SKEWNESS OF SACCADIC VELOCITY PROFILES: A UNIFYING PARAMETER FOR NORMAL AND SLOW SACCADES

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Abstract—It has become customary to make use of so-called main sequence plots to characterize the dynamic properties of saccades. However, such a description does not account for the fact that the ratio between the accelerating and the decelerating fraction of the eye movement is not constant for all saccades. In this paper we introduce a new parameter, skewness, that characterizes this much neglected aspect of the saccade velocity profile. Human saccade data in this report demonstrate a clear relation between saccade duration (D) and skewness (S). When saccadic eye movements become extremely slow, due to fatigue or diazepam, the main sequence relation breaks down, while the S-D relation still holds. Despite large differences in amplitude, saccades of a fixed duration appear to have the same shape of velocity profile. A unifying equation relating the saccade parameters amplitude, maximum velocity and skewness, which is valid for both normal and slow saccades, is proposed.

INTRODUCTION

It is a well-documented fact that normal saccades in both man (Westheimer, 1954; Yarbus, 1956; Mackensen, 1958; Robinson, 1964) and monkey (Fuchs, 1967) obey rather stereotyped amplitude (A) vs duration (D) and amplitude vs maximum eye velocity (V_max) relations. In the literature these relations are known as the “main sequence” for saccades (Bahill et al., 1975). The typical A-D relation in man can be described by a straight line over a wide range of saccade amplitudes, while the A-V_max relation shows soft saturation for amplitudes beyond 20 deg. In both clinical and pure scientific work it has become customary to quantify the dynamic behaviour of saccades in this way. In the clinical setting the main sequence is used as a standard for the definition of pathological conditions in the saccadic system and thus has become a diagnostic tool of considerable importance. At a more fundamental level, the main sequence relations have called attention to the fact that the saccadic system as a whole is nonlinear (Westheimer, 1954; Robinson, 1964), a property which constitutes an interesting challenge for explanation from the modelling point of view. In Robinson’s internal feedback model (Robinson, 1975; Zee and Robinson, 1979; Van Gisbergen et al., 1981), the main sequence relations reflect a single nonlinearity, embodied by so called medium lead burst cells.

Although the main sequence is a readily applicable tool for characterizing dynamic properties (D and V_max) of normal saccades, with widespread clinical applications, one should be aware that it cannot provide a complete description of saccade dynamics. An important aspect which is not covered by such a reduced description based on only 3 parameters, concerns the shape of the saccade velocity profile (see Fig. 1). It has been noticed in the literature that the accelerating phase (D_a) of the eye movement in man has a roughly constant duration for all amplitudes, while the decelerating portion of the movement (D_d) is prolonged when saccade amplitude increases (Hyde, 1959; Baloh et al., 1975). This means that saccades of different amplitudes have differently shaped velocity profiles. Small saccades appear to have a rather symmetrical profile, while in large saccades the velocity profile has a more skewed appearance. Since its discovery, this phenomenon has received little further attention and has never been accounted for in models of the saccadic system.

In the present paper we propose a new, objective method for characterizing the shape of
the saccade velocity profile, based on a mathematical function fit to the entire velocity profile. Our data show a positive correlation between saccade amplitude and a shape parameter of the velocity profile, skewness, obtained by the curve fitting procedure. However, further analysis of the data has revealed that skewness (S) shows a significantly better correlation with saccade duration than with amplitude.

A second feature of the saccadic system that deserves more attention than it has received so far, is the occasional occurrence of abnormally slow saccadic eye movements. These movements, which do not obey the main sequence, are often regarded as nontypical and excluded from further analysis. Yet, under certain experimental conditions, normal main-sequence saccades are the exception rather than the rule. For example, slow saccadic eye movements occur rather systematically when subjects are required to make saccades to nonvisual targets (Smit et al., 1987) and after the application of certain centrally acting drugs (Aschoff, 1968; Rothenberg and Selkoe, 1981; Hikosaka and Wurtz, 1985). We have attempted to find a more comprehensive quantitative description of saccades, which incorporates these slow somewhat atypical movements. It will be shown that slow saccades disrupt the normal A–S relation, but still obey the same D–S relation as normal main-sequence saccades. We propose a simple generalizing equation, which incorporates all of these properties.

Part of the results in this paper were published elsewhere in a preliminary form (Van Gisbergen et al., 1984).

