Glissades—Eye Movements Generated by Mismatched Components of the Saccadic Motoneuronal Control Signal

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ABSTRACT

Human saccadic eye movements have three types of overshoot: dynamic overshoot, lasting 10–30 ms; glissadic overshoot, lasting 30–500 ms; and static overshoot, which is amended—after a delay of about 200 ms—by a subsequent corrective saccade. Glissades are the slow drifting eye movements occasionally seen at the end of saccadic eye movements. Glissades are hypothecated to be produced by mismatches in the pulse and step components of the motoneuronal controller signals. Glissades are not vergence eye movements, although the dynamics are similar.

INTRODUCTION

There are three types of overshoot in saccadic eye movements: dynamic overshoot, glissadic overshoot, and static overshoot [3]. These are shown in Fig. 1. The return phases of the dynamic overshoot (*A* and *C*) have magnitudes of 0.5 deg, peak velocities of 45 deg/sec, and durations of 18 ms. The glissade (*B*) has a magnitude of 1.1 deg, a velocity of about 8 deg/sec and a duration of 280 ms. The static overshoot (*C*) is corrected—after a delay of 180 ms—by a 0.7 deg, 50 deg/sec, 20 ms corrective saccade. The shapes, neurological controls, and dynamics of these three types of overshoot are quite dissimilar. Glissadic overshoot is proposed to be a consequence of a mismatch in the motoneuronal control signals and is the major topic of this paper.

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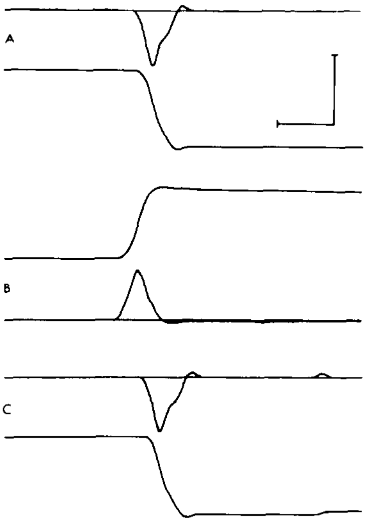

FIG. 1. Three types of overshoot. Eye position and eye velocity as functions of time for three saccadic eye movements executed in a 2 minute time span that demonstrate dynamic overshoot (*A*), glissadic overshoot (*B*), and both dynamic overshoot and static overshoot (*C*). The calibrations represent 18.2 deg, 750 deg/sec, and 80 ms.

To generate a saccadic eye movement, a motoneuronal control signal in the form of a pulse step, as shown in Fig. 2(b), is sent to the extraocular muscles [3, 6, 9, 10, 11, 16, 24]. This motoneuronal control signal consists of two portions: first, the phasic component, characterized by a high-frequency burst of motoneuronal activity for the agonist and an inhibition of motoneuronal activity for the antagonist; and secondly, a tonic component, the steady state neuronal firing rate. The duration of the phasic component is about one-half the duration of the saccade [5]. This phasic component is responsible for the large forces that rapidly move the eye from one position to another. The tonic component holds the eye in its new position. The human saccades of Fig. 2 were, according to our hypothesis, the results of variations in degree of matching of phasic and tonic components. If these two components were in concert, the resultant eye movement would be a matched saccade, as shown in Fig. 2(a). If the phasic component were greater than the tonic component, (because, for example, the pulse was too wide or too high), then the eye would travel beyond its final position and slowly drift back, as shown in the mismatched saccadic eye movement of Fig. 2(c). If the phasic component were smaller than the tonic component, then the eye would not reach the final position with one fast, smooth motion, but would stop short and slowly drift to its final position, as shown in the mismatched saccadic eye movement of Fig. 2(d). These slow drifts are called glissades.[1]

