Independent Feedback Control of Horizontal and Vertical Amplitude During Oblique Saccades Evoked by Electrical Stimulation of the Superior Colliculus

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SUMMARY AND CONCLUSIONS

1. In early local feedback models for controlling horizontal saccade amplitude, a feedback signal of instantaneous eye position is continuously subtracted from a reference signal of desired eye position at a comparator. The output of the comparator is dynamic motor error, the remaining distance the eyes must rotate to reach the saccadic goal. When feedback reduces dynamic motor error to zero, the saccade stops on target. Two classes of local feedback model have been proposed for controlling oblique saccades (i.e., saccades with both horizontal and vertical components). In “independent comparator” models, separate horizontal and vertical comparators maintain independent representations of horizontal and vertical dynamic motor error. Thus, once an oblique desired displacement signal is established, the horizontal and vertical amplitudes of oblique saccades are under independent feedback control. In “vectorial comparator” models, output cells in the motor map of the superior colliculus act as site-specific vectorial comparators. For a given oblique desired displacement, a single comparator controls the amplitudes of both components. Because vectorial comparator models do not maintain separate representations of horizontal and vertical dynamic motor error, they cannot exert independent control over the component amplitudes of oblique saccades.

2. We tested differential predictions of these two types of models by electrically stimulating sites in the superior colliculus of rhesus monkey immediately after either vertical or horizontal visually guided saccades. We have shown previously that, despite the fixed site of collicular stimulation, the amplitude of the visually guided saccades systematically alters the amplitude of the corresponding component (horizontal or vertical) of stimulation-evoked saccades. However, in the present study, we examined the effect of the visually guided saccades on the amplitude of the orthogonal component of stimulation-evoked saccades.

3. For a fixed site of collicular stimulation, vectorial comparator models predict that the initial visually guided saccade will influence both components of the ensuing stimulation-evoked saccade via the single feedback comparator. By contrast, independent comparator models permit the independent manipulation of the horizontal and vertical amplitudes of these oblique stimulation-evoked saccades. However, we collected data from 15 collicular stimulation sites. Immediately after either horizontal or vertical visually guided saccades of different amplitudes, we measured the horizontal and vertical amplitudes of saccades evoked by stimulation of the intermediate or deep layers of the superior colliculus. For each site, the duration, frequency, and current of the stimulation trains were held constant.

4. Under these conditions, stimulation-evoked saccades followed visually guided saccades with short latency (18.1 ± 6.7 ms, mean ± SD). For every stimulation site tested, although the amplitude of the component of stimulation evoked saccades corresponding to the direction of the preceding saccade (horizontal or vertical) varied systematically, the amplitude of the orthogonal component was roughly constant.

5. Thus the horizontal and vertical amplitudes of oblique saccades can be manipulated independently. Moreover, the peak velocity-amplitude relationships, the instantaneous velocity profiles, and the ratio of horizontal and vertical velocities and durations were very similar to those of visually guided saccades.

6. Independent comparator models can readily account for the ability to manipulate the amplitude of one component of oblique saccades without affecting the other. However, two-dimensional local feedback models that cannot exert independent control over the horizontal and vertical amplitudes of oblique saccades should be carefully reevaluated.

INTRODUCTION

To bring selected images onto the fovea, saccadic eye movements must be highly accurate. Yet, saccades are far too rapid for visual feedback to play a role in achieving that accuracy, nor does accuracy depend on proprioceptive feedback from extraocular muscles (Guthrie et al. 1983; Keller and Robinson 1971). As an alternative, Robinson (1975) proposed a model of horizontal saccadic control in which a nonsensory feedback signal of orbital eye position is derived from a copy of the effenter motor command. Figure 1A (Horizontal Controller) depicts a conservative modification of that model (Jürgens et al. 1981) in which a feedback signal representing horizontal eye displacement during the current saccade (HCD) is subtracted from a reference signal of horizontal desired displacement (HDD) at a comparator (COMP). The output of the comparator is horizontal dynamic motor error (HME), the remaining distance the eyes must rotate to reach the saccadic goal. A pulse generator (HPG) computes a velocity command as a high gain function of dynamic motor error, and a displacement integrator (HDI) integrates that velocity command to provide the negative feedback signal to the comparator. The pulse generator automatically drives the eyes (via the motorneurons) until the current displacement signal from the integrator matches the desired displacement signal at the comparator. After each saccade, the feedback integrator is reset to zero (Jürgens et al. 1981) with an exponential time course (Nichols and Sparks 1995) in preparation for the next desired displacement command. Although this one-dimensional model was developed to account for the control of horizontal saccades, it can account for vertical saccadic control, as well.
However, most saccades are oblique, having both horizontal and vertical components. Furthermore, just two or three synapses upstream from the motoneurons, a motor map in the superior colliculus (SC) represents saccades in all directions (Robinson 1972). Therefore the local feedback concept must be extended to explain accuracy in two dimensions. Figure 1A captures the essential features of one approach to this problem (e.g., Becker and Jurgens 1990; Grossman and Robinson 1988; Scudder 1988). In this class of two dimensional models, a vectorial desired displacement signal, represented by the locus of activity in the collicular map, is decomposed to provide separate reference signals to independent horizontal and vertical comparators downstream. These comparators drive separate pulse generators and receive feedback signals from independent integrators. Thus horizontal and vertical dynamic motor error are reduced to zero independently during oblique saccades.