METHODS

Horizontal saccades to the right were elicited by a spot of light (0.4 deg; 5 cd/m²) which jumped, after a randomly varying period of 0.5–1.1 s, from the initial position to one of 8 randomly selected peripheral locations on a tangent screen at 57 cm. Background intensity was 1.2 cd/m². Horizontal and vertical movements of the left eye were measured by double magnetic induction (Bour et al., 1984). In order to cancel the contribution of the primary magnetic field (see Bour et al., 1984), the adjustable compensation coil was positioned above the subject's right eye. The raw eye position signals were low pass filtered (−3 dB at 150 Hz) and sampled at a rate of 500 Hz in each channel. By positioning the detection coil eccentrically relative to the suction ring on the left eye, a measuring range of 0–35 deg was available in one quadrant of the visual field. Resolution was 0.25 deg or better, in the range 0–25 deg. After linearization (Bour et al., 1984), vectorial eye velocity was computed from the position signals by differentiation using the central-difference algorithm (Bahill et al., 1982) followed by smoothing with a symmetrical digital filter (−3 dB at 72 Hz; Rabiner, 1970).

Saccade duration was determined automatically by computer, making use of a 30 deg/sec eye velocity criterion. The onset was defined as 4 msec before this level was crossed, whereas saccade offset was taken to be 4 msec after eye velocity fell again below this criterion. Saccades which had abnormal double or multi-peaked velocity profiles, as well as saccades with
durations exceeding 160 msec, which were often associated with blinks, were excluded from analysis. These movements always constituted less than 3% of the raw data set.

Experiments were done on 8 subjects with ages ranging from 22 to 42 years. Seven of the subjects were experienced males; the female subject (M.J.V.G.) was naive. At least 79 saccades were measured in each subject but in four subjects more than 135 saccades were collected. Two of the subjects (J.V.G. and A.S.) participated in an experiment in which a broader range of saccade durations was required. In order to achieve this, both subjects received 7 mg of diazepam intravenously (Aschoff, 1968; Rothenberg and Selkoe, 1981; Tedeshi et al., 1983), after the calibration data and control data were collected. Informed consent was obtained.

Curve fitting of saccade velocity profiles

Saccade velocity profiles were fit with a mathematical function in order to characterize their shapes. The present results were obtained using the so-called density function of the gamma distribution \( y = \text{gamma function for short;} \) (Abramowitz and Stegun, 1972)

\[
v(t) = a \cdot \left[ \frac{t}{\beta} \right]^{-1} \cdot \exp \left[ -\frac{t}{\beta} \right] \quad t \geq 0; \beta > 0; y \geq 1
\]

where \( v(t) \) is the saccade velocity profile; \( a \) and \( \beta \) are scaling constants for velocity and duration, respectively, and \( y \) is a shape parameter which determines the degree of asymmetry. Small \( y \) values imply asymmetrical velocity profiles; as \( y \) goes to infinity the function assumes a symmetrical (Gaussian) shape.

The iteration procedure to determine the best fit started from initial parameter estimates based on computation of the first three central moments of the velocity signal (for details, see Appendix 1). Curve fitting was done using the least-squares error criterion (Hartley, 1961; Jennrich and Sampson, 1968). When the initial parameter estimates were deliberately changed, the iteration procedure generally took longer but still converged on the same solution. For most saccades, \( y \) values were in the range between 2 and 15. Since our interest is mainly in the shape of the saccade velocity profiles, the parameters \( a \) and \( \beta \), which reflect differences in maximum velocity and duration, will not be considered here.

Skewness can be derived directly from \( y \) using the relation (Abramowitz and Stegun, 1972)

\[
S = \frac{2}{\sqrt{\gamma}}
\]

It should be noted that the precise \( y \) value found by the fitting procedure varies in a rather predictable way with the definition of the onset criterion of the velocity profile. Near saccade onset, the gamma function behaves roughly as

\[
v(t) = a \cdot \left[ \frac{t}{\beta} \right]^{-1}
\]

When saccade onset is taken at an early point in time, where the velocity profile still rises rather gradually, higher \( y \) values will be found than in the case of a later onset criterion. In a previous paper (Van Gisbergen et al., 1984), where slightly different onset and offset criteria were used, accordingly somewhat lower skewness values were obtained.

Alternative measures for velocity-profile asymmetry

In order to exclude that our findings on skewness values derived from the gamma function are due to some mathematical artifact (see below), we have also explored alternative measures. Skewness can be computed directly by determining the third central moment, if the velocity signal is conceived of as a distribution along the time axis. By definition

\[
S = \frac{\int_{0}^{\infty} (t - \mu)^3 |v(t)| dt}{\sigma^3 \int_{0}^{\infty} |v(t)| dt}
\]

where \( \mu \) is the expectation value (first central moment) and \( \sigma^2 \) is the variance (second central moment) of the velocity profile, \( v(t) \). As can be seen from this equation, the contribution to \( S \) increases strongly with time. Accordingly, noise long after saccade offset may easily dominate the contribution of the actual velocity profile to \( S \). Therefore, when using relation (3), it was necessary to replace the noisy fluctuations occurring after saccade offset by zero's to get meaningful results.

A second alternative measure which has been tried on the data is derived from the beta function, since this function, unlike the gamma function, can also yield negative skewness values.

