

RESEARCH ARTICLE

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Reaction times of vertical prosaccades and antisaccades in gap and overlap tasks

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Abstract Horizontal saccadic reaction times (SRTs) have been extensively studied over the past 3 decades, concentrating on such topics as the gap effect, express saccades, training effects, and the role of fixation and attention. This study investigates some of these topics with regard to vertical saccades. The reaction times of vertical saccades of 13 subjects were measured using the gap and the overlap paradigms in the prosaccade task (saccade to the stimulus) and the antisaccade task (saccade in the direction opposite to the stimulus). In the gap paradigm, the initial fixation point (FP) was extinguished 200 ms before stimulus onset, while, in the overlap paradigm, the FP remained on during stimulus presentation. With the prosaccade overlap task, it was found that most subjects (10/13) – whether they were previously trained making horizontal saccades or naive – had significantly faster upward saccades compared with their downward saccades. One subject was faster in the downward direction and two were symmetrical. The introduction of the gap reduced the reaction times of the prosaccades, and express saccades were obtained in some naive and most trained subjects. This gap effect was larger for saccades made to the downward target. The strength of the up-down asymmetry was more pronounced in the overlap as compared to the gap paradigm. With the antisaccade task, up-down asymmetries were much reduced. Express antisaccades were absent even with the gap paradigm, but reaction times were reduced as compared to the antisaccade overlap paradigm. There was a slight tendency for a larger gap effect of downward saccades. All subjects produced a certain number of erratic prosaccades in the antitasks, more with the gap than with the overlap

paradigm. There was a significantly larger gap effect for the erratic prosaccades made to the downward, as compared to the upward, target, due to increased downward SRTs in the overlap paradigm. Three subjects trained in both the horizontal and the vertical direction showed faster SRTs and more express saccades in the horizontal directions as compared to the vertical. It is concluded that different parts of the visual field are differently organized with both directional and nondirectional components in saccade preparation.

Key words Vertical saccades · Antisaccade · Reaction time · Express saccades · Fixation

Introduction

For the past three decades, saccadic reaction times (SRTs) have been studied and used as a tool to better understand the generation of saccades, visual functions, and cognitive processes. During this time, most studies have concentrated on horizontal saccades, focussing on such topics as the gap effect, express saccades (ES), training effects, and the role of fixation and attention. This study will investigate some of these topics with regard to vertical saccades.

Saslow found in 1967 that SRTs could be reduced by introducing a temporal gap with no stimuli (optimally 200 ms) between the disappearance of an initial fixation point (FP) and the appearance of a new peripheral saccade target, known as the *gap effect*. This effect has been proposed to be the result of a modulation of saccade generation by fixation and attentional systems (Dorris and Munoz 1995). The finding of the gap effect has inspired further related studies, many with the common goal of extending our understanding of the saccadic and fixation system (Munoz and Wurtz 1993a, b; Guitton and Volle 1987; Biscaldi et al. 1996). An overview is given by Fischer and Weber (1993). Using the *gap paradigm* (200 ms between FP offset and stimulus onset; Fig. 1), ES were discovered in monkeys (Fischer and

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Boch 1983) and later in humans (Fischer and Ramsperger 1984). ES is the term used for saccades with latencies between 60 and 100 ms (in the monkey) and 80 and 135 ms (in humans). Often, these saccades occur as a separate peak in the distribution of the reaction times. Although these ES can be generated by completely naive subjects and may occur even with the overlap paradigm (Fischer et al. 1993), daily *training* with the gap paradigm usually increases the number of ES in both humans (Fischer and Ramsperger 1986) and monkeys (Fischer et al. 1984).

Although not fully understood, studies of horizontal SRT have found that humans often show SRT *directional asymmetry* (i.e., faster in a particular direction). Differences in the strength and/or time-course of the saccade-generating processes within the left and right hemisphere have been discussed as reasons for these asymmetries (Weber and Fischer 1995). They found that, in the gap paradigm, many subjects show a strong tendency to saccade faster to rightward appearing targets, although there are also subjects with a bias to the left. This asymmetry can be affected by the gap period. The asymmetry can also be strongly influenced by attentional factors, because attending to a permanent stimulus at one location reduces the frequency of ES to targets presented at that location (Weber and Fischer 1995). In an *overlap paradigm* (Fig. 1), where the FP remains on during stimulus presentation, the latency asymmetry is often reduced or absent.

The antisaccade task (Fig. 1) has also become a popular paradigm in eye movement research. This task requires subjects to suppress a "natural" saccade to the visual stimulus and look in the opposite direction (Hallett 1978). It has been proposed that the ability to plan and execute antisaccades is controlled by the frontal cortex (Guitton et al. 1985; Guitton and Volle 1987) so that a large number of erratic prosaccades in this antisaccade task (i.e., saccades mistakenly made to the stimulus) may potentially indicate mental deficits or disease such as schizophrenia (Sereno and Holzman 1995) or Alzheimer's disease (Currie et al. 1991). While correct antisaccades are usually not of the express type, normal subjects also produce a certain number of erratic prosaccades in the gap antisaccade task; these involuntary saccades are often but not always of the express type (Fischer and Weber 1992). Asymmetry is commonly observed with these erratic prosaccades; their numbers are usually higher to the right side than to the left side, but some subjects show the opposite bias. The SRTs of horizontal antisaccades are also often asymmetric and, as for the prosaccades, faster SRTs are usually observed with saccade direction to the right side (stimulus left). Again, the effect seems to be more pronounced in the gap task (H. Weber, unpublished work).

Interpretation of these results from horizontal saccades often relies on presumed differences in the underlying neural structures because of their bilateral organization at cortical and subcortical levels. Yet the gross anatomy does not support this notion, as there are virtu-

ally no differences between the representations of the right and left visual hemifields, nor between the corresponding oculomotor output structures in the brain stem.

Such a bilateral organization is not present along the vertical meridian of the upper and lower field. Yet small differences in reaction time, optokinetic nystagmus, and visual acuity for stimuli presented in the upper compared with the lower fields have been reported (Heywood and Churcher 1980; Honda and Findlay 1992; Human and Sharpe 1993; Berardi and Fiorentini 1991), which may be explained by gross anatomy, as reviewed by Previc (1990). More recently, large asymmetries in the vertical direction have been reported for the monkey with a strong bias for faster reaction times of upward saccades (Schlykova et al. 1996). There are differences in the representation of the upper and lower visual field in the prestriate cortex. Area V3 is located in the dorsal extrastriate cortex and contains a representation of only the inferior contralateral quadrant, while area VP, in the ventral extrastriate cortex, contains a representation of only the superior contralateral quadrant (Burkhalter et al. 1986). Burkhalter and colleagues have found that there are some asymmetric projections to these structures from striate cortex, area V1. They suggest that, in the monkey, there is a basic asymmetry in the way visual information is processed in the upper compared with the lower visual field and that there may be asymmetries in the proportion of cortex devoted to the upper and lower fields.

The gap and overlap task have been extensively studied for horizontal saccades and a number of asymmetries have been found in SRT, percentage ES, and erratic proerrors in the antisaccade task. Although the generation of vertical prosaccades in the gap and overlap tasks has been studied (Honda and Findlay 1992), much less is known, and almost nothing is known about the generation of vertical ES and antisaccades. In the present study, we wanted to see whether subjects would produce different numbers of ES for upward or downward targets in the gap protask, and whether such asymmetries would also exist using the antisaccade task. The results indicate that vertical ES can be obtained and that a gap effect exists, which can be different in strength for up and down directions. Vertical asymmetries are the rule for prosaccades but not for antisaccades. It is concluded that two functional subsystems contribute to saccade generation: one with a directional selectivity and the other without.

