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Express-Saccades of the Monkey: Effect of Daily Training on Probability of Occurrence and Reaction Time

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Summary. Two monkeys learned to make saccadic eye movements from a central fixation point to a peripheral target, when there was a temporal gap between fixation point offset and target onset. Under these conditions the animals made saccades after extremely short reaction times (< 100 ms), so called express-saccades. With ongoing training the rate of occurrence increased (10 to 100%) and the reaction time of the express-saccades decreased (95 to 75 ms). The training effects were mediated by the amount of previously executed express-saccades and they were also spatially selective for express-saccades to that target position that had been used during training. The training effects on the express-saccades can be saturated after less than 7 days of daily training and are reversible after another 7 days of no training. The results indicate the existence of a fast-operating visuo-to-oculomotor pathway which can be quickly and reversibly modified by daily exercise.

Key words: Eye movements – Express-saccades – Reaction time – Learning – Monkey

Introduction

The neural processes that precede voluntary goal directed movements include a number of rather complex mechanisms. In case of visually-guided changes of the direction of gaze at least 3 or 4 different operations take place: the ongoing process of active fixation of a previous target must be interrupted and the visual attention naturally changes its direction; a decision to initiate a movement of the eye must be made and finally the coordinates for the saccade must be computed.

The modern techniques of single unit and eye movement recording from monkeys that have learned to perform in different and quite specific tasks have allowed some insight into these processes with the main result that, in different cortical and subcortical structures, there exist neurons that have a visual input as well as a non-visual saccade and/or attention-related input (see review by Wurtz et al. 1980). Among these structures there is also the visual association cortex at the prelunate gyrus (Fischer and Boch 1981a and b), which seemed to have many properties in common with neurons in the frontal eye fields (Goldberg and Bushnell 1981), the superior colliculus (Wurtz and Albano 1980), and the posterior parietal cortex (Bushnell et al. 1981).

All of these structures have neurons that exhibit a spatially selective enhancement of their visual on-response prior to a saccade that is going to foveate the receptive field stimulus. The frontal eye fields, the superior colliculus, and also the prelunate cortex have in addition a signal that is independent of the on-response and precedes the changes of the direction of gaze and/or attention (Bushnell and Goldberg 1979; Mays and Sparks 1980; Fischer and Boch 1981a).

A monkey's ability to learn a specific task and to perform it better and better with an increasing amount of exercise must also have a neural correlate. In fact, we have shown that in case of visually-triggered saccades to a constantly illuminated peripheral target the neural activity prior to saccades changes with training time (Fischer and Boch 1982) and that – at the same time – the corresponding saccadic reaction time decreases (Boch and Fischer 1983). During these experiments it became clear that, in the monkey, the saccadic reaction times can be very different depending on the paradigm used to elicit the saccades. Reaction times between 140 and

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400 ms were found depending also on the amount of previous exercise.

In addition, we have recently demonstrated the existence of goal-directed saccadic eye movements (express-saccades; E-saccades) that occur after extremely short reaction times of about 75 ms with surprisingly small standard deviations in the order of a few (3 to 5) milliseconds (Fischer and Boch 1983). Express-saccades are defined by their short reaction time and their small standard deviation. In a distribution of reaction times they form a separate narrow peak besides that of the regular reaction times. E-saccades (in all animals but one) cannot be distinguished from regular saccades (R-saccades) on the basis of their accuracy in reaching the target at once. E-saccades are as correct in amplitude and direction as R-saccades. Manipulations of the visual parameters (luminance and size) of the target stimulus affect the reaction time of the E-saccades but otherwise they seemed to be quite constant (Boch et al. 1983). As we repeated our measurements over and over again and as we elicited saccades to targets of unpredictable locations in the visual field we discovered that not only the reaction time of the R-saccades was a function of daily exercise (Boch and Fischer 1983) but also changed the rate of occurrence and the reaction time of the E-saccades. The E-saccades were affected differently in different parts of the visual field depending on the amount of saccades that the animal had already made to correspondingly located targets.

Our results will show that in the monkey there exists a fast operating retino-topically organized visuo-oculomotor pathway which can be modified selectively and rapidly: its use in the past increases the probability it will be used and decreases the time it takes to use it in the future.

The existence of distinct groups of saccadic reaction times allows to decompose the process of the initiation of visually-triggered saccades and possibly to attribute them to different brain structures that are involved in the voluntary visuo-oculomotor coordination.

Materials and Methods

Two adult female monkeys (macaca mulatta) were used: "Omi" and "Pi". The methods of recording eye movements, of training the animals for stationary fixation and visually-guided saccades, as well as the determination of the saccadic reaction times, have been described in our previous papers (Fischer and Boch 1983; Boch and Fischer 1983; Boch et al. 1983). The temporal aspects of the animals' task are illustrated in Fig. 1. Upon the occurrence of a central fixation point the animals had to press a key and to hold it for a randomly varying period of time between 1 and 8 s after which either the fixation point or the target would dim, depending on which of the two happened to be on the screen. The animals were always rewarded for detecting the dimming of a visual stimulus, either the fixation point or the saccade target, and not for making correct eye movements. If they failed to make the required saccade they often failed to detect the dimming and the reward was retained. During training saccades were made to a standard target (1/4° x 1/4°; 50 cd/m^2; background 1 cd/m^2) in a standard location, 4° from the fovea, obliquely directed into one of the 4 quadrants of the visual field (see Fig. 1).

