KINEMATICS OF CENTRIFUGAL AND CENTRIPETAL SACCADIC EYE MOVEMENTS IN MAN

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Abstract—The kinematics of centrifugal and centripetal saccadic eye movements were quantified in human subjects. The maximum velocity of centripetal saccades increased with the eccentricity of the orbital starting point and was systematically higher than that of centrifugal saccades starting from primary orbital position. The slope of this linear increase was related to target step amplitude (2.6 and 3.9 deg/sec/deg for 20 and 30 deg, respectively). Despite these velocity changes, saccade amplitude was maintained by corresponding variations of the duration of deceleration. These findings, which are relevant with respect to saccadic control theories, indicate that initial eye position must be considered before comparing saccades based on their kinematic properties.

Saccade kinematics Oculomotor plant Initial orbital position Local feedback Proprioception Man

INTRODUCTION

Human subjects can perform saccadic eye movements ranging from a few minutes of arc to 90 deg. Over this wide range of movements, the maximum velocity of a saccade increases with its amplitude, with a pronounced saturation beyond 20 deg. This relationship, called the main sequence (Boghen et al., 1974; Bahill et al., 1975), shows noticeable inter-individual variations (Boghen et al., 1974); it is further affected by the visual environment (Becker and Fuchs, 1969) and the subject’s state of alertness (Jürgens et al., 1981). Nevertheless, in well controlled conditions, this relationship is quite reliable and can be used to distinguish normal saccades from both abnormal ones and non-saccadic eye movements (Boghen et al., 1974). The main sequence is plotted from data usually collected with saccades starting from the primary position of the eyes and moving toward the periphery of the orbit. However, for a given amplitude, saccades directed toward the primary orbital position (centripetal) are faster than those starting from that position (centrifugal), i.e. the former lie above the main sequence (Frost and Pöppel, 1976; Jürgens et al., 1981; Inchingolo et al., 1987).

Up to now, only two studies have investigated this phenomenon. In the first, Abel et al. (1979) showed that the maximum velocity of 10 deg saccades between 20 and 30 deg orbital positions is significantly affected by their direction, the centripetal saccades being faster than the centrifugal ones. A more recent study (Arista et al., 1986) reported that centripetal saccades starting from a 30 deg orbital position were on the average 100 deg/sec faster (maximum saccadic velocity) than centrifugal ones elicited from the primary position. In both studies, however, the type of relationship between saccade kinematics and initial eye position was not investigated. In addition, no comparison of the accuracy of the two types of saccade was provided. Finally, the underlying processes of these variations in maximum saccade velocity are still unknown; they may be related to modifications of command signals and/or mechanical properties of the oculomotor plant.

As a further insight, the present study was designed to quantify kinematics of horizontal saccades in response to two steps of the visual target originating from three different positions (corresponding to 3 initial orbital positions). Initial eye positions and target step amplitudes were purposely chosen in such a way that the eyes always moved far below their mechanical limits. The questions addressed in this experiment were: (1) Is there, for a given target step, a simple continuous relationship between saccade velocity and initial eye position? (2) Is the effect of initial eye position on saccade velocity
related to saccade amplitude? (3) Is saccade accuracy maintained despite saccade velocity changes, and in such a case, what are the relative contributions of each phase (acceleration and deceleration) of the saccade in the corresponding duration changes?

**METHODS**

The experimental apparatus consisted of a horizontal curved display composed of a dimly illuminated random dot pattern (90 × 7.5 deg of visual angle) and a set of visual targets. The targets were small numbers (10' of visual angle) imprinted on a black photographic film, each being illuminated by a red light emitting diode (LED) located just behind. The subject was seated at the center of the curved display (distance = 1.2 m) and his head was fixed by a bite-plate in a straight ahead position (aligned with the central target).

Binocular horizontal eye position was recorded by an electro-oculographic (EOG) technique with a band-pass from d.c. to 80 Hz. Just before each peripheral target presentation, while the subject was looking straight ahead at the central target, the EOG signal was reset to cancel any offset related to signal drift. After at least 15 min of adaptation to darkness, the EOG signal was calibrated as follows: eight peripheral targets 10 deg apart (from 40 deg on the left to 40 deg on the right of the central target) were presented in sequence and the EOG signal measurement was triggered by the subject himself as soon as he could identify the target. Reading the small numbers required foveating the target and ensured an accurate fixation when the EOG signal was measured. The eight calibration samples were then fitted by a polynomial function which was used for off-line linearization of EOG signal (with an 8-bit resolution, i.e. 0.5 deg). The EOG signal was calibrated before and after each experimental session so that eventual variations of EOG gain during the corresponding time could be corrected off-line, based on the ascertained hypothesis of a quasi linear relationship between EOG gain and elapsed time. Eye position recording was accurate within ±0.5 deg as estimated from the mean error after the last corrective saccade.

