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Article Title: Express-saccades of the monkey: Reaction times versus intensity, size, duration, and eccentricity of their targets.
Express-Saccades of the Monkey: Reaction Times Versus Intensity, Size, Duration, and Eccentricity of Their Targets

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Summary. Monkeys were trained to fixate a small spot of light (fixation spot) and to saccade to a peripheral target if and only if the fixation spot was turned off. If the offset of the fixation spot preceded the onset of the peripheral target by a temporal gap of more than 140 ms the animals could change their direction of gaze after saccadic reaction times of more than 70–80 ms (express-saccades). The reaction times of the express-saccades depend on the luminance and the size of the target and decrease from about 120 ms for near threshold targets by about 50 ms in a range of 2,5 log units above threshold (gap duration 200 ms). The minimum reaction time and the target size for which the minimum is reached are functions of the retinal eccentricity of the target. Comparison with response latencies of afferent visual neurons suggests that the dependence of the reaction times of express- as well as regular-saccades on the physical parameters of the target is mostly determined by retinal factors. The short reaction times of the express-saccades are discussed in relation to the reaction times of other visually-guided goal-directed movements.

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

Introduction

The brain processes of any kind of visually-guided behavior begin only after the corresponding visual structures received the signals from the retina. An analysis of these processes implies the knowledge of when they take place and how much time any one of them takes for completion.

In the case of visually-triggered saccadic eye movements one would like to decompose the saccadic reaction time into different periods during which operations like break of previous fixation, decision making, and computation of size and direction for the saccade, take place. As a first step then one has to take into account the delay times that are due to the type of visual stimulus used to initiate the movement. Unfortunately, saccadic reaction times reported so far are in the order of 150–300 ms and exhibit variation of about ±20 ms or much more. This means that the chances of seeing changes in the order of 20–40 ms are not very good.

The existence of saccadic eye movements in the monkey after extremely short and stable reaction times of about 70 ms with a standard deviation in the order of ±3 ms (Fischer and Boch 1983), however, allows us to study the effect of stimulus parameters and, thus, to separate afferent delay times from central processing times.

The express-saccades (E-saccades) occur if the previous fixation spot is extinguished some time before the new target appears, i.e. if there is a gap between fixation spot offset and target onset. Since the reaction time of the E-saccades is so extremely short (as compared to the regular saccades with reaction times between 140 ms and more than 250 ms) and since their value is so precisely repeated from saccade to saccade one expects that those physical parameters of the peripheral target that influence the response latency of the afferent visual neurons (e.g. retinal ganglion cells) also affect the reaction time of the E-saccades as well as any other reaction time of visually guided movements.

We have, therefore, recorded saccadic eye movements of monkeys and measured their reaction times when they were trained to change their direction of gaze from one visible target to another. We determined the effects of the luminance, size, duration,
and eccentricity of the target on the reaction time of E-saccades and regular saccades (R-saccades). The results show that the reaction time of E-saccades can be consistently reduced from 120 ms by as much as 50 ms by increasing the visibility of the target from near threshold to 2.5 log units above threshold.

Any other goal directed movement that follows these eye movements or that needs them as a concomitant event might have a chance of being executed according to the same rules as E- and R-saccades. For example, in man, goal-directed saccades always precede the corresponding head and reach movements but the muscle activity for all three movements occur about at the same time (Biguer et al. 1982; Zangemeister and Stark 1982) opening up the possibility that there is only one command center. If one enabled the eye to move 100–150 ms earlier by erasing the fixation target before the peripheral gaze and reach target occurs one would have a chance to see whether the arm and/or head takes advantage of the preceding eye movement.

Methods

Two animals (macaca mulatta) by the names of “Omi” and “Pi” were trained to press a key upon the onset of a fixation spot which dimmed after randomly varying periods of time between 1 and 6 s. The animals were rewarded by a drop of water if they released the key within 700 ms after the occurrence of the dimming. After they had learned this task their head was rigidly fixed by a permanently implanted metal bar. Surgery was done under (10 mg/kg, i.m.) Ketamin and (25 mg/kg, i.m.) Nembutal. During the subsequent training sessions the x- and y-components of eye movements were continuously monitored by an infrared light sensitive device with a resolution of 0.1 deg (Bach et al. 1983). The x-y-coordinate system of the eye position signal could be rotated electronically such that one axis of the rotated system coincided with the line between the fixation point and the target.