In an alternative approach (e.g., Arai et al. 1994; Keller 1979; Van Opstal and Kappen 1993; Waitzman et al. 1988, 1991), the output neurons of the SC lie within the local feedback loop and serve as site-specific, vectorial comparators. In this class of models, illustrated in Fig. 1B, each locus in the collicular motor map serves as the single comparator for a different saccade vector. For an oblique saccade of a particular direction and amplitude, the output neurons at a single active locus receive input from a reference signal of vectorial desired displacement (VECT DD), also specified by the locus of collicular activity, and negative feedback from both horizontal and vertical displacement integrators (HDI and VDI). The discharge rate of the active locus represents vectorial dynamic motor error, whereas the relative weighting of projections from the active locus to the horizontal and vertical premotor circuitry determines the appropriate ratio of horizontal and vertical dynamic motor error (i.e., the direction of vectorial dynamic motor error). The horizontal and vertical pulse generators then compute component velocity commands from their respective motor error signals. Thus the two dimensional model in Fig. 1B differs from the model in Fig. 1A primarily in the nature of its comparator. Vectorial comparator models maintain a single representation of dynamic motor error during oblique saccades, whereas independent comparator models maintain independent representations of horizontal and vertical motor error.

Under many circumstances, these models will behave similarly. But, if it were possible to manipulate the amplitude produced by one pulse generator without changing the locus of activity in the collicular map (and consequently, without changing either vectorial desired displacement or the locus of the putative vectorial comparator), then the vectorial comparator and independent comparator models would make qualitatively different predictions. Logically, vectorial comparator models cannot exert independent feedback control over the horizontal and vertical amplitudes of oblique saccades, because they maintain only one representation of dynamic motor error. Thus, if both the desired displacement vector and the comparator locus in the SC are fixed, it is not possible to alter the amplitude produced by one pulse
generator without affecting the amplitude produced by the other (for a related argument, see Van Opstal and Kappen 1993). By contrast, in independent comparator models, independent feedback loops control horizontal and vertical dynamic motor error downstream from the SC. Thus, even if the locus of collicular activity is fixed, altering the component amplitude produced by the horizontal pulse generator will have no effect on the amplitude produced by the vertical pulse generator, and vice versa. We tested these differential predictions for saccades evoked by electrical stimulation of the SC.

Typically, electrical stimulation at a particular site in the SC evokes saccades with very stereotyped directions and amplitudes (e.g., Robinson 1972; Schiller and Stryker 1972), and amplitude is site specific even when the stimulation train outlasts the saccade (e.g., Robinson 1972). Furthermore, the direction and amplitude of stimulation-evoked saccades vary systematically with electrode location across the colliculus (Robinson 1972). These findings, among others, have been widely interpreted as evidence that collicular stimulation evokes a site-specific desired displacement signal (for reviews, see Fuchs et al. 1985; Sparks and Mays 1990).

However, despite their normally stereotyped trajectories, saccades evoked by collicular stimulation deviate from their normal direction and amplitude when they are elicited during (e.g., Schlag-Rey et al. 1989) or immediately after (Kustov and Robinson 1995; Nichols and Sparks 1995) visually guided saccades. In one study, Nichols and Sparks (1995) applied electrical stimulation to collicular sites immediately after either purely horizontal or purely vertical visually guided saccades of different amplitudes. Under these conditions, the interval between the end of the visually guided saccade and the beginning of the stimulation-evoked saccade was ~20 ms, much shorter than the shortest interval between visually guided saccades. Furthermore, the amplitude of the initial visually guided saccade systematically influenced the corresponding component amplitude (horizontal or vertical) of the stimulation-evoked saccade. For example, consider a collicular site at which stimulation normally produces an oblique saccade up and to the right (the “control” saccade). Immediately after a rightward visually guided saccade, the rightward component of the stimulation-evoked saccade will be reduced in amplitude relative to control. Immediately after a leftward saccade, the rightward component of the stimulation-evoked saccade will be increased relative to control. In general, for a fixed intersaccadic interval, the amplitude of the horizontal component of the stimulation-evoked saccade will be inversely proportional to the amplitude of the preceding horizontal saccade over a wide range. This amplitude effect on the horizontal component will gradually disappear as intersaccadic interval is increased, and will be completely absent for intervals >120 ms. The same phenomenon is observed for the vertical component of stimulation-evoked saccades following vertical saccades. These systematic changes in the amplitude of one component can span a range as large as 20° despite the fixed site of stimulation in the collicular map (for a related effect, see Robinson 1972).