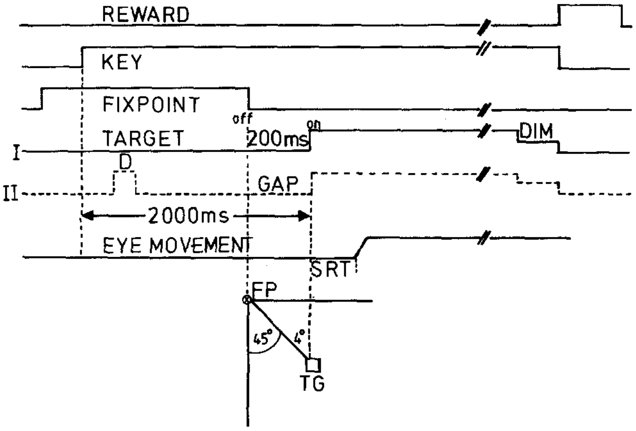

Fig. 1. Temporal and spatial arrangements of the standard paradigm used. Upon the onset of a central fixation spot (FP) the monkey pressed a key. The fixation point was turned off and, after a temporal gap, a peripheral target (TG) appeared. Depending on the randomly varying period of time either the fixation or the target (shown by trace I) dimmed and the monkey released the key for water reward. To announce the future target location the target could be exposed (D, trace II) for 120 ms 1.3 s prior to the offset of the fixation spot. Below: For standard measurements and during all training sessions the target was placed in one of the 4 quadrants of the visual field (lower left shown here) at 4° (some times 8°) of eccentricity

The trace labeled II in Fig. 1 indicates a trial where the target occurred in a peripheral position that was announced to the animal in that trial 500 ms after the beginning of stationary fixation and 1.3 s before the fixation spot went off. The announcement consisted of a short (120 ms) exposure of the target in exactly the position where it would occur 1.5 s later on the same trial. On these trials with announcement we provided the animal with the possibility to predict and to precompute the location of the target and the corresponding coordinates for the saccade necessary to reach it. We also used this temporal sequence of events on trial with "false" announcements, i.e. the target was exposed for 120 ms in one position but later it occurred somewhere else and the eye movement – had it been preprogrammed – would have to be programmed again. On "false" announcement trials we decided to locate the announcement target in the standard 4°-position, while the real target occurred somewhere else, and – in other series – announcements were made somewhere, while the real target occurred always in the same standard location, the 4°-position.

On trials indicated by the trace labeled I in Fig. 1 the target position was either completely unpredictable because its location was changed from trial to trial or the target occurred in always the same position but without an announcement on the same trial. In the latter case there exists the possibility of predicting the target position from previous trials, but the animal could never be sure. Also, in the time between the last target exposure and the next

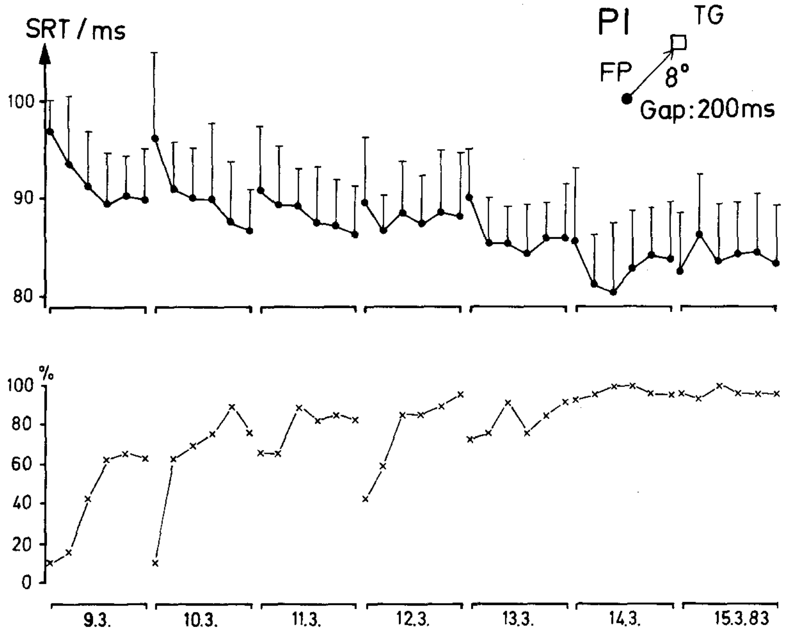

Fig. 2. Effect of training on the reaction time of E-saccades (dots) and their rate of occurrence (crosses) during 7 consecutive daily sessions each consisting of 6 groups of 30 trials

saccade the animal made other eye movements such as the initial saccade to the fixation point as it appeared at the beginning of each trial.

Throughout the experiments reported here the time between "key down" and the occurrence of the saccade target was kept constant at 2000 ms. We elicited saccades between 0.2° and 10° of size into all directions in the visual field. In each of the 4 quadrants we used the 4°-position (one of which is indicated in Fig. 1 below the traces) for continuous training of saccadic eye movements as well as for measurements where the target position was not announced but kept constant throughout a series of 20 to 100 trials.

Saccades were identified on a storage oscilloscope, and their reaction times were determined electronically. The numbers were displayed on a millisecond counter, and collected and printed by a small computer (PC 100, Siemens) for calculating mean values and standard deviations.

Unless stated otherwise reaction times between 55 ms and 100 ms were attributed to E-saccades and values between 101 ms and 1000 ms were considered as reaction times of R-saccades. That there exists such a dichotomy of the reaction times has been established earlier (Fischer and Boch 1983).

Usually, an animal works 700–1000 trials per day and makes a corresponding number of saccades. The results presented below thus rely on the analysis of a total of more than 100,000 saccades of the two monkeys.