When an animal had learned to fixate a small (3 min of arc) stationary red spot and had consistently cooperated during daily sessions of 2–4 h he was asked to make rapid goal-directed eye movements: the fixation spot was turned off 1.8 s after the beginning of a trial and a new target was turned on in the near periphery (1/2–10°) from the fovea.

If the dimming happened to occur at times when the fixation spot was off the target would dim instead. Animals realized this quickly and consequently they changed their direction of gaze if and only if the fixation spot went off. This case is illustrated by the continuous line labeled “Target” in Fig. 1. The figure also shows the usual sequence of events and the definition of the saccadic reaction time (SRT). Usually the target was placed into one of the 4 quadrants of the visual field at an eccentricity of 4° and appeared 2 s after the beginning of the trials, i.e. there was a gap of 200 ms between fixation spot offset and target onset.

In a given series the target was always presented at the same location. After the animals had learned to make consistent eye movements we began the measurements described below.

The background illumination was kept constant at 1 cd/m² throughout the series of experiments. The maximal luminance (I max) of the target was 30 cd/m² and could be reduced in steps of 0.1 log units by using neutral density filters. The size of the quadratic target was variable between 0.08° × 0.08° and 4° × 4°, its duration between 3 ms and 2000 ms. In case of brief exposures of the target it was turned on again another 200 ms later such that the animal would be able to detect the dimming of the target. This case is illustrated by the broken line in Fig. 1.

Between 30 and 80 saccades under identical conditions in successive trials were collected and their reaction times measured from the onset of the target were determined automatically by an electronic threshold detector. Each saccade was displayed on a storage oscilloscope for visual inspection. The beam was interrupted when the threshold detector detected the saccade (Fig. 2). False detections due to artefacts and micro-saccades were aborted immediately. The values of the reaction times were digitised and fed into a minicomputer to calculate mean values and standard deviations.

Saccadic reaction times shorter than 50 ms and longer than 300 ms measured from target onset were rejected from the data reported here. Also, reaction times of saccades that were anticipated and/or failed to reach the target at once by more than 10%, were discarded.

Results

Under the conditions illustrated in Fig. 1 where there is a gap between the offset of the fixation spot and the onset of the peripheral target monkeys usually maintain their direction of gaze until the new target becomes visible. Then they initiate a saccadic eye movement that brings the fovea from the position of the previous fixation spot to the position of the new target. Figure 2 shows a sequence of records of eye movements of one animal. As reported earlier two distinct cases may occur. In one instance the saccade is initiated after a regular though short reaction time of about 130 ms (regular saccade) and in another instance the reaction is executed without any delay while the animal is not fixating the target (immediate reaction).
instance the saccade begins much earlier after a reaction time of about 70 ms (express-saccade). This particular animal almost never failed to reach the target at once, i.e., without a subsequent corrective saccade. As long as an animal is not used to making express-saccades (E-saccades) to a target in a particular position there is always a good percentage of regular saccades (R-saccades) in a given sequence of trials. Nevertheless, E-saccades may occur the very first day of training of goal-directed eye movements in a gap situation. The aspects of the effect of training on the rate of occurrence and the duration of the reaction time of E-saccades will be described separately.

1. Intensity

In our previous studies the size and luminance of the saccade target was kept constant well above threshold. As one successively decreases the luminance of the target stimulus and plots the distribution of saccadic reaction times for each luminance separately a picture like that of Fig. 3 emerges. The distributions are bimodal. The E-saccades give rise to the population on the left, the R-saccades constitute the population on the right. As luminance is decreased in steps of 0.2 log units (from top to bottom) both distributions shift to the right, i.e. the reaction times of both the express and the regular saccades become longer.