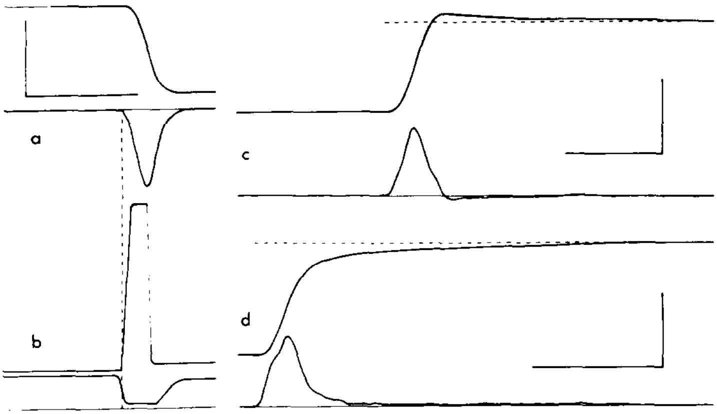

FIG. 2. Three types of glissadic behavior. Eye position and eye velocity as functions of time for saccadic eye movements with no glissade (a), glissadic overshoot (c), and glissadic undershoot (d). The hypothecated firing frequencies for the agonist (top) and the antagonist (bottom) motoneuronal pools are shown in (b). The calibrations represent 13 deg and 640 deg/sec (a), 14.6 deg and 600 deg/sec (c), and 10 deg and 500 deg/sec (d). The time calibration in each represents 100 ms. No time delay is shown between onset of motoneuronal activity and start of saccade, because this delay is not fixed; it depends upon where the motoneuronal activity is measured.

These glissades have been portrayed in a number of previous reports [15, 23, 25, 28, 29, 30]: most of these reports [15, 23, 25, 28] implied that the glissades were due to the mismatching of the phasic and tonic components of the motoneuronal saccadic controller signal.

The present paper examines glissades in the light of our new experimental data. It shows that glissades can be produced by errors in either the phasic component *or* the tonic component. When the tonic component is in error, visual feedback will produce a corrective saccade, about 200 ms after the primordial saccade, correcting for the steady state error and bringing

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[1] *Saccade* is a French word meaning a fast movement like the flick of a sail [17] or the jerk of a horse's head. It was first used by Javal [19] to refer to eye movements. *Glissade* is a French word meaning a skillful slide down a steep snowy slope. It was first used by Weber and Daroff [30] to refer to eye movements.

the eye onto the target. If the phasic component, the product of the pulse height and pulse duration, is erroneous, there need be no corrective saccade, for the eye will drift onto the target via the glissade. This paper further shows that although glissades are not vergence eye movements, the relationships between the maximum velocity and the magnitude of the eye movements are similar for glissades and vergence eye movements.

METHODS

The infrared photodiode method of eye position measurement was used [3, 27]. The bandwidth of the complete system including photodiodes, amplifiers, computer velocity algorithm, computer slowdown plotting routine, and an *X-Y* plotter extended from DC to 500 Hz. This large bandwidth was essential for studying glissades. Low pass filtering of the data distorted the true shape of the glissades and often completely obscured the smaller glissades. The data were also effected by our use of a velocity record when looking for glissades. Small glissades are easier to discern in velocity records than in position records. Figure 3 illustrates the linearity of our methods. The system is linear for more than 20 deg of eye rotation. This limit on linearity is prescribed by the size of the iris and the covering of the iris by the eyelids. The output of this exceptionally simple instrument is

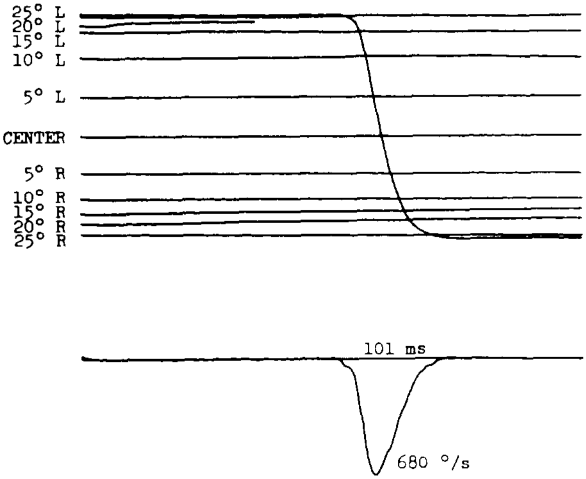

FIG. 3. Linearity of the method is illustrated by a typical 50 deg saccade (top) and its associated velocity record (bottom). The indicated values of 680 deg/sec and 101 ms are respectively the peak velocity and the saccadic duration. The background grid lines show voltage output when the subject was fixating at the indicated positions. The line for 20 deg left is incomplete, because the subject saccaded away from this point. The length of each record is 500 ms.

nonlinear for very large eye movements. We do not wish to add either more photodiodes or a computer linearization program to the instrument to compensate for this nonlinearity, because the present instrument compresses the extremes of the range and expands the central region, producing linearity and a signal to noise ratio greater than 1000 near the center, where the saccades achieve peak velocity. Yet, it still allows measurement of saccades up to 50 deg, which includes most naturally occurring human saccades. Other details of the methods and models have been discussed elsewhere [3].