Recall that independent and vectorial comparator models make differential predictions if the locus of collicular activity is constant while the amplitude produced by one pulse generator is varied. Therefore, given two basic assumptions, this experimental paradigm offers a rare opportunity to test these predictions. First, the fixed location of the stimulating electrode results in a fixed locus of stimulation-induced collicular activity. Second, the systematic changes in the amplitude of one component of stimulation-evoked saccades reflect changes in the output of the corresponding pulse generator within the feedback loop. If these two assumptions are correct (see Discussion), then vectorial comparator models predict that it will not be possible to manipulate the amplitude of one component of oblique stimulation-evoked saccades without also influencing the orthogonal component. Independent comparator models predict that manipulating the amplitude of one component will have no effect on the amplitude of the other.

Different analyses of the data in this report were used to test other classes of models in a previous report (Nichols and Sparks 1996).

METHODS

Surgery and training

Data were obtained from two adult, female rhesus monkeys (Macaca mulatta). Two sterile surgical procedures were performed on each animal under isoflurane anesthesia. In the first, a scleral search coil (Fuchs and Robinson 1966) and head restraint fixture were implanted. After training, a 15-mm-diam craniotomy was centered over the intersection of the mid sagittal plane and the interaural line. A stainless steel cylinder for a hydraulic microdrive was attached to the skull above the craniotomy. The cylinder was sealed with a replaceable Teflon plug between experimental sessions. All surgical and experimental protocols were in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and were approved by the University of Pennsylvania Animal Care and Use Committee.

Stimulating and recording sessions

During experimental sessions, animals were placed within two 23-kHz sinusoidally oscillating magnetic fields arranged in spatial and phase quadrature. The head was fixed, and the current induced in the scleral coil by the magnetic fields provided a measure of horizontal and vertical eye position with a sensitivity of <0.25° (Fuchs and Robinson 1966). During data collection, horizontal and vertical eye position signals were sampled at 500 Hz. Visual targets were presented on a tangent screen with a computer-driven laser galvanometer system. Target locations were corrected on-line for tangent screen error.

For stimulating and recording sessions, a 21-gauge syringe needle, into which a tungsten-steel parylene-insulated electrode (Microprobe) was withdrawn, was used to pierce the dura. A hydraulic microdrive was fixed to an x-y positioner (Kupf) mounted on the animal’s recording cylinder. The microdrive was then used to advance the electrode into the brain. Physiological signals were amplified and filtered (bandpass of 200–4,000 Hz) to exclude signals of the magnetic field. The electrode was advanced until the multiunit saccade-related activity was found. The electrode tip was always selected, stimulation parameters were set at either 400 or 500 cathodal pulses per second and at either 40 or 50 μA. Pulse width was 0.5 ms. The duration of the stimulation train was set between 50 and 100 ms, depending on the amplitude and duration of the sac-
cade normally elicited from the site under study. Because stimulation-evoked saccades can be truncated if the stimulation train is not sufficiently prolonged (Freedman et al. 1996; Stanford et al. 1993, 1996), at the beginning of each session, we qualitatively assessed the train duration required to produce the full amplitude specified by the collicular stimulation site. Once set, stimulation parameters were fixed for the remainder of the session.

**Experimental design**

Three trial types were used to test the predictions of the vectorial and independent comparator models.

**CONTROL STIMULATION TRIALS.** Animals fixated an initial target for 800–1,200 ms. Either 50 or 70 ms after the fixation light was extinguished, but before any eye movement could occur, electrical stimulation was applied to the SC, producing a saccade. A variable time after the stimulation-evoked saccade, a second visual target appeared in a randomly selected location, and the animal was rewarded for looking to that target.

**VISUAL TRIALS.** Animals fixated an eccentric initial target for a variable period and then received a reward for looking to a briefly presented central target. In some experimental sessions, the extinction of the fixation light and the illumination of the target occurred simultaneously. The target light was subsequently extinguished at a variable time during the reaction time of the animal. In other sessions, the target and the fixation light were both illuminated for a variable period (500–700 ms) before the extinction of the fixation light cueing the animal to look to the target location. In these sessions, the target light was extinguished as the eyes left the electronically defined fixation window. In both cases, however, the target light was extinguished before the animal acquired the target position.

