Fig. 2A), which is consistent with the previous observation by Krauzlis and Miles (1996). The changes in the distribution of latencies caused by a gap period are very similar in the pursuit and fixation paradigms (compare Fig. 2A and 2B). A large number of saccades fell into the 'express range' (e.g. < 150 ms) when a gap was introduced.

Although the smooth pursuit system is thought to be different from the fixation system (Luebke and Robinson 1988, Goldreich et al. 1992, Schwartz and Lisberger 1994), recent psychophysical (Tam and Ono 1994; Krauzlis and Miles 1996) and physiological (Munoz and Wurtz 1993a,b) studies suggest that the mechanism underlying active fixation is shared by these two systems. Fixation cells in the rostral SC continue firing when the monkeys perform smooth pursuit (Munoz and Wurtz 1993a, but Krauzlis et al. 1997) as well as when they are fixating a stationary target. The activity of these cells is thought to inhibit the presaccadic burst neurons located in the caudal SC (Munoz and Wurtz 1993b). Although no quantitative data are available for the activity of fixation cells during pursuit termination, possible decay of activity of these cells may explain the reduction of the latency in gap trials when the subjects are pursuing a target.

Forward-backward asymmetry of saccade latency

In this study, the latency of saccades was affected by the direction of preceding smooth pursuit eye movements. We believe that the asymmetry of mean saccade latency, which was up to 36 ms, was not due to orbital mechanics. Pursuit velocities are much lower than saccadic

velocities so any asymmetry due to mechanical effects should be much more prominent during saccades (cf. Robinson 1964, 1965). The observation that the asymmetry was similar even when pursuit velocity decreased by at least half in the gap trials (Fig. 4) also supports this interpretation.

We have to examine whether the effect of pursuit direction on saccade latency was merely due to differences in the visual inputs, because the forward and backward targets were different with respect to the eye in retinal eccentricity and in target motion toward or away from the fovea. To exclude the possible effect of retinal eccentricity of the targets, we examined latencies of two subjects in the non-gap trials in which the saccade target was illuminated when the eyes reached the center of the screen (see Results). We still observed significant differences in latencies between forward and backward saccades. Furthermore, a similar change in latencies was also observed in gap trials. In these trials, eye position was close to the center of the screen when the saccade target appeared, because the eyes continued to move smoothly during the 200 ms gap interval. Therefore, the difference in the retinal eccentricity of the targets alone can not explain the asymmetry in saccade latencies during pursuit.

In the paradigm used here, the subjects initiated a saccade to a stationary target. Therefore, before a saccade, the retinal image of the saccade target in the same direction as the preceding pursuit (forward) moved toward the fovea, whereas the retinal image of the target in the opposite direction (backward) moved away from the fovea. We do not have any data to exclude the possibility that the direction of retinal image motion affect the latencies. A previous study examined the latency of saccades during pursuit (Krauzlis and Miles 1996). They moved the target for saccades at the same speed as the target for pursuit. Although the motion of target image before saccades was greatly reduced in their experiments, one may see a similar asymmetric change in saccade latencies along with pursuit direction in three of their four subjects (see Fig. 2 of Krauzlis and Miles 1996).

Another question that remains is whether the asymmetry of the latency is specific for saccades. There are no data, such as manual reaction time tasks during pursuit eye movements, to answer this question directly. However, it is known that the response to a visual target at a previously attended location is delayed (Posner and Cohen 1984). This inhibitory effect is observed whenever subjects are asked to respond by ocular as well as by manual movements (e.g. Maylor 1985; Rafal et al. 1989; Abrams and Dobkin 1994; Tanaka and Shimojo 1996). Furthermore, this effect is determined by the ‘environmental’ coordinates rather than by the retinotopic coordinates, because the inhibitory effect is still evident when the retinal location of target is dissociated from that of the cue by introducing saccades (Posner and Cohen 1984; Maylor and Hockey 1985; Rafal et al. 1989). Because the subjects should move their attention in space with a moving target during smooth pursuit eye movement, it is very likely that the forward-backward asymmetry of saccade latency reflects the difference in attentional state along the pursuit path.

Recently, it has been suggested that the latency of saccades is determined by the activity of buildup cells as well as that of fixation cells in the monkey SC (Dorris et al. 1995). Because fixation cells are thought to reduce the entire activity of the caudal SC bilaterally, changes in their activity should influence the latency of saccades of all amplitudes and directions (Munoz and Wurtz 1993a,b; Dorris et al. 1995). Therefore, the asymmetric change in saccade latency depending on the direction of pursuit must be determined by neural activity which relates saccades with a specific amplitude or direction, such as the preparatory activity of SC cells (Glimcher and Sparks 1992; Munoz and Wurtz 1995; Kustov and Robinson 1996) or cortical cells (Bruce and Goldberg 1985; Schlag and Schlag-Rey 1987; Schall 1992). The asymmetry of saccade latency presented here suggests that the activity of these cells may be influenced by smooth pursuit eye movement. The present results showing that the effect of pursuit direction on saccade latency was much smaller than the ‘gap effect’ may reflect the difference between the local and global changes in neural activity in the saccade generating map(s) located in the SC and/or the cortices.

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