RESULTS

Figure 4 shows a typical glissade. The right eye reached the target with one smooth saccade, while the left eye's fast saccadic portion fell short of the target, and the movement was completed with a glissade. For the rest of this report we show only the eye that has the glissade.

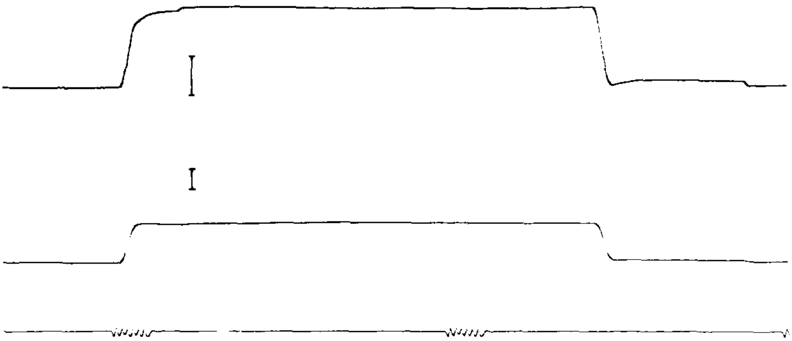

FIG. 4. Glissades are monocular. The left eye (top) has glissadic undershoot and glissadic overshoot, while the right eye (middle) has neither. The lowest trace is a timing record with a 60 Hz burst each second. The calibration marks represent 10 deg for each channel.

The three basic types of glissadic behavior due to the matching or mismatching of the phasic and tonic components of the motoneuronal controller signal have been shown in Fig. 2. Because the phasic and tonic components are each capable of making their own separate errors, 13 types of glissadic behavior are logically possible: the phasic component could be oversized, undersized, or correct, and the tonic component could also be oversized, undersized, or correct, yielding the 13 possible combinations shown in Fig. 5.

Each of these 13 types can be distinguished from the others. When the tonic component was oversized or undersized, a steady state error existed at the end of the eye movement. This required a subsequent corrective saccade about 200 ms after the primordial saccade. So, in all cases where the tonic component was incorrect (*A*, *C*, *D*, *F*, *G*, and *I* of Fig. 5), there was a subsequent corrective saccade in a direction appropriate to eliminate the steady state error between target and eye position.

When only the phasic component was incorrect, there was no subsequent corrective saccade, but only a slow corrective glissade at the end of the saccadic eye movement (*B* and *H* of Fig. 5).

When both the phasic and the tonic components were oversized or undersized, the resulting saccadic eye movement could have a positive glissade (upward in Fig. 5), a negative glissade (downward in Fig. 5), or no glissade, depending upon which component had the larger error. These six