Materials and methods

Subjects

Thirteen subjects participated in this study. Seven subjects (between the age of 19 and 26 years) were completely naive with respect to the purpose of the study and had never served as subjects in eye movement experiments before. Six subjects (between the age of 24 and 53 years), referred to as horizontally trained (HT), were previously trained for horizontal saccades in the gap and overlap task until they reached stable reaction time distributions

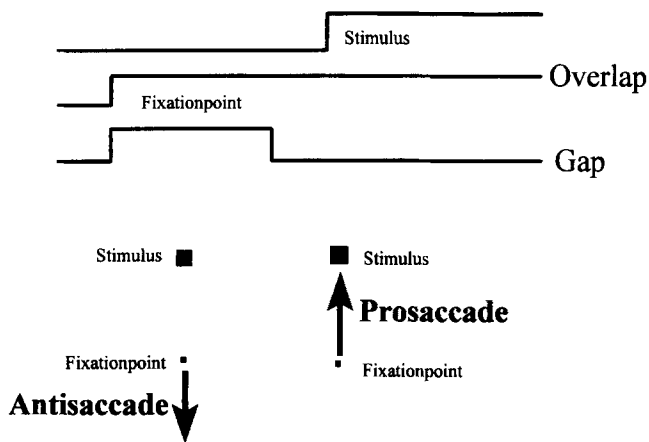


Fig. 1 Temporal and spatial arrangements of the saccade paradigms. Gap and overlap trials are depicted *above*, pro- and antisaccade tasks are shown *below*. In the gap task, the fixation point (FP) was extinguished for 200 ms before the onset of the stimulus, while in the overlap task, the fixation point remained on during the stimulus presentation. Subjects were instructed to look to the target (protask), or away from the target (antitask). The stimulus appeared randomly at 4° above or below the FP

(Fischer and Ramsperger 1986). One of the naive subjects qualified as an ES maker (Biscaldi et al. 1996) for saccades in the upward, leftward, and rightward direction and will be treated separately.

Stimulus presentation

The visual stimuli, consisting of a central red fixation point (Fp; 0.1°×0.1°) and white target stimuli (St, 0.2°×0.2°) on a 20°×15° green background, were generated by a personal computer and presented on an RGB color monitor using a high-resolution graphic interface (micrograph 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 (stimuli generated at 4° in the upper field occurred 8 ms earlier than stimuli generated 4° in the lower field). The luminance of all stimuli was well above perceptual threshold (65 cd/m²). Viewing distance was 57 cm from the subjects' eyes. While performing the tasks, the subject's head was stabilized by a chin rest.

The tasks

The gap and the overlap paradigms were used. The temporal sequence of events is shown in the upper part of Fig. 1. The Fp was presented for 1000 ms on gap trials and for 2000 ms on overlap trials. The stimulus was presented for 800 ms, 1200 ms after Fp onset. The intertrial interval was set at 1000 ms. A gap duration of 200 ms was used throughout. Two instructions were given to the subjects. In the *prosaccade task* (protask), subjects were instructed to look to the stimulus when it was presented and, in the *antisaccade task* (antitask), they were instructed to make a saccade in the direction opposite to the stimulus. The stimuli were randomly presented at 4° above or below the Fp. In the control horizontal tasks, the stimuli were presented randomly at 4° to the right or left of the fixation point. Twelve subjects performed the pro- and antitasks. In a later set of experiments, 9 subjects also performed a *no-target saccade task* consisting of two blocks. In one block, subjects were instructed to make upward saccades (about 4° in amplitude) upon Fp offset and, in another block, to make only downward saccades. No stimulus was present and thus the saccades were voluntary (not reflexive).

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°. SRTs were detected on-line by velocity threshold detection and presented as a histogram.

SRTs of all saccades within 700 ms from target onset were determined again off-line on the basis of the analog-digital (A-D)-converted eye position signal stored on disc. The reaction time was defined by the time when the velocity signal exceeded 15% of its maximum within the saccade under consideration. Calculations of all mean SRTs used latencies between 80 and 400 ms in both the pro- and antitask. The SRT distributions were constructed and smoothed using a Gaussian kernel of 5 ms width.

Calibration

Before the start of each experimental session, the subjects had to fixate a small fixation stimulus, which could be moved manually using the mouse. Both the stimulus and the eye position were superimposed on the computer screen. The stimulus was moved up and down from the center of the screen and the subjects were instructed to track it. The gain was set at 0.3 V/deg such that it would fit linearly with the respective position of the fixation stimulus on the screen. After off-line analysis of the data, we multiplied all amplitude and velocity values by a factor to achieve a mean value corresponding to the respective target position. This factor, depending on the quality of the on-line calibration, usually had values between 0.98 and 1.02. This procedure was applied only for prosaccades.

Data analysis and statistical tests

For the identification of anticipatory saccades, we made use of the occurrence of direction errors in the protask. In agreement with earlier investigations (Wenban-Smith and Findlay 1991; Fischer et al. 1993) we found that direction errors occurred with SRTs below about 80 ms. This value was thus taken as the upper time limit for the presence of anticipatory saccades, and as the lower limit for visually guided saccades.

Mean SRT values were compared using Student's two-tailed *t*-test. The Kolmogorov-Smirnov test was used with a significance level of 0.01 to determine whether SRT distributions could be considered as statistically similar.

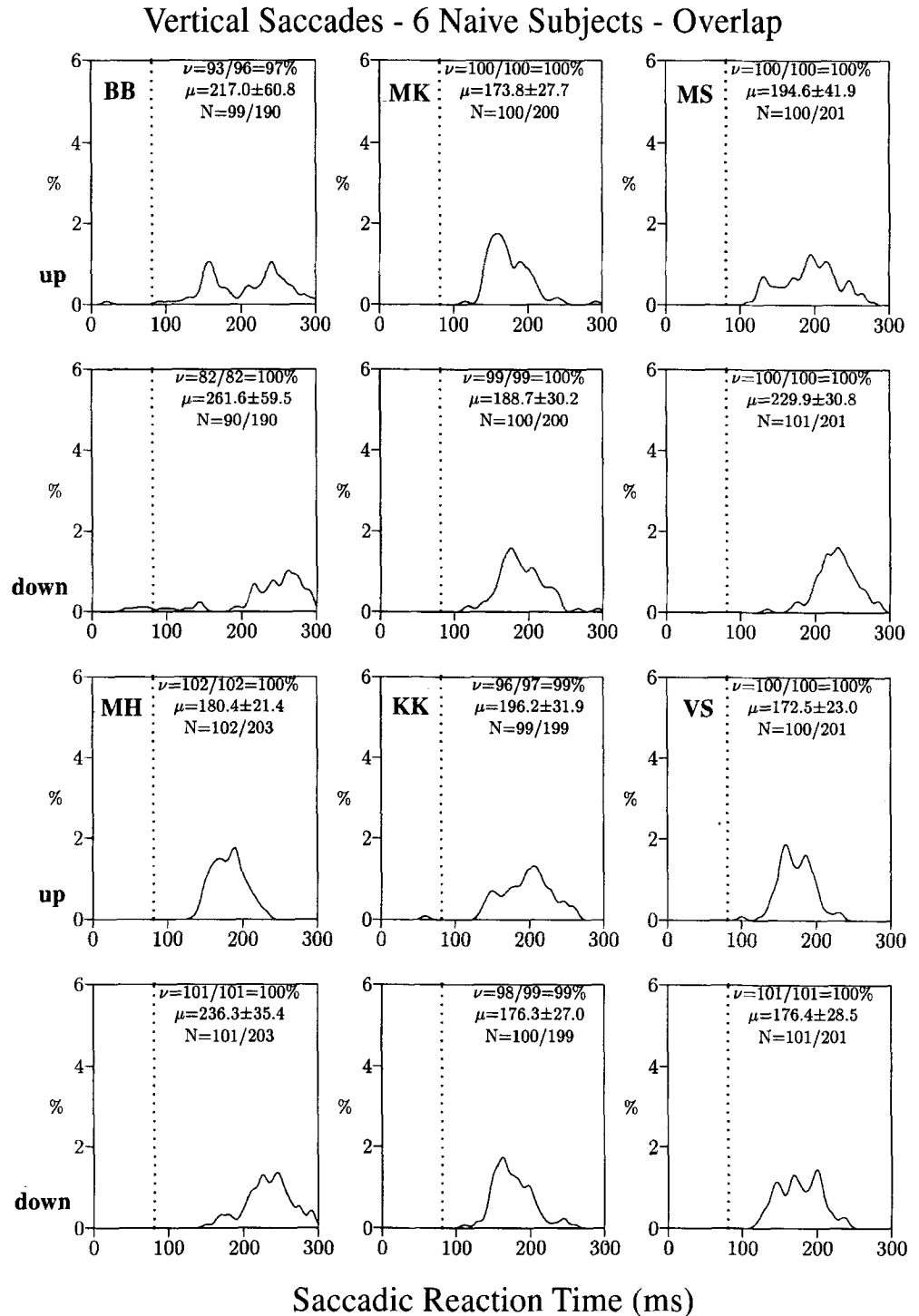
Results

Prosaccades

Overlap versus gap

Naive subjects. The upward and downward SRTs for the 6 naive subjects in the overlap task are displayed in the 12 panels of Fig. 2. The SRT distributions are broadly scattered and somewhat complex, some showing unimodality and some bi- or trimodality. There is virtually no indication of ES (SRT 80–135 ms) or anticipations (SRT <80 ms). All mean SRTs are above 170 ms, reaching as high as 260 ms. Some subjects are dramatically asymmetric with respect to their SRTs to the upward or downward target. As can be seen from Fig. 2, subjects B.B., M.H., M.K., and M.S. show greatly reduced SRTs to the upward target, while K.K. appears faster to the downward target. All these differences were statistically significant at the 1% level. Subject V.S. shows virtually no difference in the up and down mean SRTs.

