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Experimental test of two models for the generation of oblique saccades

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Summary. In this paper, we report a detailed study of the dynamic properties of horizontal, vertical and oblique saccades. These eye movements were measured with an improved version of the double-magnetic induction method in two rhesus monkeys. We found that onsets of orthogonal components of oblique saccades are so well synchronized in the monkey that a common initiation system seems likely. Saccade vectors obeyed a nonlinear peak-velocity/amplitude relationship in all directions. The peak-velocity/duration/amplitude relationship for components was not fixed, but depended on the relative size of the orthogonal component: for a component with a given size, its duration increased and its peak velocity decreased, as the saccade vector to which it contributed turned away from the component direction under consideration. This stretching effect, which reflects a nonlinearity in the system, was negligible for small saccade vectors but became very pronounced in large oblique saccades. These experimental data were confronted with quantitative predictions derived from two different models for the generation of saccades in two dimensions. It appears that a model which assumes the existence of synchronized, but otherwise independent, pulse generators for horizontal and vertical components must be rejected. An alternative model, featuring a nonlinear vectorial pulse generator followed by a decomposition stage which generates component velocity command signals from the vectorial eye velocity signal, provides good fit with the data. According to this common-source model, the two nonlinear phenomena observed, viz., the curvilinear peak-velocity/amplitude relationship of saccades in all directions and component stretching in large oblique saccades, are due to a single nonlinearity in the proposed vectorial pulse generator. A possible neural basis for the common-source model is discussed.

Key words: Oblique saccades – Component stretching – Nonlinearity – Neural coding – Models

Introduction

Studies aimed at characterizing the properties of saccadic eye movements, or at revealing the neural signal processing underlying their control, have mainly been limited to horizontal and vertical saccades. The lack of data on oblique saccades made it impossible, so far, to distinguish between two different models of the saccadic system which can account equally well for most data in the literature. In this paper, these two models are described and tested by comparing experimental data on dynamical properties of oblique saccades in the monkey with quantitative predictions made from each model.

Single-unit recordings at the level of premotor and motoneurons, as well as lesion studies, have resulted in an already rather detailed picture of how horizontal and vertical saccades are generated at a peripheral level. It has been established that the paramedian pontine reticular formation and the mesencephalic reticular formation contain so-called medium-lead burst cells (MLBs) whose firing rate is tightly related to eye velocity in horizontal and vertical saccades, respectively (Luschei and Fuchs 1972; Keller 1974; Büttner et al. 1977; King and Fuchs 1979; Hepp and Henn 1982). It is generally assumed that these cells are responsible for the high-frequency bursts in agonist motoneurons during saccades. The picture emerging from the literature is that at this peripheral level the saccadic system is organized in a Cartesian coordinate system and that the information is temporally coded.

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Much less is known on precisely how horizontal and vertical MLBs are driven. Studies using a variety of techniques (see Wurtz and Albano 1980; Schiller et al. 1980) have established that at a more central level both the superior colliculus and the frontal eye fields are involved in the visual guidance of saccadic eye movements. Neural maps in both structures encode retinal error and probably also motor error (Mays and Sparks 1980) and specify the desired saccade vector. It is generally assumed that at this level the information is spatially coded, which means that the location of the active population of neurons in the neural map, rather than their precise firing rate, is important.

A problem of central interest in oculomotor control is how the spatially encoded position signal in the visuomotor system, which represents the desired saccade vector, is ultimately converted in the temporally encoded, component related, eye velocity signals carried by MLBs in the motor system. For the purpose of this paper, it is useful to distinguish two different aspects of the signal transformations which must occur in this spatio-temporal translation process:

1) A *vector* is decomposed into signals related to the horizontal and vertical *components* of saccades, and

2) A *position* signal is converted into *velocity* command signals. Since the latter process results, ultimately, in the high-frequency bursts of MLBs, it is denoted as *pulse generation.* As will be shown, it is important, from the standpoint of modelling, to know in what sequence these two signal transformations (vector decomposition and pulse generation) occur.

Robinson (1975) has proposed a specific model of how the pulse generator may work. In his model, horizontal (vertical) MLBs are driven by horizontal (vertical) motor error. According to the model, the nonlinear relation between saccade peak velocity and saccade size reflects a nonlinearity in MLBs, which causes peak firing rate in the burst to be a nonlinear function of saccade size. Whatever the precise mechanism of generating the pulse (burst), the idea that the nonlinear peak-velocity/amplitude relation of saccades (Fuchs 1967; Bahill et al. 1975; Baloh et al. 1975) reflects a nonlinearity before or at the level of MLBs – rather than in the oculomotor plant – seems a reasonable hypothesis in view of the fact that burst rate in burst neurons and oculomotoneurons saturates for large saccades (Robinson 1970; Keller 1974).

There is also evidence that, as predicted by the model, firing rate in horizontal MLBs is tightly related to horizontal motor error (Van Gisbergen et al. 1981). Robinson's model accounts reasonably well for various relations among motor error, burst cell firing rate and eye velocity in purely horizontal saccades but, since it is one-dimensional, was not meant to provide a description of the signal processing underlying the generation of *oblique* saccades. The experimental data discussed so far are equally compatible with either of two schemes which can be proposed to extend the model to two dimensions. These two schemes (Fig. 1) differ in the sequence of the two signal transformations in the spatio-temporal translator which were distinguished above.

In the *independent model* (Fig. 1B), vector decomposition *precedes* pulse generation. The idea here is that vectorial error is first decomposed into horizontal and vertical error signals which, subsequently, are transformed independently into horizontal and vertical eye velocity command signals. This arrangement is implicit in Robinson's model, where MLBs are driven by a position signal, and is consistent with the data presented by Van Gisbergen et al. (1981). Furthermore, the curvature in human oblique-saccade trajectories (Bahill and Stark 1975; Viviani et al. 1977) shows that horizontal and vertical components may have different dynamics, which would be expected if the independent model is correct.

There are, however, other experimental data which are not readily explained by the independent model. First, it has been established in the cat that the dynamics of a given saccade component are not fixed but depend on the size of the orthogonal component (Evinger and Fuchs 1978; Guitton and Mandl 1980; Evinger et al. 1981). The present paper confirms several preliminary reports in the literature (King et al. 1983; Keller 1980) that such crosscoupling effects are also present in the monkey's saccadic system. Second, Hepp and Henn (1982) have presented some evidence that the tight relation between horizontal motor error and firing rate in horizontal MLBs, found earlier for purely horizontal saccades, is quantitatively different for oblique saccades.

This, together with new data and ideas in a more recent paper from this group (Hepp and Henn 1983), has led us to explore another possibility of how the spatio-temporal translator may work. In this scheme (Fig. 1A) the sequence of vector decomposition and pulse generation is reversed. Suppose that the motor error vector signal in the neural maps is first converted into a vectorial eye velocity command signal carried by long-lead burst cells (LLBs) in such a way that the location of active neurons in an array determines the *direction* of the saccade velocity vector (spatial coding) while their instantaneous firing rate determines its *magnitude* (temporal cod-