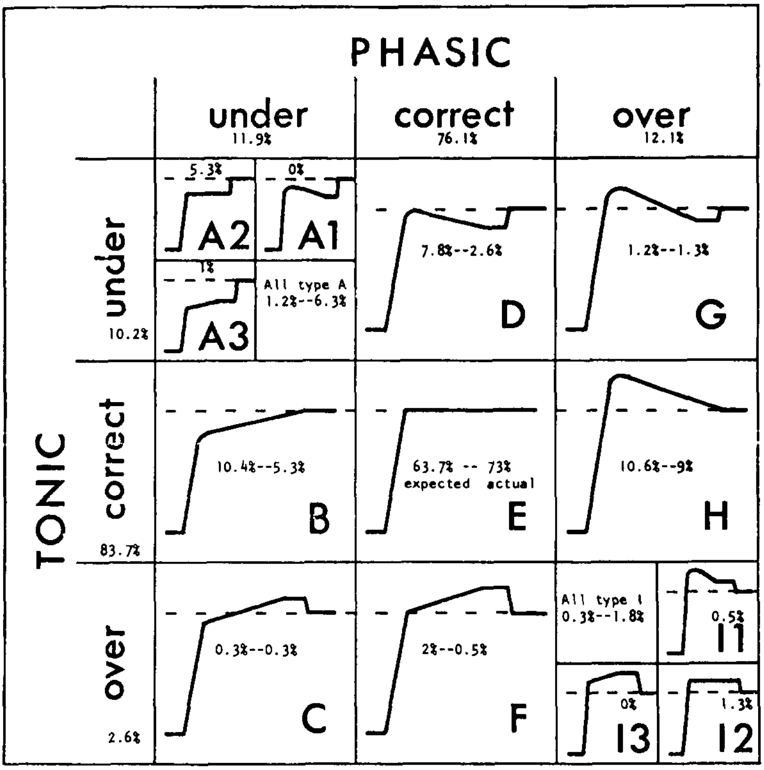

FIG. 5. The 13-fold way, showing all of the glissades that are possible, due to amplitude mismatches of the phasic and tonic components of the motoneuronal controller signal. The first number in each block represents the actual percentage of occurrence of each type, and the second number represents the percentage that would be expected if the phasic and tonic components were completely independent.

possibilities are shown in *A* and *I* of Fig. 5.

Two of these 13 types (*A*2 and *I*2) have static undershoot and static overshoot. They look like type *E* saccades. Two other types (*A*1 and *I*3) have not yet been observed experimentally.[2] Therefore, the display of actual eye movements has been reduced to the ninefold way shown in Fig. 6.

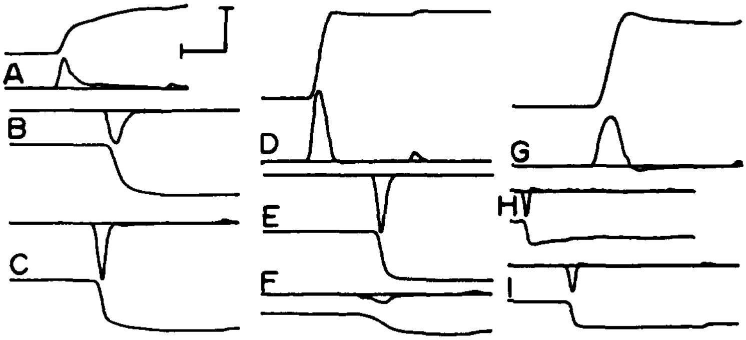

FIG. 6. Eye position and eye velocity for the nine basic types of saccadic eye movements shown in Fig. 5. The calibration shown in *A* represents: 10 deg and 425 deg/sec for records *A*, *B*, *C*, *D*, *E*, and *F*; 15 deg and 550 deg/sec for record *G*; one degree and 100 deg/sec for record *H*; and 4 deg and 270 deg/sec for record *I*. The time calibration is 100 ms and applies to all records.

Figure 5 shows the relative frequency of occurrence of each of these 13 types in normal unfatigued human subjects. Fatigue greatly increases the percentage of type *B* responses [2]. These percentages are based on the 617 saccadic eye movements remaining after saccadic eye movements with dynamic overshoot [3] have been removed from our data base of 2500 saccades. The percentages based on all 2500 saccades are roughly similar, but some saccadic eye movements possessing dynamic overshoot were very difficult to catagorize.

The velocity and duration of these glissades depended upon their magnitude. The eye was being driven by the difference in tonic activity of the agonist and antagonist muscles and not by a pulse step controller signal as in saccades, so glissades were slower than saccades of the same magnitude. Vergence eye movements are driven by a step change in motoneuronal activity [14], and have similar velocities to glissades. Figure 7 is a *main sequence* diagram showing the velocity of saccadic eye movements [4], the

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[2] We have recorded a solitary type *I*3 glissadic eye movement in a patient with a cerebellar tumor (Bahill, Hoyt, Ochs, Selhorst, Spire, and Stark, ENG Laboratory, Neurology Department, University of California at San Francisco).