Fig. 2 The saccadic reaction time (SRT) distributions obtained from six naive subjects as identified by the two letters in each pair of boxes. Data from the overlap prosaccade task are shown. Saccades to the upward or downward stimulus are depicted in the boxes labeled up or down. The vertical broken line indicates the 80-ms cut-off for anticipatory reactions. Each box contains the mean SRT (μ), and the percentage of saccades used for calculation (ν). N indicates the number of trials taken over the total number of trials

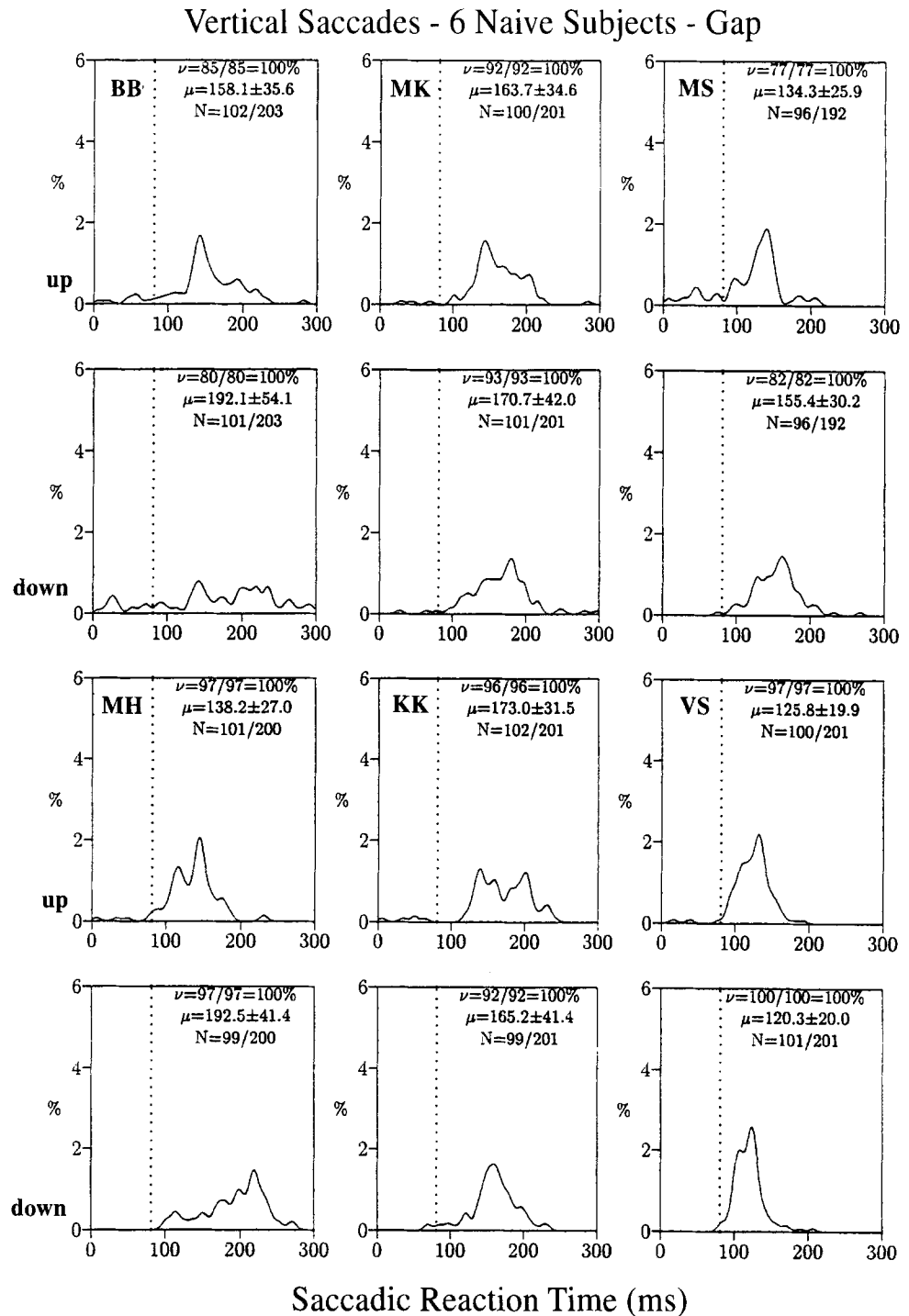


All subjects had reduced SRTs in the gap task (see Fig. 3) as compared to the overlap results. The distributions are not all unimodal. In the gap task, there were significantly more anticipations in all subjects and indication for express saccades can be seen, especially in M.H., (up saccades) and V.S. (down saccades). Smaller numbers of express saccades are present in subjects M.H. (down), M.K. (down), and M.S. (up and down). All five subjects who were asymmetric in the overlap task

showed the same kind of asymmetry in the gap task, but M.K. and K.K. failed to reach significance.

HT subjects. The SRT distributions for the 6 HT subjects in the overlap task are displayed in Fig. 4. The SRT distributions are complex with slightly less scatter as compared to the naive subject data. The mean standard deviation of the SRT mean values was 6.2 ms smaller for the trained subjects. The SRT distributions show signs of

Fig. 3 Same format as Fig. 2. Data from the gap prosaccade task are shown from the six naive subjects



both unimodality and bimodality. There is only indication of ES in one subject (N.D.) for upward saccades and very little indication of anticipations. All subjects showed significant directional asymmetry, with shorter SRTs to the upward target, except S.G., who was symmetrical.

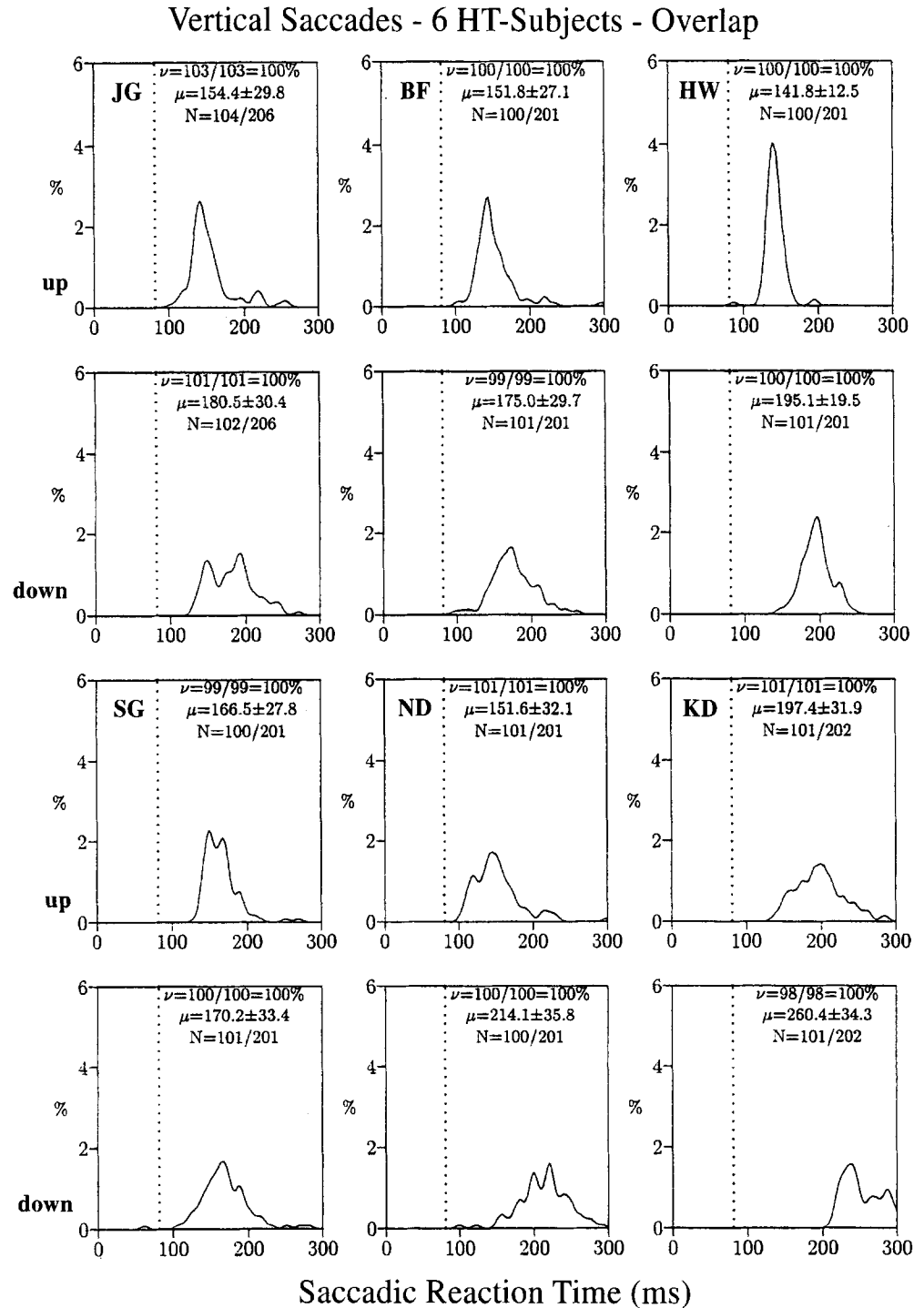
All HT subjects had reduced SRTs in the gap task (Fig. 5), and the distributions are generally bimodal, with the exception of S.G. and H.W. (“up”) who were unimodal. ES are seen in all subjects, at least in one direction, except K.D. Directional asymmetry was significant in