**VISUAL/STIMULATION TRIALS.** These trials were exactly like visual trials except that at the end of the saccade to the location of the brief visual target, stimulation was applied to the SC. Stimulation onset was locked to the eyes entering an electronically defined window (less than or equal to ±2.5°) around the target position and occurred after a delay of 0, 5, or 10 ms. Because of the latency from the onset of stimulation to saccade onset, stimulation-evoked movements began only after visually guided saccades ended near the location of the extinguished target. Because the target light was always extinguished before the eyes arrived in the target window, there was never a visual stimulus to fixate when electrical stimulation was applied. Furthermore, because stimulation-evoked saccades always began from roughly the same orbital position, differential orbital position effects on saccade amplitude, direction, velocity, and duration were minimized.

Once a stimulation site was selected in the intermediate layers of the SC (see Stimulating and recording sessions) and the site-specific direction and amplitude were determined with the use of Control Stimulation Trials, the goal was to obtain stimulation-evoked saccades with a large range of amplitudes in one component. As described in the Introduction, Visual/Stimulation Trials permitted the systematic manipulation of the amplitude of one component of stimulation-evoked saccades without any corresponding change in the location of collicular stimulation. In “horizontal” data sets, stimulation immediately followed horizontal visually guided saccades; in “vertical” data sets, stimulation immediately followed vertical saccades. Visual/Stimulation Trials were randomly interleaved with Visual Trials, and stimulation occurred on ~40–50% of the trials.

**Quantitative predictions**

To formulate detailed predictions for vectorial and independent comparator models, we must consider two possible interpretations of the previously observed amplitude effect on stimulation-evoked saccades.

First, the changes in component amplitude in this paradigm can be readily explained in terms of the resettable feedback integrator without assuming any change in the desired displacement signal evoked by collicular stimulation (Nichols and Sparks 1995). In the horizontal and vertical controllers in Fig. 1A, the saccadic velocity command from the pulse generator to the motoneurons terminates when the feedback signal from the displacement integrator matches the desired displacement reference signal. After each saccade, the feedback integrator must be reset to zero in preparation for the next desired displacement command. Otherwise, residual value on the integrator from the previous saccade would be subtracted automatically from the next desired displacement command at the comparator, causing amplitude errors (Jürgens et al. 1981). Ordinarily, saccades occur with sufficient temporal separation to obscure the putative resetting process of the feedback integrator. But by electrically stimulating sites in the SC immediately after either horizontal or vertical visually guided saccades, desired displacement signals can be injected before or during the resetting of the integrator. If the stimulation-evoked saccade occurs at a fixed time during this postsaccadic resetting process, the component amplitude of the stimulation-evoked saccade should vary in inverse proportion to the amplitude of the preceding visually guided saccade. This prediction was confirmed (Nichols and Sparks 1995).

In an alternative interpretation of this phenomenon, the initial visually guided saccade might transiently alter the intrinsic excitability of the pulse generator, which could, in turn, alter the time integral of the pulse generator’s discharge in response to a given desired displacement signal. Because that integral determines component amplitude, systematic changes in excitability could alter the amplitude gain (the ratio of actual to desired amplitude) of the pulse generator even in the absence of residual value on the feedback integrator. Nichols and Sparks (1995) rejected this interpretation of their data based on a number of arguments, but it is raised again here for the sake of generating a more complete set of predictions for the independent and vectorial comparator models.

Under either interpretation, the independent comparator model in Fig. 1A makes a straightforward prediction. Consider a collicular site (Fig. 2A) at which stimulation normally evokes a 45° oblique saccade with a 10° vertical and a 10° horizontal component (oblique arrow in Fig. 2B). Following vertical saccades of various amplitudes, the vertical amplitude of the stimulation-evoked saccade will be altered systematically. But manipulating the amplitude produced by the vertical pulse generator in response to a given desired displacement command can have no effect on the amplitude produced by the horizontal pulse generator, because neither the vertical feedback integrator nor the vertical pulse generator has any interaction with the horizontal comparator. Therefore, despite variations in the vertical amplitude, the horizontal amplitude will be constant, and the endpoints of all stimulation-evoked saccades will fall along the dashed vertical line (labeled IC) in Fig. 2B.

By contrast, the vectorial comparator model in Fig. 1B predicts that the horizontal and vertical amplitudes of oblique stimulation-evoked saccades will interact systematically. However, the nature of the predicted interaction depends on the theoretical interpretation of the amplitude effect.