Results

After an animal had learned to fixate a stationary small spot straight ahead, we elicited saccadic eye movements by turning the fixation spot off and – after a gap of 200 ms – turning a peripheral target on (Fig. 1). Within less than 60 min an animal usually learned to execute these eye movements consistently and correctly. As one looks at the reaction times at the first day one can see that most saccades have reaction times in the order of 150 ms but every once in a while values as short as 85 to 95 ms occur. These are typical values for E-saccades and the observation shows that the mechanism which mediates these eye movements is already established at the beginning of training but it is not used very often. To find out how selectively one can facilitate the use of this pathway we required an animal to make saccades to a standard target in a standard position in one quadrant of the visual field, while the other three quadrants were not used, always using the gap paradigm.

1. The Occurrence of E-Saccades

The data shown in Fig. 2 were taken from "Pi" who had to make 180 saccades per day in groups of 30 to a constant standard target position in the upper right quadrant. The figure shows the reaction times (dots) and rates of occurrence (crosses) of E-saccades for each of the 6 samples during each of the 7 consecutive days. As the reaction time decreases the rate of occurrence increases quickly on the first day. The following day both values are partly resetted but then they follow the same trend. After 6 days both curves reach a constant final plateau of 100% E-saccades having reaction times of 85 ms. Note, that the 100% – level is reached earlier than the final value of the reaction time.

It should be born in mind that whenever less than 100% of the saccades were E-saccades the distribution of the reaction times were bimodal. This means

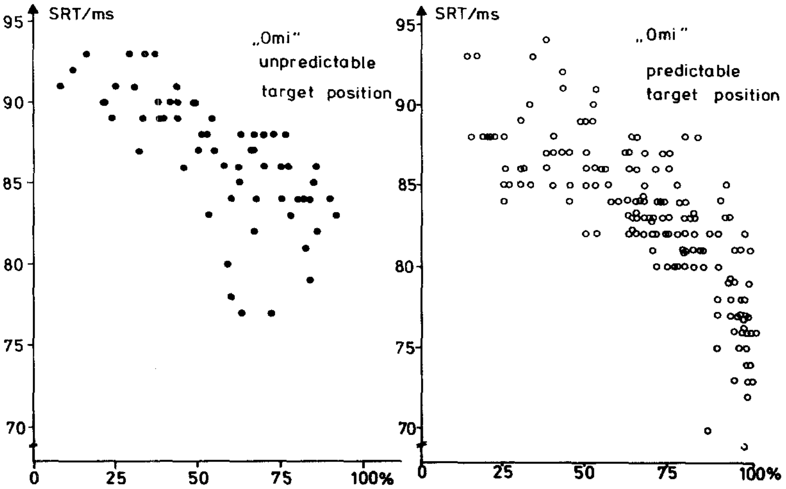

Fig. 3. Correlation between reaction time of E-saccades and their rate of occurrence for targets of unpredictable (left) and predictable (right) location

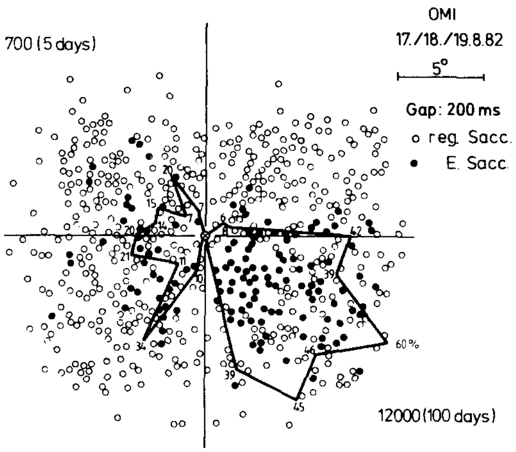

Fig. 4. Map of the central visual field of a monkey who made gap-saccades to targets of unpredictable locations indicated by the dots and circles. Locations reached by E-saccades were marked by the dots, those reached by R-saccades by circles. The lower right quadrant was used for about 12,000 saccades, the upper left for about 700 regular saccades. The other two quadrants were unused so far

that by daily training the two peaks in the distribution may shift and the regular peak at the same time gets smaller. But they do not merge into each other.

In this animal we controlled the training sessions as exactly as possible and also continued during the weekend. The earlier animal, "Omi", had to perform in different tasks by different amounts of trials and there were also breaks during the weekends. As a consequence, we obtained quite a lot of variations from day to day. However, as we plotted the reaction time versus the rate of occurrence of E-saccades we obtained a pretty good correlation shown in Fig. 3, right.

If, in a series of trials (30 to 60) the animal for some reason happened to make only a few E-saccades, their mean reaction time is long and vice versa. This correlation, of course, is clear for the data of Fig. 2 as well.

So far all saccades had been made to the standard position in one quadrant. After about 3 months where the animal "Omi" made about 12,000 saccades of all kinds to the standard target in the lower right quadrant we obtained the map shown in Fig. 4. The map displays the animal's visual field and the locations of the saccade targets as they occurred in *unpredictable* positions from trial to trial. If the saccade happened to be of the express type the position was marked by a black dot and if the saccade had a regular reaction time the position was marked by a circle. The distribution of the black dots shows that almost all saccades between 1° and 5° into the lower right quadrant, which had been used so extensively, are express-saccades, whereas saccades to targets in other positions are mostly regular, even though a few express-saccades occur everywhere. This animal had previously also made about 700 regular saccades on 5 days into the upper left quadrant. Yet the amount of E-saccades is as small as in the other two quadrants. The continuous line in Fig. 4 was obtained by plotting the percent numbers of E-saccades in a polar diagram (sector size 15°) centered on the fixation point. Note that the targets on the vertical meridian were never reached by saccades with reaction times below 100 ms.