five of the six subjects. As with the naive overlap results, four subjects (B.F., N.D., K.D., H.W.) had significantly reduced SRTs to the upward saccades, one subject (S.G.) was significantly faster during down and saccades, and one subject (J.G.) was symmetrical.

The gap effect

The gap effect is defined as the reduction of the mean SRT in the gap task (with a gap of 200 ms) as compared

Fig. 4 Same format as Fig. 2. Data from the overlap pro-saccade task are shown as obtained from six subjects who have been trained for horizontal saccades in the gap task (HT subjects)

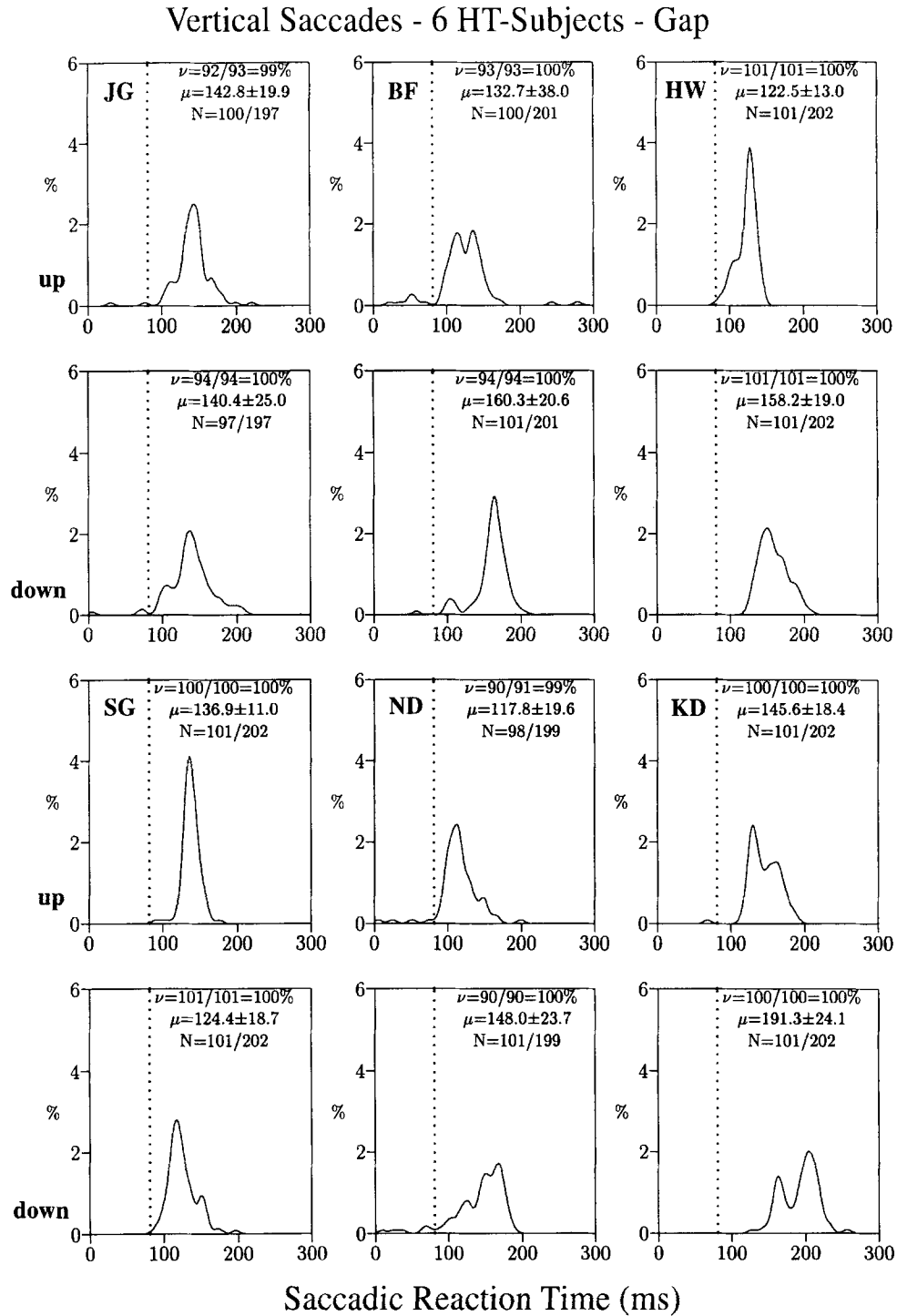


to the overlap task. We calculated these mean values to give an idea of the strength of the gap effect, despite the fact that these numbers are not very meaningful in the cases of clear bimodality. The gap effect in the protask is visually displayed in the top panel of Fig. 6A, plotting mean gap SRT against mean overlap SRT. Data for the 12 subjects, both naive and HT subjects, are plotted (for the upward and downward target). There was very little difference between the naive and trained subjects with respect to the gap effect, so that the data points could be

combined in the scatter plots. As one can see, the gap SRTs are all reduced as compared to the overlap (i.e., data points lying above the 45° line), and there is a clear, positive correlation between the two sets of latencies. The difference between the mean gap and overlap SRTs was 39.7 ms, a significant difference. Ten subjects showed a larger gap effect for downward saccades, as compared to upward; the other two did not reach significance.

The top panel of Fig. 6B displays the mean SRT of downward versus upward saccades. Gap and overlap data

Fig. 5 Same format as Fig. 2. Data from the gap prosaccade task are shown from six HT subjects



have been combined. From the plot, one can see that there was a general tendency for subjects to saccade faster to the upward target in the protask (most data points lie below the 45° line). When comparing the mean upward and downward SRTs for all 12 subjects, upward saccades were significantly faster by 24.7 ms. One can also see a positive correlation between the downward and upward SRTs.

Antisaccades

Overlap versus gap

Naive and HT subjects. The SRT plots for the naive subjects are displayed in Fig. 7 from the overlap antitask and in Fig. 8 from the gap antitask. All subjects were slower in the antitasks as compared to the corresponding protasks (except subjects M.H. and M.S. with the downward stimulus). The SRT distributions range between