**Prediction 1.** Continuing with the above example, if the initial visually guided saccade transiently alters the intrinsic amplitude gain of the vertical pulse generator, then the amplitude of the horizontal component will be altered inversely so that vectorial amplitude is constant. For example, if the amplitude produced by the vertical pulse generator is reduced, the amplitude produced by the horizontal pulse generator must increase so that the total feedback is constant. Regardless of the particular ratio of horizontal and vertical amplitudes (i.e., saccade direction), vectorial dynamic motor error will continue to drive the movement until actual vectorial amplitude matches desired vectorial amplitude (effectively,
FIG. 2. Quantitative differential predictions of vectorial and independent comparator models. A: schematic of the motor map in the left superior colliculus (SC). Latitude lines represent isoamplitude contours; longitude lines represent isodirection contours. A stimulating electrode is indicated at a collicular locus (gray circle) that normally specifies a 45° oblique saccade with a 10° upward amplitude and a 10° rightward amplitude. B: predictions of the independent and vectorial comparator models. The gray oblique arrow represents the saccade vector normally produced by electrical stimulation at the collicular locus shown in A. Dashed vertical line (IC); prediction of the independent comparator model. Dotted arc (VC1); one prediction of the vectorial comparator model. Dotted oblique line (VC2); alternative prediction of the vectorial comparator model. C: predictions from B replotted as vectorial amplitude vs. direction. Filled square indicates the direction and amplitude specified by the site of stimulation. With these axes, the dotted arc in B becomes a horizontal line; dotted oblique line becomes a vertical line; and the dashed vertical line predicted by the independent comparator model becomes the nonlinear function, \( R = c / \cos(\theta) \), where \( R \) is vectorial amplitude, \( \theta \) is direction, and \( c \) is a constant corresponding to the x-intercept of the dashed vertical line in B.

Until desired vectorial amplitude equals the square root of the sum of the squares of the actual component amplitudes, \( R \). Thus the vectorial amplitude \( R \) of stimulation-evoked saccades will be constant across a wide range of directions, \( \Theta \), and saccade endpoints will fall along the dotted arc in Fig. 2B (labeled VC1).

Prediction 2. If the observed amplitude effect on stimulation-evoked saccades is due to residual value on the vertical feedback integrator after the initial saccade, then that residual value will be subtracted at the vectorial comparator. Even at the onset of the stimulation-evoked saccade, vectorial dynamic error already will differ from vectorial desired displacement. Because vectorial dynamic error is decomposed into horizontal and vertical contribution, both horizontal and vertical amplitudes will be influenced. Thus vectorial amplitude will vary systematically while vertical direction remains constant. This prediction is represented by the oblique dotted line in Fig. 2B (labeled VC2).

Unlike the slope of the vertical dashed line predicted by the independent comparator model (Fig. 2B), the slope of the oblique line of prediction 2 depends on the particular saccade direction specified by the stimulation site. Therefore relying on the difference between these predicted slopes to differentiate the models has the undesirable consequence that the magnitude of that difference will vary from one stimulation site to the next. However, all three predictions are qualitatively different and independent of the site of collicular stimulation when they are recast in terms of the vectorial amplitude and direction of stimulation-evoked saccades. With these axes, prediction 1 of the vectorial comparator model (Fig. 2C) becomes a line with zero slope (dotted horizontal line in Fig. 2C). Prediction 2 of the vectorial comparator model (dotted oblique line in Fig. 2B) becomes a line with infinite slope (dotted vertical line in Fig. 2C), regardless of the saccade vector encoded by the stimulation site. Therefore, according to both predictions of the vectorial comparator model, vectorial amplitude \( R \) and direction \( \Theta \) will be independent of each other. The independent comparator model, on the other hand, predicts a strong, nonlinear relationship between vectorial amplitude and direction. The vertical line (horizontal amplitude = constant) illustrated in Fig. 2B becomes the nonlinear function \( R = c / \cos(\theta) \) (1) where \( R \) is vectorial amplitude, \( \theta \) is saccade direction, and \( c \) is a constant corresponding to the x-intercept of the vertical line in Fig. 2B. If Eq. 1 provides a good description of the data, then vectorial amplitude and direction are strongly correlated, in contrast to both predictions of the vectorial comparator model. It should be emphasized that, although the independent comparator model predicts independent control over the horizontal and vertical amplitudes of oblique saccades, it predicts a strong dependence between vectorial amplitude and direction.

**Data measurement and analysis**

The amplitudes (in Fick coordinates) for the horizontal and vertical components of all visually guided and stimulation-evoked saccades were measured. In general, saccade onset and offset were marked automatically on the basis of objective velocity criteria. On some trials, the objective criteria obviously failed, and saccade onset and offset were marked by hand. One criterion was applied for selecting stimulation-evoked saccades for analysis: the amplitude of one component of the initial visually guided saccade fell between 0.5° and −0.5°. In other words, the visually guided saccade was essentially purely horizontal or purely vertical. Once the data were selected, we assessed both qualitatively and quantitatively how well the predictions of the vectorial and independent comparator models described the data (see **RESULTS** for details).