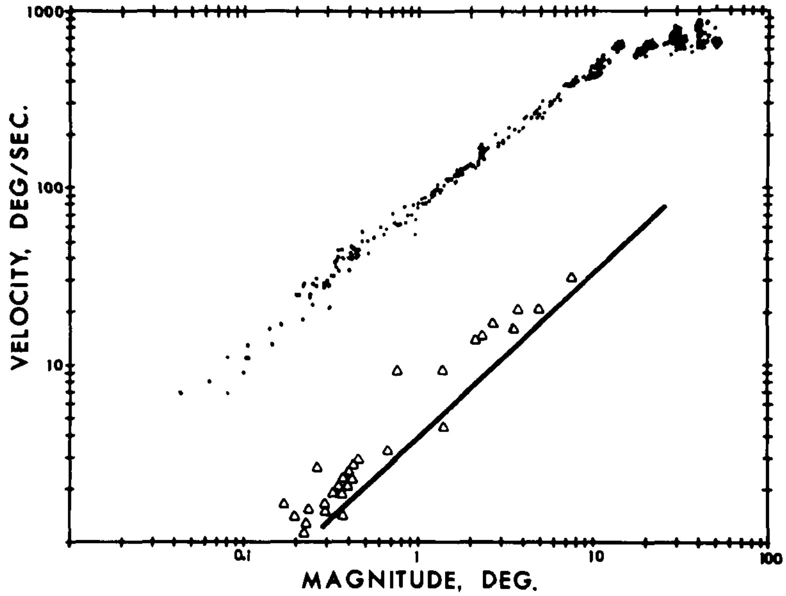

FIG. 7. A main sequence diagram showing velocity versus magnitude for saccades (●), glissades (△), and fusional convergence (—).

fusional convergence eye movements [21, 22, 32], and the glissades of this report. It is clear that glissades are much slower than saccades and are of about the same velocity as vergence movements.

To further test the theory that the nine types of glissadic behavior were caused by mismatches of the phasic and tonic components, a simulation was performed on the Clark-Cook-Stark model for the extraocular plant [3, 11, 12]. A phasic oversized component could be produced by having the motoneurons fire at too high a rate during the phasic burst, by having too many motoneurons recruited for the phasic burst, or by having the duration of the burst too long. To avoid confounding effects, we have varied only the duration of the pulse in our model and have produced the ninefold way. Figure 8 shows saccades from our model of types *B*, *D*, *E*, *F*, and *H*. Types *B*, *E*, and *H* have equal, correct tonic components; the only parameter that is different between them is the duration of the phasic component of the controller signal. Types *D*, *E*, and *F* all have identical phasic components; the only parameter that is different for the primordial saccades of this figure is the tonic component of the controller signal. A corrective saccade follows for the two movements when this tonic component was erroneous. These simulated glissades have dynamics that match recorded human glissades. For example, the glissade at the top of Fig. 8 has a magnitude of 1.3 deg, an

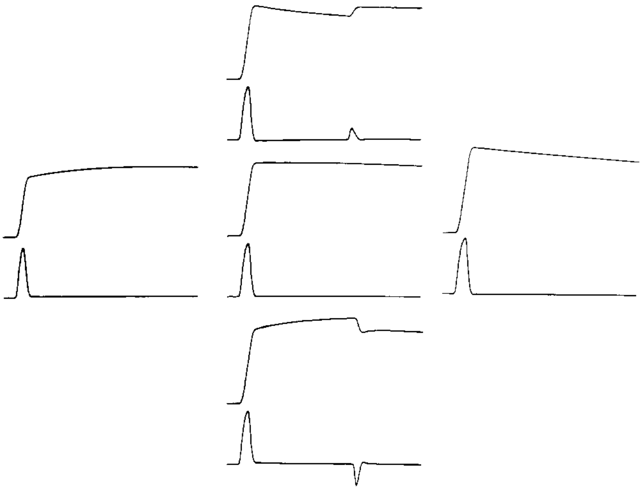

FIG. 8. Simulated 10 deg saccadic eye movements of type *B*, *D*, *E*, *F*, and *H*. The glissades were created by mismatching the pulse and step components of the saccadic controller signal. The dynamics of these simulated glissades match the dynamics of actual human data. Each record lasts 500 ms.

average velocity of 5.5 deg/sec, and a duration of 230 ms. This velocity matches the glissadic velocities of Fig. 7, and the duration is the same as for the human glissade of Fig. 6C. So, the shapes, sizes, velocities, and durations of the simulated glissades match actual human glissades.