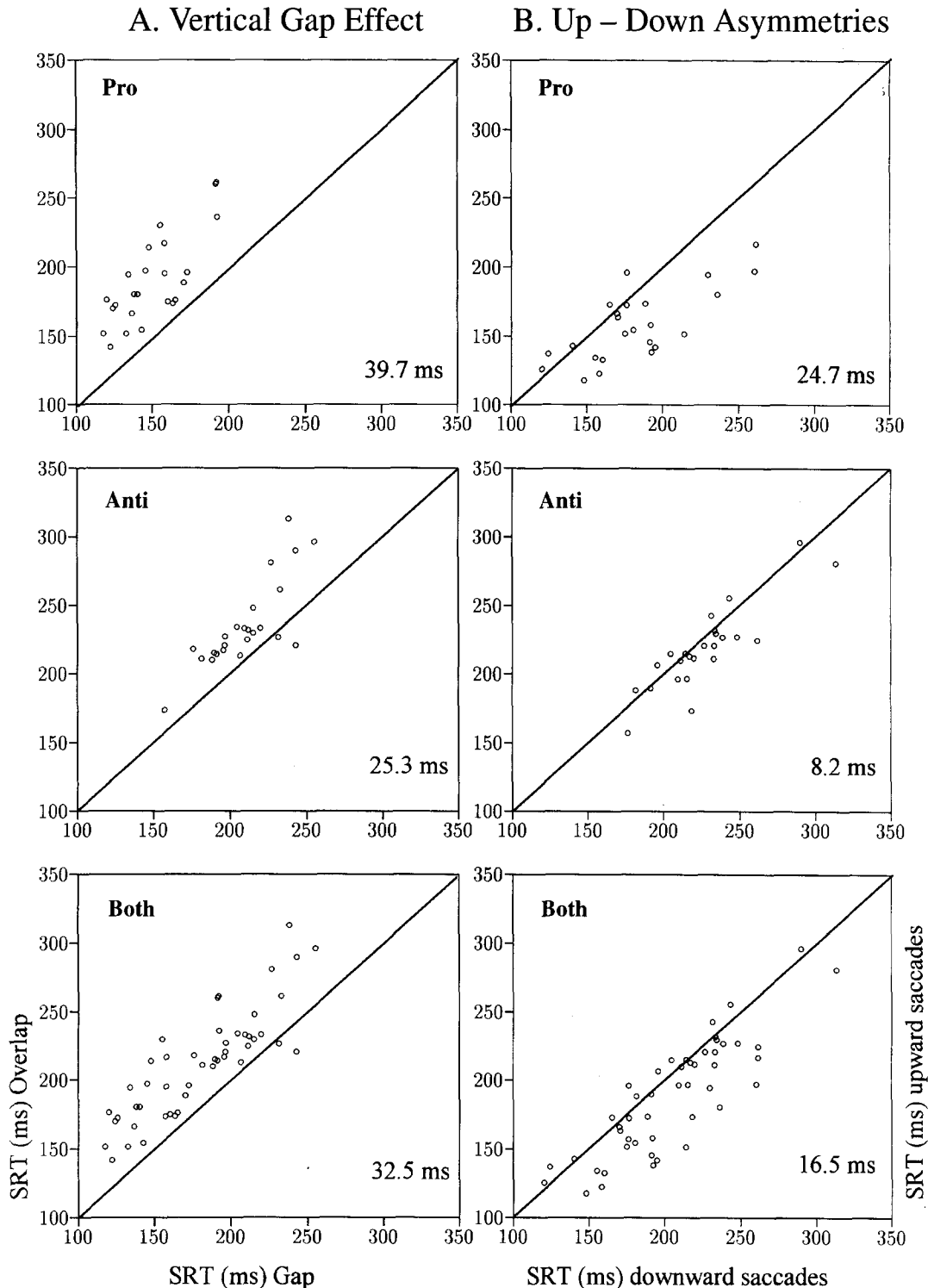
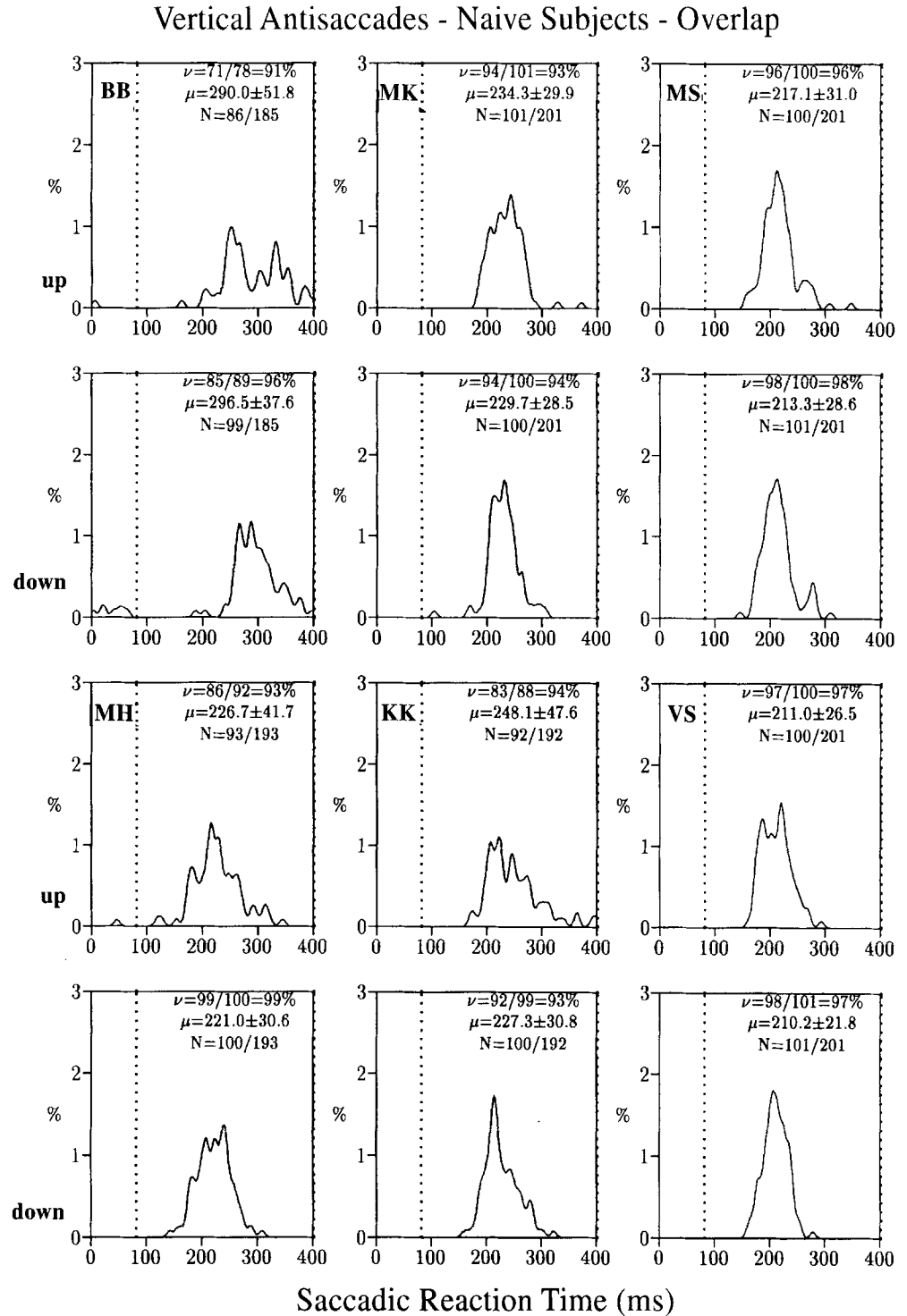


Fig. 6 **A** For each direction (up and down) and each subject (six naive and six HT subjects) the mean SRT from overlap trials is plotted against that from gap trials. The deviation of the data points from the continuous 45° line indicates the strength of the gap effect. Data from the prosaccade and antisaccade tasks are shown separately, with the mean value of the differences in milliseconds given in each box. The pooled data are shown in the *bottom* box. **B** For each paradigm (overlap and gap) and each subject, the mean SRT from the upward saccades is plotted against that from the downward saccades. The deviation of the data points from the continuous 45° line indicates the up-down asymmetry of the SRTs (i.e., data for faster upward saccades falls *below* the line). The mean values of the differences are given in each box

about 170 and 320 ms in the overlap data and between about 150 and 240 ms in the gap data.

When the data from the six HT subjects were analyzed, a two-sided *t*-test indicated that there was no statistical difference between the naive and HT data. Therefore, the data of the HT subjects are not shown here. Note that both subject groups were untrained in the vertical direction. The respective group means for the overlap SRTs of naive and HT were 235.43 ± 29 ms and 235.16 ± 35.9 ms. In the gap task, the corresponding numbers are 214.86 ± 23.7 ms

Fig. 7 Same format as Fig. 2. Data from the overlap antisaccade task are shown from the six naive subjects