Calibration procedure, random target selection during experimental sessions, EOG signal sampling (1000 Hz frequency), off-line EOG linearization and interactive display of every single response were under the control of a program running on a DEC PDP 11/23 computer. This program allowed anticipated responses or those contaminated by EMG noise or blink to be rejected, the corresponding trials being represented later on in the same experimental session. After linearization, onset and completion of each main saccadic response were manually detected by positioning cursors on the eye position trace displayed by the computer (resolutions: 2 msec and 0.6 deg): duration, amplitude and their ratio (mean velocity) were thus obtained. Eye position was differentiated with a 30 Hz filtering by a polynomial regression method to compute 3 other parameters: maximum velocity, duration of acceleration and deceleration phases.

**SUBJECTS AND PROCEDURE**

Eight members of the laboratory (4 males and 4 females) without known visual or oculomotor deficits went successively through the experiment; they were required to carefully track the visual target whenever its position changed. Centrifugal (CFG) and centripetal (CPT) saccadic responses to 20 and 30 deg target steps were studied in 3 separate conditions which differed only by the initial position of the target before the step. In the first condition ("CFG-0"), the initial target position corresponded to the central position (0 deg) so that the saccades started from the primary orbital position and were purely centrifugal. In the second condition ("CPT-10") in which the target crossed the center by stepping from a 10 deg eccentric position, saccadic responses had a 10 deg centripetal component. In the last condition ("CPT-20"), depending upon the amplitude of the step which originated from a 20 deg eccentric position, the target crossed the center (30 deg target step) or jumped toward primary position (20 deg target step), eliciting either saccades with a 20 deg centripetal component or purely centripetal saccades, respectively. Each target step was presented 16 times (8 on each side) in a random order; the order of testing of the three conditions was balanced over the 8 subjects.

The general shape of the responses were first qualitatively determined: 6 (2 target steps × 3 initial eye positions) position and velocity time-courses were averaged over 128 responses each (8 subjects × 16 repetitions). In order not to produce a distortion of the mean profile, individual velocity profiles (filtered at a 40 Hz cut-off frequency) were first scaled in the time
domain only, i.e. they were compressed or expanded to fit the mean saccadic duration. Then, after averaging, the 6 velocity profiles were integrated to obtain the corresponding position profiles. Only for this particular qualitative shape description did we use a scaling procedure.

In a second stage, the parameters computed on each individual raw eye response (see above) were submitted to a 2 level (3 conditions x 2 target steps, 8 repetitions) analysis of variance. Each of the 8 repetitions considered in the analysis is the average over 16 responses for a given subject, a given target step and a given condition.

RESULTS

Figure 1 shows the average shape of saccades in response to 30 and 20 deg target steps. Individual responses being synchronized with respect to saccade onset, the duration of averaged signal (solid lines) does not include the non-synchronized corrective saccades. Thus, in the upper part of the figure, the dotted lines drawn on the right of the responses represent mean eye position after the main saccade, irrespective of corrective saccades which were actually observed to bring the eye on target. By examining only eye position time-courses, it would be tempting to conclude that there is a similarity between the different saccadic eye movements, especially in response to the 20 deg target step. However, kinematic differences appear much more clearly when examining the corresponding velocity profiles (Fig. 1, bottom). Indeed, a more eccentric initial orbital position leads to greater maximum velocity and shorter duration of the saccade. This holds for both targets steps, although less pronounced for the smaller one. These averaged responses show a striking invariance of the acceleration phase duration, defined as the time elapsed between onset and maximum velocity of the saccade. This invariance of velocity rise-time combined with the observed changes in saccade duration result in a gradual variation of velocity profile asymmetry according to initial eye position. Finally, the accuracy of the saccades is similar in all conditions: indeed, the main saccade falls short of the target roughly to the same extent in all three conditions (Fig. 1, top). A quantitative analysis of these effects of initial eye position is presented below.

