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## Interaction of extraretinal eye position signals in a double-step saccade task: psychophysical estimation

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**Abstract** The time course of extraretinal eye position signals (EEPSs) for visually guided saccades made successively with a short intersaccadic interval was estimated on the basis of perceptual errors in localizing a visual target flashed between the two saccades. The EEPSs for the first and the second saccades were shown to interact in a specific way when the intersaccadic interval was short. The pattern of interaction depended on the direction of the second saccade. It is suggested that when the second saccade was made in the opposite direction to the first saccade, the EEPS for the first saccade was interrupted before its completion in preparation for the onset of the second saccade. When the two saccades were made in the same direction, the EEPS for the first saccade developed more quickly than in a single-saccade condition. The results are discussed in relation to the findings of recent neurophysiological studies.

**Key words** Eye position signal · Corollary discharge · Double-step saccade · Visual localization · Saccade generation

### Introduction

How is the current position of the eye represented in the brain during saccadic eye movements? This question is very important, especially when we consider the well-known perceptual phenomenon of visual position constancy; that is, visual stability during eye movements in spite of the shift of the visual image on the retina. To explain this phenomenon, Helmholtz (1866) proposed the cancellation theory, according to which the brain provides visual stability by comparing the neural signal for the retinal position of the visual image with that for the eye position in the orbit (extraretinal eye position signal: EEPS). This explanation requires that the brain knows

the accurate position of the eye during eye movements. However, recent psychophysical experiments have shown that this is not the case (Dassonville et al. 1992a; Honda 1990a, 1991). In Honda's studies a flashed target was presented when the subject made a saccade in the dark, and he or she was asked to report the apparent position of the target. At the same time, the position of the eye was recorded and the position of the target image on the retina was calculated. Usually the target was mislocalized, in particular when it was flashed near the time of the saccade. The time course of EEPS was estimated on the basis of the size of mislocalization and the position of the target image on the retina. The rationale of the psychophysical estimation adopted in these studies is as follows. According to the cancellation theory, the perceived position of the target seen during saccades is determined by the combination of the EEPS and the signal for the position of the target image on the retina (retinal signal). Provided the retinal signal correctly transmits the target position on the retina to the central visual system, the phenomenon of mislocalization can be explained by assuming that the EEPS the visual system receives is incorrect. In other words, mislocalization reflects the discrepancy between the EEPS and the actual eye position.

In previous studies (Honda 1990a, 1991), I psychophysically estimated the time course of the EEPS for 8-deg saccades. Typically the EEPS occurred about 100 ms before saccade onset. However, its development was very slow and it did not catch up with the actual eye position even after the completion of the saccade. Thus, it was concluded that the EEPS did not reflect the actual eye position, suggesting that the visual localization system in the brain did not know the accurate position of the eye when it moved in a saccadic fashion. Recently, Dassonville et al. (1992a) conducted similar experiments using human and monkey subjects. In their experiment, the subjects made a 20-deg rightward initial saccade from the original fixation point placed at eye level. When the saccade was made, a visual target stimulus was flashed in one of five possible locations 10-deg above eye level, and the accuracy of the second saccade made to the target

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stimulus was measured. Dassonville et al. (1992a) estimated the time course of EEPS from the oculomotor mislocalization, and found that the EEPS began to change 114–249 ms before the saccade in human subjects, while the inflection point in the monkey subject was 51 ms before saccade onset. Thus, their results were very consistent with those reported by Honda (1990a, 1991).

The aim of the present study was to investigate how the EEPS changes when a subject is asked to make a double-step saccade rather than a single saccade. I am interested in the time course of the EEPS, especially when the two saccades are made successively with a relatively short intersaccadic interval. This is because when the subject is asked to make the second saccade immediately after the first saccade as rapidly as possible, the EEPS for the first saccade is expected to be modified so as to prepare for eliciting the second saccade. On the other hand, when the intersaccadic interval is long, there may be no interaction between the EEPSs for the two saccades.

In this study, I employed two types of double-step saccade: the opposite direction and the same direction. In the former condition (experiment 1), the second saccade was made toward the original starting position of the first saccade. In the latter condition (experiment 2), the direction of the two saccades was the same. In both conditions, the time course of the EEPS was estimated on the basis of the perceptually judged position of the target briefly presented during a double-step saccade and the position of the target image on the retina. It was expected that the EEPS for the first saccade would be modified differently depending upon the direction of the second saccade.

As described above, this study was conducted to explore EEPS modification in double-step saccade conditions by using psychophysical data on visual mislocalization during saccades. The results demonstrated large mislocalization of visual targets when they were flashed near the time of saccades. However, it should be noted here that this type of mislocalization is never noticed in everyday life, because our normal visual behavior is usually performed in an illuminated environment and therefore we can make use of many visual cues for judging locations of objects around us (Honda 1993). In addition, it is rare that we make successive saccades as quickly as required in the present experiments.