A more general way to describe the saccade velocity profile is by means of a polynomial function. We fitted a 6th order polynomial to
the velocity signal, and used it to compute its skewness by relying on equation (3).

Finally, a more direct procedure for characterizing the shape of the saccadic velocity profile which is not based on an estimation of skewness (in the mathematical sense), is to determine the acceleration fraction defined as the ratio $D_a/D_s$ of the accelerating phase ($D_a$) and saccade duration ($D_s$) (see Fig. 1). All five measures yielded qualitatively comparable results (see Results). This paper deals primarily with the results obtained by the gamma-fit procedure. Further details on the other measures applied in this study are outlined in Appendix 2.

RESULTS

Gamma function fit results

Figure 2 shows three typical examples of curve fits of the gamma function for saccades of different amplitudes, together with the difference between the measured data points and the best-fit function (the residue) for a few saccades. The fit, as judged from the correlation coefficient, is good ($0.920 < r < 0.999$). The mean amplitude of the residue (18.7 deg/sec in subject J.V.G., computed between onset and offset of 325 saccades) is slightly above the velocity-noise level of about 6 deg/sec (computed similarly from the post saccadic velocity signal of 30 saccades over 80 msec). Systematic discrepancies from the noise can be noted in the superimposed residues. In general, peak velocity as well as the tail of the velocity profile are slightly overestimated, especially in small and intermediate-sized saccades.

Relation between gamma skewness of velocity profile and saccade amplitude

The shape parameter $\gamma$ has a clear relation with saccade amplitude; for normal small saccades we find larger $\gamma$ values than in large amplitude eye movements (see Fig. 2). Since the goodness of fit is quite satisfactory, and similar for all saccade amplitudes, these differences must reflect changes with $A$ which cannot be accounted for by any combination of amplitude and time scaling [see Fig. 3(A, B)] and thus do not trivially reflect the fact that in large saccades the eye moves faster and longer than in smaller saccades. This is illustrated by way of example in Fig. 3(B), where three saccades of different

![Fig. 2. Examples of vectorial eye velocity profiles of horizontal saccades (sampled every 2 msec) with their best fit curve (continuous line). Subject F.P.O. Error in fit (residue) for a number of saccades of the same size is shown below (note difference in scale). Positivity in residue means that data points lie above fit curve. The residue is only slightly greater than the noise level, but errors tend to be systematic. Abbreviations: $r$, correlation coefficient; $A$, amplitude in deg; $\gamma$, see text.](image)
amplitudes have been normalized to their own peak velocities and durations. These representative examples clearly illustrate that, as saccade amplitude increases, the relative duration of the accelerating phase decreases: the velocity profile becomes more skewed in larger saccades. It can be noted in Fig. 3(A) that peak eye velocity is reached roughly at the same time in all three saccades.

When a plot is made of $S$ vs $A$ for normal saccades, a clear linear relation is found [Fig. 4(A)]. Together with Fig. 3(A), this plot confirms earlier suggestions in the literature (Baloh et al., 1975) that skewness increases with amplitude. Contrary to what would be expected, however, the plot in Fig. 4(A) also assigns some positive skewness to small saccades. It is very probable that this is due to a subtle but systematic failure of the gamma function to fit the tail of saccade velocity profiles (Fig. 2). While the fit curve has an exponential decay and, by definition [see equation (2)], is confined to positive skewness values only (computed for an infinite time-domain), in small saccades the eye clearly stops more abruptly. Compared with computations of the third central moment directly from the measured data (see Methods), the $S$ values derived from $\gamma$ are systematically higher by a nearly constant amount of 0.6 (see Discussion). Since we were interested in establishing trends rather than in absolute skewness values and because this alternative method had its own problems (see Discussion), the main results in this paper are based on $\gamma$-derived $S$ values.

**Gamma skewness of velocity profile and saccade duration**

From the data [Fig. 4(B)] it follows that $S$ and $D$ have an approximately straight-line relation-
Table 1. Correlations and multiple regression for normal saccades