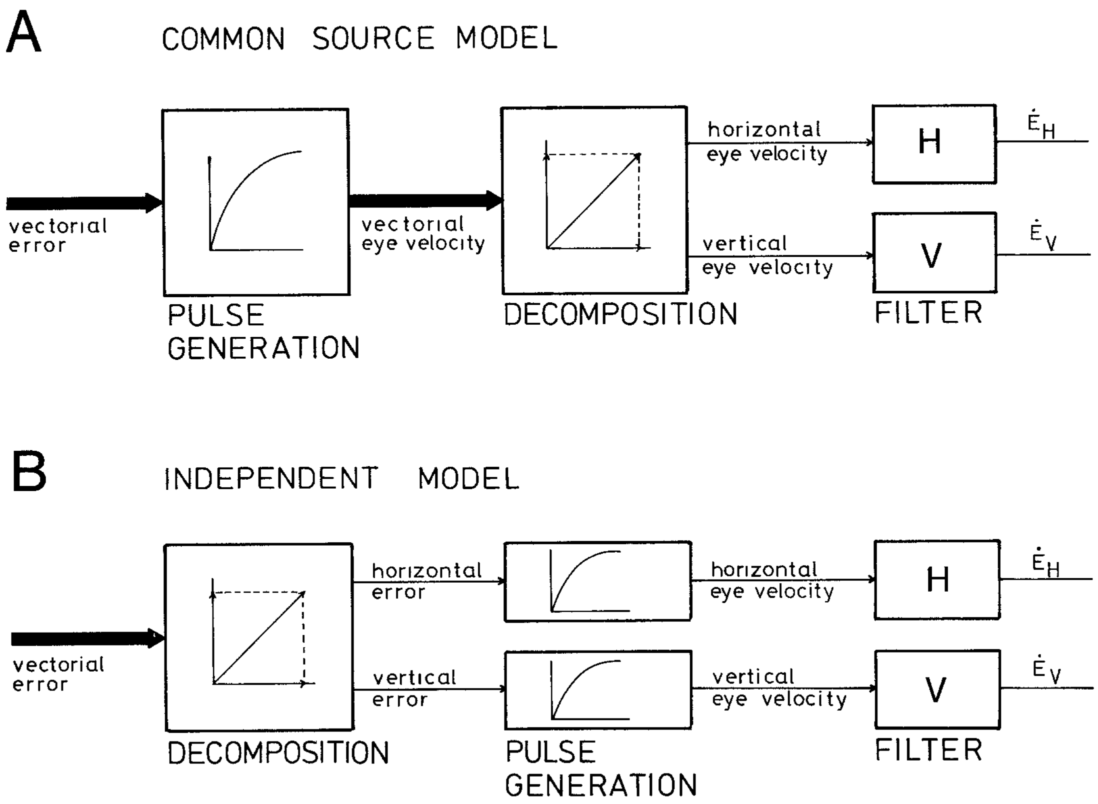

Fig. 1A and B. Schemes emphasizing common elements and differences in the common-source model **A** and the independent model **B**. In both models the transformation of vectorial error into horizontal and vertical eye velocity command signals involves a nonlinear signal transformation (pulse generation) and vector decomposition. The two models portray the two logical possibilities for the sequential order of these processes. In the scheme vectorial signals are indicated by a heavy line; thin lines represent component-related signals. The filters on the right (H and V) comprise all signal processing after medium-lead burst cells and thus include: creation of pulse-step signal found at the level of motoneurons and the oculomotor plant. Since the peripheral filters are assumed to behave linearly in first approximation, the nonlinear peak-velocity/amplitude relation of saccades must reflect a nonlinearity further back in the system

ing; see Hepp and Henn 1983). In the next step of the alternative scheme for the spatio-temporal translator, this vectorial eye velocity signal is decomposed into the component related horizontal and vertical eye velocity signals of MLBs. To achieve this, the synaptic strength of the connections between the LLBs and the MLBs would be fixed for any given LLB but would have to differ from cell to cell dependent on the direction of its movement field. Because the horizontal and vertical MLBs in this scheme are driven by a common signal, we will denote this scheme as the *common-source model.* As we will show below, this model can account for crosscoupling between components of oblique saccades and for Hepp and Henn's (1982) finding in a natural way if it is assumed that the vectorial pulse generator is nonlinear. If the nonlinearity can be characterized mathematically, quantitative predictions of the expected amount of crosscoupling in each component as a function of saccade size and direction can be made (see below).

The reason why reversing the sequence of vector decomposition and pulse generation can have such a profound effect (presence or absence of crosscoupling) is that pulse generation is assumed to be a nonlinear signal transformation. It is well known that in a system composed of linear and nonlinear subsystems, their precise sequence may affect the input-output relations of the total system (Marmarelis and Marmarelis 1978). Just because this is true, it is sometimes possible to discriminate between alternative models by confronting the predictions made from them with the experimental data. We have tried to do so in the present paper. Since the common-source model entails that the amount of crosscoupling should increase with the size of the saccade vector and may be negligible with small saccades (see below), we have investigated saccades in a large amplitude range. Before the data can be confronted with what would be expected based on the two models, it is necessary to make the models explicit and to formulate their predictions mathematically.

A. Common-source model

In what follows we will examine the implications of an idealized common-source model for the saccadic system. Its main purpose is to sketch a mathematically tractable alternative to the independent model, which leads to quite different predictions. It is suggested that horizontal and vertical components of oblique saccades are derived from a common vectorial velocity command signal which specifies the time course and the direction of the saccade. Such a system generates oblique saccades with straight trajectories since the signals which drive the horizontal and vertical eye muscle systems are scaled versions of the vectorial command signal so that both have the same time course.

Saccade and component peak velocity. We assume, in this model, that the nonlinear peak velocity/amplitude relation for horizontal and vertical saccades reflects the nonlinearity of a central pulse generator that transforms (motor) error into vectorial eye velocity. Because of the assumed nonlinearity of the vectorial pulse generator, peak amplitude of the velocity signal does not increase linearly with saccade vector amplitude but shows soft saturation and its duration increases with saccade size. According to the model, the well-known nonlinear relation between peak eye velocity and saccade amplitude for horizontal saccades is only a special case of a universal relation valid for saccade vectors in any direction. Let us suppose that the nonlinear peak velocity/amplitude relation can be represented by:

$$\mathrm{VEC_p(R)} = \mathrm{VEC_a}\left[1 - e^{-R/R_c}\right] \qquad (1)$$

where $\mathrm{VEC_P}$ represents the magnitude of vectorial peak velocity; $\mathrm{VEC_a}$ represents asymptotic vectorial peak velocity; R represents the size of the saccade vector (in degrees) and R_c represents an angular constant (in degrees). The same type of equation has been used before by Baloh et al. (1975).

Given the assumptions made above, it is now possible to specify peak velocity of saccade *components*. For example, peak velocity in the horizontal component (H_p) depends on the size (R) and the direction (φ) of the saccade vector as follows:

$$H_p(R,\varphi) = \mathrm{VEC_a} \cdot \cos\varphi\left[1 - e^{-R/R_c}\right]. \qquad (2)$$

To obtain the relation between component peak velocity and *component* size, this can be rewritten by eliminating R:

$$H_p(\Delta H,\varphi) = \mathrm{VEC_a} \cdot \cos\varphi\left[1 - e^{-\Delta H/R_c\cos\varphi}\right] \qquad (3)$$

where ΔH represents horizontal component size ($\Delta H = R\cos\varphi$). Similarly, the relation among vertical peak velocity (V_p), size of the vertical component (ΔV) and saccade direction (φ) is given by

$$V_p(\Delta V,\varphi) = \mathrm{VEC_a} \cdot \sin\varphi\left[1 - e^{-\Delta V/R_c\sin\varphi}\right]. \qquad (4)$$

It follows from Eqs. (3) and (4) that the relation between component peak velocity and component amplitude, according to the common-source model, depends on the direction of the saccade vector.

To illustrate these relations with an example, let us suppose, for simplicity, that the saccadic system has rotational symmetry (this assumption is not crucial for making predictions and will be abandoned later) and that $\mathrm{VEC_a}$ and R_c in Eq. (1) have values of 1000 deg/s and 10 deg, respectively, in any direction (Fig. 2A). One implication of the model is that when saccades are elicited as in Fig. 2B, the eye will move in a straight line with a peak velocity which saturates for large saccade amplitudes (Fig. 2C). Another consequence is that components of oblique saccades show stretching. The peak velocity of a given component size depends on the direction of the saccade vector (Fig. 2D, E). In the present example, the peak velocity of a large component will drop by 50% when φ changes from 0 to 60 deg. The amount of stretching is modest for $\varphi = 30$ deg saccades.

At this point, it is interesting to note that component stretching in oblique saccades betrays a nonlinearity somewhere in the system. This can be illustrated as follows. Suppose the system responds with a horizontal saccade with velocity profile x(t) to a horizontal stimulus displacement H and with a vertical saccade, having a velocity profile y(t), to a vertical stimulus V. If stretching occurs, the response to both stimuli *simultaneously* (H, V), by definition, will not be simply the combination of velocity profiles x(t) and y(t). A stretched component of the oblique saccade to (H, V) will still have the correct size, but will be executed more slowly. According to the common-source model, the violation of linear superposition, expressed in the stretching phenomenon, is simply a consequence of a saturating vectorial eye-velocity/amplitude relationship (Fig. 2A). If this relation were linear, stretching would not occur. In line with this, the common-source model predicts that stretching will almost be negligible in components participating in small oblique saccades, where this relation is still almost linear (i.e., for small horizontal components; see Fig. 2D, E). In contrast, as R increases, vectorial peak velocity saturates and the component stretching effect should become progressively more noticeable.

