

RESEARCH ARTICLE

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Effects of stimulus conditions on the performance of antisaccades in man

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Abstract We investigated the effect of different spatial and temporal parameters on the saccadic reaction times (SRTs) of the antisaccades and on the frequency and the SRTs of erratic prosaccades in five adult human subjects. The subjects were instructed to aim their saccades to the side *opposite* to where a visual go-stimulus occurred. Parameters under consideration were: the gap duration (between 0 and 600 ms, and an overlap paradigm); the stimulus size (sizes of 0.1°, 0.2°, and 0.4°, using the gap 200-ms paradigm); and the stimulus eccentricity (1°, 2°, 4°, 8°, and 12°, with the gap 200-ms paradigm). A decrease in the anti SRTs and an increase in the error rate were observed with medium gap durations (200 ms, 250 ms), while the anti-SRTs were longer and the error rates lower with the shorter values (0 ms, 100 ms, and with the overlap paradigm) and with the long values (600 ms). A slight decrease in the anti-SRTs and an increase in the error frequency occurred with increasing eccentricity; the SRT distributions of the errors resembled closely those of prosaccades in corresponding prosaccade tasks with the same eccentricities. The stimulus size had only modest or no effects at all. Analysis of the distributions of the correction times of the erratic prosaccades showed that the intersaccadic intervals could be very short: in the range of express saccades, with a peak at 100 ms; or in some subjects even shorter, with a peak at 40–50 ms. It is concluded that the performance of antisaccades is influenced by parameters that interact with the fixation and/or attention system of oculomotor control. Parameters supporting a disengagement of fixation at the time of stimulus onset provoke a reduction of the saccadic reaction times not only of prosaccades but also of antisaccades. Moreover, a certain state of disengagement seems to facilitate the occurrence of reflex-like errors.

Key words Saccade · Reaction time · Antisaccade · Fixation · Gap effect · Human

Introduction

The reaction and correction times of visually guided saccadic eye movements have often been used as a tool to investigate the generation of these movements or for the understanding of visual psychophysical or cognitive processes. The most frequently used paradigm employs the presentation of a central fixation point at the beginning of a trial and requires the subject to maintain fixation of gaze until a peripheral saccade target stimulus is presented. Reaction time and size of primary and secondary (corrective) saccades, as well as their velocity, have usually been measured as independent variables.

Several years ago it became clear that both the presence and absence of the fixation point at the time of stimulus presentation, and the presence and absence of a stimulus at the goal location for the saccade play a basic role in its generation: when the fixation point is switched off some time before the peripheral stimulus is presented, the so-called gap condition, the reaction times of saccades to the stimulus (prosaccades) are generally reduced as compared to the case where the fixation point remains visible, i.e., the so-called overlap condition (Saslow 1967). This effect is known as the gap effect. Later on it was discovered under gap conditions that the reaction time distribution can become multimodal with an early mode of express saccades (at about 70 ms in the monkey; Fischer and Boch 1983; at about 100 ms in man; Fischer and Ramsperger 1984). The express saccade was interpreted as a reflex-like orienting movement that can be produced when active fixation and/or attention is disengaged. It is also known that in the primate the express saccade is mediated through the retino-cortico-tectal pathway and can be generated without the frontal eye fields (Schiller et al. 1987).

If, on the other hand, a saccade is aimed toward a location where no target stimulus is presented, the saccadic

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reaction times (SRTs) are prolonged. A special paradigm with no saccade target is the antisaccade task (Hallett 1978). In this task the subjects are required to direct their gaze from the initial fixation point toward the direction opposite to where the stimulus is presented. For a successful performance of this task the subject must be able to suppress a reflex-like prosaccade to the stimulus, and, second, the subject must be able to voluntarily generate a saccade toward the opposite side. Therefore it did not come as a surprise that antisaccades are usually not of the express type, because there is no reflex-eliciting stimulus for the antisaccade (Fischer and Weber 1992). Moreover, as revealed by studies in neurological patients, antisaccades – unlike express saccades – need an intact frontal cortex (Guitton et al. 1985). Patients with frontal lesions are impaired in the antisaccade task and very often produce reflex-like movements to the stimulus, with reaction times of about 100 ms (Guitton et al. 1985). They also produce considerably larger numbers of express saccades in a gap prosaccade task than normal control subjects (Braun et al. 1992). These observations lead to the idea that patients with other syndromes such as schizophrenia, who are also impaired in the antisaccade task (Matsue et al. 1994a, b), suffer from neural degenerations involving the frontal cortex. The simple experimental manipulation of taking away the fixation point prior to stimulus presentation (gap condition) increases the error rate and decreases the reaction time of the correct antisaccades significantly (Fischer and Weber 1992). Children around 9–12 years of age have considerable difficulties with the antisaccade task producing an average of more than 50% errors (Fischer et al. 1997).

While the existence of a gap effect for prosaccades has been widely acknowledged (Mayfrank et al. 1986; Reuter-Lorenz et al. 1991; Currie et al. 1993; Dorris and Munoz 1995; Weber and Fischer 1995), the reports on a gap effect for antisaccades are controversial. A gap effect for antisaccades was clearly established in previous experiments in our laboratory (Fischer and Weber 1992; Goldring and Fischer 1997); H. Weber and N. Dürr, submitted). Reuter-Lorenz et al. (1991), on the other hand, claimed that the gap effect was unreliable for antisaccades or considerably smaller (Reuter-Lorenz et al. 1995). They suggested that the observed decrease in the reaction times of the antisaccades in gap as compared to overlap trials resulted in part from a warning effect due to the fixation point offset and in part from a release of fixation prior to stimulus onset.