Vertical glissades have also been recorded. They had slightly different distributional percentages than horizontal saccadic eye movements. The biggest differences were that about 10% of upward saccadic eye movements were type *A*3 (compared to 1% for horizontal) and that about 10% of downward saccadic eye movements were type *I*1 (compared to 0.5% for horizontal). With these exceptions their percentages were similar to the percentages of Fig. 5. Oblique saccadic eye movements have been recorded with glissades in the horizontal component, the vertical component, and even in both components simultaneously, as is shown in Fig. 9. In this figure the vertical eye movement was composed of two overlapping saccades (see Bahill and Stark [2] for a discussion of overlapping saccades), followed by the negative glissade. Overlapping saccades and an excessive number of glissades are signs of fatigue [2]. The glissades of Fig. 9 were recorded from the right eye while the left eye was covered with a black patch.

It should be possible to have both eyes in error for the same saccadic eye movements, thus producing binocular glissades. If these binocular glissades

FIG. 9. A saccadic eye movement with glissades in both the vertical and horizontal components: in the left column, from top to bottom, as functions of time are vertical eye position, vertical eye velocity, horizontal eye position, and horizontal eye velocity. The right column displays the X-Y trajectory representing the position of the eye in X-Y space (top), and the horizontal eye position trace rotated 90 deg and aligned with the trajectory above. The calibration represents 4 deg, 150 deg/sec, and 250 ms. These eye movements were recorded under monocular viewing conditions.

caused the eyes to move in opposite directions, then it would be hard to differentiate them from vergence eye movements. However, if the eyes were moving in the same direction, it would be easy. We have specifically looked for binocular glissades in the records of three of our subjects. We found them in all three records. Figure 10 shows binocular glissades. Figure 10(a) shows type *A*3 glissades. The normal occurrence of this type of movement is about 1% (from Fig. 5), so the behavior exhibited by the saccadic eye movements of Fig. 10(a) would be a rare chance occurrence, occuring about once in 10,000 saccadic eye movements. The glissades of Fig. 10(b) were type *I*1, which have a frequency of occurrence of 0.5%. So this type of binocular glissade would occur once in 40,000 saccadic eye movements. Thus, although binocular glissades are rare, they do exist.

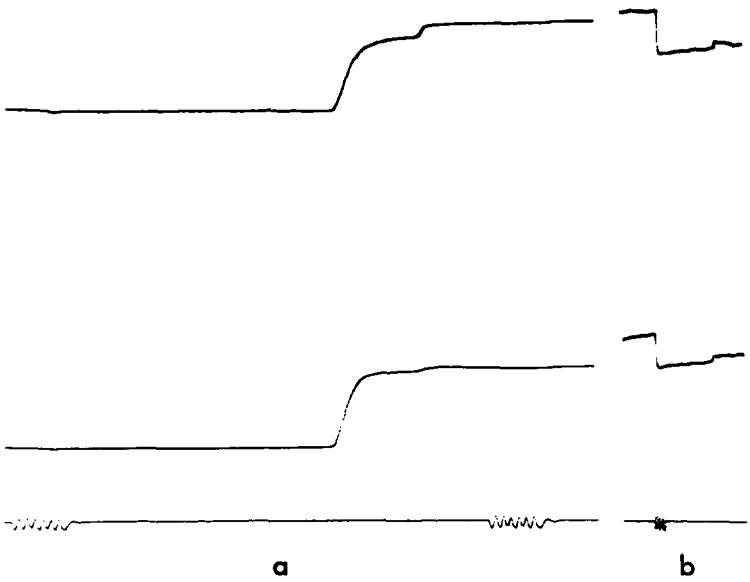

FIG. 10. Binocular glissades. Both eyes are glissading, and the glissades carry the eyes in the same direction. Shown, as functions of time, are left eye position (top) and right eye position (middle) for (a) 10 deg, and (b) 2.5 deg saccadic eye movements. The lowest trace is a timing record with a 60 Hz burst every second. The time scale for (b) is one-fifth that for (a). Leftward eye movements are represented by upward deflections in these records.

DISCUSSION

The shapes of the glissadic velocity records (Figs. 1, 2, 6, 8, and 9) are roughly exponential. The peak velocity occurs near the start of the glissade, and the velocity decays toward zero in an approximately exponential manner. This is what would be expected if the glissades were driven by the difference between the erronous eye position and the tonic motoneuronal activity, which codes the correct eye position.