Saccade and component duration. When small (< 5 deg) saccades are excluded, saccade duration and saccade amplitude have an approximately straight-

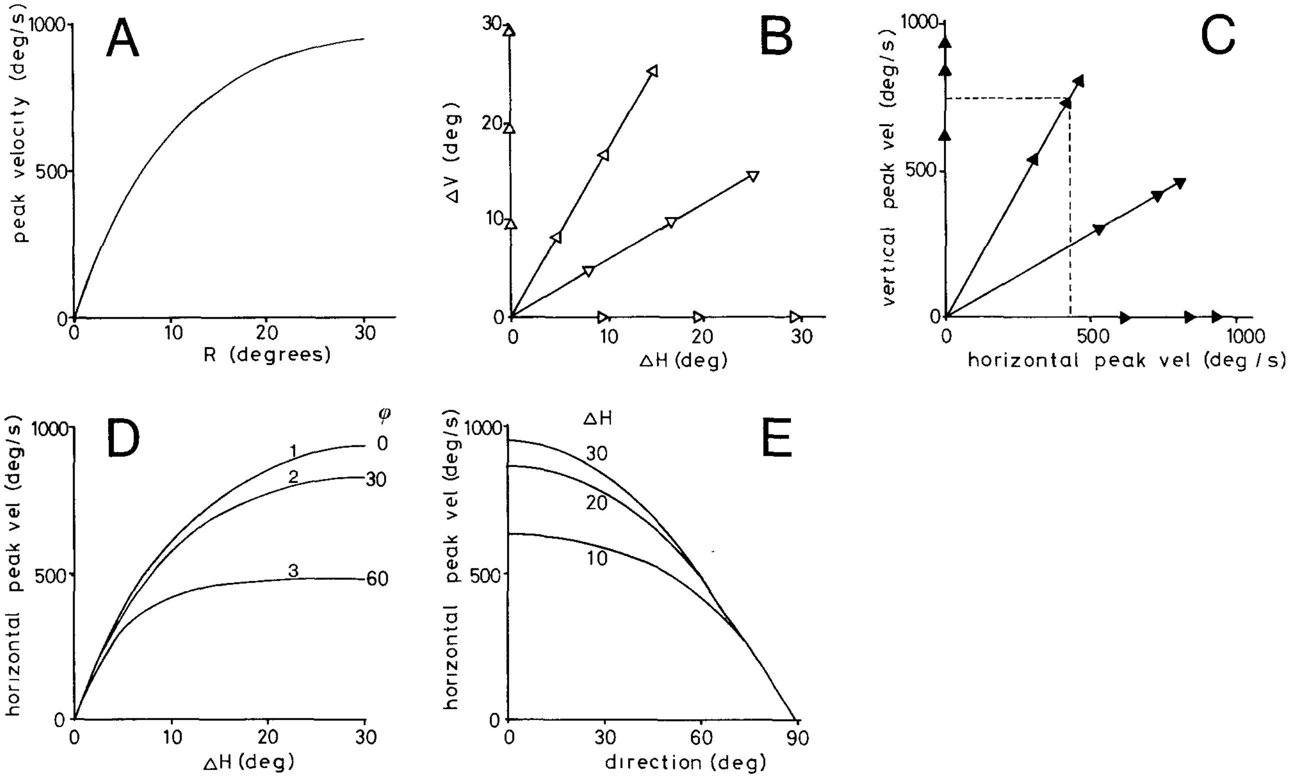

Fig. 2A–E. Graphical illustration of implications of common-source model. **A** It is assumed that saccades obey a universal nonlinear relation between peak vectorial eye velocity and vector size: $VEC_p = 1000\,(1 - e^{-R/10})$. **B** Saccade vectors, with amplitudes of 10, 20 and 30 deg, in the directions $\varphi = 0, 30, 60$ and 90 deg. **C** Peak-velocity vectors of the saccades in **B** as specified by the nonlinear relation in **A**. The velocity vector points in the direction of movement; its magnitude signifies peak velocity. Notice stretching in horizontal component of $R = 20$, $\varphi = 60$ deg oblique saccade which has the same *amplitude* as a 10 deg pure horizontal saccade (**B**) but a 31.6% lower *peak velocity* (**C**); this effect is a direct consequence of the nonlinearity in **A**. **D** Peak velocities reached in the horizontal component of horizontal (curve 1) and oblique saccades (curves 2 and 3) as a function of component size, ΔH. These curves are cross-sections of the $H_p(\Delta H,\varphi)$ surface specified by Eq. (3). Curve 1: asymptote = 1000 deg/s; angular constant = 10 deg; same curve as in **A**. Curve 2: asymptote = 866 deg/s [see Eq. (3)]; angular constant = 8.66 deg. Curve 3: asymptote = 500 deg/s; angular constant = 5 deg. **E** Different cross-section of the $H_p(\Delta H,\varphi)$ surface specified by Eq. (3). As saccade vector turns away from horizontal axis (φ increasing), peak velocity of a given horizontal component size drops (stretching). This is most marked in large components.

line relationship in both man (Yarbus 1967; Bahill et al. 1975) and monkey (Fuchs 1967). We assume that this is true for saccades in all directions:

$$D_{VEC}(\varphi) = p(\varphi) + q(\varphi) \cdot R \qquad (5)$$

where $D_{VEC}(\varphi)$ represents vectorial saccade duration for saccades in direction φ; p and q represent constants which may be φ dependent, and R represents the amplitude of the saccade vector. According to the common-source model, both components as well as the saccade proper, all have the same duration:

$$D_H(\Delta H,\varphi) = p(\varphi) + \frac{q(\varphi)}{\cos\varphi} \cdot \Delta H \qquad (6)$$

$$D_V(\Delta V,\varphi) = p(\varphi) + \frac{q(\varphi)}{\sin\varphi} \cdot \Delta V \qquad (7)$$

where D_H and D_V represent horizontal and vertical saccade component duration. This means that, if the model is correct, the $D_H(\Delta H)$ and the $D_V(\Delta V)$ relation must have φ dependent slopes. This has in fact been noticed in the cat (Evinger and Fuchs 1978) and is a manifestation of crosscoupling. The model makes it possible to make quantitative predictions.

B. Independent model

Saccade and component peak velocity. In this model we assume that the saccadic system has two separate saccadic pulse generators, one horizontal and one vertical, which, once enabled by the initiation system, are driven by horizontal and vertical motor error, respectively. To keep the model simple, we suggest that both components start simultaneously. In the independent model, in striking contrast with the common-source model sketched above, the dynamics of horizontal (vertical) components are determined entirely by horizontal (vertical) motor