Transient peripheral cues presented 100 ms before and always at the side opposite to the go-stimulus in an antisaccade task (thus indicating correctly the direction for the next antisaccade) should decrease reaction time and error rate. Instead, the opposite result was obtained (Fischer and Weber 1996). These results cannot be accounted for by warning effects, nor by common hypothesis of attention allocation.

Considering these open questions, we decided to investigate the effects of some temporal and spatial stimulus parameters on the generation of antisaccades. The re-

sults show that as for prosaccades the duration of the gap is critical for the reaction times and for the percentage number of erratic prosaccades. While there was no essential effect of stimulus size on antisaccade latency or error rate, both variables were substantially influenced by the stimulus eccentricity, in a similar way to the reaction times of prosaccades (Boch et al. 1984; Weber et al. 1992, 1993). For all conditions where the subjects made reasonable numbers of errors we analyzed also the time of the beginning of the corrective saccades. This analysis revealed that different modes can be used to correct anticipatory saccades, involuntary erratic prosaccades, or voluntary prosaccades that miss the target.

Materials and methods

Subjects

Five adult human subjects (aged 24–53 years), two of them being the authors, participated in this study. All of them had normal or corrected-to-normal vision. All were right-handed and viewed the stimuli with both eyes. They were all trained for horizontal prosaccades in the gap and overlap task until stable reaction time distributions were obtained (Fischer and Ramsperger 1986). The subjects also had experience in performing the antisaccade gap task.

Eye movement recording and analysis

Eye movements were measured by an infrared reflection method (Skalar Medical Iris System), with a temporal resolution of 1 ms and a spatial resolution of 0.1° . SRT and size of all saccades detected within 700 ms from stimulus onset were determined off-line on the basis of the analog-digital-converted eye position signal stored on disc. The reaction time was defined by the time when the velocity signal exceeded 15% of its maximum for the saccade under consideration.

Calibration

Before the start of each experimental session, the subjects had to fixate a fixation stimulus, which could be moved manually using the computer mouse. Both the stimulus and the eye position signal were superimposed on the experimenter's computer screen. The stimulus was moved to the left and right from the center of the screen and the subjects were instructed to track it. The gain was set to 0.3 V/deg such that it would fit linearly with the respective position of the fixation point on the screen. For experimental blocks with antisaccades, this calibration was maintained.

Stimulus presentation

The visual stimuli, a central red fixation point (Fp; $0.1^\circ \times 0.1^\circ$) and white target stimuli (St; 0.1° , 0.2° , or 0.4°) on a $20^\circ \times 15^\circ$ green background, were generated by a personal computer and presented on an RGB color monitor using a high-resolution graphic interface (mirograph 510). Target onset time was synchronized to the screen (frame rate 83 Hz), taking into account also the constant time delay between the synchronization pulse and the horizontal level at which the stimuli were presented. The luminance of all stimuli was well above perceptual threshold (Fp and St, 50 cd/m², background, 10 cd/m²). Viewing distance was 57 cm.

Saccade tasks

In the antisaccade task (antitask) the subjects were instructed to make a saccade in the direction opposite to the side of the stimulus

to the mirror-imaged position. In the prosaccade task they were required to look to the stimulus when it appeared. Stimulus presentation was always randomized to the right or left of the fixation point. The gap or the overlap paradigm was used in different experimental blocks. The fixation point was presented for 1000 ms on gap trials and for 2200 ms on overlap trials. On overlap trials the stimulus was always presented 1200 ms after fixation point onset and remained on for 1000 ms; on gap trials stimulus onset was determined by the respective gap duration, stimulus duration was again 1000 ms. The intertrial interval was set to 1000 ms throughout. The following parameters were varied (with the other parameters as described above):

1. *Gap duration.* Gap durations of 0, 100, 150, 200, 250, 300, 400, and 600 ms and the overlap paradigm were used in separate blocks of 200 trials. Stimulus eccentricity 4°; size 0.2°).
2. *Stimulus eccentricity.* Eccentricities of 1°, 2°, 4°, 8°, and 12° on either side (left and right) were employed in separate blocks of 200 trials each. (Gap duration 200 ms, stimulus size 0.2°.) Both the anti- and the protask were used.
3. *Stimulus size.* Sizes of 0.1°, 0.2°, 0.4° were applied. Size combinations were: 0.1° left and 0.2° right, and vice versa; 0.4° left and 0.2° right, and vice versa; and 0.2° left and right (gap duration 200 ms; stimulus eccentricity 4°).

The subjects performed the blocks in a pseudorandom order.

Data analysis

For the identification of anticipatory saccades, we made use of the occurrence of direction errors in the protask (Wenban-Smith and Findlay 1991; Fischer et al. 1993a). They found that all direction errors occurred with SRTs below about 80 ms. This value was therefore taken as the upper reaction time limit for the presence of anticipatory saccades and as the lower limit for visually guided saccades. Calculations of mean SRTs and the mean amplitudes included the latency range between 80 and 400 ms. The histograms were constructed using a bin-width of 5 ms.

Statistical tests

Mean SRT values were compared using Student's two-tailed *t*-test with a significance level of 0.01. The ANOVA was performed on the data obtained with the gap duration and with the eccentricity series.

Results

Effects of the gap duration

Antisaccade latency

The SRT distributions of correct antisaccades from selected blocks with different gap durations obtained from a single subject (S.G.) are shown in Fig. 1. With increasing gap duration from no gap (overlap) to a gap of 200 ms, the reaction times of the antisaccades decrease significantly by about 25 ms. For longer gap durations, the reaction times increase again, reaching the reference value with a gap duration of 400 ms. A further latency increase is observed for both left and right stimuli with still longer gap durations.