Maximum saccade velocity is plotted against initial eye position in Fig. 2 (upper part). The leftmost points show that centrifugal responses (initial eye position = 0 deg) to both target steps reach a similar maximum velocity (400 deg/sec) in agreement with the known saturation of the main sequence relationship beyond 20 deg (Becker and Fuchs, 1969; Boghen et al., 1974;...
Frost and Pöppel, 1976). However, when the centripetal component of the saccade increases (initial position 10 and 20 deg), a corresponding increase in maximum velocity is observed, which reaches a statistically significant level ($F_{2,42} = 4.6, P < 0.05$). It should be emphasized that, although maximum saccade velocity shows a great inter-subject variability (individual means over both target steps range from 329 to 486 deg/sec for “CFG-0” condition and from 397 to 546 deg/sec for “CPT-20” condition), a statistically significant increase in maximum velocity between “CFG-0” and “CPT-20” conditions is present in every subject and for both target steps ($t$-test, $P < 0.05$). This almost linear relationship is observed for both saccade amplitudes, with a steeper slope for the larger (3.9 deg/sec/deg) than for the smaller saccades (2.6 deg/sec/deg).

In the lower part of Fig. 2 is plotted the ratio of maximum over mean velocity. Its average value ($1.6 \pm 0.1$), as well as its invariance with respect to initial eye position, both confirm previous data (Inchingolo et al., 1987). Neither initial eye position nor target step amplitude significantly affect this parameter ($F_{2,42} = 1.5$ and $F_{1,42} = 0.0$; NS), indicating a tight covariation of maximum and mean saccade velocities. Indeed, the different experimental conditions qualitatively affect mean as well as maximum saccade velocity in the same way: the mean velocity increases significantly with initial eye position ($F_{2,42} = 8.1, P < 0.01$); for each of the 2 target steps, this relationship can be approximated by a linear function, whose slope is steeper for the larger (3.0 deg/sec/deg) than for the smaller saccades (1.5 deg/sec/deg). This increase of mean velocity results only, as seen from the shape of average saccadic responses (Fig. 1), from a shortening of saccade duration while keeping saccade amplitude constant.

To show the relative contributions of acceleration and deceleration components in the observed variations of saccade duration, these components were separately analyzed. They are represented in Fig. 3 for 20 and 30 deg target steps, and the total saccade duration corresponds to the height of both super-imposed hatched and white columns. As expected from these observations, the duration of saccades to both target steps decreases when the eyes start farther away from the midline ($F_{2,42} = 8.2, P < 0.01$). Furthermore, it should be pointed out that the deceleration phase is fully responsible for this shortening of saccade duration since it is significantly related to initial eye position ($F_{2,42} = 14.6, P < 0.001$) while the slight variations of the acceleration phase are not statistically significant ($F_{2,42} = 0.4, NS$). These results indicate that, for a given target step amplitude, the duration of acceleration is rather stereotyped while the maximum velocity reached depends largely upon initial eye position. Regarding the lengthening of saccade duration with
Centrifugal and centripetal eye saccades

Fig. 4. Saccade accuracy. Histograms of main saccade amplitude were constructed on 128 responses to the target steps indicated by vertical arrows; means are shown by short vertical lines (X). Neither the means nor the scatter of the distributions are affected by initial eye position.

target step size, the two phases of saccadic responses are again differentially affected. Although both significantly increase with target step amplitude ($F_{1,42} = 9.8$ and 144, $P < 0.01$ and $P < 0.001$ for acceleration and deceleration phases, respectively), most of the saccade duration difference between 20 and 30 deg responses is accounted for by the second phase (Fig. 3).

The last parameter analyzed, saccadic accuracy, is shown in Fig. 4 by the distributions of saccade amplitude. The main saccade generally undershoots the target by an average of 7% as classically reported (Becker, 1972; Prablanc et al., 1978). In addition, our different experimental conditions do not significantly affect saccade amplitude ($F_{2,42} = 1.2$, NS). The figure also shows that the variability of saccadic accuracy is similar in all conditions. It should be added that after the main saccade, glissadic eye movements were rarely observed; in addition, such atypical responses, present in only one subject, were totally unrelated to initial eye position.