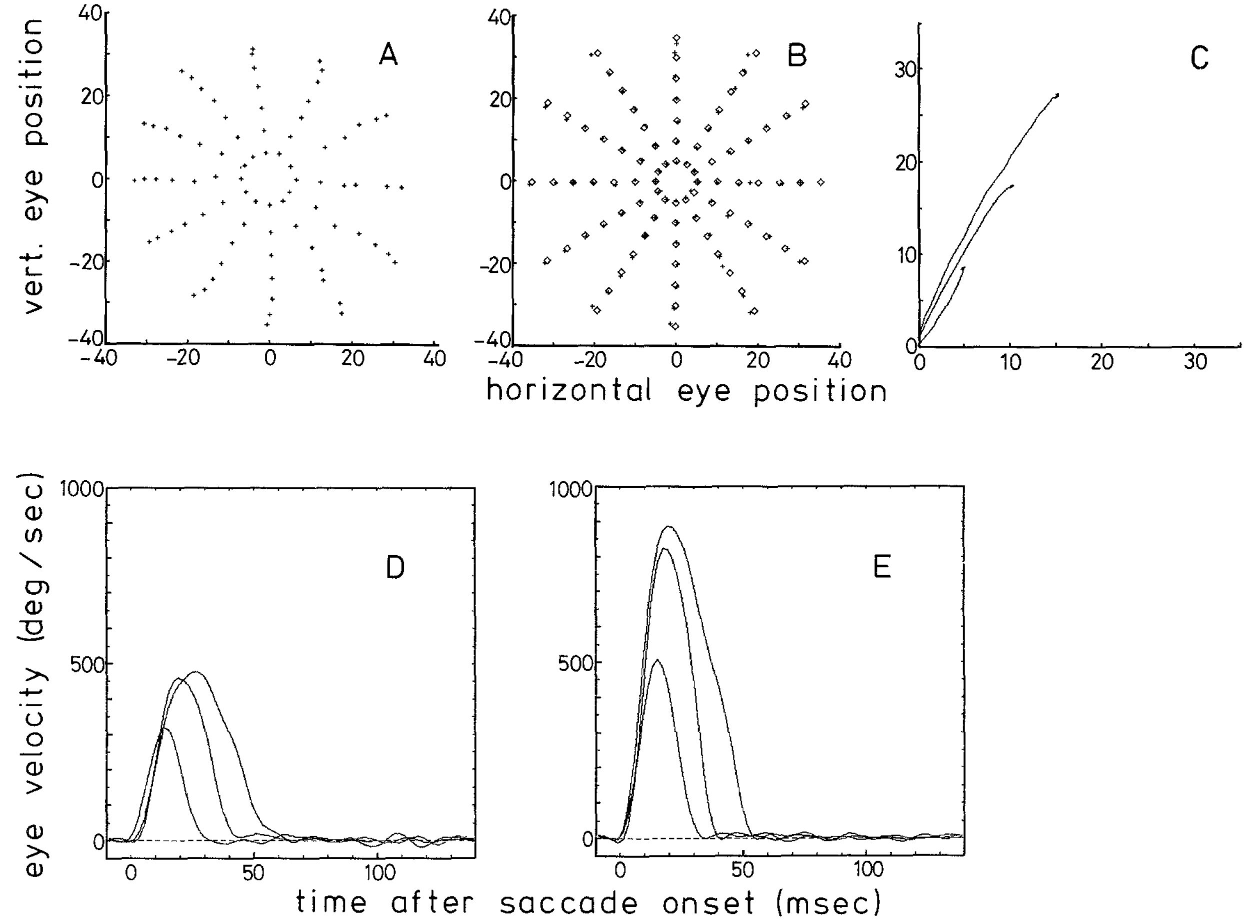

Fig. 3. **A** Plot of raw eye position signals measured when monkey 11 was fixating the target at each of 82 peripheral locations. Responses in two trials missed by the monkey ($\varphi = 0$, $R = 35$ deg; $\varphi = 30$, $R = 10$ deg) are not shown. Note that, due to nonlinearity inherent in eye movement recording system, the response increment decreases as stimulus eccentricity increases. Scale in arbitrary units. **B** Same responses after linearization procedure in the computer (crosses) plotted together with stimulus locations (diamonds). After linearization, the eye movement recording technique has a useful measuring range of 0–35 deg in all directions. Scales in degrees. **C** First-saccade responses in direction $\varphi = 60$ deg having amplitudes (R) of 10, 20 and 31 deg (after linearization). Scales in degrees. **D and E** Horizontal and vertical eye velocity profiles of saccades shown in **C**. Horizontal axis: time since vectorial saccade onset. Velocity profiles were smoothed digitally as described in text. Note that noise level remains below 30 deg/s

error. Thus, no stretching effects would be expected and components of oblique saccades would have the same dynamics as when executed as pure horizontal (vertical) saccades of the same size. Consequently, because the vector sum of two orthogonal vectors is larger than either alone, oblique saccades would have larger peak velocities than either horizontal or vertical saccades of the same size and would be 'superfast' in Bahill and Stark's (1975) terminology. These predictions from the independent model will be tested in the Results.

Saccade and component duration. If the duration/amplitude relation is known for each component, it is possible to predict the relation between horizontal and vertical saccade component duration in oblique saccades of a given direction. Suppose that the duration/amplitude relation approximates a straight-line relationship both for horizontal:

$$D_H = a_H \mid \Delta H \mid + b_H \tag{8}$$

and vertical saccades:

$$D_V = a_V |\Delta V| + b_V \tag{9}$$

then, since $\Delta V = \Delta H \tan\varphi$ for a saccade in direction φ, we obtain:

$$D_V(\varphi) = \frac{a_V}{a_H} |\tan\varphi| \, (D_H - b_H) + b_V \tag{10}$$

where D_V is the duration of the vertical component; D_H is the duration of the horizontal component; b_V and b_H are intercepts of the duration/amplitude relation of horizontal and vertical saccades, respectively, and a_V and a_H are the corresponding direction coefficients in this relation. Note that according to the common-source model, the duration of horizontal and vertical components of oblique saccades is always equal ($D_H = D_V$; see above).

Methods

Eye movements were recorded in two rhesus monkeys who were rewarded for tracking a small (0.4 deg) spot of light (luminance: 5 cd/m^2) which was rear projected on a translucent screen, with a background luminance of 1.2 cd/m^2, placed at a distance of 57 cm. Vision was binocular. In each trial, the spot first appeared at the primary position for a period varying from 0.8 to 1.8 s and then jumped randomly to one of 84 positions in a polar-coordinate grid ($R = 5, 10, 15, \ldots, 35$ deg; $\varphi = 0, 30, 60, \ldots, 330$ deg). At the peripheral position, the spot remained stationary for at least 1.7 s until it was switched off and the intertrial pause (duration: 1–2 s) began. After this resting period the next trial began, and so on, until saccadic responses to all 84 positions had been elicited. The animals had been water deprived for 16 hours and were rewarded with apple juice for fixating the target both in the central and the peripheral position. The results reported here were collected in at least ten separate sessions over a period of several months. In most cases, data from the first stimulus sequence on each experimental day were used.

Recording of eye movements

Eye movements from the right eye were measured with our improved version (Bour et al. 1984) of the double-magnetic induction method originally described by Reulen and Bakker (1982). Raw horizontal and vertical eye position signals were low-pass filtered (-3 dB at 150 Hz), digitized at a rate of 500 samples/s with a precision of 12 bits and stored on disk in a PDP 11/34 computer. The data were corrected off line, to compensate for the static nonlinearity inherent in this method, as described by Bour et al. (1984; see also Fig. 3A, B). If, for some reason, the correction procedure did not yield a satisfactory result, the data were discarded. In the monkey, the double magnetic induction method has a range of 35 deg in all directions. After correction, angular resolution in the eye position data was 0.25 deg, or better, up to 25 deg from the primary position. To give an impression of the data obtained, linearized saccadic eye movements of 10, 20 and 31 deg ($\varphi = 60$ deg) are shown in Fig. 3C–E.

Saccade onset, offset and velocity

Using the linearized data, eye velocity was computed in both the horizontal and vertical channel using a central-difference differentiation algorithm (T = 2 ms; Bahill et al. 1982). Subsequently, a symmetrical digital low-pass filter was used to smooth the eye-velocity profile (-3 dB at 72 Hz; Rabiner et al. 1970).

Saccade onset and offset were detected separately in each channel using a 30 deg/s velocity criterion. For each component, peak velocity was computed and stored together with on- and offset moments. Vectorial eye velocity was computed as the Pythagorean sum of horizontal and vertical eye velocity. The resulting vectorial eye velocity signal was used to detect vectorial saccade onset and offset (criterion: 40 deg/s) and vectorial peak velocity. The results in this paper all refer exclusively to first saccades made in response to the stimulus displacement. First saccade vectors whose overall direction (determined by a straight line through onset and offset position) deviated from the stimulus direction by more than 10 deg, were discarded. Therefore in the Results, φ refers to the direction of stimulus movement and to overall saccade direction within 10 deg.

Results

Onset synchronization of saccade components

Since it was assumed in both the common-source and the independent model (Introduction) that orthogonal components of oblique saccades start simultaneously, this important point must be checked first. An extreme opposite point of view is to suppose that both components have separate, completely independent, initiation mechanisms (cf. Bahill and Stark 1975). If this were the case, the latency variability from trial to trial would be expected to occur independently in each component. On the other hand if, as we assumed, the process triggering the saccade has stochastic variability but is common for both components, horizontal and vertical component latency should show strong correlation.

It appears that, indeed, the orthogonal components of oblique saccades have strongly correlated latencies (Fig. 4). The result shown, from monkey 10, is representative for all oblique saccade directions tested (30, 60, . . ., 330 deg) in both monkeys. The amount of component onset asynchrony was investigated in detail in monkey 11. In the large majority of oblique saccades (84.9%), the latency difference remained below 4 ms (N = 577). A more cursory inspection of the data indicates that this result is representative also for the other monkey. Because of these results, we feel that our assumption of a common initiation mechanism for both components is reasonable.