Error production

Figure 2 shows the distributions of the reaction times of the erratic prosaccades from the same subject. While er-

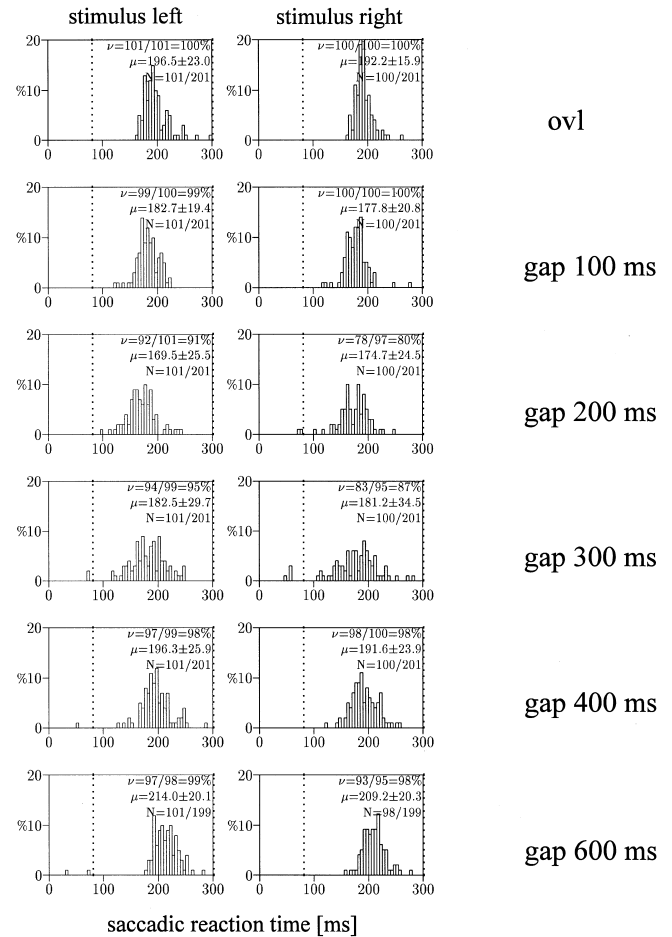


Fig. 1 Frequency distributions of saccadic reaction times (SRTs; bin-width 5 ms) of correct antisaccades from a single subject (S.G.) obtained with the overlap (*ovl*) and with five different gap durations as indicated at the *right*. Distributions obtained with left stimulus presentation (antisaccade right ward) are given at the *left*, those with right stimulus presentation (antisaccade left) at the *right* (ν number of values included in the panel/all values > 80 ms obtained with left or with right stimulus presentation, respectively; μ mean SRT and the SD of the values included in the panel; N number of values measured with left or with right stimulus presentation/the number of values measured in the respective session)

atic prosaccades are absent for overlap trials and short gap durations below 150 ms, the error rate increases abruptly, in particular with right stimulus presentation for the medium gap durations (gap 200 ms and 300 ms). The error frequency decreases again for longer gap durations. The reaction times of the errors are almost all in the range of 100 ms, i.e., the latency range of express saccades.

These systematic changes in the mean reaction times of the correct antisaccades and in the frequency of error production were observed in all subjects, but with different absolute values. One subject (J.G.) showed only a small gap effect (about 10 ms) for the mean reaction times of the antisaccades even at “optimal” gap durations. Her error rate followed the general trend quite closely (about 10% increase between overlap and gap

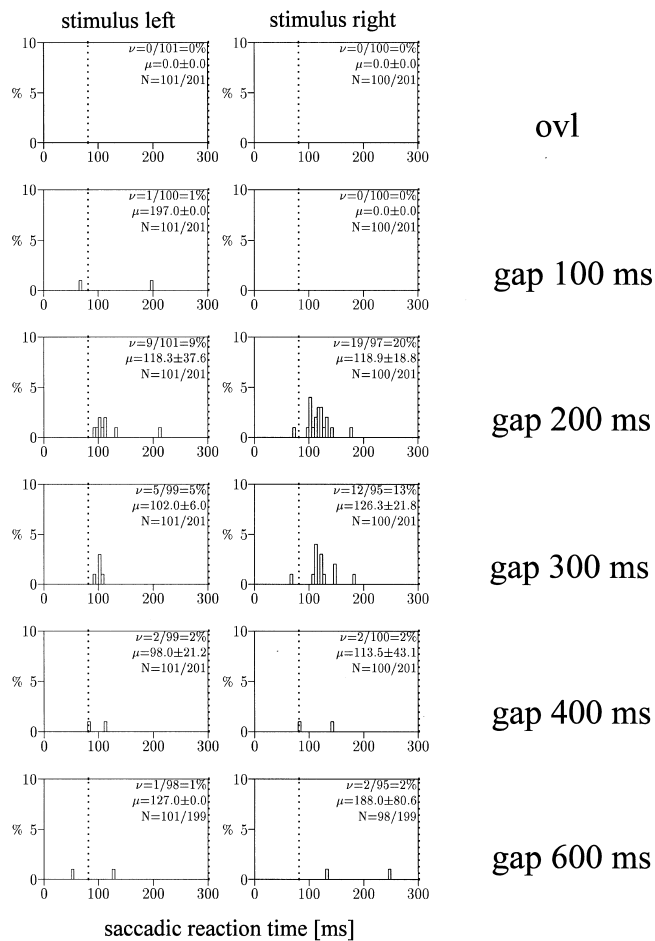


Fig. 2 Frequency distributions of saccadic reaction times (bin-width 5 ms) of erratic prosaccades from a single subject (S.G.) obtained with the overlap and with five different gap durations as indicated at the right. Data presentation as in Fig. 1

200 ms). Subject K.D. showed a clear gap effect for the reaction times of the antisaccades (about 55 ms), but she produced very low numbers of errors (below 3%) throughout; yet the reaction times of her correct antisaccades were rather short, starting in the region of 100 ms. Subject H.W. showed also a clear gap effect (about 40 ms), and her error rate increased by about 10% between overlap and gap 200 ms. The results from subject B.F. were very similar to those from subject S.G. (Figs. 1, 2). All subjects produced more errors to the right as compared to the left stimulus, and almost all the errors occurred in the latency region of 100 ms.