The statistics of Fig. 5 were derived from saccadic eye movements where both eyes could view the target, but the movements of only the left eye were recorded. We have done a similar statistical analysis for saccades recorded with a black patch over the nonrecorded eye; the percentages were similar to those of Fig. 5. We have also done an analysis of data derived when both eyes viewed the target and both eyes were recorded. Although the target motion had no vergence inducing component, we found that some vergence eye movements were made. These saccades with appended vergence movements looked qualatatively different than saccades with glissades appended. Removing the responses with vergence eye movements from the data base yielded percentages similar to that of Fig. 5, except that the percent of ideal type *E* responses increased by about 5%.

With the eye abducted 35 deg from primary position we found glissadic undershoot to be slightly more prevelant in abducting than in adducting saccadic eye movements. However, tracking targets in this position produces fatigue very rapidly, and this increases the occurrence of undershooting glissades in all directions [2].

The velocities used in Figs. 2 and 7 have slightly different definitions. The velocities for saccades [4] and dynamic overshoot [3] are maximum velocities, while those of vergence [21, 22, 32] and glissades are averages over the first portion of the movements. Vergence eye movements have nearly constant velocities over the first portion [22], so the average for this portion and the maximum velocities are similar. Saccadic maximum velocities are about 20 times larger than vergence and glissadic average velocities. If the data for saccadic peak velocities were converted into average velocities, then the saccadic average velocities would be about 12 times larger than glissadic and vergence average velocities. The differences would still be large, and we felt that it was best not to transform the data of Fig. 7.

Glissades are not vergence eye movements, although glissadic velocities have been compared to vergence velocities. First of all, only one eye is moving during a glissade, and during most vergence eye movements the two eyes move in opposite directions and by the same amount. Asymmetrical vergence eye movements (where only one eye moves) can be induced for slowly moving targets. However, abrupt target steps will usually produce saccades plus symmetric vergence eye movements (Robert Kenyon, personal communication). Second, vertical glissades (Fig. 9) are common. Third, glissades can occur under monocular viewing conditions (Fig. 9). Fourth, there is no latency between the occurrence of the error and the start of the glissade. Fifth, binocular glissades exist. The glissades of Fig. 10 are binocular glissades. Each eye is moving in the same direction, and with the same dynamics during the glissadic portion of the eye movement. Vergence eye movements do not move the eyes in the same direction. There is no moving target, and therefore it is unlikely that this movement is smooth pursuit.

Some of the glissades of Fig. 7 have velocities slightly greater than equivalent sized vergence eye movements; this may have been caused by the initial conditions imposed on the glissade by the preceeding saccade. The glissades of Figs. 2 and 6 were specially selected so that their behavior would be readily apparent; thus, they are unusually large glissades.

The distribution shown in Fig. 5 for the types of glissades reveals that the tonic and phasic components are interdependent. If the components were independent, then the percentage shown in any particular block of Fig. 5 would be the product of its row and column percentages. For instance, 76.1% of the eye movements of Fig. 5 had correct phasic components, and 10.2% had undersized tonic components. The product of these is about 7.8%. If each component were independent, then 7.8% of the eye movements should have been type *D*. The actual data show that only 2.6% were type *D*. The types where only one component was in error (types *B*, *D*, *F*, and *H*) were all less numerous than would be expected for independence. The sum of the actual percentages for these four is 17.4%, while the sum of the expected percentages is 30.8%. Assuming that the number of eye movements of any one type is adequately represented by a Poisson distribution, then this paucity of type *B*, *D*, *F*, and *H* movements could occur by chance in only one of ten thousand cases. The individual probabilities that the scarcity of types *B*, *D*, *F*, and *H* occurred by chance are respectively 0.27, 0.03, 0.04, and 0.34. Thus, when one component is in error, it is likely that the other component will also be in error. Therefore, the components are interdependent.