Vectorial eye velocity

A further step in the procedure to test both models presented above, is to fit an exponential curve [Eq. (1)] through the vectorial peak eye velocity/amplitude data obtained for 12 different meridians. As Fig. 5 shows, the exponential function can fit the data quite reasonably (see also Table 1), not only in the cardinal directions, but equally well for intermediate directions. Another conclusion allowed from Fig. 5 and Table 1 is that the simplest version of the common-source model – a rotation symmetrical (isotropic) saccadic system – must be rejected right away. In the panel displaying the $\varphi = 270$ deg curve, the slowest direction in this monkey ($VEC_a = 700$ deg/s;

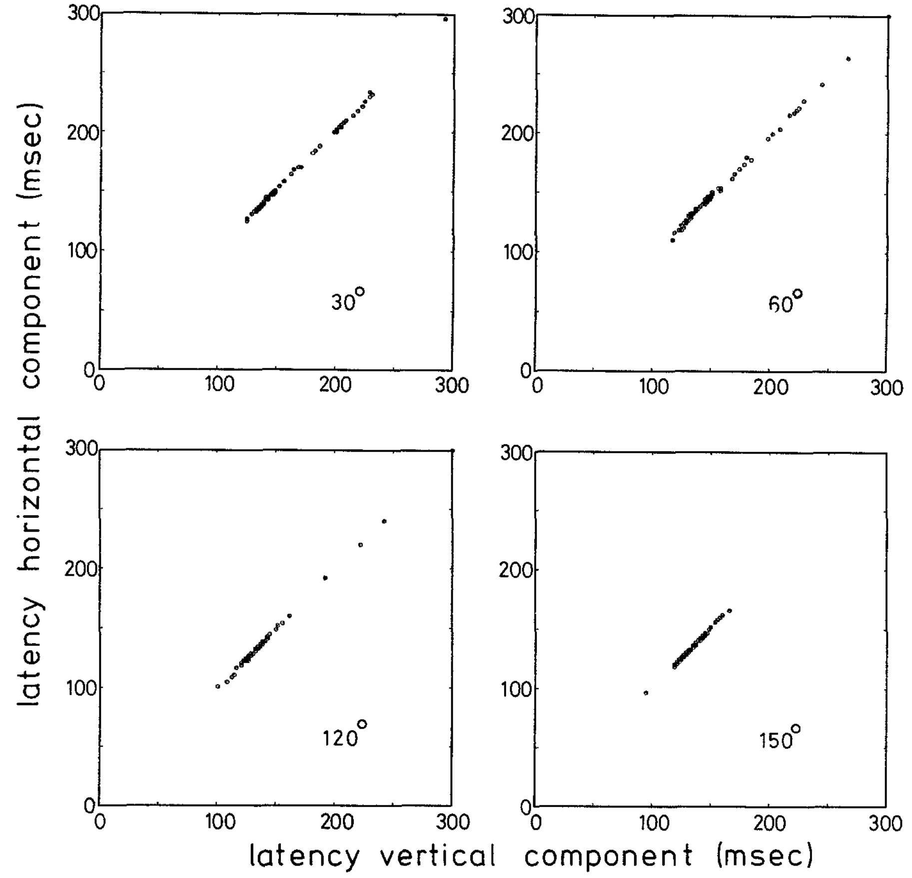

Fig. 4. Onset synchronization of horizontal and vertical components of oblique saccades in various directions. Data from monkey 10. Best fit lines drawn through the data points (not shown) appear to have a slope of 1.00 ± 0.01 in the data shown. Extremely high correlation coefficients (0.99 or higher) show that component onsets are nearly perfectly synchronized

R_c = 7.3 deg), we have retraced the curve from the φ = 150 deg direction where saccades are faster (VEC_a = 1100 deg/s; R_c = 12.5 deg). Curves from the other directions lie somewhere in between these two extreme examples. As summarized in Table 1, the best fit parameter values for the asymptote and the angular constant in Eq. (1) varied considerably for various directions. Horizontal saccades in our monkeys had peak velocities comparable with values reported by Fuchs (1967) but seem slightly slower than in the study by Optican and Robinson (1980).

Are oblique saccades superfast?

To investigate the idea that oblique saccades are perhaps superfast (Bahill and Stark 1975; see Introduction), we constructed oblique saccades in the computer in the same way as a saccadic system, operating as envisaged in the independent model, would do this. Searching through 4 data files containing velocity profiles of purely horizontal and vertical saccades of various amplitudes and corresponding to each of the four cardinal directions right, up, left and down, the computer composed as many oblique saccades in the directions φ = 30, 60, 120, 150, 210, 240, 300 and 330 deg as it could, with a precision of ±1 deg, by selecting appropriate horizontal and vertical saccade combinations and synchronizing their onsets. By computing peak vectorial velocity from a large number of such synthesized oblique saccades, of various sizes, it is possible to determine mean peak velocity for a given direction and saccade amplitude. These independent-model simulation val-

Fig. 5. Peak vectorial velocity as a function of saccade size for 12 different meridional axes. Number in each box denotes saccade direction. Data from monkey 11. Exponential curve [Eq. (1)], which gave best fit, has been drawn through the data points. Note that this curve gives a reasonable characterization of the trends visible in both cardinal and oblique directions. To illustrate extremes in the shapes of the fit curves for various directions, the curve for φ = 150 deg has been retraced in the 270 deg panel, for comparison. In general, curves showing early saturation have relatively low asymptotic velocity levels (see also Table 1)

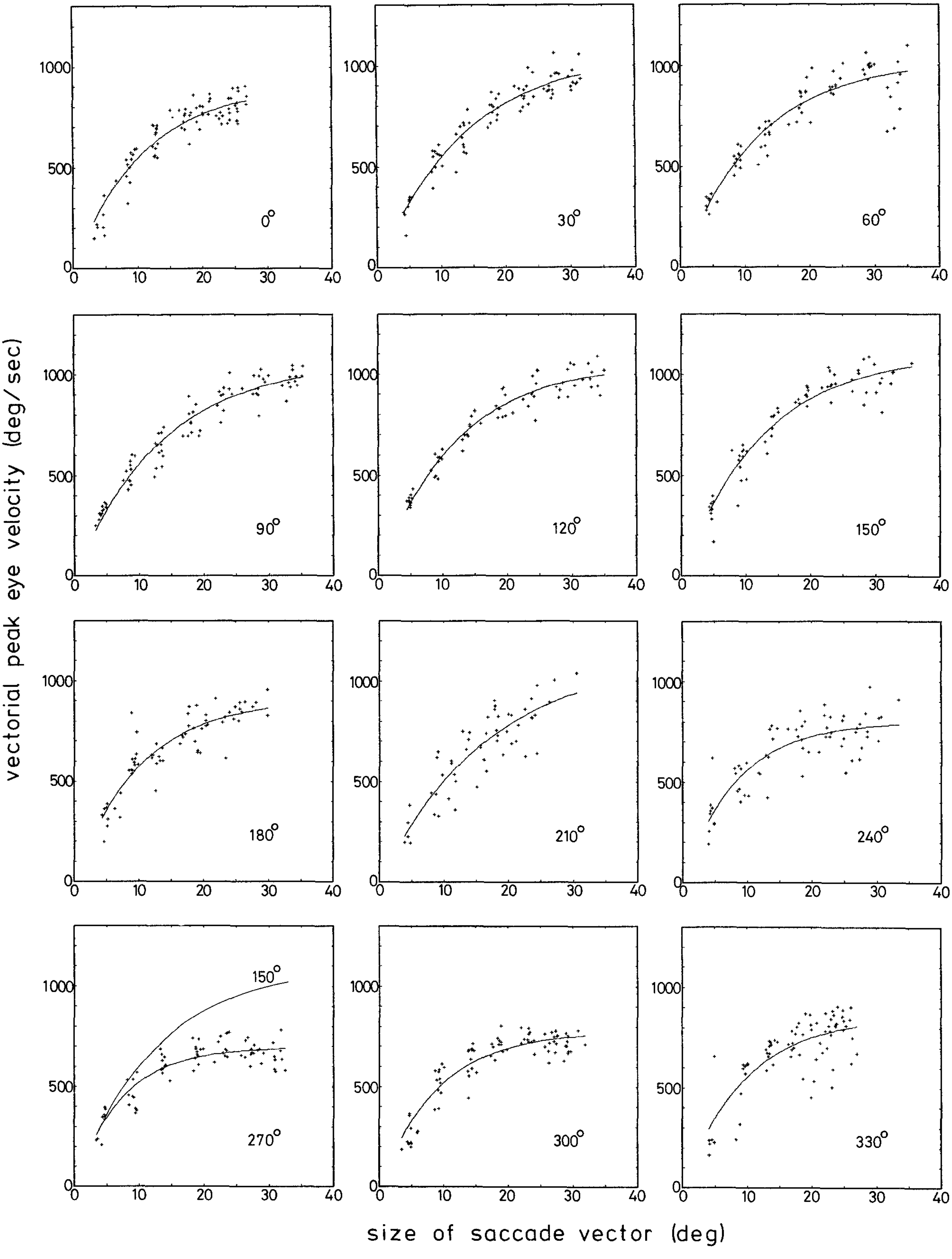
vectorial peak eye velocity (deg/sec)
size of saccade vector (deg)
0°
30°
60°
90°
120°
150°
180°
210°
240°
270°
150°
300°
330°
0
500
1000
0
10
20
30
40

Fig. 5

Table 1. Dependence of parameters asymptote (VEC_a) and angular constant (R_c) in Eq. (1) on saccade direction (φ). The goodness of fit of Eq. (1) with the data points can be judged from Fig. 5 and the correlation (r) between data points and the fit curve

	Monkey 10			Monkey 11		
φ (deg)	VEC_a (deg/s)	R_c (deg)	r	VEC_a (deg/s)	R_c (deg)	r
0	950	9.2	0.97	910	10.8	0.94
30	1030	9.7	0.92	1070	13.9	0.96
60	1250	13.3	0.95	1020	12.1	0.94
90	1150	11.6	0.93	1060	13.5	0.97
120	1470	16.9	0.96	1050	11.9	0.97
150	1360	16.3	0.98	1100	12.5	0.96
180	1100	10.9	0.98	910	10.0	0.90
210	1140	12.2	0.98	1130	16.8	0.87
240	1080	10.7	0.87	800	8.3	0.84
270	910	8.2	0.77	700	7.3	0.90
300	840	8.8	0.93	780	9.1	0.93
330	850	7.8	0.90	860	9.6	0.82
mean	1090	11.3	0.93	950	11.3	0.92

ues are compared with the experimentally determined values (from data as in Fig. 5 and Table 1) in the polar plots of Fig. 6.