The gap duration curves for the mean SRTs of the correct antisaccades and the mean error rates averaged across all five subjects are shown in Fig. 3 separately for left and right stimulus presentation. The gap duration being most effective in decreasing reaction time (Fig. 3A) and increasing error rate (Fig. 3B) is in the order of 200 ms.

The statistical evaluation of the averaged data (Student's two-tailed t -test) revealed that the mean SRT values obtained with gap durations of 100, 150, 200, 250,

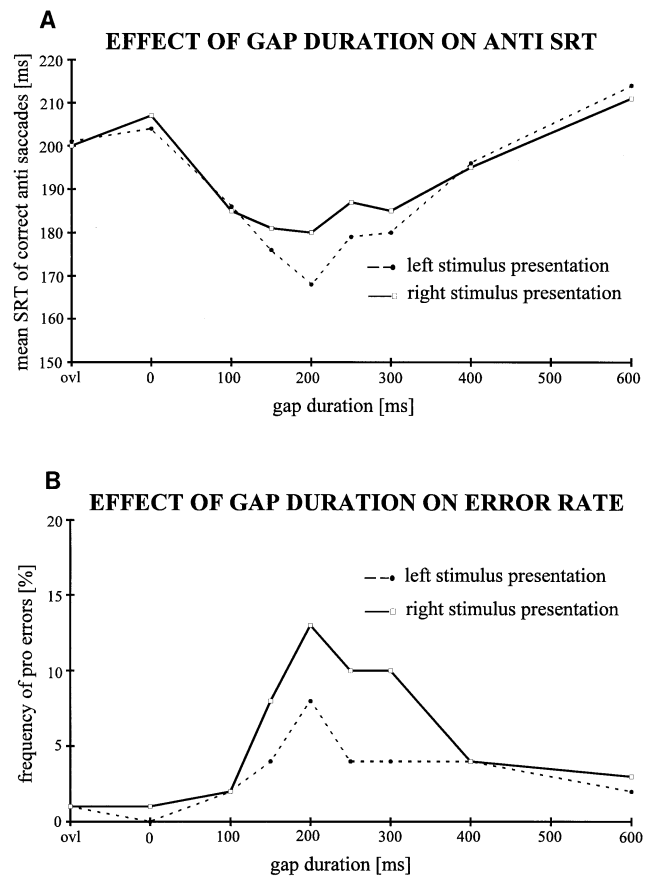


Fig. 3 **A** Mean saccadic reaction times (SRTs) (averaged over all five subjects) of the correct antisaccades as a function of the gap duration. The data obtained with left stimulus presentation (dashed line) and with right stimulus presentation (solid line) are considered separately. **B** Frequency of erratic prosaccades in percent (averaged over all five subjects) as a function of the gap duration. Again data obtained with left stimulus presentation (dashed line) and with right stimulus presentation (solid line) are considered separately. Note the pronounced asymmetry in the error production: more errors occur with right stimulus presentation

and 300 ms were all significantly different from the overlap value ($P < 0.01$ for both left and right). The mean SRT values obtained with the gap 0 ms and the overlap value were statistically similar for left stimulus presentation ($P = 0.1$), but different (slower!) for right stimulus presentation ($P < 0.01$). The mean SRT values from the gap 400 ms and the overlap value were statistically similar ($P = 0.01$ for both left and right). The mean SRT value from the gap 600 ms was again significantly different from the overlap value ($P < 0.01$ for both left and right), with longer latencies in the gap condition.

The ANOVA was performed on the SRT data for each subject separately and revealed significance values below 0.01% in each case, with F -values varying between 15.99 (for J.G.) and 63.3 (for H.W.). The ANOVA for the group means of the SRTs was significant for both sides of stimulation ($P = 0.014$; $F(7;32) = 3.04$ for the left stimulus and $P = 0.016$; $F(7;32) = 2.98$ for the right

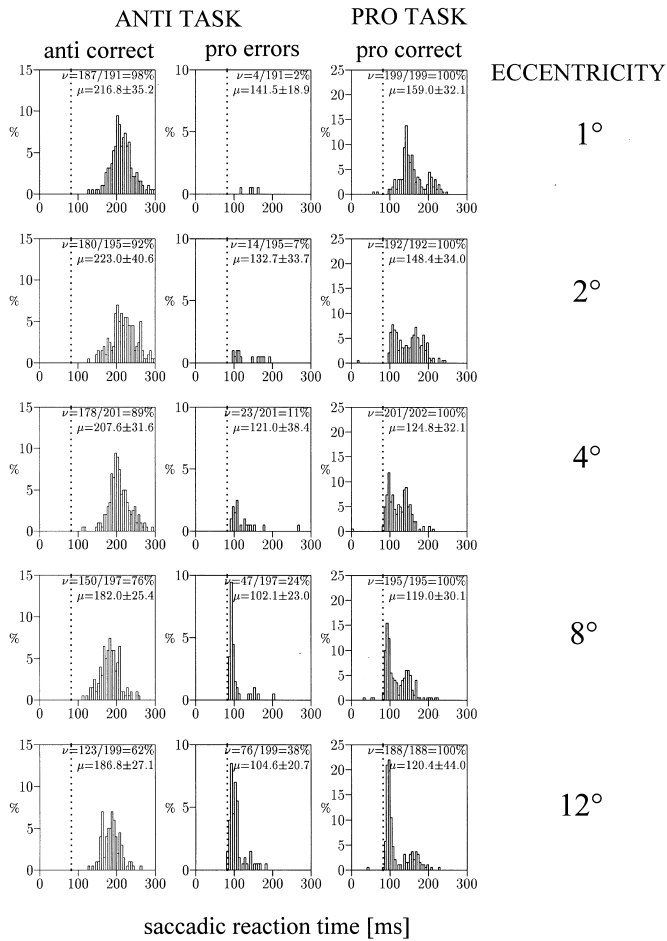


Fig. 4 Frequency distributions of saccadic reaction times (bin-width 5 ms) from a single subject (J.G.) obtained with five different stimulus eccentricities as indicated at the right. Distributions obtained in the antisaccade task (correct antisaccades and erratic prosaccades) are given in the left two columns, those obtained in the prosaccade task in the right column. Saccades obtained with left and right stimulus presentation are pooled, because the subject showed no clear asymmetries (ν number of values included in the panel/all values > 80 ms; μ mean SRT and SD of the values included in the panel)