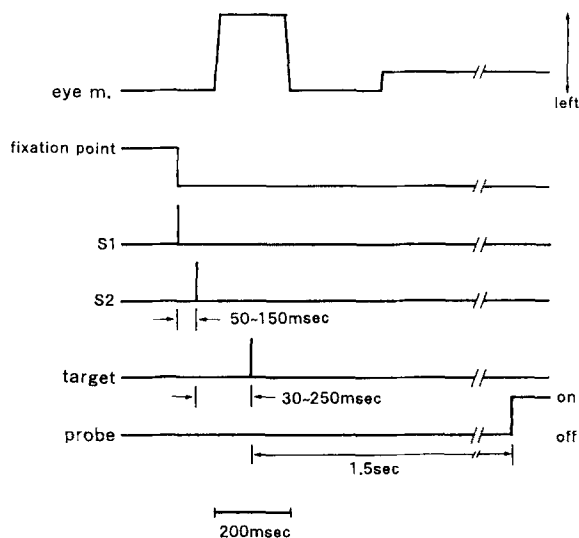
## Experiment 1

### Perceptual mislocalization and the EEPS at the time of a double-step saccade when the second saccade was made in the direction opposite to that of the first saccade

#### Method

##### Double-step saccade trial

A subject was seated in the dark with the head fixed by a chin- and forehead-rest. Horizontal eye movements of the right eye were monitored by a photoelectric limbus tracking method. The subject's right eye was illuminated by an infrared light-emitting diode (Toshiba, TLN101), and the reflected light from the two points of



**Fig. 1** Schematic description of experiment 1 in which subjects sequentially made two saccades: the first to the right and the second, returning saccade to the left. *Eye m.* eye movement, *upward* and *downward deflections* show saccades to the right and the left, respectively, *fixation point* the original fixation point, *S1* and *S2* visual stimuli for the first and second saccades, respectively (in reality, *S2* was presented by relighting the original fixation point: see text), *target* a visual target stimulus for the localization task, *probe* a probe stimulus, by moving which the subjects reported the apparent position of the target

the lower limbus (iris-sclera boundaries in 4 o'clock and 8 o'clock positions) was collected by a pair of phototransistors (Toshiba, TPS601). By amplifying the difference between the two phototransistor outputs, horizontal eye movements were monitored, and recorded by a digital data recorder (TEAC, DR-F1) with an accuracy of about 0.5 deg and a sampling rate of 500 Hz. On each trial, a buzzer warning signal was given, and then a fixation point (white LED, 0.3 deg in diameter, 20 cd/m<sup>2</sup>) was presented at the center of the visual field for about 2 s. The subject was asked to keep watching the fixation point. When the fixation point was turned off, a visual stimulus (white LED, 0.3 deg in diameter, 20 cd/m<sup>2</sup>) for eliciting the first saccade was presented for 20 ms at a position 10 deg right of the fixation point. The subject was asked to make a horizontal saccade (the first saccade) toward the first stimulus. Immediately after the presentation of the first stimulus, the original fixation point was relit for 20 ms as a visual cue stimulus (the second stimulus) for the second saccade. The inter-stimulus interval between the first and the second stimuli was varied randomly from trial to trial between 50 ms and 150 ms. The subject made the second returning saccade as rapidly as possible after completion of the first saccade. (When the second stimulus was presented near the time of the first saccade, it was often seen at a position different from its actual position. In this case, the subject was instructed that the second stimulus was a signal for making a backward saccade to the position of the original fixation point and that he or she should not necessarily move the eyes to the illusory position of the second stimulus.) Between 30 and 250 ms after presentation of the second stimulus, a visual target stimulus for localization was presented for 2 ms at the position exactly between the first and the second stimuli, i.e., 5 deg to the right of the original fixation point. The target consisted of four vertically arranged small square red LEDs (0.3 deg×0.3 deg; 40 cd/m<sup>2</sup> each). The subject was allowed to move the eye toward the target only after the completion of the second saccade. Figure 1 schematically represents the paradigm of double-step saccade trials in experiment 1. As mentioned above, the inter-stimulus interval between the second stimulus and the target was varied randomly from trial to trial between 30 ms and 250 ms. Thus, the timing of target presentation depended on the latency of the saccades and the inter-stimulus in-

interval between the second stimulus and the target, and the target usually appeared during the time interval between the first and the second saccades. About 1.5 s after disappearance of the target, a probe stimulus (yellow LED, 0.5 deg in diameter, 30 cd/m<sup>2</sup>) was presented for 5 s. The subject could move the horizontal position of the probe stimulus by turning a knob with the right hand. The subject reported the apparent position of the target by moving the probe to that position.

#### Single-saccade trial

In addition to the double-step saccade trial, localization was also examined in a single-saccade trial, in which only the first stimulus was presented and the subject made the first saccade only. The target was presented at a time near the saccade, and the subject reported its apparent position by moving a probe stimulus in the same way as in the double-step saccade trial.

#### Subjects and procedure

Three subjects participated in this experiment. Subject HH was the author and the remaining two subjects were university students. They served as subjects for 6 days. On each day, about 160–180 trials, divided into eight or nine sessions, were conducted. In each session, the single-saccade and the double-step saccade trials were presented in random order. After the experimental session, a few sessions of control trials were conducted. On the control trials, either the first stimulus or the second stimulus was presented for 2 s, and the subject kept watching these stimuli. Immediately after the stimulus was turned off a target was presented for 2 ms, and the subject reported its apparent position. The control trials were conducted to examine localization accuracy when the subject did not make a saccade.