The independent model predictions fit very well for 10 deg saccades but deteriorate progressively, in both monkeys, as saccade size increases. Clearly, for large oblique saccades, the actual vectorial peak velocity falls systematically below the predicted value. While this discrepancy argues against the independent model, it cannot be construed as a point in favour of the common-source model. The latter, in its present form, cannot make quantitative predictions on this point.

Component peak velocity

As has been made clear in the Introduction, once the peak-velocity/amplitude relation for saccade vectors is known (see Fig. 5 and Table 1), predictions can be made for either component, using the common-source model [Eqs. (3) and (4)]. In Fig. 7 we present data from the first quadrant (φ = 30 and 60 deg) in monkey 11. Each panel shows peak velocity as a function of component size. In addition, predictions stemming from both models by using procedures explained in the Introduction, have been entered. The curve representing the independent model prediction is simply the peak-velocity/amplitude curve for purely horizontal (or vertical) saccades elicited in the same quadrant. The common-source curve for horizontal and vertical components was computed using Eqs. (3) and (4), respectively. It can be noticed right away that the predictions for the larger component (horizontal for φ = 30; vertical for φ = 60 deg) differ very little for the two models and fail to provide a reason for preferring one or the other. As for the smaller component predictions, the common-source model curve is closer to the data points than the independent model prediction. The data in Fig. 7 are quite representative for the results in all quadrants. The reason behind the fact that the common-source model gives better predictions, at least for the smaller component, is that the latter shows clear evidence of stretching.

Saccade component duration

Another way to explore both models, outlined in the Introduction, is to study saccade and component *durations*. To make quantitative predictions from the common-source model, the relation between vectorial saccade duration and amplitude was studied for all 12 directions in both monkeys. It is well known that, in the amplitude range studied here, this relation is linear for horizontal saccades (Fuchs 1967). We obtained about equally good straight-line fits for the amplitude/duration relation in the other directions (mean correlation coefficient: 0.88; range 0.67–0.97; data from two monkeys).

For each direction, intercept p and slope q in Eq. (5) were computed and used, by applying Eqs. (6) and (7), to predict the amplitude/duration relation for horizontal and vertical components in each oblique saccade direction tested. The resulting common-source model predictions for component duration yield straight lines with φ dependent slopes (Fig. 8; see Introduction). In contrast, the independent model proposes that the duration of a given component is independent of the direction of the saccade vector and is the same as when it is executed as a purely horizontal (or vertical) saccade.

Fig. 6. Polar plots to show relation between peak vectorial eye velocity and saccade amplitude (R) for all directions tested. Directional differences in peak velocity are most clear in large saccades. In both monkeys, large saccades in the fourth quadrant are slower than in any other direction. This reflects the observation (Fig. 5, Table 1) that, for these meridians, eye velocity saturates more rapidly as R increases and settles at a lower asymptotic value. Predictions of the independent model, that oblique saccades should be superfast, are not borne out by the data

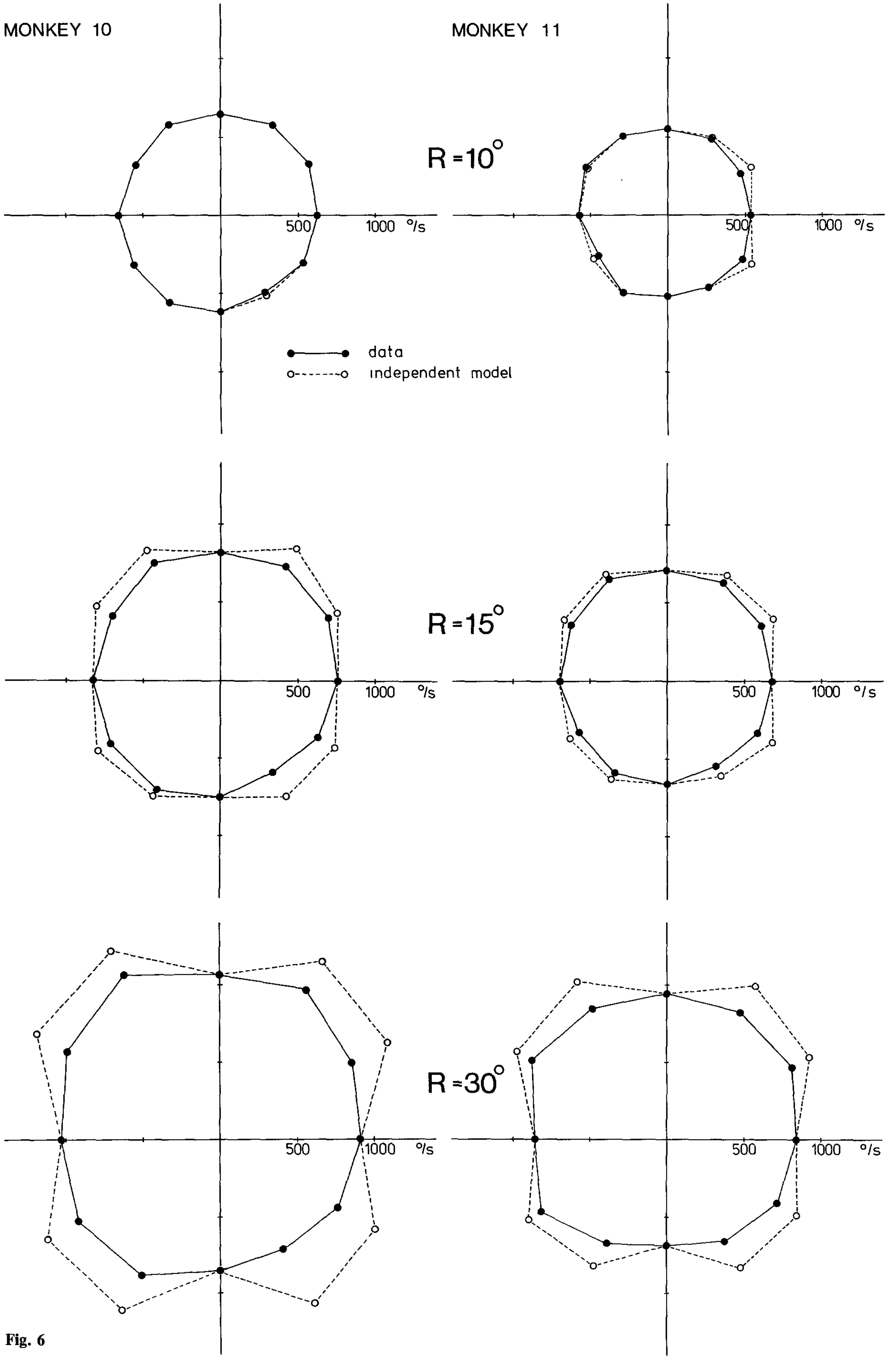
MONKEY 10
MONKEY 11
R =10°
R =15°
R =30°
500
1000 °/s
data
independent model