stimulus). The ANOVA of the error rate gave significant variations for the right stimulus ($P = .012$; $F(7;32) = 3.17$) but was insignificant for the left stimulus ($P = 0.27$; $F(7;32) = 1.32$). This latter result was due to one subject, who showed no significant variations of the error rate only to the left side. The analysis of the saccade size revealed a mean value of $4.4 \pm 1.6^\circ$ for the correct antisaccades and $3.0^\circ \pm 1.0^\circ$ for the proerrors (averaged over all gap durations and subjects).

Effects of the stimulus size

While the size of both the left and the right stimulus was set to 0.2° in the control block, the size of one of the stimuli, either the left (in one block) or the right (in an-

other block), was changed in the test blocks. All subjects therefore had to perform five blocks of 200 trials each.

For left stimulus presentation, there was a tendency for producing shorter antisaccade latencies with the larger (0.4°) than with the smaller (0.1°) stimulus ($P < 0.001$). The latency variation obtained in the three cases with the same stimulus size (0.2°) is, however, in the same range, and the latency difference between the largest and the smallest mean SRT value measured with this stimulus size is also significantly different ($P < 0.001$). For right stimulus presentation, there is no effect at all of the stimulus size on the antisaccade latencies ($P = 0.1$). Again, the subjects generally produced more errors to the right stimulus. In no case did the size of the stimulus reverse this asymmetry. The variation in the error rates within subjects ranged from 2% (K.D.) to 14% (B.F.). The variations observed with the same stimulus size in the same subject were always larger than the differences of the mean values for the different stimulus sizes. The reaction time of the errors were largely in the range of express saccades and generally shorter than 150 ms.

Effects of stimulus eccentricity

The stimulus for the antisaccade was presented at different eccentricities along the horizontal meridian in different blocks using the gap paradigm. In each block the location was randomized symmetrically between left and right. All subjects performed the same blocks again with the prosaccade gap task for sake of comparison with the latencies of the erratic prosaccades obtained from the antisaccade gap task.

The data from a single subject (J.G.) are shown in Fig. 4. This subject had essentially symmetric reaction times for left- and right-directed saccades, and therefore we pooled the data obtained with the two stimulus directions. The left and the middle column depict the SRT data from the antisaccade task: in the left panels, the SRTs of the correct antisaccades; in the middle panels, those of the erratic prosaccades are shown. The SRT distributions of the correct prosaccades from the blocks from the prosaccade task are presented in the panels of the right column. A clear decrease in the mean latencies (30 ms) of the correct antisaccades is seen with increasing stimulus eccentricity. In parallel, the frequency of erratic prosaccades increases from 2 to 38%. The majority of the proerrors, in particular those obtained with the largest stimulus eccentricities, is in the range of express saccades. A similar picture is observed for the correct prosaccades in the prosaccade task: almost no express saccades are seen with the 1° stimulus eccentricity, while their number increases successively with increasing stimulus eccentricity. Note the close similarity of the SRT distributions of the proerrors from the antisaccade task and the correct prosaccades from the prosaccade task with the 12° eccentricity. Note also the consistent bimodality of the pro-SRT distributions.

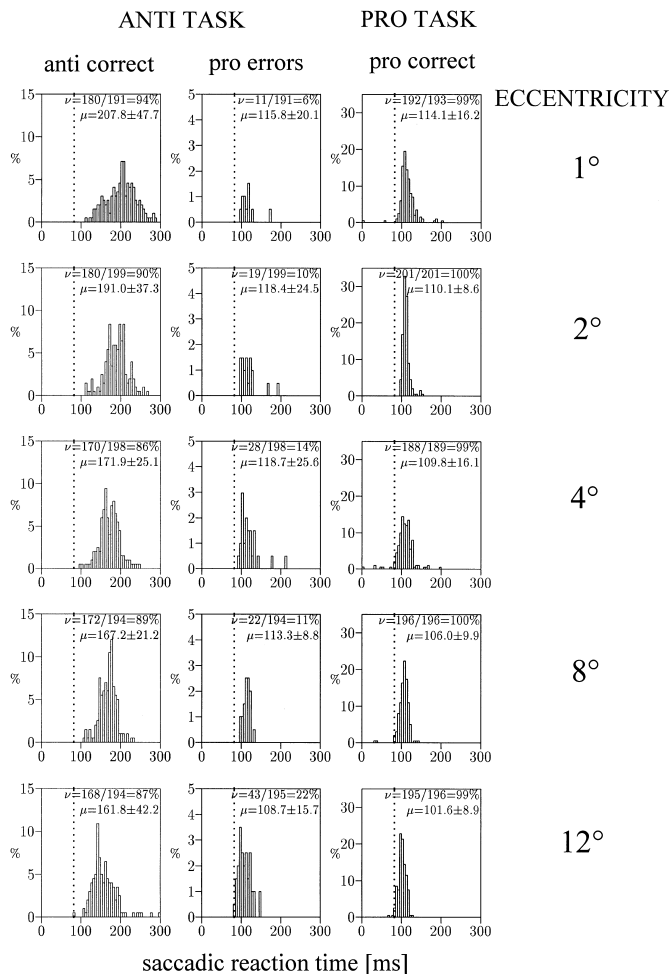


Fig. 5 Frequency distributions of saccadic reaction times (bin-width 5 ms) from a single subject (S.G.) obtained with five different stimulus eccentricities as indicated at the *right*. Data presentation as in Fig. 4