**RESULTS**

Data were collected at 15 collicular stimulation sites in two rhesus monkeys. At 10 sites, either a vertical or a horizontal data set was collected; at 5 sites, both were collected. Of these 20 data sets, 7 were from 1 animal and 13 from the other. For each stimulation site, we first collected control stimulation-evoked saccades that followed periods of fixation lasting 800–1,200 ms. Electrical stimulation of the SC under these conditions produced saccades with highly stereotyped, site-specific trajectories, and it was assumed that the horizontal and vertical amplitudes of these saccades (see Table 1) provided estimates of the horizontal and vertical...
Values in Control Stimulation are means ± SD for the horizontal (top) and vertical (bottom) amplitude of control stimulation-evoked saccades. The table shows a summary of the function fitting for stimulation-evoked saccades. Each row in the table contains data from a single collicular stimulation site. The designation of the stimulation site is given in Site. The component that was systematically manipulated is indicated (H, horizontal; or V, vertical) next to each site designation. At some sites, both horizontal and vertical data sets were collected and are presented in consecutive rows. In Slope the slope of the best fitting line is given for stimulation-evoked saccades plotted as the amplitude of one component vs. the amplitude of the other. In % Variation the percentage of variance in vectorial amplitude accounted for by Eq. 1 is presented. Control stimulation-evoked saccades were not included in the function fits.

desired displacement signals evoked by stimulation at each site. On visual/stimulation trials (see METHODS), stimulation-evoked saccades followed either horizontal or vertical visually guided saccades with very short latency. The mean intersaccadic interval between the end of the visually guided saccade and the beginning of the stimulation-evoked saccade for all visual/stimulation trials was 18.1 ± 6.7 (SD) ms. Although stimulation was applied at a fixed site in the SC for each data set, the amplitude of one component of stimulation-evoked saccades depended systematically on the corresponding component amplitude of the preceding visually guided saccades.

For all 20 data sets, despite wide variation in the amplitude of one component of these redirected stimulation-evoked saccades, either there was no effect on the amplitude of the

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**TABLE 1. Independent control of component amplitudes in oblique stimulation-evoked saccades**

<table>
<thead>
<tr>
<th>Site</th>
<th>Control Stimulation (H&lt;sub&gt;amp&lt;/sub&gt;, V&lt;sub&gt;amp&lt;/sub&gt;)</th>
<th>Slope</th>
<th>% Variation</th>
</tr>
</thead>
<tbody>
<tr>
<td>T17mr.95 (V)</td>
<td>8.2 ± 0.7°, 3.4 ± 0.5°</td>
<td>0.06</td>
<td>89</td>
</tr>
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<td>T17mr.95 (H)</td>
<td>6.6 ± 0.3°</td>
<td>0.20</td>
<td>83</td>
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<tr>
<td>T22mr.95 (V)</td>
<td>5.0 ± 0.4°</td>
<td>-0.01</td>
<td>99</td>
</tr>
<tr>
<td>T24mr.95 (V)</td>
<td>14.8 ± 1.2°</td>
<td>0.05</td>
<td>99</td>
</tr>
<tr>
<td>T06jn.95 (V)</td>
<td>4.3 ± 0.3°</td>
<td>0.05</td>
<td>98</td>
</tr>
<tr>
<td>T08jn.95 (V)</td>
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<td>0.01</td>
<td>97</td>
</tr>
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<td>99</td>
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<td>0.15</td>
<td>91</td>
</tr>
<tr>
<td>T29jn.95 (H)</td>
<td>-4.7 ± 0.4°</td>
<td>-0.05</td>
<td>97</td>
</tr>
<tr>
<td>T04jl.95 (V)</td>
<td>11.0 ± 0.6°</td>
<td>0.05</td>
<td>94</td>
</tr>
<tr>
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<td>-0.16</td>
<td>77</td>
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<tr>
<td>T26jl.95 (V)</td>
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<td>0.06</td>
<td>93</td>
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<td>-0.07</td>
<td>83</td>
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<td>90</td>
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<td>0.00</td>
<td>96</td>
</tr>
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<td>0.09</td>
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<td>S27au.95 (V)</td>
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<td>0.05</td>
<td>93</td>
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<tr>
<td>S27au.95 (H)</td>
<td>8.4 ± 0.3°</td>
<td>0.06</td>
<td>97</td>
</tr>
<tr>
<td>S28au.95 (V)</td>
<td>-6.0 ± 0.3°</td>
<td>0.06</td>
<td>97</td>
</tr>
</tbody>
</table>