There are three conceptual schemes for generating the complex pulse step controller signal. First, a saccadic signal could be sent to two separate elements that operate in parallel. One of these would create the step, and the other the pulse. These two would then be added together to produce the pulse step controller signal. When the input to the system was in error, both components would most likely be incorrect. This hypothesis is in concert with the data of Fig. 5. The second and third schemes, the differentiator and integrator hypotheses, use serial processing. The differentiator hypothesis states that the initial signal is the tonic step, which is differentiated to produce the pulse. (This pulse is the part of the motoneuronal controller signal that drives the eye to its new position with a large saccadic velocity.) Then a summer adds the pulse back into the tonic step, and the complete pulse step controller signal is obtained [6]. On the other hand, the integrator hypothesis states that the initial signal is the pulse, which is integrated to produce the tonic step. (This step is the characteristic part of the controller signal that holds the eye in its new position.) Then a summer adds the step back into the pulse, and the complete pulse step controller signal is obtained [1, 8, 13, 25]. The data in Fig. 5 contain suggestive evidence supporting the differentiator operator hypothesis, but not supporting the integrator hypothesis.

We remarked above that Fig. 5 showed a deficiency of occurrence for error in either the tonic or the phasic components alone. We now examine this deficiency in more detail. Although blocks *B*, *D*, *F*, and *H* were all underrepresented, blocks *D* and *F* were most significantly scarce, with probabilities of 0.03 and 0.04 that this scarcity occurred by chance. Block *D* has one-third and block *F* one-fourth of the expected number of glissadic eye movements. For these blocks the tonic component is incorrect. Therefore, when the tonic component is incorrect, the phasic component is very seldom correct. The differentiator hypothesis accommodates this well. If the input—the tonic step—were incorrect, then the result of differentiation—the phasic pulse—would seldom be correct, and would be correct only by chance. The integrator hypothesis does not fit these data well. This hypothesis would require that when the input (the phasic pulse) is incorrect (e.g. blocks *B* and *H*), the result of integration (the tonic step) should seldom be correct. But the data of Fig. 5 do not show this. The percentages of type *B* and *H* responses are only slightly reduced.

These arguments are, of course, only suggestive in supporting the differentiator and the parallel processing hypotheses. A main reason for putting them forward is to stimulate the oculomotoneurophysiologists to obtain more clear-cut evidence.

There are neurophysiological studies which facilitate speculation about the locus and operation of the differentiating or integrating operator. The complex pulse step controller signal must be generated from one simple signal somewhere in the CNS, because information in the retina specifies only static error between target and eye position. Furthermore, stimulation of only one point in either the superior colliculus, or the frontal eye fields, or the visual cortex, or the cerebellum, or the thalamus will produce a saccadic controller signal with both the tonic and phasic components that are necessary for normal saccades. This implies that the pulse step controller signal may be generated in the brain stem. The differentiator hypothesis is bolstered by the finding that the oculomotor neuronal membranes act as differentiators [6], because when a step of depolarizing current is applied intracellularly, the motoneuronal firing frequency responds in a pulse step manner. The parallel processing and integrator hypotheses are bolstered by the findings that there are two pools of neurons in the reticular formation that are related to eye movements [7, 13, 18, 20, 26, 31]. One of these pools seems to be related to the tonic eye position, and the other to the saccadic pulse. For the integrator hypothesis, the activity of the tonic neuronal pool would be created by integrating the activity of the pulse pool, and the two would then be summed by the oculomotor neurons in order to produce the pulse step controller signal.

Both tracking saccades and saccades of regard were recorded. The tracking saccades were recorded while the subject attempted to follow a target that jumped predictably from one point to another. Frequencies between 0.25 Hz and 1.5 Hz were used. Saccades of regard were made as the subject voluntarily shifted his gaze between two clearly visible targets. The distributional percentages were the same for these two types of movements.

SUMMARY

Glissades are one of the three types of overshoot (and undershoot) seen in saccadic eye movements. Glissades are generated by amplitude mismatches of the pulse step saccadic motoneuronal controller signal shown in Fig. 2. They may be produced by errors in either the phasic or the tonic components. The driving force for glissades is the difference in tonic levels of innervation, and therefore, glissadic velocities are similar to vergence eye movement velocities. However, glissades are not produced by the vergence system, for binocular glissades have been observed, vertical glissades are common, and glissades have been recorced under monocular viewing conditions. Statistical analysis of the relative frequency of occurrence of each of the 13 types of glissadic eye movements lends support to the differentiator hypothesis, which proposes that the step of neural activity is the input to the motoneuronal controller signal generator and that the pulse of neural activity is produced from it.

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