## Results

### Eye movements

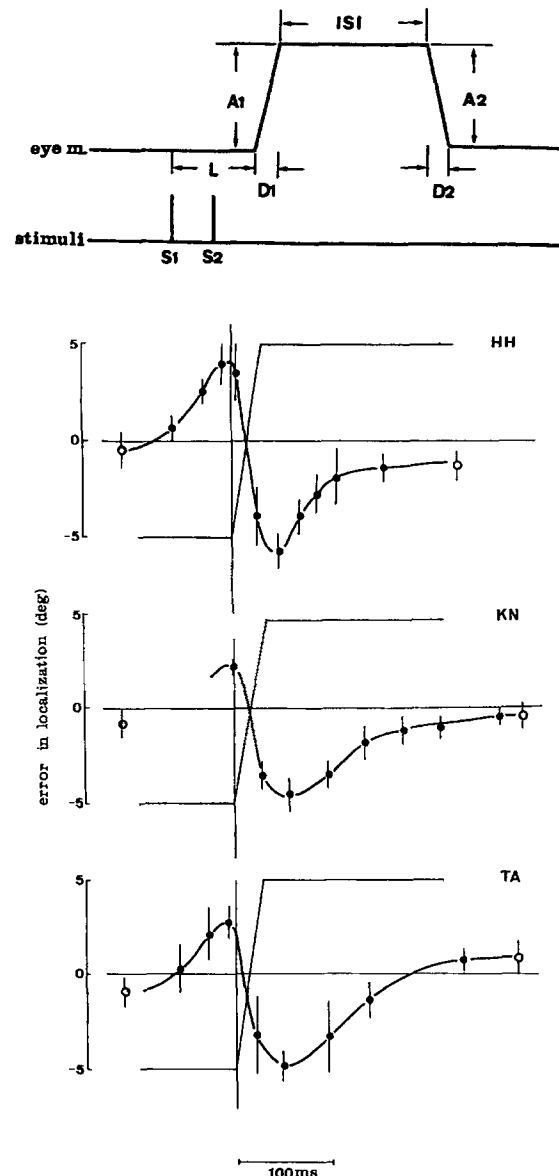
There was a slight difference in the amplitude of the saccades between the three subjects (Table 1). However, the most striking difference was observed in the latency of the first saccade and the intersaccadic interval (interval between the end of the first saccade and the beginning of the second saccade). The mean latency of the first saccade of subject TA was distinctively different from that shown by the remaining two subjects. In addition, he showed the longest intersaccadic interval among the three subjects. One possible reason for this difference was that subjects HH and KN were very experienced in eye-movement experiments, while subject TA was naive.

### Mislocalization

Figure 2 shows the time course of mislocalization in the single-saccade trials. The error curves shown in Fig. 2 are very consistent with those reported in previous studies (Matin et al. 1969, 1970; Kennard et al. 1971; Honda 1990a, 1991; Dassonville et al. 1992a). All subjects mislocalized the target to the saccade direction when it was presented immediately before or at the beginning of the saccade. In contrast, when the target was presented at the end of the saccade, the subjects mislocalized the target in the direction opposite to the saccade's direction. The er-

**Table 1** Means and SDs of latencies (ms), durations (ms), intersaccadic intervals (ms), and amplitudes (deg) of the two saccades in experiment 1 (*L* latency of the first saccade, *D1* and *D2* durations of the first and second saccade, respectively, *ISI* intersaccadic interval, *A1* and *A2* amplitudes of the first and second saccades, respectively)

Subject	L	D1	D2	ISI	A1	A2
HH	179 (48.1)	33 (3.2)	32 (4.9)	140 (25.6)	10.1 (0.9)	7.9 (1.7)
KN	182 (55.0)	34 (4.5)	35 (9.6)	261 (69.0)	9.7 (1.6)	9.0 (2.0)
TA	265 (91.0)	40 (10.2)	47 (11.2)	307 (101.0)	11.5 (2.7)	12.5 (3.5)



**Fig. 2** Time course of mislocalization in the single-saccade trials in experiment 1. The results are shown separately for the three subjects. The vertical line indicates the onset of the saccade, and the time course of the saccade is schematically shown. The ordinate shows mislocalization (deg). A minus sign in the ordinate indicates mislocalization in the direction opposite to the first saccade. Each dot indicates the mean of error of about 5–20 trials, and the bar on each dot is the size of the SD. The error curves were fitted by eye based on the average errors (dots). Open circles indicate the results in control trials in which the subject kept watching S2 (left circle) or S1 (right circle)