<table>
<thead>
<tr>
<th>Subject</th>
<th>N</th>
<th>D-S</th>
<th>A-S</th>
<th>A-D</th>
<th>a_D</th>
<th>a_A</th>
</tr>
</thead>
<tbody>
<tr>
<td>J.V.G.</td>
<td>114</td>
<td>0.88*</td>
<td>0.86</td>
<td>0.98</td>
<td>0.95</td>
<td>-0.06</td>
</tr>
<tr>
<td>A.S.</td>
<td>83</td>
<td>0.72</td>
<td>0.74</td>
<td>0.86</td>
<td>0.33</td>
<td>0.47</td>
</tr>
<tr>
<td>M.J.V.G.</td>
<td>75</td>
<td>0.92*</td>
<td>0.90</td>
<td>0.97</td>
<td>0.78</td>
<td>0.13</td>
</tr>
<tr>
<td>F.P.O.</td>
<td>84</td>
<td>0.93**</td>
<td>0.88</td>
<td>0.94</td>
<td>1.69</td>
<td>-0.79</td>
</tr>
<tr>
<td>H.G.</td>
<td>84</td>
<td>0.90**</td>
<td>0.88</td>
<td>0.98</td>
<td>0.95</td>
<td>-0.05</td>
</tr>
<tr>
<td>J.R.</td>
<td>135</td>
<td>0.94**</td>
<td>0.90</td>
<td>0.98</td>
<td>1.48</td>
<td>-0.53</td>
</tr>
<tr>
<td>W.S.</td>
<td>79</td>
<td>0.97**</td>
<td>0.92</td>
<td>0.97</td>
<td>1.31</td>
<td>-0.35</td>
</tr>
<tr>
<td>J.D.V.</td>
<td>88</td>
<td>0.28</td>
<td>0.36*</td>
<td>0.91</td>
<td>-0.28</td>
<td>0.61</td>
</tr>
</tbody>
</table>

Correlation coefficients $r_{DS}$, $r_{AS}$, $r_{AD}$ and normalized multiple regression coefficients for saccade duration ($a_D$) and amplitude ($a_A$) in eight subjects for normal main-sequence saccades. The multiple regression coefficients were determined by using the equation (Spiegel, 1961)

$$S - \mu_S = a_D \left( \frac{D - \mu_D}{\sigma_D} \right) + a_A \left( \frac{A - \mu_A}{\sigma_A} \right)$$

where $\mu$ and $\sigma$ denote mean and standard deviation, respectively, of $S$, $D$ and $A$. Note that six out of eight subjects yield higher regression coefficients for saccade duration than for amplitude. The coefficient for amplitude is negative in five cases, suggesting that for these data, skewness tends to decrease with amplitude, when $D$ is kept constant (see also Fig. 6B). Six out of eight subjects yield higher correlation coefficients for the $D$–$S$ relation than for the $A$–$S$ relation, which is significant in all cases ($*P < 0.05; **P < 0.005$).

Subject J.D.V. yielded poor gamma fits (see Discussion).

By comparing plots of $S$ vs $A$ and $D$ for normal main sequence saccades, it seems that both relations are about equally tight [Fig. 4(A, B)]. This may seem not too surprising since $A$ and $D$ in such saccades are tightly related (see Table 1). Nevertheless, six out of our eight subjects systematically yielded a slightly better correlation for the $D$–$S$ relation of normal saccades. The difference was statistically significant in all cases (Sterling and Pollack, 1968; see Table 1). To determine more directly the extent to which the variability in the skewness parameter $S$ relates to differences in amplitude and duration of saccades, normalized multiple regression coefficients (Spiegel, 1961) were also computed. Again, six out of eight subjects yielded higher coefficients for duration than for amplitude (Table 1). This result suggests that skewness is predominantly determined by saccade duration.

To explore further whether the $D$–$S$ relation is indeed more fundamental than the $A$–$S$ relation, we have also compared both plots in conditions where the normal $A$–$D$ relation is disrupted. This was achieved in two subjects (J.V.G. and A.S.) by an intravenous injection of diazepam (see Methods). Further relevant data were obtained from a fatigued subject (M.J.V.G.) near the end of a long session. Interestingly, while the $A$–$S$ relation deteriorated, the same $D$–$S$ relation remained valid under these conditions [Fig. 5(A)–(F)]. In Table 2 the correlation coefficients for the $D$–$S$, $A$–$S$...

Table 2. Correlations and multiple regression for pooled saccades

<table>
<thead>
<tr>
<th>Subject</th>
<th>N</th>
<th>D-S</th>
<th>A-S</th>
<th>A-D</th>
<th>a_D</th>
<th>a_A</th>
</tr>
</thead>
<tbody>
<tr>
<td>J.V.G.</td>
<td>325</td>
<td>0.88</td>
<td>0.71</td>
<td>0.71</td>
<td>0.76</td>
<td>0.17</td>
</tr>
<tr>
<td>A.S.</td>
<td>209</td>
<td>0.83</td>
<td>0.74</td>
<td>0.85</td>
<td>0.73</td>
<td>0.12</td>
</tr>
<tr>
<td>M.J.V.G.</td>
<td>156</td>
<td>0.93</td>
<td>0.86</td>
<td>0.89</td>
<td>0.78</td>
<td>0.16</td>
</tr>
</tbody>
</table>