It is only near threshold that the distribution corresponding to the regular saccades becomes flat. During this session the percentage of E-saccades was almost constant at about 40% and decreased only near threshold. At an intensity of log I/I max = −1.4 the animal failed in about 75% of the trials to make an eye movement, and in about 20% the saccades had a regular reaction time. There were almost no E-saccades at this low luminance. We reliably observed that the threshold for E-saccades was a little (about 0.2 log units) higher than the threshold for regular saccades. These thresholds might become equal after an animal has been used extensively in these experiments. The data of Fig. 3 were all obtained from saccades to targets placed in the upper right quadrant at 4° of eccentricity as indicated by the small arrow at the top of the figure. To obtain the plot of saccadic reaction time versus log intensity shown in Fig. 4 we placed the target in the lower right quadrant, because we noticed that this animal in its present state of training would make almost exclusively E-saccades. This is indicated by the open circles which display the percentage of E-saccades as a function of intensity. Over about one log unit this percentage is little affected but the reaction time changes quite regularly by more than 40 ms. The curve is still decreasing at our highest luminance value indicating that the reaction time of the E-saccades could be still shorter. In fact, as we used larger (instead of brighter) targets we were able to obtain still shorter values (see also Chap. 2). The threshold of the target was at log I/I max = −1.5 and is indicated by the arrow at the abscissa. The total range of luminance over which the reaction time changes is about 2.5 log units. Typi-
Fig. 3. Distributions of saccadic reaction times (abscissa) for different luminances of the target (¼° × ¼°) as indicated by the values of log \( I_{\text{max}} \) at the left. The narrow peaks at the left represent the subpopulation of express-saccades, the broader peaks to the right correspond to the regular saccades. The bars at the right hand side of the figure illustrate the percentage of express-saccades (E, hatched), regular saccades (R, white), and trials, where the animal failed to make an saccade (M, black) within less than 400 ms from target onset. Total numbers of trials for each luminance are given by \( n \). The bar at the lower right corner shows, that just above threshold the animal made almost no E-saccades, but still some R-saccades. In most of these trials \( n = 44 \) the animal failed to saccade to the target and, therefore, also missed the dimming and consequently stopped to cooperate after 44 trials.

2. Size and Eccentricity

The plot of Fig. 4 indicates, that the SRTs of the E-saccades would have been still shorter at still higher intensities of the target stimulus. Instead of increasing the luminance (which was limited in our apparatus) we increased the size of the target. As a consequence the SRT became still shorter. This led us to systematically look at the effect of target size versus reaction time, when the luminance was kept constant at 50 cd/m².

Figure 5 shows the results. Target size is plotted along the abscissa (log-scale of area) and eccentricity of the target is the parameter indicated for each curve. The figure shows the systematic decrease of the SRTs as target size increases. For eccentricities up to 12°, reaction times increased again from 23.9 ms to 72 ms, but then they did not change any further.

The graph in Fig. 6 shows how the SRTs vary with the value of log \( I_{\text{max}} \). The value 1.4 log units is the average of the excursion of the deviation from zero of the data points.

The black dots in the diagram correspond to data points.
Fig. 5. Plot of the reaction times of E-saccades versus size of the peripheral target expressed by the logarithm of its area (A) over an area A0, selected arbitrarily as a square of 0.25° x 0.25°. The parameter at each curve is the eccentricity of the target as indicated also by the inset. FP = Fixation point.

Fig. 6. Data taken from Fig. 5 are plotted versus eccentricity. Black dots represent the size of the target (square) at which the reaction time was minimal, and the circles represent the corresponding minimal value of the reaction time.

up to 8° the SRTs reach a minimum and increase again for larger targets. At still larger eccentricities (12°, 16°; not shown) we obtained similar curves but they did not show a minimum but rather remained flat up to target sizes of 4° x 4°.

The minimum value decreases with eccentricity and is reached at increasingly larger sizes of the target. Figure 6 illustrates the relationship between the values of the minimal SRTs (circles) and the corresponding “critical” size of the target (dots) and the eccentricity of the target. Even though the values of the minimum at 1° of eccentricity (72 ms) and the value at 8° (64 ms) differ by only 8 ms this is a significant difference because of the small standard deviations of the reaction time of E-saccades.