The map of Fig. 4 combined data obtained on three different days. One day later the animal had to make 800 saccades to the standard target placed in the standard 4°-position in the upper left quadrant. Two days later (they happened to be a weekend without training) we repeated the mapping of the upper half of the visual field. The result is shown in Fig. 5. Now the animal made about as many E-saccades into the upper left quadrant as into the

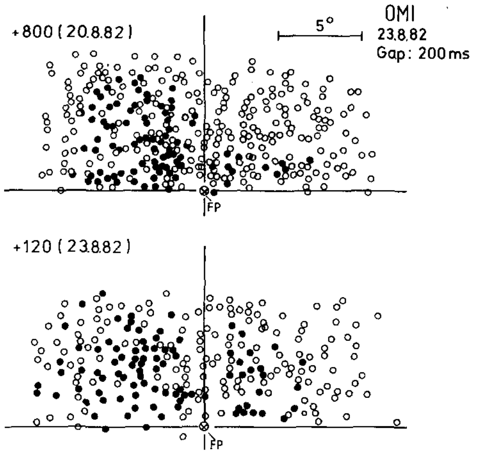

Fig. 5. Maps of the upper half of the visual field of the same monkey 4 days later. Meanwhile the animal made another 800 gap-saccades into the upper left quadrant but no further saccades to the upper right quadrant. Below: Same after another 120 gap-saccades to the upper left quadrant. Dates of training days are given in brackets and number of trained saccades in front

lower right, while the upper right quadrant remained unchanged.

After this map was completed the animal had to make another 120 saccades to the upper left standard target (4°-position). Again we repeated the map (on the same day) and obtained the lower part of Fig. 5. Now all saccades to targets in the standard position were of the express type.

These results indicate that the pathway that mediates the E-saccades can be rapidly modified in terms of the frequency in which it is used. They also show that this modification does not apply to just any saccade to any target location, but rather the training effects are spatially selective (for the details see Sect. 5). Implicit in the maps is also that E-saccades can be made to targets of unpredictable location (Sect. 4).

Moreover, the correlation between rate of occurrence and reaction time of E-saccades to the standard position is also obtained for E-saccades to unpredictable target positions as shown by Fig. 3, left side.

2. *Regular Versus Express-Saccades as a Conditioning Factor*

So far we have used only the gap situation during training and it is clear that the corresponding saccades increase the rate of occurrence of E-saccades. The question then arises whether or not regular saccades alone would have the same effect on E-saccades. Therefore, "Omi" had to make 840 regular saccades to the standard position in the upper right quadrant, which was unused up to that point and almost empty of E-saccades (see Figs. 4 and 5). (To prevent E-saccades during training we used a task where the target occurred 1.5 s before the fixation point went off. Under this condition we have never seen E-saccades.) The map of Fig. 6 was obtained one day later. It shows, that there was only a slight increase of E-saccades in both quadrants. Then, on the same day, "Omi" made 600 saccades to the standard position in the same (upper right) quadrant in the gap situation. As we repeated the mapping right after, we obtained the lower part of Fig. 6, which shows that the quadrant is now as heavily filled by dots as the others that had been used extensively before. This indicates that R-saccades are far from being as effective as E-saccades. (This experiment was also repeated with the other animal and gave the same result even more clearly.)

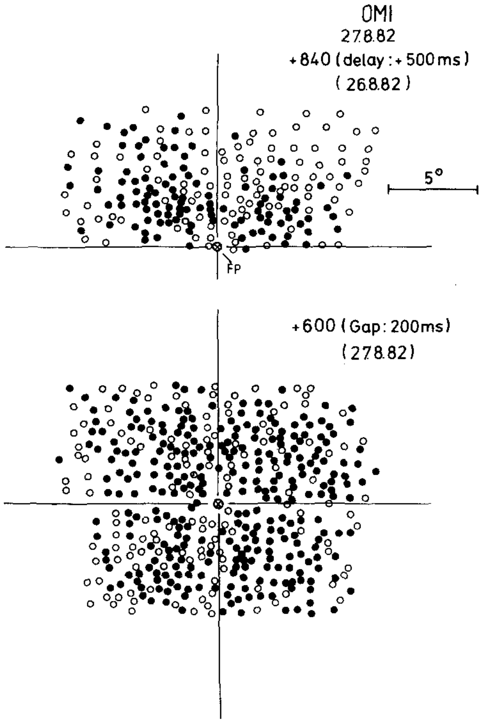

Fig. 6. Same as Fig. 5 another 4 days later. Meanwhile the animal made 840 regular saccades to the upper right quadrant and then one day later another 600 gap-saccades

3. *Reversibility*

The observations documented in Figs. 4 and 6 were made in the end of August, 1982. During the next 6 weeks this animal made saccades only to targets in the lower right quadrant, whereas the other three quadrants were not used. When we repeated the map