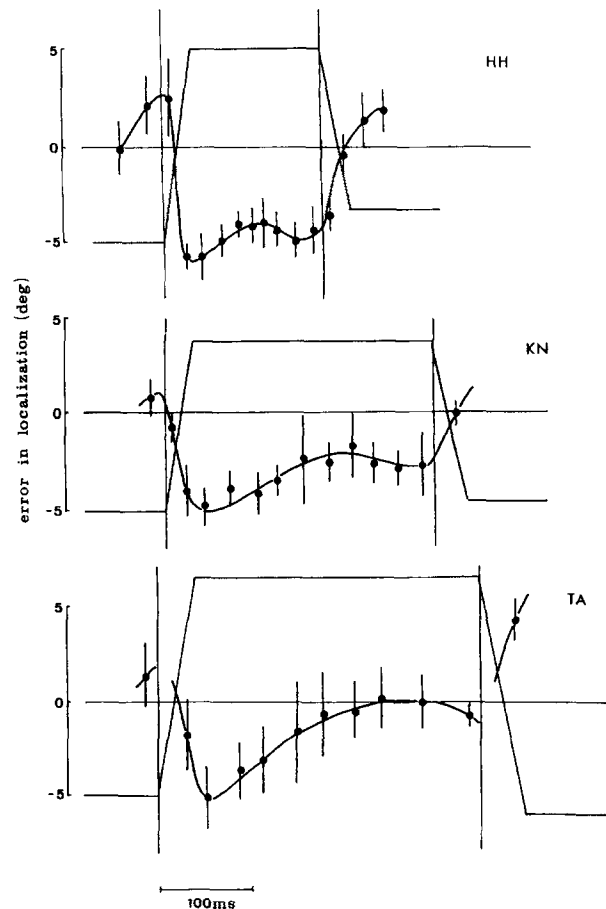
ror disappeared by about 150 ms after the end of the saccade; the data points reached the  $\pm 1$  SD range of the localized position on the control trials.

Mislocalization in double-step saccade trials is shown in Fig. 3. Note that in this figure the means of mislocalizations during the intersaccadic interval are plotted as a function of the relative position in time of the target's presentation with respect to the total length of the intersaccadic interval. For example, when the target was presented 20 ms after the end of the first saccade and the intersaccadic interval was 160 ms, its relative position was 12.5% (20/160). Thus, before calculating the means of mislocalization, each datum obtained during the intersaccadic interval was rearranged on the relative timing of the target presentation. This type of normalization was applied so as to know exactly how visual mislocalization was influenced by conducting the second saccade, because localization of targets flashed during the intersaccadic interval was determined exclusively by the relative position of target presentation in time during the intersaccadic interval, not by the timing of target presentation relative to the first saccade onset, nor by that relative to the second saccade onset.

The shape of the error curve was different among the subjects. In particular the error curve for subject TA was remarkably different from that of subjects HH and KN. In these latter two subjects, microlocalization in the direction opposite to the first saccade (i.e., downward deflection in Fig. 3) continued until the end of the second saccade. In subject TA, on the other hand, mislocalization gradually decreased and disappeared by about 200 ms after the end of the first saccade. Note that the error curve for subject TA was the same as that shown in the single-saccade trial (Fig. 2). Evidently, the reason for the difference in the error curves between subject TA and the remaining two subjects (HH and KN) is that subject TA was experimentally naive and showed a relatively longer intersaccadic interval between the two saccades. Presumably, in subject TA, mislocalization produced by the first saccade was not influenced by making a subsequent second saccade.

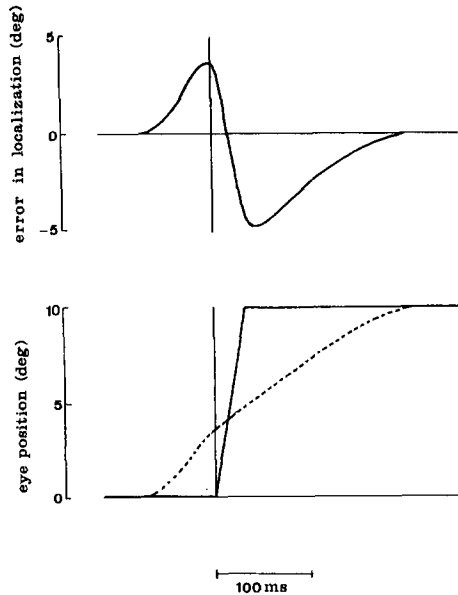
#### Time course of the EEPS

The time course of the EEPS was estimated from the mislocalization (error) curve and the change in position of the target image on the retina produced by saccadic movements of the eye. In Fig. 4, the upper trace represents the idealized time course of mislocalization in the single-saccade trial which is drawn based on the findings shown in Fig. 2 that mislocalization (1) started about 80 ms before saccade onset, (2) reached its maximal upward error (i.e., error in the saccade direction) of about 4 deg at saccade onset, (3) went back to the maximal downward error (i.e., error in the direction opposite to the saccade) of about 5 deg at saccade offset, and (4) diminished about 200 ms after saccade offset. The lower two traces schematically show the typical time course of a



**Fig. 3** Time course of mislocalization in the double-step saccade trials in experiment 1. Notation is the same as in Fig. 2 except that the two vertical lines indicate the onset of the first (left-hand line) and second saccades (right-hand line)

saccade (continuous line) and that of the estimated EEPS (dashed curve). The EEPS was obtained by subtracting the retinal signal from the perceived position of the target as estimated from the mislocalization curve. For example, consider the point of maximal mislocalization when the target is presented after the saccade in Fig. 4 (top). Mislocalization is approximately  $-5$  deg. Given that the target was flashed after the saccade, the retinal signal is also  $-5$  deg. The perceived location of the target in absolute coordinates (i.e., relative to the starting point of the trial) is approximately  $0$  deg. EEPS is then  $0 - (-5)$ , or  $+5$  deg, as indicated by the dashed line (Fig. 4, bottom). The retinal signal was calculated on the basis of eye position at the time of target presentation. In calculating EEPS, mislocalization curves were corrected by using the error in the control trial, because the results of the control trial indicated that there was a small indigenous error (open circles in Fig. 2). As shown in Fig. 4 (bottom), the time course of the estimated EEPS did not coincide with that of actual eye movements. The EEPS appears about 80 ms before saccade onset, but it develops so slowly that it cannot catch up with the actual position of the eye until more than 100 ms after the end of the saccade. The time course of the EEPS is very consis-