The data of Figs. 2–6 were all taken from the animal “Omi”. The second animal (“Pi”) delivered the same typical curves. The minimal reaction time for targets at 1° of eccentricity was 81 ms and decreased to 69 ms for targets at 8° of eccentricity. This difference in absolute values of the reaction time is mostly due to the fact that the corresponding data were taken in an early stage of training. The target size at which the minimal values were reached varied from 0.35° at 1° of eccentricity to 1.0° at 8° of eccentricity and, therefore, closely resembled the data of Fig. 6 (black dots).

3. Duration of Target Exposure

There are two points of interest in changing the time of exposure, i.e. the duration, of the target stimulus: Do express-saccades also occur if the target stimulus is extinguished before the eye begins to move and how long has the stimulus to be exposed in order to compute the coordinates for the eye movements? As one changes stimulus size and luminance the latencies and the strength of the neural responses of afferent visual neurones also change. If the duration of the stimulus changes there are changes of response strength but only little changes of response latency. As long as the stimulus lasts longer than the latency there are no latency changes at all. Therefore, one expects only little if any systematic changes of the reaction time of express-saccades as far as they are determined by retinal factors. To elicit saccades to briefly visible targets we used the paradigm illustrated in Fig. 1 by the broken line. The second occurrence of the target was necessary to provide the possibility for the animal to detect the dimming of the target.

As we successively shortened the target exposure from 2 s to 3 ms (!) we observed that the animal made
express-saccades at the same rate (97%) and with the same reaction time (76 ± 6 ms; n = 290) at all durations. In other words: even a light impulse of no more than 3 ms duration is sufficient to elicit a correct express-saccade. It should also be noticed that for target exposure times below 70 ms the eye begins and stops to move when there is no target present. The fovea also reaches the exact position that the target had before, such that no further eye movement is needed when the target appears again after the second gap of 200 ms.

4. Reaction Time of Regular Saccades

Figure 3 shows the distribution of the reaction times of both express and regular saccades. It is evident that the mean reaction times of the regular saccades also increase as the luminance of the target is lowered. At the same time their scatter increases as well, such that for low luminances near threshold mean values and standard deviations are not very meaningful. We, therefore, determined the differences between the mean values of regular and express-saccades only in the range of 0.3 to 1.3 log units above threshold. We found that this difference hardly changes with intensity, but rather stays constant at about 55 ± 8 ms (mean and standard deviation of 39 differences of mean values) for this particular animal ("Omi") in its present state of training.

In the other animal ("Pi"), which produced no regular saccades with a gap duration of 200 ms, we used a shorter gap of 80 ms to obtain more regular saccades and also the target size was increased from 0.25° × 0.25° to 0.5° × 0.5° in order to cover the full range over which the reaction times would change. The result is shown in Fig. 7. The reaction times of the regular saccades (circles) decrease by about the same amount as those of the express-saccades (dots) indicating again that the difference between the two stays about constant. This animal, however, in its present stage of training produced a difference of only 35–40 ms. It remains open, for the time being, to which extent the extra central processing time that is needed for a regular saccade, in comparison to an express-saccade, depends on the amount of previous exercise and/or on the individual animal under study. In earlier experiments (Fischer and Boch 1983) we found a difference of 70 ms between regular and express reaction times, and that animal had much less experience.

Discussion

a. Reaction Times of Express and Regular Saccades and Retinal Latencies

In a previous study we have shown that the reaction times of E-saccades are rather constant both in a given series of trials under identical conditions and for different eccentricities of the target (Fischer and Boch 1983). In this study we have manipulated those physical parameters of the saccade target that would also affect the latency of the neural responses in the retina. It seems that most of the systematic changes of the reaction time of E-saccades can be explained by retinal factors. For instance, the latencies of the responses of retinal ganglion cells of the cat (Bolz et al. 1982) change over about the same range of luminance (2.5 log units) and by about the same amount (50 ms) as the reaction time of E-saccades. Also the increase of the reaction time for targets that exceed a certain range in size could be interpreted as a consequence of retinal lateral inhibition that causes the reaction time to increase with increasing target size. 