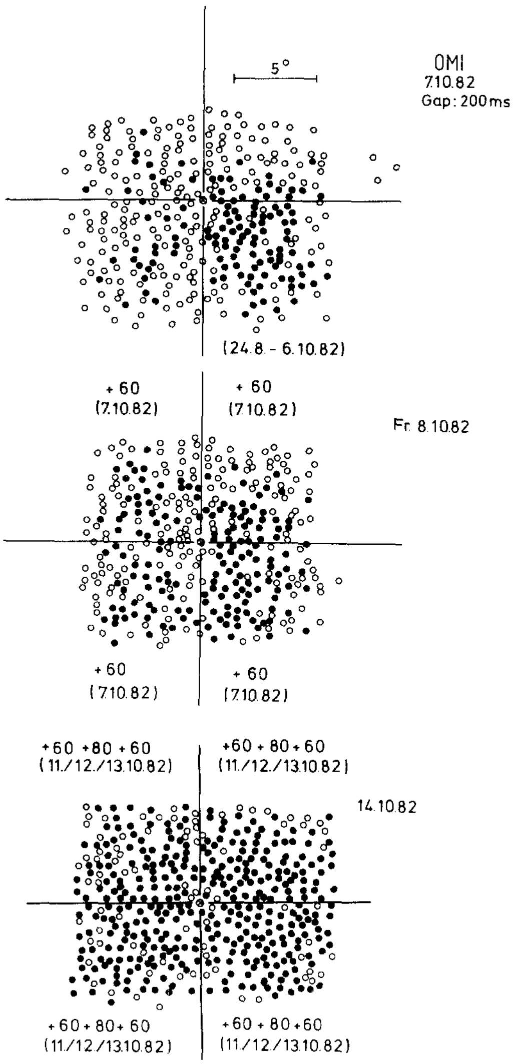

Fig. 7. Same animal 6 weeks later. Meanwhile only the lower right quadrant was used. The upper map is hardly different from that of Fig. 4. After a few days of training (60 gap-saccades per day and quadrant) the picture of Fig. 6 (lower part) is restored

it turned out that the saccades in the "unused" quadrants had predominantly regular reaction times as can be seen from the upper part of Fig. 7. The facilitation of the E-saccades that had been reached by the end of August was completely gone. In fact the map of Fig. 4 and upper Fig. 7 are hardly different.

The other animal, "Pi", which was trained for E-saccades during 7 successive days and reached the 100% level within that time (Fig. 2) was tested after only one week, during which the animal kept making saccades to another quadrant. As a result all E-saccades had disappeared from the quadrant that was unused for only 7 days.

During the next days we tried to restore the occurrence of the E-saccade of "Omi" by allowing only 60 saccades per day and quadrant. After one day the map in the middle of Fig. 7 was obtained and after another 3 days of training the lower map was taken. It is quite clear that the small numbers of daily saccades are sufficient to restore the state of almost exclusively occurring express-saccades. Again very small (< 1°) and larger (> 6°) saccades still have a good chance to be of the regular type because during the conditioning sessions the targets were always in the standard 4°-position in each of the quadrants. Of course, taking the map always interferes with the conditioning, because it requires saccades which increase the probability of occurrence of E-saccades. This probably explains why not only saccades to the standard location are modified but also – to a lesser extent – saccades to neighbouring locations.

4. Prediction and Precomputation

When we first discovered the existence of the E-saccades the target was always located at the same position in the visual field (4°-standard position) and its occurrence was also fixed in time at 2000 ms after the animal's key pressing. We showed later that the possibility of *predicting the time* of target onset was not a determining factor for the occurrence of E-saccades (Fischer and Boch 1983). The maps of Figs. 4–7 show in addition that neither is the possibility of *predicting the location* of the target from previous trials a determining factor. What might change though with an increasing chance of prediction is the rate of occurrence and the reaction time of E-saccades. In this section we describe the result of experiments where the location (and time of occurrence) of the target was not only predictable from previous trials (and previous sessions) but rather the target position was spatially announced in the same trial by briefly exposing the target 1.5 s before its (future) appearance in the same position (see traces II of Fig. 1). The corresponding saccades will be compared with those elicited when the spatial announcement was 'false', i.e. when we briefly exposed the target at some position different from that to which finally the saccade had to be made.

The basic result is that on trials with 'correct' announcements animals had a tendency to initiate saccades about 220 ms after the offset of the fixation point, i.e. they did not wait for the peripheral target to occur. These saccades are in a way anticipatory with respect to the occurrence of the target and almost all of them failed to reach the anticipated location by 20 to 70%. But most of the saccades after 'correct' announcements were E-saccades and only a few (< 15%) regular saccades were seen. On trials

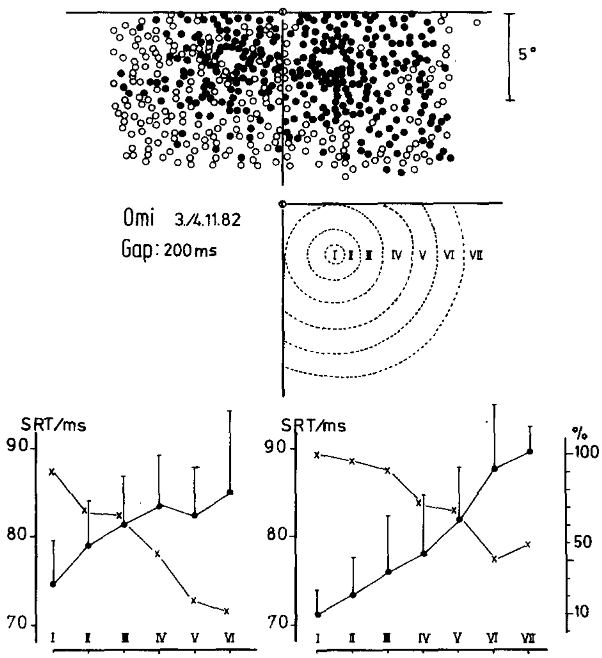

Fig. 8. Above: Map of the lower half of the visual field (same animal, 4 weeks later). Middle: Each quadrant is divided into circular regions concentric to the standard target location. Saccades into these regions were counted and their rate of occurrence (crosses) as well as the mean reaction time of the E-saccades (dots) were plotted below as a function of the distance from the standard location (number I to VII along the abscissa)