Correlation coefficients and normalized multiple regression coefficients for pooled normal and slow saccades in three subjects. In all three subjects $r_{DS}$ was significantly higher than $r_{AS}$ ($P < 0.005$). Note that multiple regression yields comparable results for the three subjects. See also Table 1.
Fig. 5. Relation between skewness and saccadic amplitude (A, B, C) and between skewness and saccade duration (D, E, F) for three different subjects. Normal and slow (A, B) and J.V.G. (C). J.V.G.: Dashed line. The relation between skewness and saccade duration is more tight than the relation with saccade amplitude (D, E, F). Number of Saccades: A, S., 60, J.V.G.: 325 and M.J.V.G.: 156.
Fig. 6. Saccades of a fixed amplitude (A) still exhibit a relation between skewness and duration (C). Number of saccades, N = 34; parameters: $a = 6.0$, $b = 0.7$. Saccades of fixed duration (D), however, do not yield a significant relation between amplitude and skewness (B). Therefore, the relation between skewness and duration is more fundamental than the relation with amplitude. Subject: A.S.; diazepam experiment, normal and slow saccades pooled together; N = 21.

and $A-D$ relations are given, together with the normalized multiple regression coefficients for pooled (normal + slow) saccades. In all three cases the $r_{DS}$ correlation coefficient is significantly higher than the $r_{AS}$ coefficient ($P < 0.005$). Furthermore, the normalized multiple regression coefficients are much higher for saccade duration than for amplitude. We conclude that the $D-S$ relation can be considered as more fundamental than the $A-S$ relation.

In Table 4 linear regression coefficients for the $D-S$ relation (a and b) are given for normal and pooled saccades. No significant difference was found between both conditions. These findings are exemplified in Fig. 6 where $S$ values have been plotted for saccades of a given amplitude (left-hand column) and for saccades of a given duration (right-hand column). Figure 6(A) shows the $A-S$ relation for fixed-amplitude saccades. Clearly, there is no significant relation. However, when the $D-S$ relation of these saccades is plotted [Fig. 6(C)] a very significant relation emerges. When saccades of a given duration [Fig. 6(B, D)] are selected, no significant $D-S$ or $A-S$ relation is found. These data show once more that saccades of a given amplitude can still have different shapes of velocity profiles whereas, on the other hand, saccades of a certain duration always have the same shape of velocity profile, despite differences in amplitude.

Results based on alternative measures for velocity-profile asymmetry

If skewness is chosen as the parameter to express the degree of asymmetry in the velocity profile, the most straightforward procedure would be to compute the 3rd central moment directly from the datapoints [equation (3)]. This has the advantage of not requiring a fitting procedure but appeared to be very susceptible to equipment noise and "biological" noise in the signal (see below). To avoid this undesired effect we have preferred to use the skewness parameter based on a smooth fit curve through the data points. There are, however, no strong a priori
Therefore, saccades where the accelerating provides a reasonable deception of the velocity profile. The gamma function was straightforward and fast. Ideally, the fit signal, yet be able to mimic the overall shape since it cannot yield negative skewness values. Variations but may not be applicable in all cases for this purpose because the fitting procedure was straightforward and fast. Ideally, the fit function should not be affected by noise in the signal, yet be able to mimic the overall shape of the velocity profile. The gamma function provides a reasonable description of the velocity profile (Fig. 2) and is quite immune to noisy variations but may not be applicable in all cases since it cannot yield negative skewness values. Therefore, saccades where the accelerating period lasts longer than the decelerating period cannot be described satisfactorily by the gamma function. This was the main reason why the fit was rather poor in subject J.D.V. where this phenomenon could be noticed for saccades up to 20 deg amplitude which were the largest saccades measured in this subject. Second, overlapping saccades or saccades with double-peaked velocity profiles, which have a very nontypical shape, cannot be described by such a simple three-parameter function.

We were concerned that the slight but apparently systematic shortcomings in the fit (see Fig. 2) might have biased the results. Therefore, to exclude that our major conclusions so far were in fact based on systematic errors in the fit we have also studied the A–S and D–S relations based on the alternative methods for quantifying the degree of asymmetry in the velocity profile outlined in the Methods section.

Not surprisingly, by using more complex mathematical functions such as the beta function and the 6th order polynomial (see Methods and Appendix II), the goodness of fit improved (mean absolute residue for gamma function: 18.7 deg/sec; for beta function: 11.6 deg/sec and for 6th order polynomial: 6.7 deg/sec; subject J.V.G.; N = 325).

On the other hand, the better the mathematical function approaches the actual velocity profile, the more details of the velocity signal which are irrelevant for the present purpose (biological noise) will affect the skewness value obtained by applying equation (3). Consequently, as expected from the 3rd central moment of the velocity profile, the beta function and the 6th order polynomial all resulted in less tight A–S and D–S relations than the gamma fit results (Table 3). Nevertheless, our main result that the D–S relation is more tight than the G–S relation remains valid. We conclude therefore that this result is not simply an artifact of the imperfect fit of the gamma function.