Fig. 6

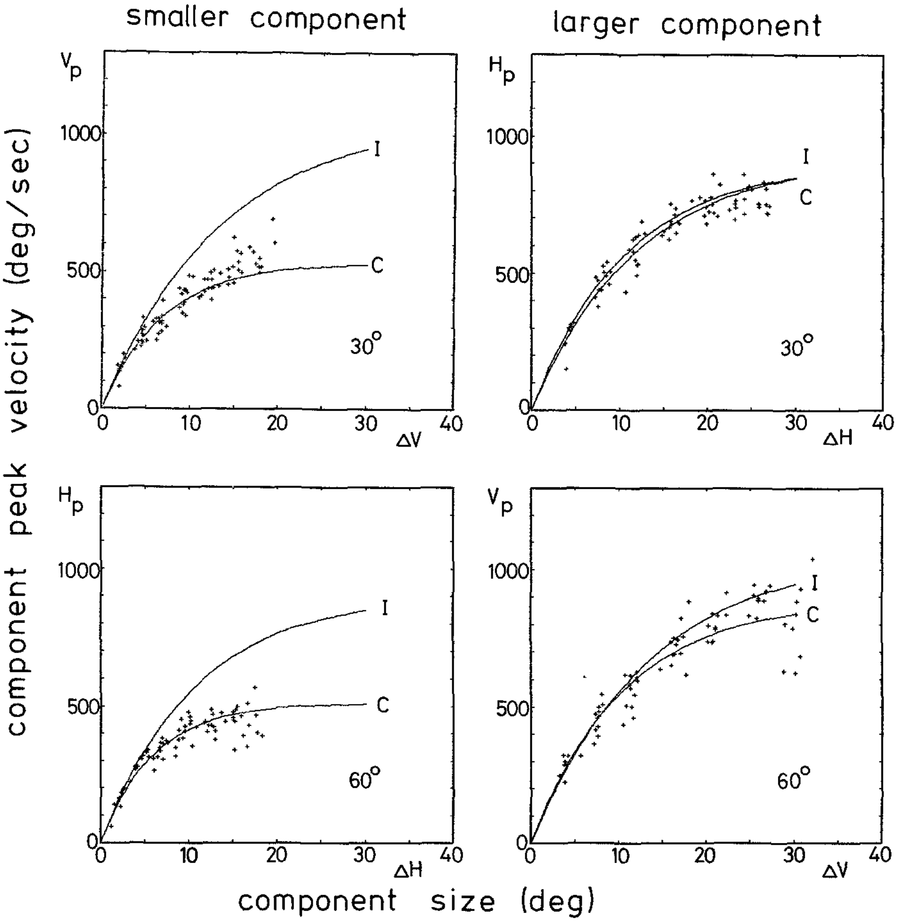

Fig. 7. Component peak velocity, as a function of component size and saccade vector direction, in the first quadrant. Predictions of both models agree about equally well with the experimental data for the larger component (horizontal for $\varphi = 30$; vertical for $\varphi = 60$ deg). For the smaller component, the common-source prediction (C) is clearly better. The common-source predictions were derived from the vectorial peak velocity/amplitude relation by using Eqs. (3) and (4). The independent model prediction (I) for horizontal and vertical component peak velocity is the best-fit curve through the peak velocity/amplitude data of purely horizontal and purely vertical saccades, respectively. Data from monkey 11

Again, it appears that both models are about equally successful in predicting durations of the larger component of oblique saccades (Fig. 8, middle column). When it comes to the smaller component, the common-source model's predictions are clearly better (Fig. 8, left-hand column). This reflects the fact that the smaller component is stretched, a phenomenon the independent model cannot account for. To make the comparison of the two models more quantitative, the peak velocity/amplitude relation and the duration/amplitude relation were fit with a least squares error criterion using an exponential relation (Baloh et al. 1975) and a straight line [Eqs. (8) and (9)], respectively. Each of these fit curves is completely characterized by two parameters: asymptote and angular constant (peak velocity); slope and intercept (duration). These experimentally determined best fit parameters were confronted with the predictions from the common-source model and the independent model. In most cases, variations in a particular parameter were predicted with an accuracy of 20–25% by the common-source model. In contrast, the independent-model predictions failed completely to explain these variations.

If the common-source model is correct, horizontal and vertical components should have equal durations. To check the extent to which this is actually the case, a plot of vertical component duration versus horizontal component duration was constructed for every oblique direction (Fig. 8, right-hand column). Again, the prediction from the common-source model (a line through the origin with a slope of 45 deg) fitted much better with the actual data than the prediction inspired by the independent model, based on Eq. (10). An appreciation of these differences, based on all data, can be gained from Table 2. This table shows more thoroughly that the same trend can be noticed also for other directions in both monkeys.

Discussion

The results in this paper show that the dynamics of oblique saccade components in the monkey can be reasonably understood by the common-source model. The alternative model, incorporating the idea that components are generated synchronously but otherwise independently, must be rejected.

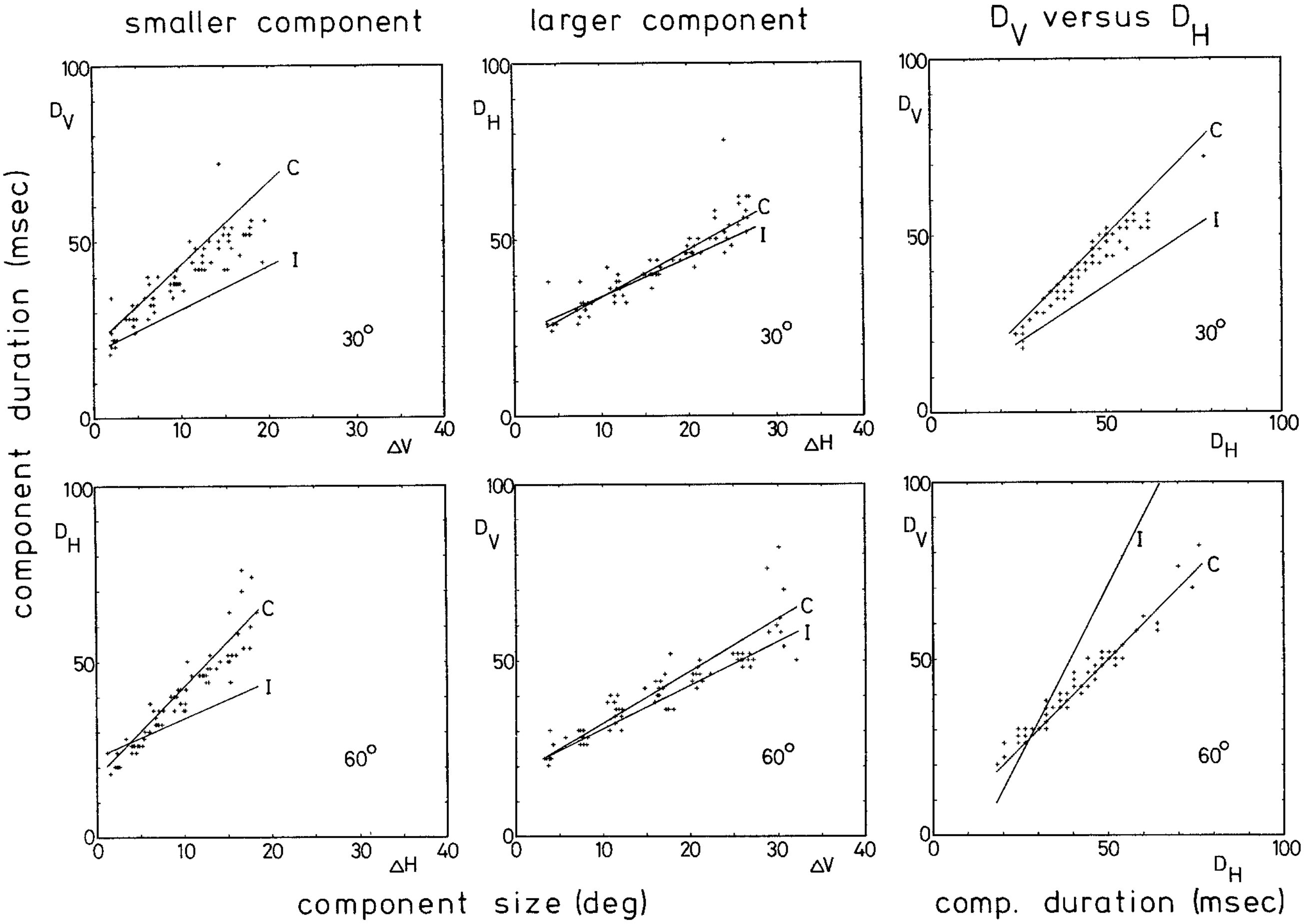

Fig. 8. Saccade component duration/amplitude relations for oblique saccades in the first quadrant. Data from monkey 11. The prediction from the common-source model (C) is at least a good (larger component) or better (smaller component) than the prediction based on the independent model (I). Panels on the right show plots of vertical component duration versus horizontal component duration. The deviation from a perfect 1 : 1 relationship predicted by the common-source model is small. The prediction from the independent model is far off, especially for $\varphi = 60$ deg. See Table 2 for further details

Table 2. Straight-line fits through vertical component duration/horizontal component duration plots, as in Fig. 8 (right-hand column), for all oblique directions tested in the two monkeys. Each fit line is characterized by a slope and an intercept (ms) and was based on at least 50 data points (left-hand columns). The correlation coefficients, characterizing the goodness of the straight-line fit with the experimental data points, ranged from 0.93 to 0.99 (mean: 0.96) for the 8 directions tested in monkey 10. In monkey 11 the fit was still better (range: 0.97–0.99; mean: 0.98). The slope and intercept were predicted according to the independent model (middle columns) using: slope = $\frac{a_V}{a_H}|\tan\varphi|D_H$; intercept = $b_V - \frac{a_V}{a_H}|\tan\varphi|b_H$.