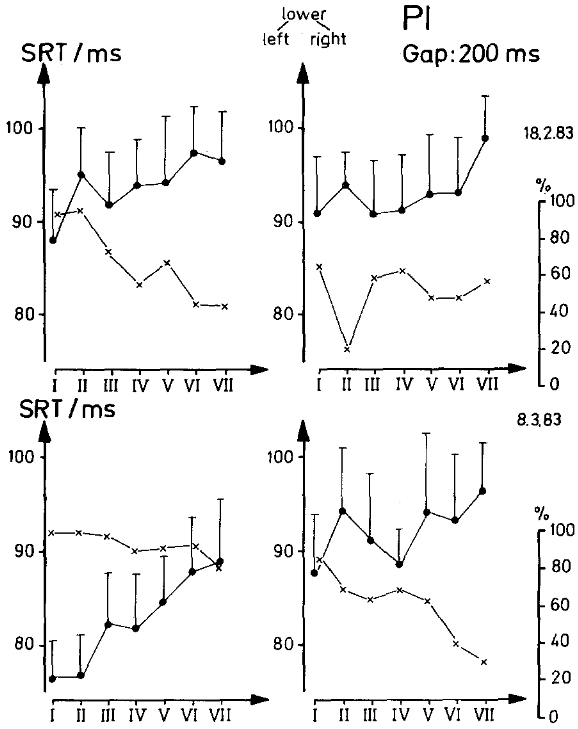

Fig. 9. Like Fig. 8, lower part, but for two different quadrants (lower left and right). The upper two graphs show the absence of any clear local structure of the two quadrants tested at the 18th Feb. 83: The lower left quadrant then received training with the target at the standard position, whereas the lower right quadrant was unused during that time. Repeating the maps at the 8th March shows the decrease of the reaction time of the E-saccades to the standard position from about 90 ms before training to about 78 ms after. The lower right quadrant remained about as unstructured as before

with 'false' announcements the animals made some anticipatory saccades to the falsely announced position but most of the saccades were correct E-saccades of about the same reaction time. This was also true if the 'false' announcement was made across the vertical meridian. This shows that even if the saccade coordinates were already computed (and stored) at the time of the announcement, they will be computed again after the actual occurrence of the target at its final location.

5. Spatial Selectivity of the Training Effects

From the maps of Figs. 4–7 it is immediately evident that the probability of occurrence of an E-saccade depends on the location of the target. In both animals only the quadrant within which the target was located during training showed an increase of the number of E-saccades, whereas unused quadrants remained about as empty as in the beginning. Even after excessive training of a given quadrant the spread across the vertical and horizontal meridians was small (Figs. 4–7). Moreover, in both animals it was not the distance from the fovea but rather the distance from the standard position that turned out to be the relevant parameter that determined the reaction time and the rate of occurrence of E-saccades. To establish the local structure of the map in more detail we took another map of the lower half of the visual field of "Omi" (see Fig. 8) with the modification that the standard position was used many times but on unpredictable trials. (Target positions within 1/4° from the standard position were all reached by E-saccades but not marked by dots in the map for the sake of clarity.) Below the map we plotted the rate of occurrence of E-saccades (number of E-saccades divided by the sum of R- and E-saccades) as a function of the distance from the standard position as indicated by the dotted circles in the middle of Fig. 8.

Also plotted are the reaction times of the E-saccades (mean of the values within each of the dotted circular regions in the middle of Fig. 8) as a function of the distance from the standard position. The figure shows that reaction times of E-saccades close to the standard position are shorter when compared to those to targets farther away. The obvious quantitative difference between the two