Finally, we have explored what picture emerges if, instead of the skewness parameter, the acceleration fraction is used to characterize the degree of asymmetry of the velocity profile. This measure can be derived directly from the velocity signal (see Methods) and can serve as an independent check to verify whether our conclusions so far depend critically upon precisely which measure is used to quantify the shape of the velocity profile. Because the acceleration fraction decreases with increasing amplitude (or duration) the resulting correlation coefficients in Table 3 are negative. Again, with this measure as well, the relation with duration is significantly more tight than with amplitude [Fig. 7(A, B)].

In summary, it can be stated that all measures used support the conclusion that the relation between the degree of asymmetry and saccade duration is more tight than with saccade amplitude. As shown in Fig. 7(C) and Table 3 (right-hand column), there is a strong correlation \(r = -0.904\) between the acceleration fraction and the gamma skewness parameter derived from the same data set. The comparison with the other skewness measures (Table 3) shows that the gamma skewness data correlate significantly better \((P < 0.005)\) with the relative acceleration measure than the alternative skewness measures. Therefore we conclude that the gamma function can be used reliably to express the degree of asymmetry in the saccadic velocity profile.

Table 3. Correlation coefficients of A–S and D–S relations for five measures of the degree of asymmetry in the saccadic velocity profile

<table>
<thead>
<tr>
<th>Measure</th>
<th>A–S</th>
<th>D–S</th>
<th>Rel. acc.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gamma function</td>
<td>0.71</td>
<td>0.88</td>
<td>-0.90</td>
</tr>
<tr>
<td>Beta function</td>
<td>0.55</td>
<td>0.70</td>
<td>-0.84</td>
</tr>
<tr>
<td>6th order polynomial</td>
<td>0.43</td>
<td>0.79</td>
<td>-0.80</td>
</tr>
<tr>
<td>3rd central moment</td>
<td>0.44</td>
<td>0.77</td>
<td>-0.80</td>
</tr>
<tr>
<td>Relative acceleration</td>
<td>-0.66</td>
<td>-0.90</td>
<td>—</td>
</tr>
</tbody>
</table>

Correlation coefficients for the A–S and D–S relations, computed for five different methods for determining skewness. Subject J.V.G., N = 325. Normal and slow saccades pooled together. Each of the five measures yields a significantly higher correlation for the D–S relation \((P < 0.005)\). Correlation coefficients of the relation between the relative acceleration measure and each of the other four measures applied in this paper are given in the right-hand column. Note that the gamma function yields a significantly better correlation \((P < 0.005)\). Because the relative acceleration fraction decreases with amplitude, negative correlations are found.
A unifying equation relating $A$, $V_{\text{max}}$, and $S$

By incorporating also the shape of the velocity profile, this paper adds a third equation to the well known main sequence relations between amplitude/duration and amplitude/maximum velocity. We wondered whether it would be possible to present all saccade parameters in a single comprehensive equation.

From the literature it is known (Evinger et al., 1981) that maximum eye velocity, at least in the cat, is proportional to mean velocity (computed as $A/D$). This makes it possible to combine the three main sequence parameters $A$, $V_{\text{max}}$, and $D$ into a single equation

$$V_{\text{max}} \cdot D = c \cdot A$$  \hspace{1cm} (5)

where $c$ is a dimensionless proportionality constant. Apart from a small intercept, this relation is also very tight ($r \geq 0.97$) in the human [Fig. 8(A, B)]. Linear regression yields a mean value of 1.64 for $c$ (8 subjects) which is slightly lower than the value of 1.9 in the cat. Table 4 gives a survey of the $c$-values found in our 8 subjects.

![Graph showing relative acceleration fraction ($D_a/D$) of the velocity profile also has a much tighter relation with saccade duration ($B$) than with saccade amplitude ($A$). Skewness as determined by the gamma function has a strong relationship ($r = -0.90$) with $D_a/D$ ($C$). Subject: J.V.G., $N = 325$ (pooled normal and slow-saccade data).]
Fig. 8. Relation between $A$ and $V_{\text{max}} \cdot D$ in two subjects. Note that this relation is very tight ($r > 0.97$), for normal as well as slow saccades. The slope, $c$, is somewhat higher for slow saccades (C, D). Note also that the slope tends to increase for large saccades (see Discussion).

When the data set included very slow saccades due to diazepam or fatigue, equation (5) remained valid but $c$ increased slightly by 4–13% [Fig. 8(C, D)]. By recombining equations (4) and (5) into a single equation, the interrelations among the various saccade parameters can be succinctly summarized

$$V_{\text{max}} = \frac{a \cdot c}{S - b} \cdot A.$$  

(6)

What equation (6) entails can perhaps best be appreciated from a scatter plot like in Fig. 9, where the amplitude/maximum velocity plane has been subdivided into a few sectors by lines of equal skewness which can be computed from constants $a$, $b$ and $c$ in equation (6) (see Table 4). Although the data sometimes overlap the sectors, most data points belonging to a certain skewness range fall within the theoretically predicted sectors [equation (6)]. Hence, equation (6) seems to provide a reasonable description for normal as well as slow saccades. Three points are worth noting:

First, the graphical expression of equation (6) in Fig. 9 incorporates the fact that, for normal main sequence saccades, $S$ increases with $A$. Since the $A-V_{\text{max}}$ relation of normal saccades in man and monkey shows soft saturation, the data points from large saccades lie in a sector which is closer to the horizontal axis (larger $S$) than is the case for small saccades.