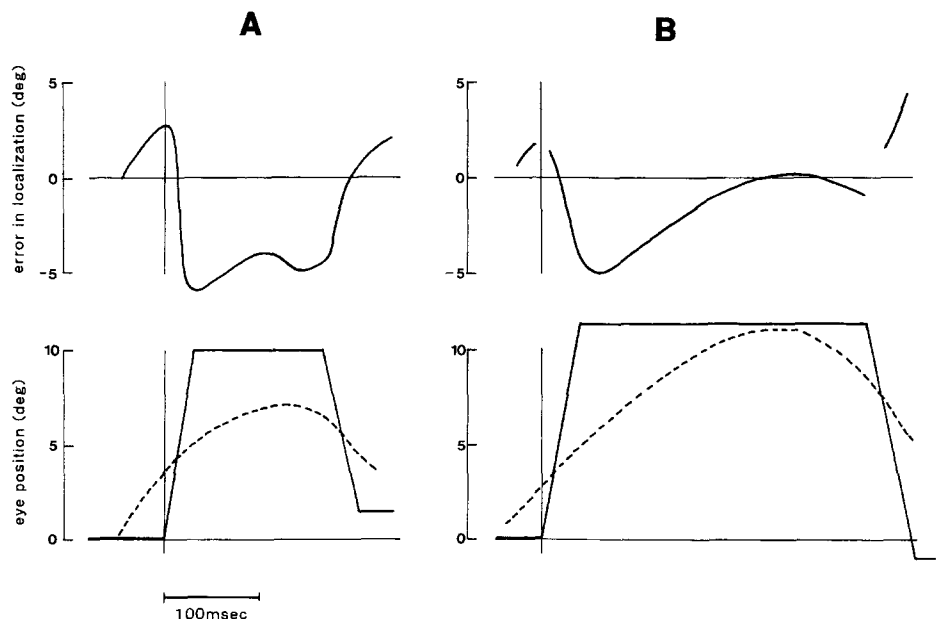


**Fig. 4** Upper trace shows the idealized time course of mislocalization in the single-saccade trials. Lower two traces show the typical time course of the psychophysically estimated EEPS (dashed curve) and that of saccadic eye movements (continuous line)

tent with that reported in previous studies (Honda 1990a, 1991).

Figure 5A shows the time course of the EEPS for a double-step saccade estimated on the basis of the mislocalization shown by subject HH. It is apparent that the EEPS for the second saccade began before the EEPS for the first saccade had fully developed. In contrast, when the intersaccadic interval was long (subject TA: Fig. 5B), the time course of the EEPS was the same as that shown in the single-saccade trial (Fig. 4). Thus, it is evident that the modification of the EEPS in the double-step saccade trial was shown only in the subjects who made the two saccades with a relatively short intersaccadic interval.

**Fig. 5** **A** Upper trace shows the time course of mislocalization in the double-step saccade trial shown by subject HH. Lower two traces show the EEPS (dashed curve) and actual eye position (continuous line). **B** Mislocalization curve (upper trace) and the EEPS (dashed curve) for double-step saccades made by subject TA



## Experiment 2

### Perceptual mislocalization and the EEPS at the time of a double-step saccade when the second saccade was made in the same direction as the first saccade

#### Method

The method and procedure of experiment 2 were basically the same as those of experiment 1 except for the direction of the second saccade. The original fixation point was presented at a position 5 deg left of the center of the visual field. The first and the second stimulus were presented at positions 10 deg and 20 deg right of the fixation point, respectively. The subject therefore made two saccades successively in the same direction. The target for visual localization was flashed at the position exactly between the fixation point and the first stimulus, and the subject reported its apparent position in the same way as in experiment 1.

Three subjects participated in experiment 2. However, one subject could not make double-step saccades even after many practice trials. Therefore, data were obtained from the remaining two subjects, HH and MT. Subject HH was the author and subject MT was a female university student with no experience in eye-movement experiments.

#### Results

##### Eye movements

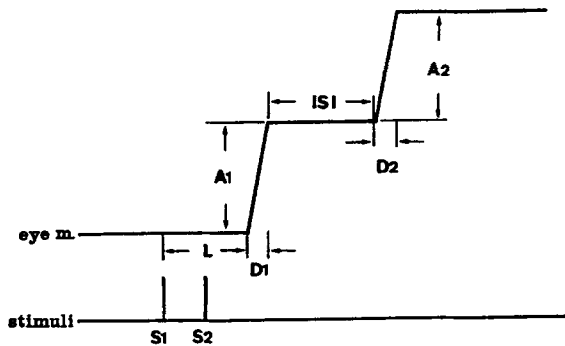
Although there was a slight difference in the amplitude of the saccades between the two subjects, the intersaccadic interval was approximately the same (Table 2). In addition, the intersaccadic interval was very short compared with that in experiment 1, indicating that both subjects were able to make the second saccade very quickly after completion of the first saccade.