These relations follow directly from Eq. (10); see Introduction. As explained in the text, the common-source model predicts that in all oblique saccades both components have equal duration (right-hand columns)

Direction	Experimental data				Predictions independent model				Common-source model	
	Monkey 10		Monkey 11		Monkey 10		Monkey 11		Monkey 10/11	
(φ)	slope	interc.	slope	interc.	slope	interc.	slope	interc.	slope	interc.
30	0.87	1.7	0.95	–1.1	0.40	13.6	0.65	3.8		
60	0.99	2.9	0.93	4.1	1.20	3.6	1.94	–25.7		
120	1.01	2.2	1.11	–2.3	1.59	– 7.2	1.73	– 9.7		
150	0.96	–1.0	1.01	–2.1	0.53	10.0	0.58	9.1		
210	0.93	1.0	1.01	–1.3	0.66	6.3	0.94	– 7.0	1.00	0.0
240	0.89	6.2	1.00	2.4	1.99	–15.2	2.83	–37.7	(same for all	
300	0.96	3.8	1.00	2.9	1.50	– 1.7	3.16	–63.8	directions)	
330	0.95	1.5	0.85	5.2	0.50	10.9	1.05	–15.7		

Recently, we have repeated the same study in the human. In each of two subjects investigated, we found that onset synchronization of orthogonal components is about as good as it is in the monkey. Furthermore, we have obtained clear evidence for component stretching in oblique saccades. As in the monkey, and in agreement with Bahill and Stark (1975), the amount of component stretching in small (e.g., < 15 deg) saccades was negligible. We could also confirm Viviani et al.'s (1977) finding that oblique saccades in man are not as straight as they are in the monkey. Whatever the cause of this phenomenon, it is unlikely from our data that it is due to a saccadic system functioning as suggested by the independent model.

It may be useful to contemplate alternative schemes which might also be able to explain the crosscoupling between components of oblique saccades which is so obvious in the monkey. One could modify the independent model by providing a possibility for crosscoupling between the horizontal and vertical channel which it now lacks (Fig. 1B). To do this at the level of horizontal and vertical pulse generators (i.e., in the neural control system) would seem to be rather ad hoc.

It should be possible, by future neurophysiological studies on coding of oblique saccades by burst neurons and motoneurons, to get more insight into the stretching phenomenon. The idea gained from the literature is that this is almost virgin territory. A start in the right direction has been made by Hepp and Henn (1982, 1983). To test the common-source model further, the interrelations among vectorial error, vectorial eye velocity, component velocity and firing rate, need to be studied for various classes of neurons.

The remaining Discussion will concentrate on the potential role of neural mechanisms to explain the observed crosscoupling effects. The common-source model can explain component stretching as a natural consequence of a *nonlinear vectorial* pulse generator without necessitating additional assumptions. It has been suggested that the pulse generator is nonlinear to explain the curvilinear peak velocity/amplitude relationship of horizontal saccades (Robinson 1975; Van Gisbergen et al. 1981). By proposing a single nonlinear pulse generator fed by a vectorial error signal (Fig. 1A), the curvilinear peak velocity/amplitude relation for horizontal saccades is generalized to all directions, in good agreement with the experimental data (Fig. 5). An interesting consequence of this key assumption is that it can also explain the occurrence of another nonlinear phenomenon: component stretching in oblique saccades. As we have shown (Introduction), quantitative predictions can be made from this model concerning the expected degree of component stretching as a function of saccade vector direction and amplitude (Fig. 2). These predictions appeared to be largely correct and thus attest of the model's capability to bring insight into what would otherwise have been a puzzling set of data (Figs. 7 and 8). Since, so far, the common-source model was discussed only in rather abstract terms, it is essential to give more thought to the problem of how such a scheme could be embodied in a realistic neural network.

Possible neural basis for common-source model

A possible neural basis for the common-source model will now be discussed. We assume that the desired saccade vector is spatially encoded in a neural map, which can be exemplified by the collicular map. The problem to be addressed is how the spatially encoded collicular map is converted into the temporally coded signals of horizontal and vertical MLBs (see Introduction). What seems to be needed, in view of the results of this paper, is a neural scheme which generates a vectorial eye velocity signal which is then decomposed in the component-related velocity command signals of MLBs.

We take up Hepp and Henn's suggestion that the spatio-temporal recoding may have an intermediary step where direction is still spatially coded (i.e., by which group of neurons in the total population is active) whereas vectorial eye velocity is already coded temporally (i.e., in the precise firing rate of these neurons). The LLB subclasses, called vector and direction burst cells by Hepp and Henn (1983; see Introduction), may represent different stages in this recoding process.

Thus, an array of LLBs, each of which codes eye velocity in a certain direction, embodies the vectorial pulse generator proposed in the common-source model (Fig. 1A). Because, according to the common-source model, the vectorial pulse generator is nonlinear, our scheme requires that burst firing rate in this LLB population (representing vectorial eye velocity) has a nonlinear relation with retinal error.

Decomposition is the subsequent stage in the proposed chain of neural signal transformations (Fig. 1A). Following suggestions made by Hepp and Henn (1983), we propose that LLBs with an oblique movement field drive both horizontal and vertical MLBs. The idea that LLBs may play an intermediary role in interfacing MLBs with the collicular map seems reasonable from a study by Raybourn and Keller (1977). The synaptic weight with which each individual LLB cell drives horizontal and vertical

MLBs must of course depend on the direction of its movement field (φ) and would be cosφ and sinφ, respectively [see Eqs. (3) and (4)]. For LLBs corresponding to the φ = 45 deg meridian, for example, these synaptic weights would both be 0.707. As a result, horizontal and vertical eye velocity would be equal which is appropriate for a 45 deg oblique saccade. It should perhaps be emphasized that the synaptic weights with which each LLB cell drives the two populations of MLBs, are *fixed*. We do not, however, exclude the possibility of slow plastic changes under certain conditions.

We are well aware, of course, that the scheme is partly conjectural and still very incomplete. Some of the problems which cannot be resolved at the moment are worth pointing out:

1) If a population of long-lead burst cells is recruited into activity, what ascertains that the total sum of all the individual movement tendencies produced will yield a normometric saccade? This problem was solved elegantly in Robinson's one-dimensional model by assuming an internal-feedback loop. There is good evidence to favour the notion of some form of internal feedback (Robinson 1975, 1981) but how this idea should be generalized in a two-dimensional model of the saccadic system is not a trivial problem (Keller 1980; Van Gisbergen et al. 1982; Sparks and Mays 1983) and certainly beyond the scope of this paper.

2) Another problem is how the pause cell saccade-initiation system (Keller 1974) is interfaced with LLBs and MLBs. So far, it has been widely assumed that the omnidirectional pause cells inhibit MLBs directly. As far as we know, such connections have not yet been proven. From a functional point of view, we think it cannot be excluded that they exert their presumed gating function at a more central level. At any rate, every scheme attempting to model the monkey's saccadic system will have to account for the rather tight synchronization of component onset and offset in oblique saccades.

3) Finally, there is the unresolved question of how the rather noisy eye velocity signals of LLBs can give rise to the neat velocity signals in MLBs.

This list, which could be expanded further, makes clear that we are still far from a complete two-dimensional model of the saccadic system. Yet, we think the common-source model deserves further attention. An important asset of this model is that it permits a rather simple explanation of the complicated crosscoupling effects which we found in the monkey. Bahill and Stark (1977), apparently reasoning from the standpoint of an independent model, suggested that "a great deal of computational effort" would be necessary to create tight crosslinking of horizontal and vertical components of oblique saccades. Also the very term "stretching", which has become entrenched in the literature, seems reminiscent of the idea that a deliberate control strategy in the saccadic system is responsible for component crosscoupling. The common-source model, instead, suggests that stretching may be a corollary of a nonlinear vectorial pulse generator. Thus, both the nonlinear peak velocity/amplitude relationship of saccades and the stretching phenomenon in components of oblique saccades may be consequences of a single nonlinearity.

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