Express-latencies, on the other hand, were quite different in one of the animals ("G") and fairly constant in the other ("Omi"). When the target was set to 40° × 40° (the size used in the earlier experiments) and the gap time increased from 120 to 300 ms, the reaction times increased almost linearly from 35 to 70 ms. When the gap time was set to 100 ms, the reaction time was around 25 ms. In this case the gap was probably the limiting factor and the reaction time limited for the latency of the neural responses in the retina. In the other animal ("Pi") this was also somewhat true, but the reaction time was much smaller and more variable. In this case the latency of the neural responses in the retina was probably the limiting factor. These results thus show that the reaction time of E-saccades is at least partly determined by retinal factors, whereas the reaction time of express-saccades is not.
the area-threshold curves and the latencies to increase again for stimulus sizes above the critical value (Bolz et al. 1982).

By subtracting the minimal retinal response latencies from the reaction time of the E-saccades one gets an idea of how long it takes to program the eye movements (its size and direction) and to finally set the eye in motion. This number turns out to be in the order of 60–70 ms depending on the state of training.

If, on the other hand, one subtracts the reaction times of the E-saccades from those of the R-saccades one obtains a figure of about 40–60 ms, which may also depend on the amount of previous training.

A full discussion of the aspects of the initiation of visually-guided saccades in relation to the properties of the E-saccades will have to take into account the quantitative data that characterize the modifications of the system during prolonged periods of training. These data will be described subsequently.

b. Temporal Aspects of the Initiation of Visually-Guided Saccades

The extremely short and constant reaction times of the E-saccades and the retinal latencies after which the visual system is first informed about the presence and location of the saccade target opens up the question of which of the eye movement related central brain structures would operate fast enough both in terms of receiving the visual information and initiation of the movement.

Visual cortical structures that contain neurons with a saccade-related activity are the frontal eye fields (A9) (Goldberg and Bushnell 1981), the parietal cortex (A7) (Robinson et al. 1978), and the prelunate cortex (Fischer and Boch 1981a, b). The latencies of the visual responses of the neurons are in the order of 60–120 ms in frontal eye fields (Goldberg and Bushnell 1981), 50–200 ms in the parietal cortex (Robinson et al. 1978), 50–120 ms in the prelunate and parietal cortex of the primate gyrius (Boch and Fischer 1983). The latencies of saccadic eye movements following electrical stimulation are 25 ms for the frontal eye fields (Robinson and Fuchs 1969), 30 ms for the prelunate and parietal cortex (Shibutani et al. 1983). Consequently, one predicts a minimal saccadic reaction time of 75 ms. This consideration makes it quite unlikely that any one of these cortical structures can be involved in the computation of the coordinates for an E-saccade or in its final initiation, unless one assumes that the minority of cells that respond after the shortest latencies are the ones that prepare and initiate the saccade. The visual responses of collicular cells have a latency of about 40–80 ms (Wurtz and Albano 1980), respectively, 35–60 ms (Wurtz and Mohler 1976) and saccades occur 20–30 ms after electrical stimulation of the superior colliculus (Robinson 1972; Schiller and Stryker 1972). Thus, from the central visual structures that have not only a passive visual on response but also a presaccadic extra-visual input and from which eye movements can be elicited by electrical stimulation the superior colliculus seems to be a good candidate to be involved in the initiation of the E-saccades. Also, because almost all E-saccades were made as precisely as regular saccades the structure—which ever it is—must provide the correct coordinates for the eye movements in a retinotopic coordinate system. Again the superior colliculus is well suited on the basis of its retinotopical organization. From a viewpoint of timing the primary visual cortex could also mediate the E-saccades. Because latencies of visual cortical responses are in the order of 35–70 ms (Wurtz and Mohler 1976) and also electrical stimulation results in eye movements (Walker and Weaver 1940; Wagmann et al. 1958; Bender 1980). But neurons in the primary visual cortex have no spatially selective enhancement related to saccades (Wurtz and Mohler 1976) and also small spots flashed onto the retina are not very effective stimuli as compared to moving or stationary bars (Hubel and Wiesel 1968). Moreover, the primary cortex alone should be insufficient, because after ablation of the colliculus electrical stimulation of the primary visual cortex no longer elicits saccades (Schiller 1977). On the other hand, the colliculus alone is also insufficient, because after ablation of the striate cortex monkeys can neither detect nor saccade to a visual target (Mohler and Wurtz 1977). After all, the question of the pathway for the express-saccades and the cortical contribution remains open until corresponding experiments are available using the gap paradigm.