Second, the skewness sectors also give a graphical illustration of our finding that, for a given amplitude, $V_{\text{max}}$ and $S$ are inversely related [i.e. slower saccades are more skewed; see also Fig. 5 (D, E, F)].

Third, equation (6) is a useful addition to equation (5), which appears to provide a very tight description of both normal and slow saccades, by specifying explicitly how the shape of the velocity profile depends on saccade duration.

**DISCUSSION**

**Main findings**

One of the main findings of the present work...
Fig. 9. The $V_{\text{max}}/A$ plane can be subdivided into an array of sectors, fanning out from the origin, where saccades have similar skewness (equation (6)). Skewness and saccade duration [see equation (4)] increase in the clockwise direction: actual datapoints (crosses: $S < 0.9$; circles: $0.9 < S < 1.1$; plus signs: $S > 1.1$) were obtained from pooled normal and slow saccades (see text). Subject: J.V.G., $N = 325$, Subject M.J.V.G., $N = 156$.

is that, for some yet unknown reason, there appears to be a relation between the duration of a saccade and the shape of its velocity profile. In addition, we have found that normal and slow saccades obey the same $D-S$ relation. Our data indicate that the skewness relation with amplitude in “alert” saccades (Hyde, 1959; Baloh et al., 1975) is indirect: it seems that large saccades are more skewed because they last longer.

The relation $V_{\text{max}} \cdot D = c \cdot A$

Apart from a small intercept, the $V_{\text{max}} \cdot D = c \cdot A$ relation [equation (5)] is valid in the human (Fig. 8, Table 4) and is very tight ($r > 0.97$) in all subjects. This is true despite
considerable scatter in both the $A-V_{\text{max}}$ and $A-D$ relations. This scatter would be not at all surprising if all saccades had the same shape of velocity profile. For example, suppose that the velocity profile could be described simply by a triangle with height $V_{\text{max}}$ and base $D$. Obviously, equation (5) then holds for every kind of triangle since $V_{\text{max}} \cdot D = 2 \cdot A$ so that, in this case, $c = 2$. One may wonder, however, whether in our data, where a strong relation appears to exist between skewness and duration of saccadic velocity profiles, the relation expressed by equation (5) could still be valid.

Assuming that all saccades can be described by a gamma function [equation (1)], under the boundary condition that the gamma function reaches its maximum height at the same moment for all amplitudes [see Fig. 3(A)], it is possible to show numerically, that the parameter $c$ is not independent from $\gamma$. This may seem to contradict the tightness of relation (5). However, $c$ depends only very moderately on $\gamma$ and is highest for the smallest $\gamma$-values (i.e. the largest saccades). The slight upward curvature noticeable for the largest amplitudes in Fig. 8 can, in fact, be interpreted to reflect this expected relation between $c$ and $\gamma$.

**Generalizing equation for saccades**

As can be seen in Fig. 9, the actual values of $S$ for normal saccades and abnormally slow saccades conform at least qualitatively with the “predictions” from equation (6). The mild violations which occur probably reflect mainly the scatter in the $D-S$ relation. Yet we feel that Fig. 9 must be interpreted with caution. First, as explained above, the precise value for intercept $b$ in the $D-S$ relation remains to be determined. Second, there is some uncertainty as to whether the linear $D-S$ relation, which emerges from the gamma fit results, is really valid for small (short duration) saccades. Despite the considerable amount of scatter, the $S$-values computed directly from the eye velocity data [equation (3)] hint that the $D-S$ relation and by implication also equation (6) are perhaps oversimplified. Therefore we regard equation (6) as an interesting working hypothesis, which requires further investigation, rather than as an established fact.