##### Mislocalization

The error curves in the double-step saccade trial (Fig. 7) were essentially the same in the two subjects except that,

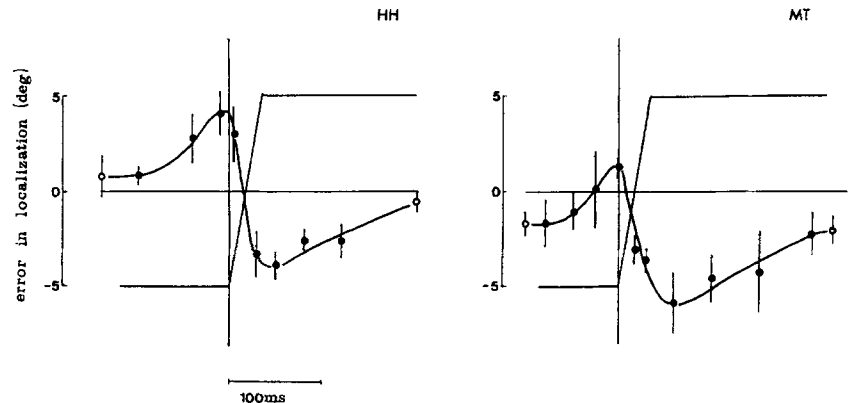
**Table 2** Means and SDs of latencies (ms), durations (ms), intersaccadic intervals (ms), and amplitudes (deg) of the two saccades in experiment 2 (abbreviations as in Table 1)

Subject	L	D1	D2	ISI	A1	A2
HH	128 (37.6)	36 (5.2)	29 (4.7)	115 (49.4)	12.3 (1.7)	8.0 (2.0)
MT	163 (70.5)	37 (7.4)	38 (6.5)	126 (47.6)	9.8 (2.7)	9.6 (2.8)

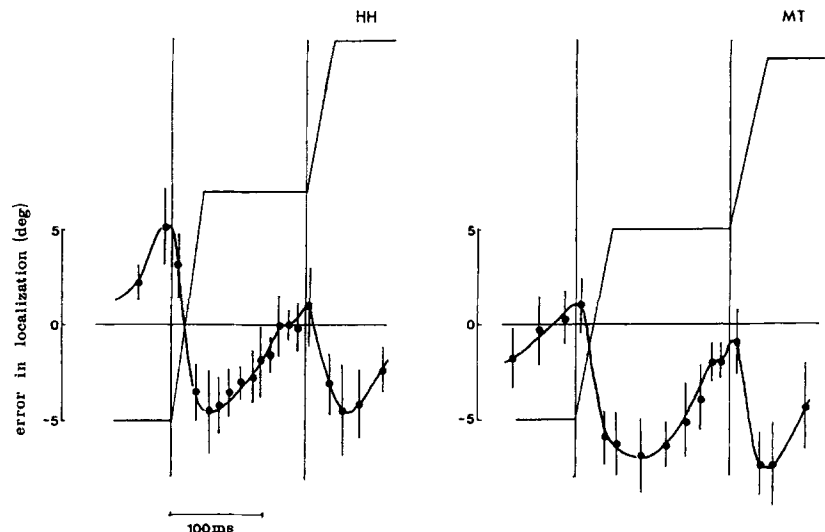


in subject MT, the entire error curve shifted in a downward direction because of an indigenous constant error in localization (Fig. 6). The error curves in experiment 2 were rather complex. As in experiment 1, a large mislocalization in the direction opposite to the first saccade

**Fig. 6** Time course of mislocalization in the single-saccade trials in experiment 1. *Notation is the same as in Fig. 2*



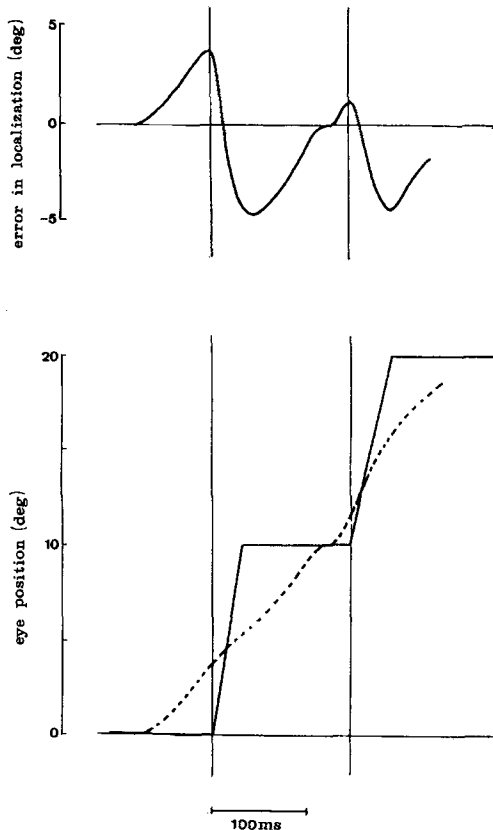
**Fig. 7** Time course of mislocalization in the double-step saccade trials in experiment 2. *Notation is the same as in Fig. 3*



(i.e., downward deflection in Fig. 7) was observed when the target was presented at the end of the first saccade. However, it rapidly decreased and disappeared immediately before the onset of the second saccade. Furthermore, the large error in the direction opposite to the saccade's direction appeared again and reached a maximum at the end of the second saccade. An interesting finding here is that the mixlocalization (downward deflection) which appeared between the two saccades decreased more quickly than in the single-saccade condition (Fig. 6 vs Fig. 7).