Figure 5 shows the data of another subject (S.G.), who produced almost exclusively express saccades with the correct prosaccades (right column). As for J.G. the SRTs of the correct antisaccades decrease continuously with increasing stimulus eccentricity by 46 ms. At the same time the frequency of the proerrors increases from 6 to 22% and their latency decreases. A corresponding latency decrease (12 ms) with increasing stimulus eccentricity is seen for the correct prosaccades in the prosaccade task.

The ANOVA was performed on the SRT data for each subject. High significance levels (values below 0.01%) were obtained in all cases, with F -values varying between 6.7 and 84.8. When the ANOVA was applied to the reaction time and error rate group mean values, significance at the 5% level was achieved only for the SRT values of the left prosaccade gap task ($F(4;20) = 3.3$; $P = 0.03$). This means that the interindividual variations of the five subjects was larger than the eccentricity effect.

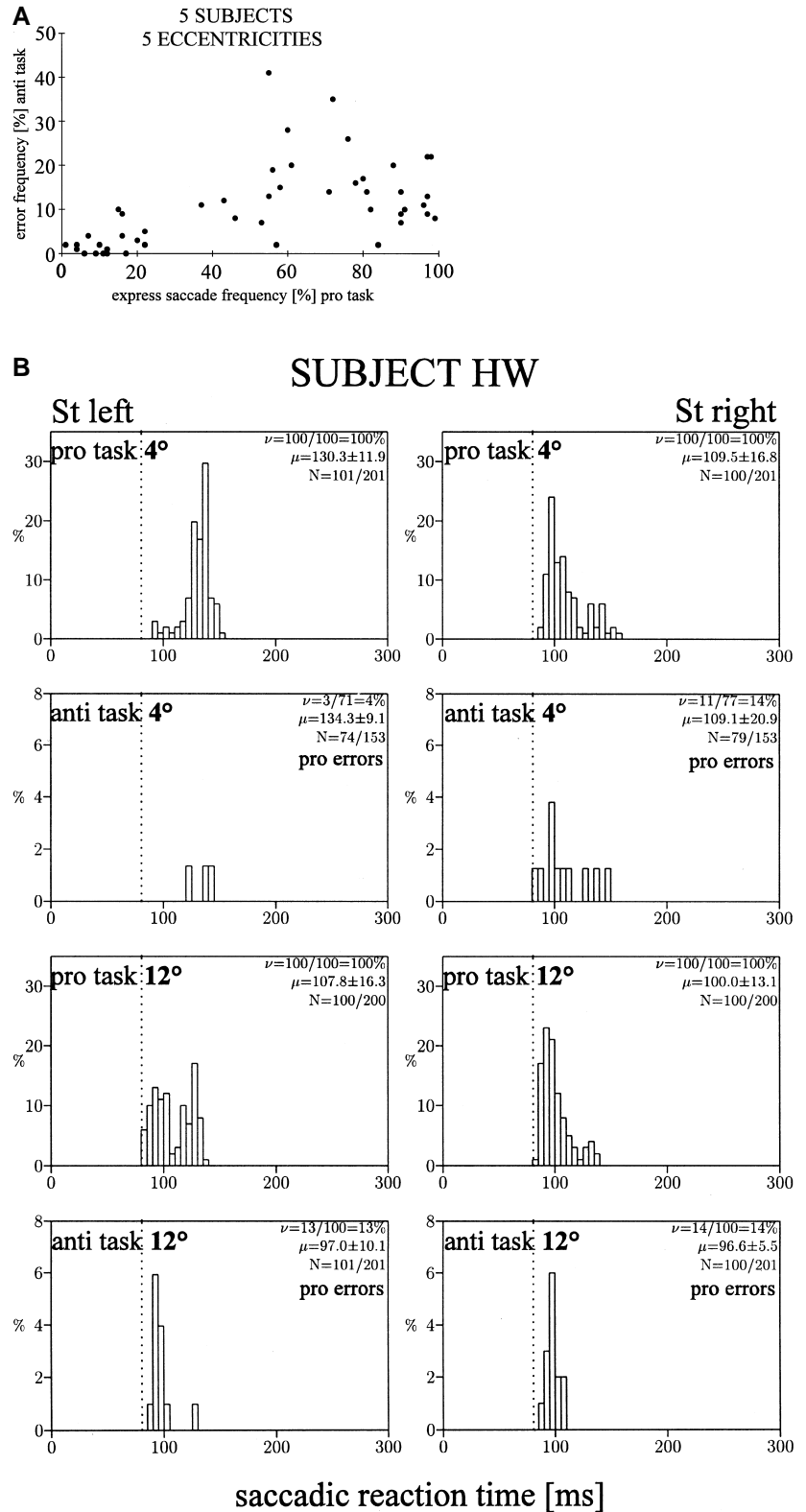
To see whether the subjects made their antisaccades in accordance with the instructions, we analyzed their mean size as a function of the stimulus eccentricity and compared it with the corresponding mean values determined from the prosaccade task. The result was a high correlation (better than 0.9). For small eccentricities, the antisaccades were relatively large (2.5° vs 1.0°), while for large eccentricities they were relatively small (10.2° vs 10.9°). The size of the erratic prosaccades was also correlated with the stimulus eccentricity, but considerably smaller errors were made with the stimulus at larger eccentricities. For eccentricities of 1, 2, 4, 8, and 12° , the mean amplitude values were 1.6, 2.1, 2.8, 5.0, and 6.9° , respectively.