**Implications for models of the saccadic system**

One might wonder, whether current models of the saccadic system (Robinson, 1975; Van Gisbergen et al., 1981; Scudder, 1985; Fuchs et al., 1985) can explain the observed phenomena. To our knowledge, no special attention has been paid to the shape of the saccade velocity profile. Simulations indicate that these models in their present form, are incapable of replicating our finding that skewness increases with duration. Therefore, an interesting problem which remains is why saccades, which last equally long, but whose amplitudes may be quite different, tend to have the same shape of velocity profiles [Fig. 6(B)]. The behaviour of the skewness parameter reflects the fact that the saccadic system is nonlinear. If the total system were linear, neither duration nor skewness of the saccade would change with amplitude. To the extent that the oculomotor plant can be assumed to behave as a linear system (Robinson, 1981; Goldstein, 1983; Van Opstal et al., 1985), differences in the time course of saccadic velocity profiles must reflect shape differences in the structure of the neural control signals generated for saccades of different amplitudes. We are currently exploring the implications of a burst generator which, instead of a fixed, static nonlinear characteristic (Van Gisbergen et al., 1981), has a dynamic nonlinear characteristic, whose parameters change during a saccade. Similar suggestions were made earlier by Lee and Robinson (1979) on different grounds.

An alternative to the idea that the peculiarities in saccade velocity profiles, described in this paper, reflect properties of the neural control signals, would be to assume that nonlinearities in the oculomotor plant may play a role. While this possibility cannot be excluded from our experimental data, the fact that the shape of saccade velocity profiles is affected by centrally-acting drugs (this paper) as well as by the visuomotor task (visually vs nonvisually triggered saccades, see Smit et al., 1987) strengthens the belief that the time structure of input signals must be a major determining factor. This same reason also seems to exclude artefacts related to the method of measuring eye movements (i.e. the presence of the eye ring).

In conclusion, we think that skewness is a revealing new parameter for saccades which deserves further attention and which seems to be a useful extension of the widely used main sequence plots as a tool for documenting their dynamic properties in pure scientific and clinical studies.

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REFERENCES


APPENDIX 1

*Estimation of Initial-parameter Values for the Gamma Function Fitting Procedure*

The velocity profile is taken to begin at 4 msec before the first 30 deg/sec crossing (see Methods) so that, at this time, \( v(0) = 0 \). For an estimation of starting values for \( a \), \( \beta \) and \( \gamma \) (equation (1)), we made use of a procedure described by Grashuis (1974): The gamma function, described by equation (1), has an expected value \( \mu = \beta \cdot \gamma \), a variance \( \sigma^2 = \gamma \cdot \beta^2 \) and a skewness \( S \) given by equation (2). It is easy to show, that the squared version of the velocity profile, \( v^2(t) \), is also a
gamma function with parameters, $\alpha$, $\beta$ and $\gamma$

$$v^2(t) = \alpha \left[ \frac{t}{\beta} \right]^{\gamma-1} \exp \left( -\frac{t}{\beta} \right)$$  \hspace{1cm} (A1)

where

$$\alpha = \frac{\gamma}{\beta}$$

$$\beta = \beta/2$$

$$\gamma = 2\gamma - 1.$$  

Therefore, the expectation value $\mu$, and the variance, $\sigma^2$, can be written as

$$\mu = (\gamma - 1/2) \cdot \beta$$  \hspace{1cm} (A2)

and

$$\sigma^2 = (2\gamma - 1) \cdot \beta^2.$$  

Determining $\mu$ and $\sigma^2$ of the squared velocity profile then yields reasonable initial values for $\gamma$ and $\beta$

$$\gamma = 1/2 + \frac{\mu^2}{2\cdot\sigma^2}$$

and

$$\beta = \frac{\mu}{\gamma - 1/2}.$$  \hspace{1cm} (A3)

Since the gamma function reaches its maximum at $t_m = \beta \cdot (\gamma - 1)$, the starting value for parameter $\alpha$ can be computed from maximum eye velocity according to

$$\alpha = \frac{V_{max}}{(\gamma - 1)^{-1}}.$$  \hspace{1cm} (A4)

When forced to start with these initial parameter values, the fitting procedure reaches the final values after about 10 iterations.

APPENDIX 2

The Beta Function

An alternative function which can also yield negative skewness values is derived from the beta function (Eadie et al., 1971). This function is defined as

$$v(t) = \alpha \cdot \left[ \frac{t}{\beta} \right]^{\gamma-1} \cdot \left[ 1 - \frac{t}{\beta} \right]^{\delta-1} \quad \text{for } 0 \leq t \leq \beta$$  \hspace{1cm} (A5)

and $v(t) = 0$ elsewhere.

In this equation, $\alpha$ is a scaling parameter, $\beta$ equals saccade duration and $\gamma$ and $\delta$ determine skewness

$$S = \frac{2 \cdot (\delta - \gamma) \cdot \sqrt{\delta + \gamma + 3}}{(\delta + \gamma + 4) \cdot \sqrt{\delta + 1}(\gamma + 1)}.$$  \hspace{1cm} (A6)

The Sixth Order Polynomial Function

The velocity profile $v(t)$ is most generally described by the equation

$$v(t) = \sum_{i=1}^{\infty} a_i \cdot t^i$$  \hspace{1cm} (A7)

We determined the first six coefficients $a_i$ of this equation and computed skewness by applying equation (3).