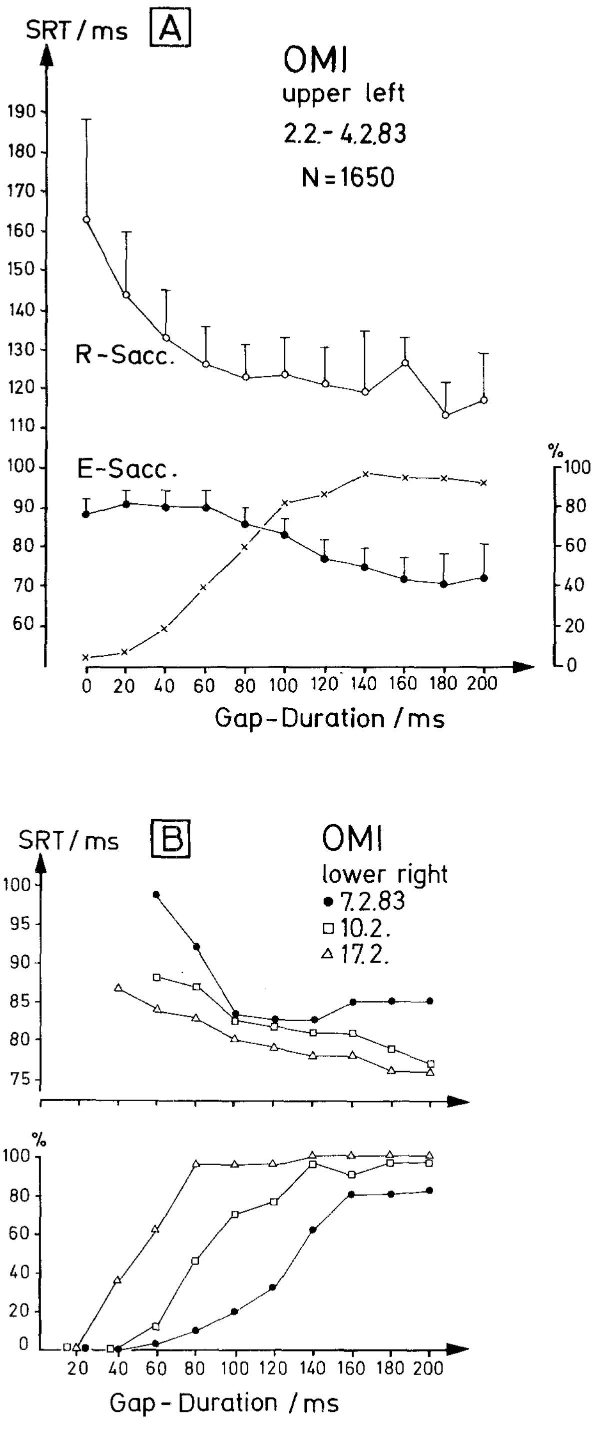

Fig. 10A and B. The influence of the duration of the gap **A** and training **B** on the reaction time and rate of occurrence of E-saccades and R-saccades. **A** As the duration of the gap increases from zero to 200 ms both the reaction time of E- and R-saccades decreases and the rate of occurrence of E-saccades (×) increases. These measurements were taken from the well-trained upper left quadrant. **B** Using the untrained lower right quadrant on successive days of training (3 days selected out of 7) shows that reaction time curves are shifted down and the rate of occurrence curve shifted to the left

lower quadrants is due to the different amount of previously made saccades: The lower right quadrant had been used throughout the weeks before whereas the lower left quadrant had been used only occasionally.

To see the development of the local structure as a function of training we used animal "Pi", which happened to produce enough E-saccades after short training. The lower two quadrants were tested on the same days, one with daily training the other with no more exercise as was implicated by taking the data. Figure 9 shows the local structures of the two quadrants as they appeared on two different days. Little or no preference of any point in the visual field is seen in the untrained quadrant whereas a clear local structure develops after a few days in the quadrant that had received the training. The figure also shows that it is not so much the rate of occurrence of E-saccades that shows the structure but rather their reaction times.

6. *Gap Duration*

One of the conditions for an E-saccade to occur seems to be the break of active fixation, which – in our experiments so far – is initiated by the offset of the fixation point. If one decreases the duration of the gap from 200 ms to zero the rate of occurrence of E-saccades decreases (Fischer and Boch 1983). The data shown in Fig. 10A have been taken from "Omi" whose upper left quadrant had been used extensively at that time already. It shows that not only the rate of occurrence decreases but also that at the same time the reaction time of the E-saccade increases by about 20 ms. Also shown are the reaction times of the R-saccades (see Sect. 8). As we began to use the lower right quadrant again (after it had been left alone for some weeks) the curves of Fig. 10B were obtained on the days indicated. The data show that the rate of occurrence at any given gap duration increases whereas the reaction time of the E-saccades decreases. A plot of reaction time versus rate of occurrence (not shown) resulted in a very similar picture to that of Fig. 3, irrespective of the gap duration. Note that with increasing exercise on a day by day basis (only 3 out of 7 consecutive days are shown in Fig. 10B) the minimal gap duration at which E-saccades occur also decreases from about 100 ms to less than 40 ms and even with zero gap duration there may be a few E-saccades (Fig. 10A).

7. *E- Versus R-Saccades*

Depending on the duration of the gap and on the state of training a monkey makes E-saccades on some trials and R-saccades on others and at present we do not know what the determining factor on a given trial might be. However, the existence of both types within a series opens up the possibility of looking at the difference of their reaction times, for example the difference between the upper and middle curves in Fig. 10A. As can be seen from the figure and as revealed from the measurements in the lower right quadrant (Fig. 10B) the difference between the mean values of E- and R-saccades in a given situation does not change with gap duration. It rather stays constant at (44 ± 5) ms in this case. This mean value was calculated out of 37 difference values, each of which was obtained from 30 gap-saccades elicited for gap durations between 40 and 200 ms on 7 consecutive days (including the data of Fig. 10B). Of course, for very short gap durations and at the beginning of training one obtains almost no E-saccades. Similarly, for longer gap duration and at the end of training one obtains almost no R-saccades. Therefore, in the above computation of the mean we included only those difference values where the rate of occurrence of E-saccades (R-saccades) was between 10% (90%) and 90% (10%).

We also tried to determine the effect of training on the differences between R- and E-saccades in the gap situation. No clear tendency was observed in either of the two animals. We, therefore, give only the mean values taken from all experiments where they were available (gap = 200 ms).

Omi: Difference (R-E)-SRT = 51.6 ± 12.6 ms (N = 4300; 83.5%)

Pi: Difference (R-E)-SRT = 39.1 ± 10.8 ms (N = 3689; 71%)

N is the number of saccades that contributed to the mean value of the difference, and the amount of E-saccades among them is given by the percent in brackets.

8. Further Observations

During the course of the experiments described above we made a number of observations, that we could not follow up in any detail, but nevertheless should be communicated.

(i) Saccades to target occurring at the vertical meridian had a reaction time in the order of 100 ms. Without further knowledge they were difficult to classify as E- or R-saccades of longer or shorter reaction time, respectively. There could exist another local structure of the visual field with respect to saccades to targets at the vertical meridian.

(ii) 'False' announcements of the target position in the hemifield contralateral to the final target position (and consequently contralateral to the following saccade) did not abolish the occurrence of E-saccades.

(iii) If the monkey was not required to fixate anything, but rather was sitting in his chair making spontaneous saccades with long intersaccadic intervals one could elicit E-saccades by suddenly presenting the target. In trials with very long gap durations (500 to 1000 ms) the monkey would frequently lock away from the position of the previous fixation point and make a number of saccades. When finally the target occurred he would foveate it frequently by an E-saccade.