The frequency of proerrors in the antitask and of express saccades in the protask

In all blocks using the antisaccade task, all subjects produced a certain number of erratic prosaccades. This number varied interindividually and depended on the exact conditions of the antisaccade task. In this section we analyze whether the error rates in the antisaccade tasks correlate with the respective frequencies of express saccades in the corresponding prosaccade tasks, because both constitute the same oculomotor actions, with the only difference that the former are executed involuntarily as unwanted reflexes, while the latter are classified as voluntary movements. For this analysis we used the data from the series with different stimulus eccentricities. The express saccade frequency was determined by calculating the percentage of saccades within the limits of 75 ms and 130 ms.

Figure 6A shows a scatter plot of the percentage of errors compared with the percentage of express saccades. High numbers of errors used to occur along with high numbers of express saccades. But high numbers of express saccades may occur along with small error rates. This tendency can be seen not only when comparing different subjects, but particularly also in single subjects producing very different numbers of express saccades to the right and left in one situation and similar numbers in another situation. Figure 6B depicts the data from subject H.W., who, when, tested with the stimuli at 4° , made almost no express saccades (7%) to the left, but 81% to the right target in the prosaccade task. With the target at 12° , H.W. produced 55% express saccades to the left and 90% to the right in the prosaccade task. When looking at the errors from the corresponding antisaccade tasks, HW produced only 4% errors to the left 4° stimulus, but 14% to the right 4° stimulus. This asymmetry disappeared at 12° , where the error rate is 13% to the left and 14% to the right. This tendency was also seen in the other subjects. In each case the side that received fewer express saccades in the prosaccade tasks was also the side to which fewer errors were made in the antisaccade task.

Fig. 6 **A** Scatter plot of the percentage number of errors in antisaccade tasks versus the percentage number of express saccades in prosaccade tasks. Data points originate from all subjects, all stimulus eccentricities, and left and right stimulus presentation. **B** Frequency distributions of saccadic reaction times (bin-width 5 ms) from a single subject (H.W.). The *upper quadruplet of panels* show data obtained with 4° stimulus eccentricity, the *lower quadruplet*, data with 12° eccentricity. The distributions of correct prosaccades from the prosaccade task are given above those of erratic prosaccades from the corresponding antisaccade task (*pro errors*). Distributions obtained with left stimulus presentation are given at the *left*, those with right stimulus presentation at the *right*. Data presentation as in Fig. 1



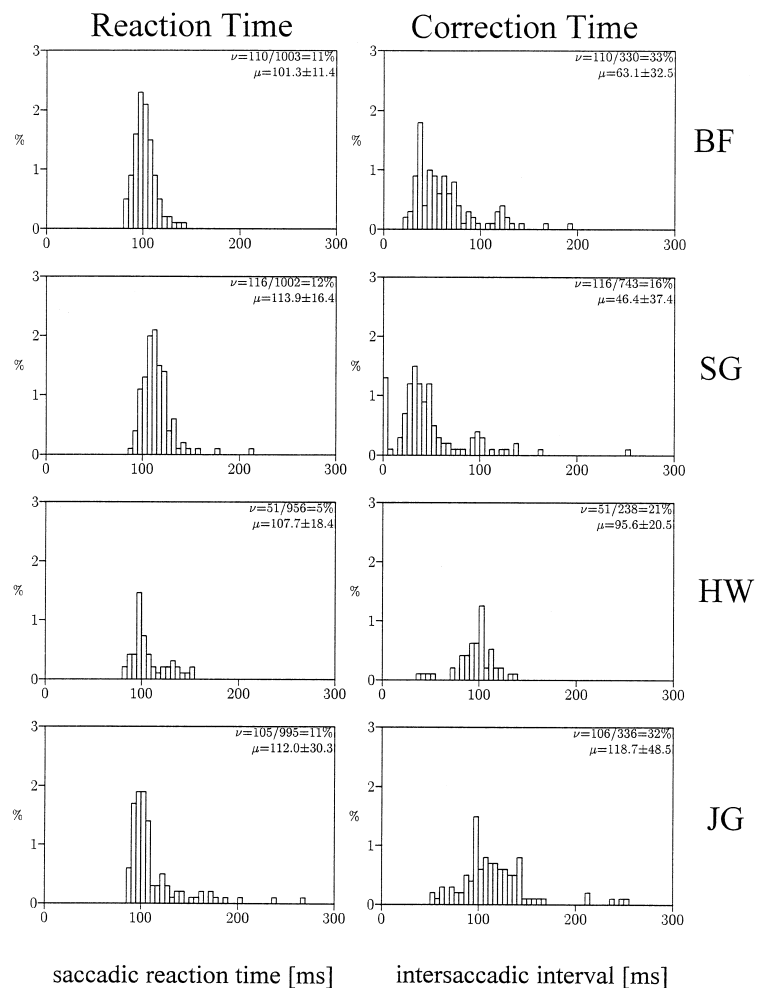
Error correction

In all cases of erratic prosaccades, these were followed by a corrective saccade to the opposite side. This section considers the correction time by calculating the time

from the end of the first (erratic) saccade to the beginning of the second (corrective) saccade.

Figure 7 shows the SRT distributions of the errors (left panels) and of the correction times (right panels) from four subjects. The data from subject K.D. are not

Fig. 7 Frequency distributions of saccadic reaction times (*left*) and of correction times (*right*) of direction errors from four subjects. For each subject the data from the sessions with different stimulus sizes and with right and left stimulus presentation have been pooled. In the *left column*: ν the number of values included in the panel/the number of values included in the pooled file; mean SRT and SD of the values included in the panel. In the *right column*: ν number of values included in the panel/the number of values where a corrective saccade has occurred; μ mean SRT and SD of the values included in the panel



shown, because K.D. produced very low numbers of errors to either side. Since the error rate was generally too low to obtain reasonable numbers of errors from an individual subject in a single block of 200 trials, we collapsed the data with right and left stimulus presentation from the sessions with different stimulus sizes for each subject. This was justified, since we observed almost no effects of the stimulus size on antisaccade latency or error rate for the size ranges tested.

