Vision Res. Vol. 16, pp. 425 to 427. Pergamon Press 1976. Printed in Great Britain.

RESEARCH NOTE

DO CORRECTION SACCADES DEPEND EXCLUSIVELY ON RETINAL FEEDBACK?

A NOTE ON THE POSSIBLE ROLE OF NON-RETINAL FEEDBACK

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(*Received* 14 *August* 1975)

The saccadic response of the human oculomotor system to step-like displacements of a target frequently breaks down into two components: the main saccade that travels about 90–95% of the target distance and one or more correction saccades that eliminate the remaining error. In a recent article in this journal, Prablanc and Jeannerod (1975) investigated the question of the occurrence of correction saccades depending on the presence of a retinal error message at the end of the main saccade. These authors report that they found almost no correction saccade, if the target disappeared within the subject's reaction time, after stepping to a new position. They observed correction saccades only if, at the end of the main saccade, the target was displayed anew for a short while at or near the position from where it had disappeared. From this fact, Prablanc and Jeannerod conclude that retinal feedback is a prerequisite for the correction of the error remaining after the main saccade. The results reported by Prablanc and Jeannerod, however, seem to contradict those of Barnes and Gresty (1973) and our own research (1972), both of which provided evidence for truly corrective saccades in the absence of visual feedback. We, therefore, discussed the apparent contradictions between our work and their own with Prablanc and Jeannerod. On the basis of these discussions, we feel that the contradictions may be reasonably explained by different experimental procedures and that a hypothesis may be advanced that explains the results of both investigations.

Before developing the pertinent arguments, I should like to briefly comment on the explanations of Prablanc and Jeannerod in their paper as to the conflicting results. They reason that in our experiments the subjects had the opportunity to learn that the response is generally hypometric and that the subjects, therefore, would schematically execute a secondary saccade, the size of which, however, would be unrelated to the actual error, if the target had disappeared prior to the main saccade. This is not the case: applying an analysis of covariance to the experimental situation depicted in Fig. 1, we found that the initial error at the end of the main saccade (e) and the drift (D) resulting from the attempt to fixate an eccentric position in the dark (Becker and Klein, 1973) are by far the most important sources of variation for the sum of secondary saccades in the dark (a). Furthermore, the computation of the multivariate regression yields: $a = 0{\cdot}8\ e + 0{\cdot}7\ D$, i.e. in our paradigm we obtain truly corrective saccades that eliminate about 80% of the initial error and 70% of the error caused by drift, without the assistance of retinal signals.

Proceeding to the question of how the differences of experimental procedure lead to apparently contradictory results our reasoning is as follows:

(1) In Prablanc and Jeannerod's experiment the target always reappeared at the center position after the dark period subsequent to its short presentation at a new peripheral position. The subjects were simply

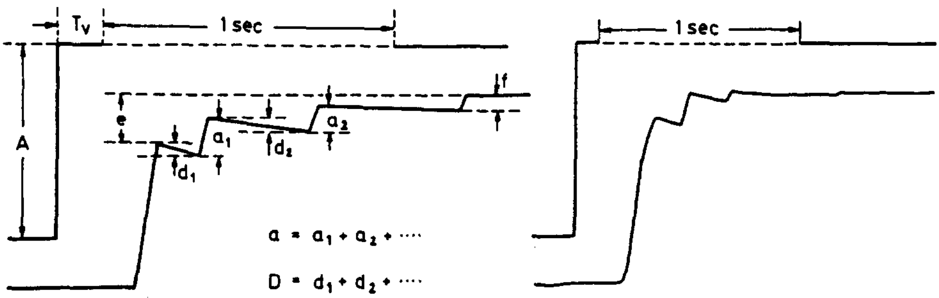

Fig. 1. Left: Stimulation pattern as used for the investigation of correction saccades without retinal feedback (upper trace) and schematized eye movement response showing the definition of the relevant parameters (lower trace). After a step of amplitude A, the target either remains continuously visible (50% of the cases) or disappears from its new position after a short presentation time T_v, reappearing only after a 1 sec period of darkness. T_v varies between 50, 100 and 200 msec and A is 20, 30, 40, 50 or 60°. All conditions are randomized. If the target disappears, the response generally consists of a main saccade having an error e, of secondary saccades during the dark period of amplitudes a_1, a_2 ... and of a final correction f, when the target reappears. In addition, there is a drift towards the center that causes a change of eye position in the dark period of magnitude D. For sake of clarity the drift is shown exaggerated. Right: Typical response to a 60° target step with 100 msec presentation time.

told to "follow the target" and therefore probably attached equal importance to both getting to the peripheral position and returning to the center. Since the target's reappearance at the center happened regularly after 1 sec, the subjects undoubtedly anticipated this, as suggested by their returning to the center after only 400 msec of peripheral fixation. To judge from experience, subjects seem to concentrate, in this situation, on regaining the center position as rapidly as possible rather than making fine adjustments for a target that has already disappeared. In our paradigm, by contrast, the target always reappeared at the position where it had disappeared from, thus inciting subjects to remain at the "virtual" target position until reappearance.