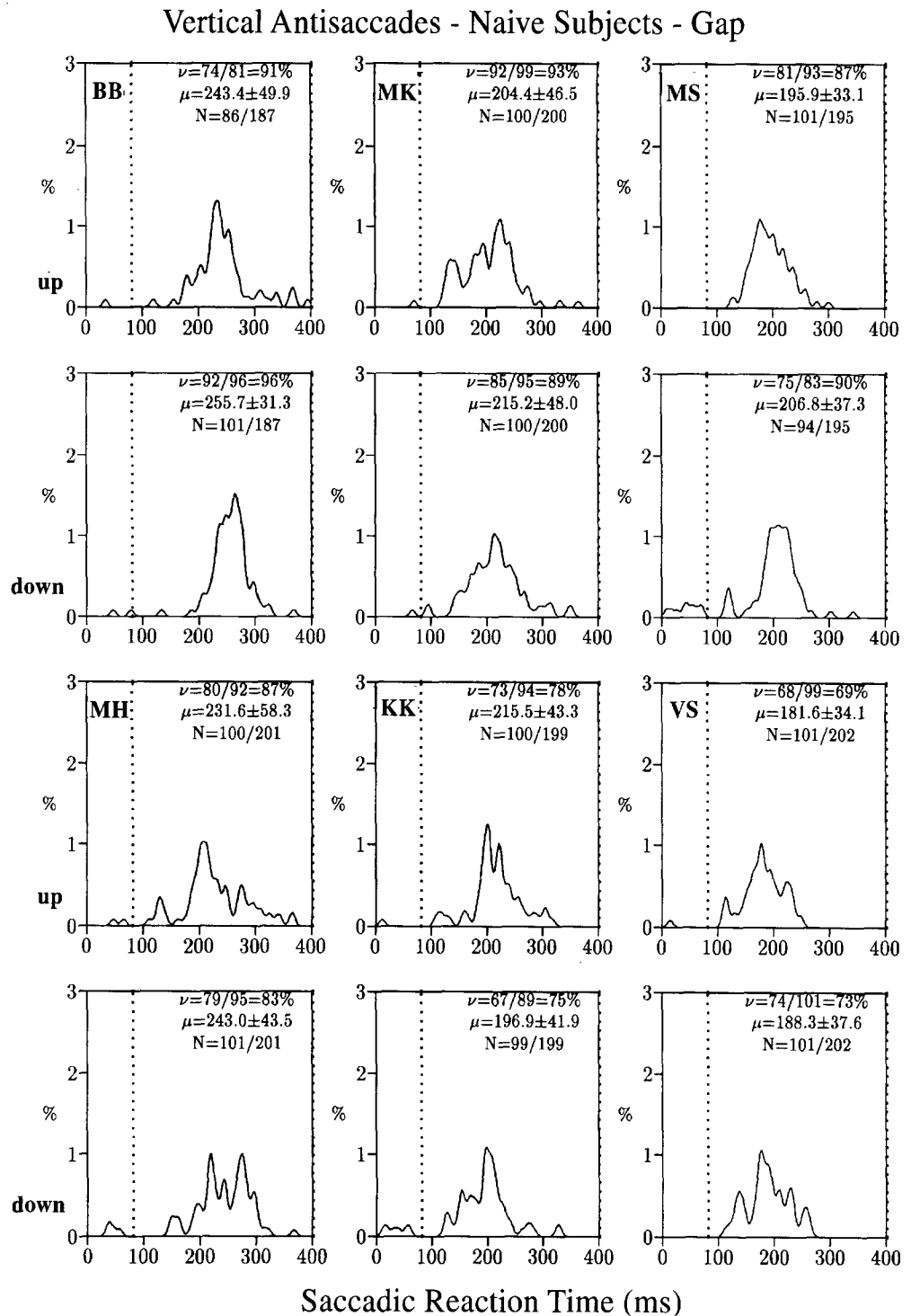
and 205.21 ± 24 ms. In the overlap and gap task, nine subjects showed no significant asymmetry, while three subjects (K.K., B.F., and K.D.) were significantly faster making upwards saccades (i.e., downward stimulus).

Percentages of erratic proerrors

Proerrors in the antitask are defined as reflexive saccades made erroneously to the stimulus. The mean percentage

of errors made in the overlap antitask by the naive and HT subjects were 4.9% and 8.4%, respectively, while in the gap task they were 15.8% and 18.1%. The differences between naive and HT error rates were not significant. After combining naive and HT error data, a comparison was also made between the percentage of errors made to the up or downward target. In the overlap task, 5.2% errors were made to the downward stimulus and 9.0% errors to the upward stimulus. In the gap task, the

Fig. 8 Same format as Fig. 2. Data from the antisaccade gap trials are shown from the six naive subjects



number of errors increased to 16.1% (down) and 17.8% (up). The differences between “up” and “down” were not significant.

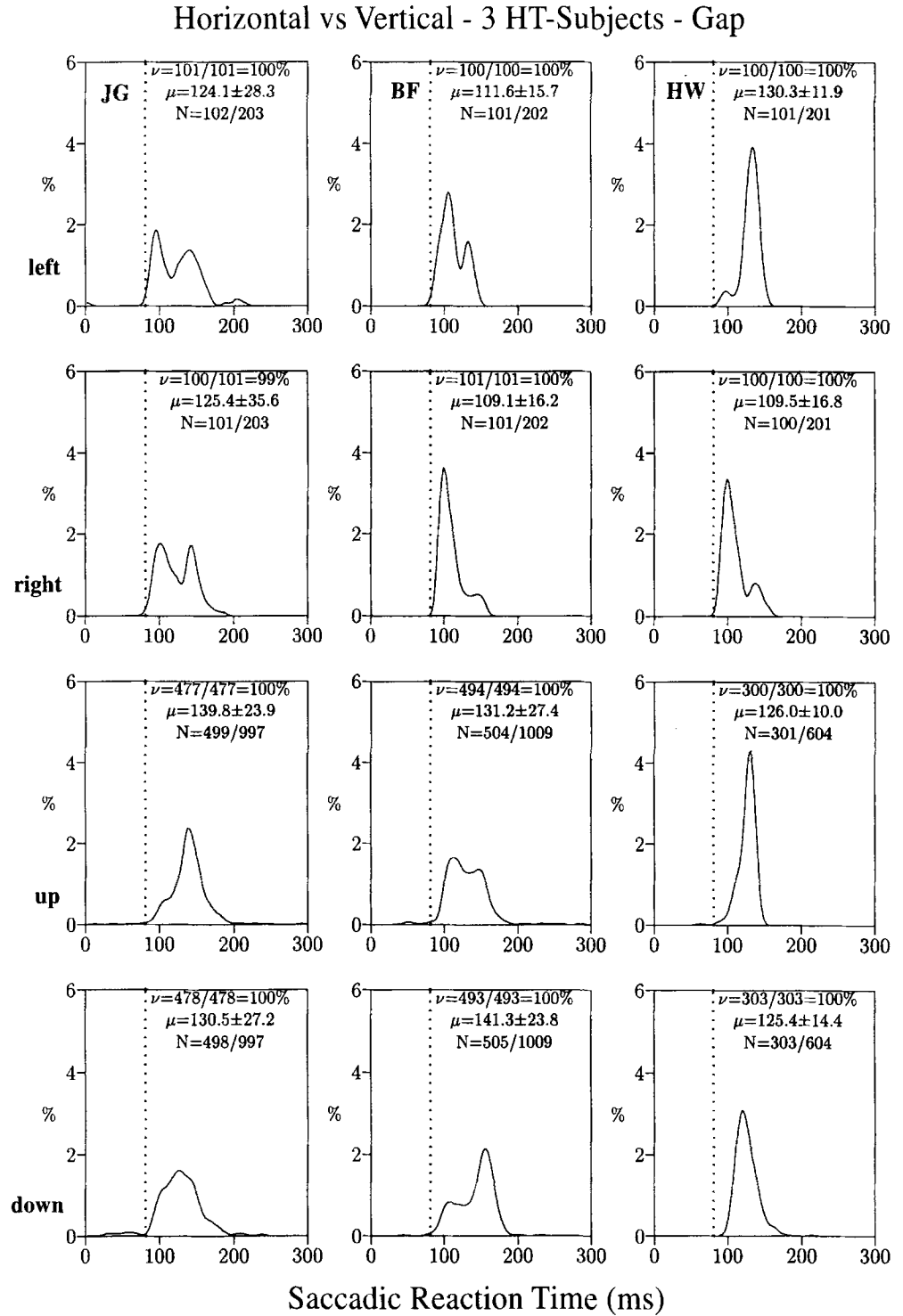
To investigate the hypothesis that subjects with fast anti-SRT make more proerrors, we plotted the mean SRT in the gap and overlap antitasks against the percentage of errors. There was, however, no correlation between anti-SRT and error rate. The SRT of the proerrors made by individual subjects was not further investigated, as the number of errors made by many subjects was too small

to calculate an accurate mean. The SRT distributions of the errors using the data files across subjects show clear peaks below 150 ms for both the up and down gap trials. The mean values will be considered below.

The gap effect

The antitask gap compared with overlap mean SRTs are displayed in the middle degrees panel of Fig. 6A.