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**FIG. 3.** Data obtained from 2 different collicular stimulation sites (T20JN.95 and T05JL.95). A: each eye position trajectory is the average of 10 saccades. Open circles represent control stimulation-evoked saccades. Filled circles represent upward visually guided saccades immediately followed by saccades evoked by stimulation at the same collicular site as the control saccades. Filled triangles represent downward visually guided saccades immediately followed by saccades evoked by stimulation at the same site. The initial positions of the stimulation-evoked saccades were aligned for easier comparison. B: vertical amplitude vs. horizontal amplitude for all saccades produced by stimulation of the same collicular site as in A. Open circles represent control stimulation-evoked saccades; filled circles represent stimulation-evoked saccades that immediately followed upward or downward visually guided saccades. C: vertical amplitude vs. horizontal amplitude for saccades evoked by stimulation at a 2nd collicular site. Stimulation-evoked saccades immediately followed horizontal visually guided saccades.
orthogonal component, or the effect was small. Figure 3 illustrates the phenomenon for two typical data sets. In Fig. 3A, each eye position trajectory represents the average of 10 saccades that had similar directions, amplitudes, and trajectories. The three groups were selected to convey the range of the amplitude interaction between visually guided and stimulation-evoked saccades for this stimulation site. Open circles represent the average trajectory (upward and to the left) of control stimulation-evoked saccades. Also shown are two conditions in which collicular stimulation immediately followed visually guided saccades. Filled circles represent the average trajectories of upward visually guided saccades (starting from ~8° below the origin) immediately followed by stimulation-evoked saccades. The vertical amplitude of the stimulation-evoked saccades was reduced from ~5° upward to slightly downward. Filled triangles represent the average trajectories of downward visually guided saccades (starting from ~5° above the origin) immediately followed by stimulation-evoked saccades. The vertical amplitude of the stimulation-evoked saccades was increased to ~9°. However, the horizontal amplitudes for all three groups of stimulation-evoked saccades are nearly the same.

In Fig. 3B, vertical amplitude is plotted as a function of horizontal amplitude for all the saccades evoked by stimulation at the same collicular site as in Fig. 3A. Open circles represent control stimulation-evoked saccades; filled circles represent stimulation-evoked saccades that immediately followed upward or downward visually guided saccades of different amplitudes. The vertical amplitude of stimulation-evoked saccades varied from approximately -1° to approximately 13°. However, despite the substantial and systematic changes in vertical amplitude, there was no systematic variation in horizontal amplitude. Figure 3C illustrates the effect for a different site at which stimulation followed rightward and leftward saccades of different amplitudes. Just on visual inspection, these two data sets clearly demonstrate that the horizontal and vertical amplitudes of oblique stimulation-evoked saccades can be manipulated independently despite the fixed site of collicular stimulation.

To quantify the effect, we performed two different analyses on each data set, as illustrated in Fig. 4. Figure 4A shows control stimulation-evoked saccades (open circles) and stimulation-evoked saccades obtained during visual/stimulation trials (filled circles) for a third stimulation site. In the first analysis (illustrated in Fig. 4B), we generated scatterplots in which the amplitude of the manipulated component of stimulation-evoked saccades was represented along the abscissa and the amplitude of the orthogonal component was represented along the ordinate. By convention, component amplitudes that fell in the same quadrant as control saccades were always assigned positive values. For example, Fig. 4B replots the redirected stimulation-evoked saccades from Fig. 4A, but with the axes interchanged and with leftward amplitudes assigned positive values. With these axes, the independent comparator model invariably predicts that a line with a slope of zero will provide the best fit to the data. Furthermore, regardless of the quadrant of the control saccades, positive slopes always indicate that horizontal and vertical amplitude are positively correlated, and negative slopes indicate a negative correlation. In Fig. 4B, the slope of the best-fitting line is 0.002. Thus, although the vertical amplitude of these stimulation-evoked saccades varies over a range of ~20°, horizontal and vertical amplitude are independent. Table 1 (column 3) provides the slope of the best fitting line for each data set. The mean slope for all the data sets is 0.04 ± 0.08. This value is close to the slope of zero predicted by the independent comparator model but suggests on average a slight positive correlation between horizontal and vertical amplitude.

In the second analysis (illustrated in Fig. 4C), we generated a scatterplot for each data set in which the vectorial amplitude of redirected stimulation-evoked saccades was plotted as a function of their direction, as shown in Fig. 4C. In general, saccades falling in the same quadrant as control saccades were assigned directions between 0° and 90°, with 0° always orthogonal to the direction of the initial visually guided saccades. For example, in Fig. 4C, a direction of 0° is defined as straight leftward, and a direction of 90° is defined as straight upward. With these axes, the independent comparator model predicts that Eq. 1 will provide a good description of the data for all the data sets. For the data plotted in Fig. 4C, Eq. 1 accounts for 96% of the variance in vectorial amplitude. In 16 of 20 data sets, Eq. 1 accounts for at least 90% of the variance in vectorial amplitude about the mean (see Table 1, column 4). In the worst case, it accounts for 71% of the variance, whereas in the best case, it accounts for 99%. Therefore, in sharp contrast to either prediction of the vectorial comparator model, vectorial amplitude and direction are strongly correlated.