As can be seen from Fig. 4c of Becker (1972), the latency of corrections without retinal feedback is rather long. This makes it probable that the anticipatory return in Prablanc and Jeannerod's experiment occurred at about the same moment the correction would have been elicited had the subject tried to remain on the virtual target. Moreover, even if the subject suppressed its premature return and executed a correction, Prablanc and Jeannerod would not consider this a "correction saccade", since, according to their terminology, correction saccades must have a short latency (Jeannerod, personal communication).

(2) The investigation of Prablanc and Jeannerod was restricted to a maximal target displacement of 20°. In the normal situation of a continuously visible target this range of target angles yields at best an average error of 2–3°, and the probability of correction saccades decreases rapidly as the target distance falls below 20°. In our experiments, we considered target angles from 20° to 60° where correction saccades occur quite regularly and reach amplitudes up to 9°. Our data show that in the situation where the target disappears, errors of less than 3° are rarely corrected whereas larger errors are almost regularly. Therefore, we feel that in Prablanc and Jeannerod's paradigm, the probability of obtaining errors that necessitate saccadic corrections, is lower than in ours and that, if there is an error, it is likely not to exceed a threshold necessary to elicit corrections without retinal feedback.

A theory accounting for most of the observed phenomena in Prablanc and Jeannerod's experiment as well as in ours would be as follows:

During the preparation or the execution of a saccade a nonretinal amplitude feedback is compared to the command amplitude. The resulting error signal is capable of preparing a correction saccade prior to the arrival of the retinal afferents. However, this signal has a range of uncertainty of about $\pm 2°$ and is therefore unsuitable for measuring errors of less than 2° or 3°. Consequently, as long as the actual error does not exceed a threshold of 2–3°, the preparation of the correction saccade is only started when the retinal error signal arises. If, on the other hand, the actual error exceeds a 2–3° threshold, the extraretinal error signal is used to prepare the correction saccade. This non-retinal correction will not be executed, however, until the retinal message becomes available for verification. If the latter confirms the prepared direction and if there are only minor differences of size, the prepared amplitude will be modified according to the retinal signal and the correction executed instantaneously thus saving time over the normal saccadic reaction time. By contrast, if there are gross discrepancies, the already prepared correction is cancelled and the retinal signal elicits a new decision process leading to a saccade within a normal reaction time.

The latter situation will happen only if the target changes its position at the end of the main saccade, as it was the case in Prablanc and Jeannerod's "double pulse" paradigm. It is obvious that the increase of correction latency observed in this paradigm does not permit any conclusion as to the dependence of the correction latency on the error size. While it takes a long time to correct large errors of, say, 20° that are induced artificially by the experimenter and which therefore contradict the non-retinal feedback, the opposite is true if errors of that size are signalled through the extraretinal pathway. The latter situation arises, if a saccade aiming at 40° or so, falls short of the intended target by 50% or more; although an exception from normal behaviour, this occurs sporadically in almost all subjects. When an error of 20° is sensed by the non-retinal feedback, a corresponding correction is executed as soon as possible without waiting for verification by the retinal signal. Thus, the latency of the resulting correction will be even shorter than the 120 msec minimum typical for correction saccades. Waiting for fine adjustments of amplitude by the retinal message would make no sense in this situation, since the required 20°-correction saccade itself will be as inaccurate as any other saccade of that size.

Finally, if the retinal signal fails to arrive after the main saccade as is the case in the present experiments, and if the error exceeds the threshold of 2–3°, the correction is executed as commanded by the non-retinal feedback, but with some delay.

In summary, this theory predicts four different cases for the normal situation of a continuously visible target:

(1) The error is below 2–3°. The correction latency equals the normal saccadic reaction time.

(2) The error is above 2–3° but not excessively large ($< 10°$ or so). A correction saccade results with a latency of 120–140 msec.

(3) The error is extremely large ($> 15°$ or so). A correction occurs within 50–80 msec.

(4) At the end of the main saccade the target position changes by a large amount. The eyes get at the new position after a normal reaction time at best.

The normal relation between the latency and the size of correction saccades as given by Becker (1972) is composed of cases 1 and 2. As mentioned above, case 3 is seen sporadically when large saccades are attempted. Case 4 has been demonstrated by Prablanc and Jeannerod in their double pulse experiment.

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