(iv) Corrective saccades have not been studied in any detail. Usually the saccades irrespective of their reaction time are correct in direction and amplitude within 10%. Correction occurs within 140 to 180 ms after the end of the primary saccade. If saccades undershot as in the case of anticipated eye movements to targets of preannounced locations their amplitude was wrong but usually their direction was not.

Discussion

The present data together with our previously published observations on saccadic reaction times (Fischer and Boch 1983; Boch and Fischer 1983; Boch et al. 1983), in particular of E-saccades, open up a number of questions:

1. What is the neural basis for the changes that enable the retinal – to – oculomotor pathway, to save 10–20 ms (in the case of E-saccades) and about 200 ms (in the case of regular saccades) as a consequence of daily exercise, and where do these changes occur in terms of anatomy?
2. Why does the reduction of the saccadic reaction time occur only for saccades of a specific direction and amplitude (spatial selectivity)?
3. Which of the different processes involved in the initiation of voluntary visually-triggered saccades change the time they need for completion? How are these different processes triggered and do they have to take place in a well-ordered sequence?

To facilitate the discussion of these questions let us assume that the execution of a correct goal-directed saccade takes the completion of at least three processes: (i) The active fixation of a foveal target must be interrupted, which takes a time f. (ii) A decision, to execute the next eye movement must be made taking a time d. (iii) The coordinates for the saccade must be computed in another time c. In addition, of course, an afferent (retinal) latency a, and an efferent delay e will elapse before the eyeball will move in response to a sensory (visual) stimulus. Therefore, given all these processes take place in sequence, the saccadic reaction time will be:

SRT = a + f + d + c + e (case I).

In case the fixation point is extinguished early enough time f could be elapsed before the new target occurs. Then the saccadic reaction time is only:

R-SRT (gap) = a + d + c + e (case II).

If, on a given trial, the animal can also complete the decision to make the saccade before the new target occurs, the saccadic reaction time is shortest:

E-SRT (gap) = a + c + e (case III).

If one identifies this reaction time with that of the E-saccades and assumes an approximate value of 50 ms for the sum of a and e, then c turns out to be in the order of 20–40 ms depending on the amount of exercise. The time c will not depend on the duration of the gap. Case II would be attributed to the regular saccades in the gap situation and the time d is in the order of 30–50 ms. We have been unable to determine training effects on d, because the difference between the R- and E-saccade reaction time scattered too much. Maybe d does not depend on training at all.

Case I occurs if the fixation point is fixated until the saccade should be executed; this happens when the offset of the fixation spot triggers the saccade, and the target has occurred earlier but *not* eliciting a saccade. In this situation (overlap) saccadic reaction times are longest and f turns out to be in the order of 100–200 ms depending also on exercise. The fact that in the overlap situation the system cannot take advantage of the visibility of the target well before the saccade shows that the coordinates – even if computed before hand – cannot be used to place the saccade unless the processing times f and d are completed. To clarify, whether or not the coordinates of the new target are computed before, one has to extinguish the target after a short exposure again before the fixation point goes off. This opens up the possibility for the animal to make a saccade to a *remembered* position. One can look at the accuracy and reaction time of those saccades (work in progress). The value of f and its dependence on exercise can also be determined from experiments, where the fixation point remains visible throughout a trial and the animal has to saccade to the target when it occurs. This, however, requires a different training of the monkey. Our preliminary observations have shown already, that – as in humans (Saslow 1967) – reaction times in this situation are rather long and dependent on exercise.

From the spatial selectivity of the training effects on E-saccades one has to conclude that the time c in this context can be short for well-trained saccades of a certain direction and amplitude, but remains longer for other E-saccades. Therefore, the neural network, which does the computation must be retinotopically organized and can be locally facilitated in terms of the time it takes to complete the computation.

It remains to be seen whether or not training effects on regular reaction times, both in the gap and in the overlap situation, are also spatially selective.

It should be noted that the training effects on saccadic reaction times must occur centrally both seen from the afferent and from the efferent viewpoint, because the animals have used their eyes throughout their lives and also because we have shown that, e.g., regular saccades in the overlap-case do not facilitate the occurrence and reaction time of E-saccades. Also the velocity – versus – amplitude relation of the eye movement are the same for all saccades elicited by the different paradigms after so clearly different reaction times. One can say that the afferent as well as the efferent part of the visuo-oculomotor pathway were already "trained", when the animals came into the experimental situation.

We have extensively discussed (Boch et al. 1983) the temporal aspects of the saccadic reaction in relation to the different anatomical structures that display saccade-related neural activity, such as the frontal eye fields (Goldberg and Bushnell 1981), posterior parietal cortex (Bushnell et al. 1981), prelunate association cortex (Fischer and Boch 1981a, b) and the superior colliculus (Wurtz and Albano 1980). From the present data it must be suspected that one or the other or even all of these structures change their functional contribution to the preparation, programming, and execution of goal-directed saccades. In principle, a structure involved in the initiation of E-saccades must receive a visual signal after latencies of less than 50 ms. This aspects favours the superior colliculus as being included in the pathway utilized by the E-saccades. Therefore, it would be interesting to see the differential effects on the occurrence of E-saccades after lesions of the superior colliculus on the one hand, and, e.g., of the frontal eye fields on the other.

Since the training effects are reversible and can be clearly observed only under a strict daily schedule of exercising, special experimentation of recording eye movements and single cell activity will be needed to clarify this type of flexibility of the visual – to – oculomotor pathway.

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