**DISCUSSION**

The present study confirms that centripetal saccades are faster than centrifugal ones, as previously reported (Frost and Pöppel, 1976; Abel et al., 1979; Arista et al., 1986; Inchingolo et al., 1987). In addition, quantification of kinematics of goal-directed saccades provides the following information: (1) for a given amplitude, saccade velocity is linearly related to the initial eye position over the 20 deg range studied, i.e. the larger the centripetal component the faster the saccade. Moreover, this effect is more pronounced for larger saccades; (2) despite these velocity changes, saccadic accuracy is maintained through corresponding variations of the duration of the deceleration phase, while the duration of the acceleration phase seems rather stereotyped.

It has been known for many years (Robinson, 1964) that for a saccade to occur, a pulse-step signal must be sent from oculomotor nuclei to the extraocular agonist muscles; a high frequency phasic activity (pulse) is required for the eyes to move quickly against high viscous forces and a regular tonic activity (step) to hold the eyes at their new position against elastic restoring forces. In addition, the kinematic parameters of the saccade (maximum velocity, duration and amplitude) are accurately encoded by pulse signal characteristics (Fuchs et al., 1985). These observations have led to a fruitful generation of models of the saccadic system, in which only one type of non-linearity, located at the level of pulse generation, is able to explain the known saturation of the main sequence relationship. In these approaches (see Robinson, 1975), the neural command sent to a given pair of muscles would appear to precisely encode the desired saccade amplitude and is thus supposed to be independent of initial eye position. The simulation of saccades from different initial eye positions through such models undoubtedly leads to equal saccade kinematics regardless of initial eye position. Thus, the changes in maximum saccade velocity, reported in our and other studies, require investigation of other possible non-linearities at the level of either command signals or ocular mechanics, or both.

The known anatomical connections between the pulse generator for horizontal saccades (the paramedian pontine reticular formation) and the muscles suggest that the antagonistic pair of muscles is organized in a push-pull arrangement (see Fuchs et al., 1985). As a consequence, the phasic command would apparently produce opposite but proportional modulations of firing frequency in the agonist (pulse of activation) and in the antagonist muscles (pulse of deactivation). However, electrophysiological recordings from motoneurons in monkey have
shown that for a given saccade amplitude (except perhaps for saccades smaller than 10 deg), antagonist motoneurons are totally inhibited irrespective of initial eye position (Fuchs and Luschei, 1970; Robinson, 1970). Therefore, since a deactivation is unable to further build up in silent antagonist motoneurons, the intensity of the deactivation is equal to that of previous tonic activity. Since this activity increases linearly with the ocular deviation toward the muscle concerned, the possibility remaining for deactivation of the antagonist muscle is proportional to the initial eye deviation in the opposite direction to the saccade (Off direction). This would imply that the pulse of deactivation is largely truncated. Moreover, the smaller the initial eye position in the Off direction (i.e. the smaller the initial centripetal component) the greater the effect of truncation of pulse deactivation. Such a loss of signal between premotor burst neurons and motoneurons, related to the low tonic activity of the latter and proportional to initial eye position, is thus a reasonable explanation of the observed linear increase of maximum saccade velocity with initial centripetal component.

Regarding the other aspect of the command, a saturation of the pulse of activation has been described in motoneurons (Robinson, 1970). Indeed, for a given saccade size, the frequency of the phasic discharge of these cells became saturated when the corresponding saccades were elicited from progressively more eccentric positions in the On direction. From this saturation, also reported at the muscular activity level in man (Collins, 1975), we can predict a progressive maximum velocity decrease with ocular deviation in the On direction. This hypothesis was not tested in the present experiment. However, it seems to be confirmed by a reduced velocity for 15 deg centrifugal saccades initiated from a 30 deg eccentric position when compared to 15 deg centrifugal saccades initiated from the primary position (Arista et al., 1986). The saturations of both agonist activation and antagonist deactivation with increased initial position from Off to On direction represent a progressive decrease of the global neural command. With regard to saccade amplitude, such a neural command non-linearity predicts that small saccades, generated by unsaturated commands, are less affected by initial eye position than are larger ones. This prediction seems to be supported by the quite different slopes of maximum and mean velocity vs initial eye position relationships found in the present experiment, and by the other data available to date (Frost and Pöppel, 1976; Arista et al., 1986; Inchingolo et al., 1987).