Fig. 9 Horizontal (*upper part*) and vertical (*lower part*) SRTs from three horizontally and vertically trained subjects in the progap task. SRTs for the left, right, up, and down target are shown separately as indicated by the labels

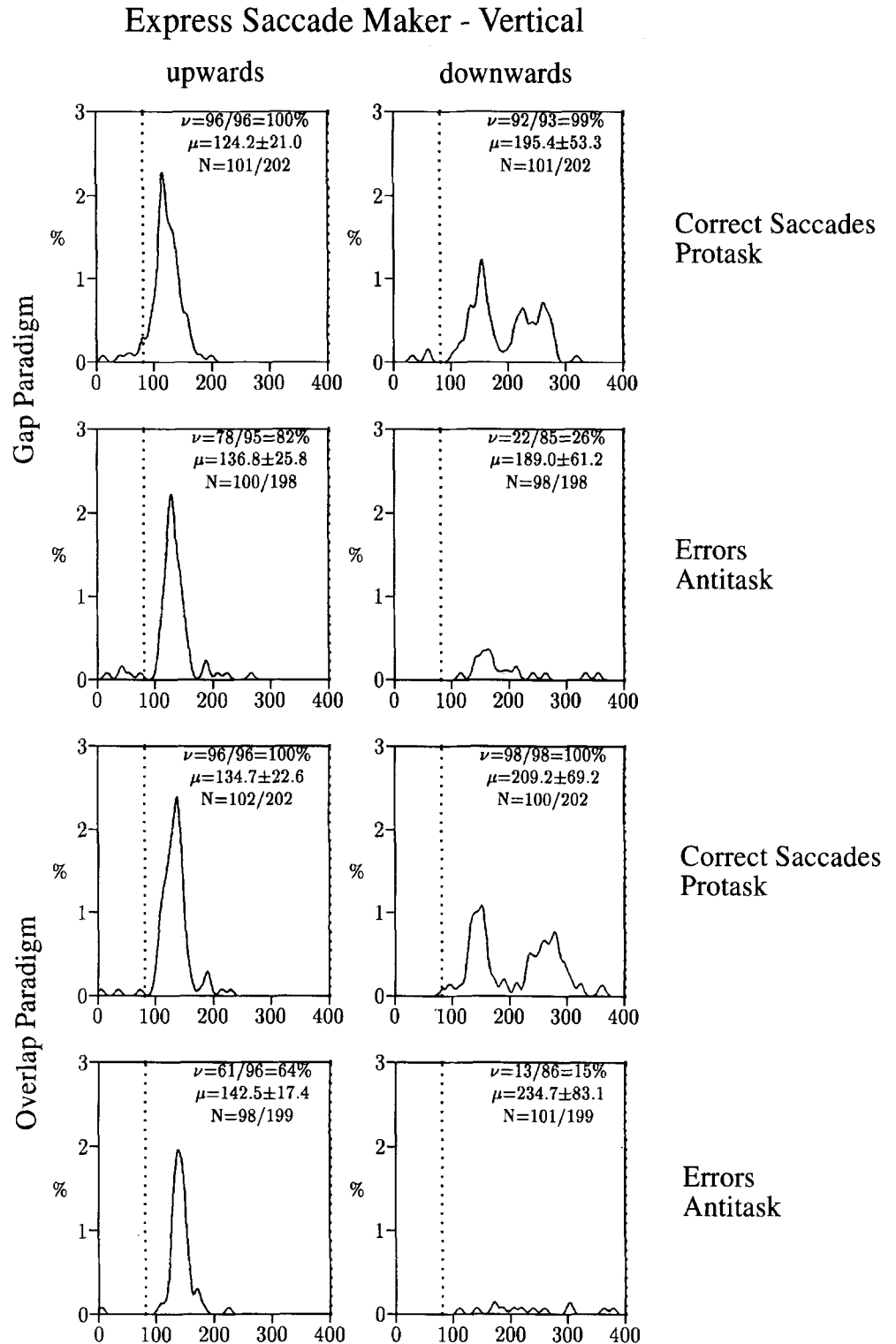


Again, the gap SRTs are shorter, with all data points lying above the 45° line, with the exception of M.H. (up and down data points), who did not show a gap effect. There is a clear positive correlation between the two sets of latencies. When comparing the group SRT means of the gap and overlap task, there was a significant difference of 25.3 ms. The gap effect was thus slightly stronger for pro- than antisaccades. The pro and antitask data are combined in the bottom panel of Fig. 6A to show the

general tendency for faster SRTs in the gap task, as well as the positive correlation between gap and overlap SRTs.

The gap effect obtained with the antisaccade task was pronounced when looking at the SRTs of proerrors to the downward stimulus (i.e., SRT difference of erratic downward saccades in the overlap compared with gap tasks). Since many subjects produced only a few errors, especially in the overlap antitask, we first collapsed the

Fig. 10 SRT distributions obtained from a subject who qualified as an express saccade maker for vertical upward saccades (*left panels*). Gap and overlap data are hardly different, with most SRTs falling within the express range. The subject produced also 82% (64%) erratic prosaccades to the upper stimulus in the gap (overlap) antitask, falling again in the express range. Downward saccades (*right panels*) are drastically different from upward saccades, showing bimodality for the correct prosaccades and fewer errors in the antitasks. In the protask, there was no significant gap effect for the downward saccades and only a small gap effect for the upward saccades. This subject was later found to be also an express saccade maker for rightward and leftward saccades



data from all subjects. In the gap trials the mean values of the proerror reaction times were 141.8 ms and 138.8 ms for the upward and downward targets, respectively. In the overlap trials the corresponding values were 162.8 ms and 198.0 ms. Thus, the gap effect was 21.0 ms for the erratic prosaccades to the upward stimulus and 59.2 ms for the downward stimulus. In a second

step we calculated the size of the gap effect for each subject separately. Only 6 of the 12 subjects produced more than 4% errors in all four conditions. The mean value of their gap effects was 22.7 ms for the upward errors and 78.7 ms for the downward errors. When all subjects were considered, these mean values were 21.1 ms and 68.9 ms, respectively.

In the middle panel of Fig. 6B, the downward versus upward SRTs are plotted for the antitask. One can see that, as with the protask results, there is a trend for shorter SRTs with upward saccades (target down), although this effect was much less pronounced (8.2 ms in antitask; 24.7 ms in protask) and did not reach significance. The data points tend to fall more on the 45° line. Again, a very strong positive correlation is seen for up and down SRTs. Pro- and antitask data are combined in the lower panel of Fig. 6B.

No-target saccades

The antitask and the no-target saccade task are similar in that the saccade must be made to a location without the target stimulus. The latter was used to measure latencies of upward and downward saccades without stimulating peripheral locations of the visual field. This no-target task thus enabled us to test the hypothesis that the observed asymmetries may depend slightly more on saccade direction than stimulus location. Nine subjects performed the no-stimulus task. In the previously performed gap protask, three of these subjects were faster down, four faster up, and two were symmetrical. In the no-stimulus task, all subjects had significantly similar upward and downward SRTs, with the exception of two subjects who were faster down. One of these was faster up, while the other was faster down in the previously taken gap protask. The mean SRTs of all subject (both up and down) were between 180 and 218 ms with indications for uni-, bi-, and trimodality. None of the subjects produced express saccades in the no-target task.

Comparison of vertical and horizontal saccades

Figure 9 displays the vertical and horizontal SRTs of three of the horizontally trained subjects (J.G., B.F., and H.W.) who had repeated the vertical gap protask (one session of 200 saccades per day) until stable distributions were obtained. All three subjects were generally faster in the horizontal directions. In particular, there are clearly more ES made to the left and right, as compared to up and down. The express peak to the left and right in J.G. and B.F. is greatly reduced in the vertical (both for up and down). In H.W., a very pronounced express peak can be seen at about 100 ms to the right and a small one to the left. In the vertical, her express peak appears to be displaced by about 15 ms.

Vertical ES maker

One additional naive subject (S.S.) was found incidentally among a group of students. S.S. fell under the criterion of an ES maker for upward saccades. An ES maker, as defined by Biscaldi and coworkers (1996), is a subject who makes spontaneously more than 30% ES in the

overlap task, at least in one direction. In both the gap and the overlap protasks, S.S. made almost exclusively ES when the target appeared in the upper field (see left column of panels in Fig. 10). In the gap antitask, this subject made 82% proerrors to the upward target, almost all in the express range. In the overlap antitask, the error rate to the upward target remained high at 64% and the latencies of the errors were fast, with a mean value of 142.5 ms. The reaction times to the downward target were in the "normal" ranges, with a clear bimodality of fast regular and slow regular saccades for both gap and overlap trials. Note that S.S. showed no significant gap effect when looking at the SRT of the correct downward prosaccades and only a small gap effect for the correct upward prosaccades, which was only due to a slight shift in the ES peak. There was also no significant gap effect when comparing the express peaks of the erratic upward prosaccades made in the gap and overlap antitask. S.S. was retested in the horizontal gap and overlap tasks (pro- and antitask) and was found to be an ES maker to both the right and the left direction. In the overlap protask, S.S. had mean left and right SRTs of 135.2 ms (61% ES) and 138.4 ms (46% ES), respectively. In the antigap task, S.S. made 51% proerrors to the leftward stimulus and 35% proerrors to the rightward stimulus.