First, one sees that in all subjects the reaction times of the errors are mostly in the range of express saccades. Subject J.G. produced some errors with longer latencies ranging up to 200 ms. Subjects B.F. and S.G. corrected their errors very fast, with almost all correction times below 150 ms (peak below 50 ms). Subject S.G. even produced some corrections with no time interval, which means that the erratic prosaccade was turned around without any delay. Subject H.W. corrected the errors after about 100 ms, subject J.G. after 100–150 ms (peak at 100 ms). It looks as if these subjects produced another saccade at express time measured from the end of the erratic primary express saccade.

Discussion

The present study has shown that the reaction times of the correct antisaccades and the frequency of erratic prosaccades to the stimulus depend on the gap duration and slightly also on the stimulus eccentricity, while the stimulus size yielded only modest or no effects. The maximum size of the gap effects depend on the subject and on the side of stimulation.

The existence of a gap effect for the latencies of antisaccades has been reported earlier (Reuter-Lorenz et al. 1991; Fischer and Weber 1992; Reuter-Lorenz et al. 1995). (In our studies the latencies of the antisaccades are shorter than in other studies. Why this occurs remains an open question and might have to do with the exact experimental conditions, the way the stimuli are generated, and how the latencies are determined. Effects on the latency are, however, described mostly in terms of differences of mean values between test and control conditions, thereby cancelling general shifts in reaction time). The latency reduction in the antisaccade task was interpreted as an effect of a general warning due to fixation offset and, in part, as a consequence of fixation re-

lease by Reuter-Lorenz and coworkers (1995). The warning hypothesis might indeed explain part of the latency reduction, but it is difficult to see how it could possibly explain the increase in error rate. If one uses cue stimuli indicating correctly the side to which the antisaccade has to be made (cue lead time 100 ms), the warning effect of fixation offset should be supported by the valid cue resulting in minimal reaction times and minimal error rates. Instead, both reaction times and error rates are increased (Fischer and Weber 1996). Therefore, one has to look for an alternative hypothesis, which should account not only for the gap effect in antisaccades but also for that in prosaccades.

For prosaccades the gap effect consists not only of a decrease in the mean saccadic latencies but also of an increase in express saccades, manifest as a separate peak in the latency distribution (Mayfrank et al. 1986; Fischer and Weber 1993). Increasing the gap duration above a certain value of about 200 ms up to 800 ms yielded a subsequent latency increase and a loss of express saccades. These results were confirmed for human subjects (Weber et al. 1995) and (Weber and Fischer 1995) and by Dorris and Munoz (1995) for the monkey, who proposed a neural correlate for the gap effect: they found that the firing rate of the fixation neurons in the rostral pole of the superior colliculus (SC) decreased with increasing gap durations up to 200 ms or 300 ms, while increasing again with longer gap durations. This and other findings from the fixation cells (Munoz and Wurtz 1993a, b) imply a function of the SC in the generation not only of reflexive (pro-) saccades (Schiller et al. 1987) but also of voluntary saccades, because, without an intact fixation system, reflex-like saccades are facilitated and proerrors in the antisaccade task become more frequent. It should, however, also be kept in mind that the collicular mechanism is under cortical control primarily from the frontal eye field (Segraves and Goldberg 1987; Dias and Bruce 1994; Dias et al. 1995).

Since clinical studies in neurological patients (Guitton et al. 1985) and neurophysiological investigations in monkeys (Schlag-Rey et al. 1993) have shown that the frontal eye field is intimately involved in the performance of antisaccades, it may be argued that the neural mechanisms for fixation engagement and disengagement play a role in the generation of antisaccades as well.

There are other details indicating a common mechanism in the generation of both types of saccades. The SRT distributions of the errors resemble the SRT pattern obtained for prosaccades in a gap prosaccade task (Fischer and Weber 1992). This finding was clearly confirmed in our present experimental series with different stimulus eccentricities, using the same eccentricities for the pro- and the antisaccade task. For the prosaccades only low numbers of express saccades were obtained, with very small stimulus eccentricities of less than 2°, corresponding to the dead zone for express saccades (Weber et al. 1992). The dead zone for express saccades has been explained by the fact that the stimulus falls in the region of the collicular fixation zone (Biscaldi et al.

1996) – which is thought to have an extension of 2° (Munoz and Wurtz 1992) – thereby activating the fixation cells and leading to a delay of the subsequent saccade. Recently it was suggested that the collicular fixation zone extends up to 10° (Gandhi and Keller 1995).

By definition, the erratic prosaccades occurring in the antisaccade task are involuntary, reflex-like saccades. Practically all of them were followed by a corrective saccade. These corrections had remarkably short intersaccadic intervals of 100 ms and below. This result is unexpected, because most of the proerrors brought the stimulus close to the fovea into the dead zone for express saccades (Weber et al. 1992). In an earlier investigation of secondary saccades obtained in a gap paradigm (Fischer et al. 1993b), we found express corrective saccades only after saccades that missed the target stimulus by far, while those that brought the target close to the fovea were followed by corrective saccades with longer intersaccadic intervals (more than 150 ms). The paradigm used in the previous study was a prosaccade task, so that the stimulus was the target for the saccade, while in the present study it was *not*. Thus the common finding in both studies is that erratic saccades in the sense of the task – such as anticipations or direction errors – can be corrected much faster than saccades that correspond to the instruction.

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