Mechanical non-linearities have been described at the level of the oculomotor plant. In cat (Robinson, 1964) and in man (Collins, 1975) extraocular muscles have non-linear length-tension relationships, with an increased stiffness of the stretched (antagonist) muscle with ocular deviation. In addition, the viscous properties of the mechanical plant also seem non-linear (Cook and Stark, 1968; Collins, 1975). However, accurate simulations of the oculomotor plant are required to assess the effect of these mechanical non-linearities and of their complex interplay on the kinematics of saccades initiated from different initial positions. In summary, although the non-linearity of neural commands seems to be a reasonable explanation of the observed velocity changes, peripheral non-linearities cannot yet be ruled out.

The present study shows a decreased duration of the saccade when its centripetal component increases. It has been well documented that the duration of a saccade is accurately determined by the duration of the pulse signal (see Fuchs et al., 1985). It could be argued that in our experiment saccade duration changes are also related to viscosity changes of the oculomotor plant with initial eye position. However, the absence of glissadic eye movements suggests the existence of a tight covariation between durations of pulse signal and saccade, regardless of initial eye position. Thus, variations in saccade duration are likely to be determined to a large extent by a modulation of phasic command duration.

It is very important to stress that, regarding the maximum velocity variations, the duration changes are very appropriate for maintaining the accuracy of saccades, whatever their starting orbital position. This finding would indicate that the amplitude of a saccade can be controlled independently of its velocity. The mere observation of different saccade durations (i.e. different pulse durations) for a target step of a given amplitude precludes pulse duration to encode only the size of the retinal error. As a consequence, one may question about the central mechanisms involved in saccade duration modulations.

The notion of a feedback control of saccadic accuracy is now well accepted (Robinson, 1975; Hallett and Lightstone, 1976a, b; Mays and...
Centrifugal and centripetal eye saccades

It has been invoked to explain the stability of saccadic accuracy through an increase of saccade duration in cases of abnormally slow saccades (Zee et al., 1976; Jürgens et al., 1981). In most models of the saccadic system, it is generally assumed that the signal fed back to the saccadic controller is an efferent copy signal of eye position [local, or internal, feedback loop (Robinson, 1975)].

Among the many studies dealing with the control of saccadic accuracy via saccade duration, one of them is critical with respect to the origin of the maintenance of saccade amplitude, for saccades originating from different orbital positions. Ritchie (1976), in a lesion study in monkey, showed that the cerebellum was involved in such a type of control. The most salient effect resulting from the lesion of vermal and paravermal zones was a saccadic dysmetria related to initial orbital position: centripetal saccades overshot the target while centrifugal ones were either normometric or undershooting. In fact, centripetal saccades, which were faster than the others, overshot the target because their duration was not correspondingly reduced. These findings clearly indicate that the mechanisms controlling the accuracy of saccades starting from different positions were no longer operating in the lesioned animals. Optican and Robinson (1980), who also reported position and direction-dependent saccadic dysmetria in cerebellar-lesioned monkeys, have suggested that the cerebellum could act as an interface between visual commands and motor performance, thereby making saccades accurate regardless of position and direction.

Since the corresponding lesioned cerebellar area receives proprioceptive afferents from extraocular muscles (Fuchs and Kornhuber, 1969; Baker et al., 1972), this would suggest an unexpected role of proprioception in saccadic accuracy control. In addition, the various nonlineairities invoked above to account for the maximum velocity variations with initial eye position, would imply that proprioceptive information is more suitable than an efferent copy information to ensure an accurate control of the saccade, as already suggested (Kornhuber, 1973; Jürgens et al., 1981). However, due to its time lag, a hypothetic contribution of proprioception can hardly be regarded as a real-time feedback process, but rather as a feedforward process. In any case, this hypothesis does not exclude the major role of the local feedback loop, the existence of which has been definitively shown by Guthrie et al. (1983). Following a perturbation of eye position induced by collicular stimulation, these authors showed that a compensation takes place with no need for proprioceptive information. However, in more natural conditions, proprioceptive information about initial eye position could introduce initial parameters within the local feedback loop to maintain saccadic accuracy despite eccentric initial eye positions.

In conclusion, our results clearly indicate that initial eye position is a parameter which should be considered when comparisons between saccadic responses are based on their kinematic properties (characterized by their main sequence and shape). The main sequence depends in fact both on the initial eye position and on the On or Off direction of the saccade (more centrifugal or more centripetal). Further, this study also shows that the accuracy of saccadic responses can be achieved independently of their velocity, even when operating in normal conditions.

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