Discussion

Three main findings came from this study: (1) asymmetry between upward and downward SRTs is the rule; (2) using a gap task for vertical saccades, the reaction times are reduced as compared to an overlap task. Different numbers of vertical ES were obtained depending on the subject and on saccade direction; (3) gap effects of different strengths occur with vertical pro- and antisaccades. The size of the gap effect can also be different for upward and downward saccades.

The first part of this study investigated the characteristics of vertical SRTs both in naive subjects and HT subjects. With respect to their vertical saccades, these two groups were found to be rather similar.

Asymmetries

In the prosaccade overlap task, 11 of the 13 subjects showed SRT asymmetry (i.e., faster in a particular direction). In agreement with earlier studies, most subjects (9/13) were faster making upward saccades (Honda and Findlay 1992; review, Previc 1990). As in studies of horizontal saccades, the gap task reduced these SRTs, increased the frequency of ES, and increased the number of anticipations as compared with the overlap task (for review see Fischer and Weber 1993). The SRT asymmetries observed in the overlap task were also seen in the gap task. In an antisaccade task, the reaction times were increased and the asymmetries seen in the prosaccade task were greatly reduced. A gap effect was also ob-

served in the antisaccade task, although not as large as in the protask. Despite the tendency to saccade faster upward in the protask, there were not significantly more errors in a particular direction in the antitask.

These asymmetries cannot be accounted for by physical differences in the visual display of the apparatus causing a relative attentional shift to the right or up, because: we have tested our apparatus carefully using photocells, there are subjects with the asymmetry in the opposite direction, and these differences are largely reduced in the antisaccade task. One possible explanation for the observed asymmetries in SRT is that the visual system operates differently on stimuli received by the different quadrants of the field. Differences exist between the extrastriate cortex areas V3 (dorsal) and VP (ventral), which are, respectively, restricted to the inferior and superior contralateral quadrant. It has been found that V3 and VP receive asymmetric projections from V1 as well as asymmetric callosal input (Burkhalter et al. 1986). These findings suggest that there may be an asymmetry in the way that visual information is processed in upper compared with lower parts of the visual field.

Our results from the protask raised the question as to whether the differences in the upward and downward SRT were dependent more on the stimulus location (i.e., area of visual field stimulated) or on the direction of the saccades. The antisaccade task was one way of probing this question of stimulus versus response specificity in the visuomotor system.

Funahashi et al. (1993) discuss two types of coding neurons: (1) stimulus-dependent, and (2) response-dependent, thought to be located in the neural structures involved with visual processing: frontal eye fields, posterior parietal cortex, supplementary motor cortex and neostriatum, and superior colliculus. If the SRT had relied more on the location of the stimulus, then, theoretically, the SRT asymmetries seen in the protask (i.e., faster to upward target) would have been seen in the antitask with similar strength for the respective stimulus location (often faster responding to upward target-downward saccades). If the SRTs had relied more on the saccade direction, than the opposite trend would have been observed. Neither of these extreme positions were found, thus suggesting that SRTs are mediated by a combination of these neurons. Individual difference (between subjects) may depend on the number and/or motor planning activity of the cell population. Although subjects may not have shown a significant asymmetry in the antitask, many were faster making saccades in the direction where they generated faster SRTs in the protask. The *slight* tendency for faster upward saccades in the antitask suggests that it may depend slightly more on the direction of the saccade. In a study on horizontal pro- and antisaccades (H. Weber, unpublished work), it has been found that subjects who saccade faster in a particular direction in the protask (usually to the right) tend to also saccade faster to this direction in the antitask (i.e., stimulus on opposite side).

In experiments measuring the reaction times of manual responses to targets in the upper and lower field, it has been found that reactions were slightly faster responding to the lower target (Berlucchi et al. 1989; Payne 1967). In a manual reaction task, however, one can detect the stimulus without making a saccade. This would support the hypothesis that the faster upward SRTs in our study were more the result of differences in the oculomotor systems generating upward or downward saccades and not in the visual system receiving the trigger stimulus for the eye movement. However, in the present study, when subjects were instructed to make upward and downward saccades on the command of FP offset, with no stimulus presentation, up-down differences in SRTs disappeared. We thus conclude that SRTs rely on both the stimulus location and the direction of the saccade.

Gap effect

Asymmetries were also observed in the strength of the gap effect being larger for the downward saccades in the protask and – only slightly so – in the antitask. In the antitask, the gap effect was pronounced for the SRTs of the erratic prosaccades to the downward stimulus, owing to increased SRTs in the overlap. This suggests that this gap effect asymmetry is strongest with prosaccades, regardless of whether they occur voluntarily in a protask or involuntarily in an antitask.

Studies on horizontal saccades have shown that the gap usually increases the SRT asymmetries, as compared to the overlap (Weber and Fischer 1995). Yet, in our study on vertical saccades, the overlap task actually increased the SRT asymmetries, due to the longer downward SRTs (and hence the larger gap effect). It is well known that, in the overlap conditions, the FP presentation has the effect of increasing SRTs due to the increased time needed to disengage active fixation, as compared to the gap task, where fixation disengagement is accomplished during the gap period. The fact that subjects have longer downward SRTs in the overlap task suggests that the FP may have a stronger inhibition on the lower field. If one assumes that directional differences in SRT are due to fixation engagement or disengagement, one has to postulate that the mutually inhibitory relationship between saccade cells and fixation cells is quantitatively different across the visual field.

The three HT subjects, although trained to the left and right, were still able to significantly reduce their downward SRTs after vertical training, but not in the upward direction. This implies that being fully trained in one direction does not mean that one is necessarily fully trained in all other directions. The additional fact that, even after training in all four cardinal directions, SRTs are different indicates that both direction-specific and nondirectional components may contribute to saccade preparation. The disengagement from active fixation may be a good candidate for the nondirectional component. The fixation system is bilaterally organized at the

tectal and cortical level and may, in principle, be different for right and left-directed saccades, but not for upward and downward saccades. As discussed by Dorris and Munoz (1995), the gap effect, and hence fixation disengagement, is a global effect; it occurs irrespective of the subject, previous training, or target direction. Further support for this hypothesis comes from the fact that training effects do not necessarily carry over from the gap to the overlap task (Fischer et al. 1984; Fischer and Ramsperger 1986). Attentional allocation is intimately related to saccade generation and, by definition, spatially selective, thus providing a possible origin for directional or even spatially selective components.

One of our subjects was found to be an ES maker, producing more than 30% ES in the overlap paradigm. This subject (S.S.) met the criteria for an ES maker in the left, right, and up direction, but not in the down direction. It has been proposed (Biscaldi et al. 1996) that EM makers may have a weakened fixation system, because this behavior (generating ES) is typical of monkeys after chemical deactivation of the fixation cells. The gap task typically reduces SRTs by allowing time for fixation disengagement. The fact that no significant gap effect was observed for the downward saccades, and only a small effect for the upward saccades, suggests that S.S. may indeed have difficulties engaging fixation. If a weakened fixation system was the only prerequisite for making ES, then we would have expected S.S. to make ES in all four directions. The downward SRT were, however, in the typical range, but showed no gap effect. Dorris and Munoz (1995) suggest that ES require not only a disengagement of active fixation but also a localized increase in activity of the saccade-related cells. Possible sources of this increased presaccadic activity could be the visual bursts of visuomotor cells in the superior colliculus, the gap-related discharge of buildup neurons in the intermedial superior colliculus, or cells in the frontal eye fields. In the case of the ES makers, it has been suggested that the second component may be hypersensitive visuomotor cells (Biscaldi et al. 1996). Subject S.S. thus may have both a weakened fixation system as well as hypersensitive visuomotor cells for the leftward, rightward, and upward direction.

Conclusions

The effect of the gap for vertical saccades cannot be predicted from that for horizontal saccades. As for right and left directed horizontal saccades, the gap effect can be different for upward and downward saccades. Earlier explanations of the gap effect due to fixation disengagement (Fischer and Weber 1993) and general warning (Reuter-Lorenz et al. 1995) need extension, because both are lacking a directional component. The present results require that the saccade generation is prepared by fixation disengagement (a nondirectional mechanism) and a spatially selective mechanism which varies in its effectiveness across the visual field. This could be related to

attentional functions but is open for further experimentation. The fact that the effects of training transfer only partly from one direction to another support this notion of direction-specific and nondirectional components contributing to saccade preparation.

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