In an intact animal there still remains the other question: Why are not all visually guided saccades of the express type? This question can be answered at least in part by looking at situations where no E-saccades are made, i.e. when the saccade target appears well before the offset of the fixation spot. In this case saccades have reaction times of more than 200 ms (Boch and Fischer 1983; Saslow 1967) and neurons in the frontal eye fields (Bushnell and Goldberg 1979), in the superior colliculus (Mays and Sparks 1980), and in the prelunate prefrontal cortex (Fischer and Boch 1981a) exhibit a presaccadic activity with a long latency measured from the offset of the fixation spot. If this activity is triggered by the breaking of active fixation (i.e. the offset of the fixation spot) and if this same activity is a prerequi-
site for a goal-directed eye movement to occur, then one understands why in the gap situation, where this process of breaking fixation is already completed at the onset of target, the saccadic reaction times are much shorter, i.e., in the order of 130–150 ms. There still remains the question, why on one gap trial an E-saccade occurs and in another the monkey makes a R-saccade.

This could be explained if in some cases the breaking of active fixation also triggers a process of decision to make a saccade, whereas in other cases this decision-making process is started by the target onset. In case the breaking of fixation and the decision are already completed at the time the target occurs, only the computation of the retinal coordinates for the saccade is needed before the final motor command can be delivered. In the latter case one could expect a rather short reaction time.


c. Comparison with Saccadic Reaction Times in Humans

Comparable measurements of saccadic reaction times in humans by using gap paradigms have been described by Saslow (1967) and Becker (1972). Shortest reaction times were in the range of 120–130 ms after gap durations of 120–160 ms between the onset of central target and the onset of peripheral target (Becker 1972). The minimal values of saccadic reaction times were in the order of 130 ms at a gap duration of 300 ms for the subject H.C. of Saslow (1967). These saccadic reaction times are about 100 ms shorter than those triggered by the onset of the peripheral target when the central spot went off simultaneously (Zambardini et al. 1982). In this saccade task the saccadic reaction times of 210–230 ms did not seem to be influenced by changing the eccentricity of the target in the range between 5° and 30°.

Using an optical forewarning signal at different times before a peripheral target appears leads to saccadic reaction times between 240 and 320 ms (Ross and Ross 1980). Because in this case the warning stimulus was presented to the fovea and remained visible throughout the rest of the trial one can assume that the process of breaking fixation was not terminated at the time of the occurrence of the peripheral target and, therefore, extended the reaction time. The saccadic reaction times obtained with this kind of foveal warning are in the same range as the saccadic reaction times described by Frost and Pöppel (1976) when the new target appears while the central fixation spot remained visible. In this case the saccadic reaction times were independent of the target eccentricity between 5° and 45°.

It should be noted that also in humans the saccadic reaction times reach minimal values of about 130 ms only if there is a gap between the onset of central fixation spot and the onset of the peripheral target (Saslow 1967). These reaction times are in the order of the SRTs of the R-saccades in the monkey as described above. So far, saccadic reaction times in the order of 70–90 ms have not been reported for humans.

Acknowledgement. The help of Mrs. U. Amann during training the animals and taking the data is gratefully acknowledged. This work was supported by the Deutsche Forschungsgemeinschaft (DFG), Sonderforschungsbereich “Hirnforschung und Sinnesphysiologie” (SFB 70, Tp B7).

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Received August 5, 1983