#### *Time course of the EEPS*

The time course of the EEPS was estimated from the error curves shown in Fig. 7. Figure 8 schematically represents the time course of the EEPS obtained when subject HH made the second saccade in the same direction as that of the first saccade. As shown in Fig. 8, the EEPS began well before the onset of the first saccade and developed rather slowly. However, it seems that the EEPS catches up with the eye more quickly than it does in the single-saccade trial (Fig. 6). It seems as though the EEPS for the first saccade is prompted to reach completion in preparation for eliciting the second saccade. Further-



**Fig. 8** Upper trace shows the idealized time course of mislocalization drawn on the basis of the data from subject HH. Lower two traces indicate the time course of the psychophysically estimated EEPS (dashed curve) and actual eye position (continuous line)

more, immediately after its arrival at the actual eye position, the EEPS for the second saccade starts to appear. Thus, it seems that the EEPS for the first saccade is rapidly switched over to the EEPS for the second saccade without a pause.

## Discussion

### Visual versus motor localization

Hallett and Lightstone (1976) asked their subjects to localize a perisaccadic flash by making a saccade to its location. Finding that oculomotor localization was accurate, they suggested that the oculomotor system knows the accurate position of the eye in the orbit at all times and therefore uses accurate EEPS when computing stimulus location. A similar finding was reported by Hansen and Skavenski (1985). In their experiment, subjects were asked to localize a visual target flashed during a saccade by hitting its apparent position with a small hammer. Hansen and Skavenski found that the subject could localize the target accurately.

In contrast to these findings, there have been many studies that indicate visual mislocalization of targets briefly presented near the time of a saccadic eye movement (Bischoff and Kramer 1968; Honda 1989, 1990a,

1991, 1993; Matin et al. 1970; Mateeff 1978; O'Regan 1984), and as shown in Figs. 2 and 6, the present study confirms these earlier findings.

Although there has been much discussion of the discrepancy between visual and motor localization (Howard 1982; Skavenski 1990; Honda 1991; Dassonville et al. 1992a; Hershberger and Jordan 1992), there is no conclusive explanation of this issue. However, it should be noted that Hallett and Lightstone's (1976) finding was not necessarily replicated by recent studies (Honda 1990a; Dassonville et al. 1992a). Honda (1990a), for example, demonstrated that when a target was presented near the time of a saccade, the eye moved to the mislocalized position of the target, not to its actual position. Therefore, there is a possibility that in Hallett and Lightstone's experiments subjects were able to use some exocentric visual cues (Dassonville et al. 1995). The same criticism may not be true of Hansen and Skavenski's experiment, because in this no visual cues to target location were available for subjects. Thus, it is not easy to explain the discrepancy between many visual localization experiments and Hansen and Skavenski's experiment. One possible explanation may be that the different tasks employ different localization mechanisms at both neurophysiological and perceptual-cognitive levels (Bridgeman et al. 1975; Honda 1990b, 1991; Skavenski 1990).

What does the EEPS estimated in this study represent?

In this study, the time course of the EEPS was estimated on the basis of the assumption suggested by cancellation theory that mislocalization occurs because the EEPS the visual system receives is incorrect. This assumption is valid only when the retinal signal correctly represents the retinal locus of the target image. Strictly speaking, however, it is not necessarily the case because as shown in Figs. 2 and 6 some subjects mislocalized the target even in the control trial in which they were not asked to make a saccade and therefore the target was presented when the eye remained stationary. Therefore, the error shown in the control trial is ascribed not only to the inaccuracy of the EEPS, but also to many other factors including the accuracy of the retinal signal. Although it is not clear to what extent the retinal signal is involved in producing mislocalization, the time course of the EEPS estimated in this study does not lose its validity because the error in the control trial is small.

The finding that the EEPS does not reflect the actual position of the eye suggests the necessity that a strict distinction should be drawn between the neural command for eliciting a saccade (motor command) and its internal representation (EEPS) the brain employs for judging the position of objects in the world observed during eye movement. As regards this distinction, it should be mentioned that some part of the brain engaged in eliciting eye movements knows to some extent the accurate position of the eye when it moves in a saccadic fashion. Barash et al. (1991), for example, recorded single-unit ac-

tivity from neurons in the lateral intraparietal area (LIP) of monkeys. The animal was required to carry out a double-saccade task in which two visual stimuli for saccades were flashed sequentially but extinguished before the animal made the first saccade. In this double-saccade paradigm, the LIP cells fired only when the saccade was made in its preferred direction, i.e., toward the cell's motion field, regardless of whether it was the first or the second saccade. This finding indicates that LIP neurons code in motor coordinates: these neurons become active if a saccade is planned into their motion field even if no visual target falls within their receptive field. At the same time, this finding suggests that LIP neurons know the accurate position the eye reached after the first saccade, because in order for these neurons to fire with the second saccade, they need to know that their motor field was moved by the first saccade to the position into which the second saccade is planned. The same type of neuron has been reported for the frontal eye field (Goldberg and Bruce 1990) and the intermediate layers of the superior colliculus of monkeys (Mays and Sparks 1980).

Another line of evidence supporting the notion that the brain knows the actual position of the eye comes from electrical stimulation experiments. Sparks and Mays (1983) applied electrical stimuli within the superior colliculus during the latency period of a visually guided saccade, and found that the visual evoked saccade compensated for the electrically produced deviation; the eyes are finally directed toward the site where the target was seen. This also implies that, in carrying the eye to the target position, the brain took into consideration the size and direction of the eye deviation produced by electrical stimulation.

Despite these findings, however, it is still unclear which of the neural activities recorded from various sites of the brain corresponds to the EEPS or corollary discharge in Sperry's (1950) term (for a recent review see Carpenter 1991; Wurtz and Goldberg 1989). This issue is discussed in more detail in the last section.

#### Does the EEPS begin before a saccade?

As shown in Figs. 2 and 6, the EEPS in the single-saccade condition began about 100 ms before the onset of the first saccade and developed rather slowly, usually reaching its destination more than 100 ms after the end of the saccade. This is very consistent with the results reported by the earlier studies (Honda 1990a, 1991). In addition, Dassonville et al. (1992b), using a colliding saccade paradigm of microstimulation to the frontal eye field, suggested that the oculomotor system uses a damped or sluggish (i.e., slowed down) representation of eye position. Their idea also fits well with the finding in this study that the EEPS develops so slowly that it cannot catch up with the actual eye position until more than 100 ms after the end of a saccade. In another experiment (Dassonville et al. 1992a), these authors psychophysical-

ly estimated the time course of EEPS based on errors in oculomotor localization of a visual target flashed near the time of a saccade, and found the same time course as that reported in the present study. However, they concluded that although the EEPS has a sluggish time course, it never begins to change before the saccade onset. This is because it takes many milliseconds for visual stimuli projected on the retina to arrive at the brain proper. For this reason, Dassonville et al. argued that in order to estimate the actual time course of the EEPS exactly, the psychophysically estimated EEPS curve should be delayed by a time equal to that required for neural processing of a visual target stimulus, with the result that the actual EEPS begins to change at the time that eye movement begins.

Their argument is quite reasonable. I think, however, that at present we cannot completely deny the possibility that the EEPS begins to develop even before the eye begins to move. First, the EEPS estimated in psychophysical studies usually begins to develop about 100 ms before saccade initiation (Dassonville et al. 1992a; Honda 1990a, 1991). In an extreme case, it was shown to begin about 200 ms before saccade onset (Dassonville et al. 1992a). By contrast, neurons in the brain begin to activate shortly after the presentation of visual stimuli: the average response latency of superior colliculus visual neurons was 40 ms (Goldberg and Wurtz 1972), and about 20% of frontal eye field neurons began to discharge within 60 ms after stimulus presentation (range 32–232 ms; Goldberg and Bushnell 1981). Second, neurons at various sites of the brain fire before saccadic eye movements (Schiller and Koerner 1971; Schiller and Stryker 1972; Wurtz and Goldberg 1972; Mohler and Wurtz 1976; Bruce and Goldberg 1985). In the lower layers of the superior colliculus, cells associated with saccadic eye movement began to discharge about 200 ms prior to the onset of saccades (Schiller and Koerner 1971). Some cells in the frontal eye field discharged about 100 ms before saccade onset (Bruce and Goldberg 1985). As will be described in the next section, the EEPS is thought to be produced based on various types of cell activities involved in planning eye movements. It seems, therefore, that the EEPS in part involves presaccadic cell activities.

Taken together, the most appropriate answer is probably that the EEPS begins to change even before saccade initiation, but by a smaller amount in time than estimated in psychophysical experiments.

#### Interaction of EEPSs in the double-step saccade trial

The results of the present study indicated that in the double-step saccade trial the EEPS for each saccade interacted in a specific way, especially when the time interval between the two saccades was short. When the subject made the second saccade in the opposite direction to the first saccade (experiment 1), the EEPS for the first sac-



cade was interrupted before its completion and was switched over to the EEPS for the second saccade. On the other hand, when the subject was asked to make two saccades rapidly in the same direction (experiment 2), it was shown that the EEPS for the first saccade developed more quickly than when a single saccade was required. Thus, the EEPS for the first saccade was modified differently by the direction of the subsequent second saccade.

At present there is no neurophysiological evidence for the above-mentioned interaction of EEPS in double-saccade conditions. However, some neurophysiological findings suggest that the neural representation for a preceding saccade is modified by conducting a subsequent saccade. Goldberg and Bruce (1990), for example, found that in a double-saccade paradigm certain postsaccadic neurons in the frontal eye field discharged during and after the first saccade if the following second saccade was made in the same direction as the first saccade. On the other hand, when the two saccades were made in opposite directions to each other, these cells ceased their activities at the instant the second saccade occurred.

Furthermore there are some neurophysiological findings that seem to have relevance to the modification of the EEPS demonstrated in the present study. Although most saccade-related neurons discharge just before a saccade and cease their activity immediately after the end of the saccade, certain neurons in the superior colliculus (Mays and Sparks 1980) and frontal eye field (Barash et al. 1991) begin discharging just after a preceding saccade and continue to activate until after the second saccade. It is, therefore, conceivable that certain neural interactions between, for example, these two types of oculomotor cells give rise to such a modified EEPS as is demonstrated in this study. In any case, it seems that EEPSs are produced by intimate neural interactions among various types of oculomotor cells at many sites of the brain.

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