**Similarities between stimulation-evoked and visually guided saccades**

In general, redirected stimulation-evoked saccades were difficult to distinguish from visually guided saccades. To illustrate this aspect of the data, Fig. 4D plots vertical eye position as a function of time for four typical stimulation-evoked saccades selected from Fig. 4A, and Fig. 4E displays instantaneous vertical velocity traces for the same four saccades. These profiles are similar to the profiles of typical visually guided saccades. The eyes hold their post-saccadic positions, the velocity profiles are bell-shaped, and the peak velocities and durations are appropriate for the amplitudes of the saccades. Figure 4F displays the peak velocity amplitude relationships for all the redirected stimulation-evoked saccades from Fig. 4A (filled circles) and for visually guided saccades (open squares) that spanned a similar range of directions and amplitudes, and that started from similar initial eye positions. Clearly, the redirected stimulation-evoked saccades exhibit a saturating peak velocity–amplitude relationship very similar to the relationship for visually guided saccades. Finally, the peak velocity of the smaller component of redirected stimulation-evoked saccades was negatively correlated with the amplitude of the larger component (see Nichols and Sparks 1996 for a quantitative analysis), as is the case with visually guided saccades (Becker and Jürgens 1990; Evinger et al. 1981; Guitton and Mandl 1980; King et al. 1986; Van Gisbergen et al. 1985).

**Deviations from predictions of independent comparator model**

Some data sets displayed a weak interaction between the amplitudes of the horizontal and vertical components of
FIG. 4. Data from a 3rd collicular stimulation site (S26AU.95). A: vertical amplitude vs. horizontal amplitude for stimulation-evoked saccades. Open circles represent control stimulation-evoked saccades, filled circles represent stimulation-evoked saccades that immediately followed upward or downward visually guided saccades. B: the same data as in A, but with the axes interchanged and leftward amplitudes assigned positive rather than negative values. The slope of the best-fitting line is 0.002, as shown. C: same data set as in A, but plotted as vectorial amplitude vs. direction. A direction of 0° is straight leftward; a direction of 90° is straight upward. Equation 1 accounts for 96% of the total variance in vectorial amplitude. D: instantaneous vertical eye position for 4 stimulation-evoked saccades from A. Trace labeled Control is a control stimulation-evoked saccade. Traces are aligned on saccade onset and on initial eye position. E: instantaneous vertical velocity traces for the 4 movements shown in D. Traces are aligned on saccade onset. F: peak velocity–amplitude relationship for the redirected stimulation-evoked saccades shown in A (filled circles) and for visually guided saccades (open squares) that were matched to the stimulation-evoked saccades in direction, amplitude, and initial eye position. Control stimulation-evoked saccades are not shown.
A (T29JN.95)

B (T04JL.95)

C

FIG. 5. Two additional data sets (T29JN.95 and T04JL.95) in which deviations from the prediction of the independent comparator model are evident. A: vertical amplitude vs. horizontal amplitude for saccades evoked by stimulation at a single collicular site. Open circles represent control stimulation-evoked saccades; filled circles represent stimulation-evoked saccades that immediately followed horizontal visually guided saccades. B: similar to A, but for stimulation at a different site following upward and downward visually guided saccades. C: data from B replotted as vectorial amplitude vs. direction. Equation 1 accounts for 97% of the variance in vectorial amplitude.

stimulation-evoked saccades. For the data in Fig. 5A, for example, as the horizontal amplitude of stimulation-evoked saccades (filled circles) was reduced relative to control (open circles), the vertical amplitude was also somewhat reduced. However, when horizontal amplitude was increased, no change in the vertical amplitude was apparent. In Fig. 5B, when vertical amplitude was reduced relative to control, the horizontal amplitude was roughly constant; but when vertical amplitude was increased, the horizontal amplitude was slightly reduced. These interactions between horizontal and vertical amplitude were small. For example in Fig. 5B, the vertical amplitude of stimulation-evoked saccades varies over a range of $\pm 20^\circ$, whereas horizontal amplitude changes by perhaps $2^\circ$. In Fig. 5C, the data from Fig. 5B are replotted as vectorial amplitude versus direction. Clearly, neither prediction of the vectorial comparator model (see Fig. 2C) describes these data. However, Eq. 1 accounts for 97% of the variance in vectorial amplitude. Equation 1 accounts for 91% of the variance in vectorial amplitude for the data in Fig. 5A.

In other data sets, although there was no apparent interaction between horizontal and vertical component amplitudes, the amplitude of the constant-amplitude component was uniformly reduced relative to control saccades (Fig. 6). This phenomenon, although not directly inconsistent with the predictions of independent comparator models, suggests that there may be other influences over the amplitude of stimulation-evoked saccades in this paradigm. Possible explanations of these effects will be considered in the DISCUSSION.

DISCUSSION

Competing classes of models have been proposed to account for saccadic accuracy in two dimensions. In one class, separate component comparators represent horizontal and vertical dynamic motor error independently during oblique saccades (Becker and Jürgens 1990; Grossman and Robinson 1988; Scudder 1988). In another, a single vectorial comparator in the SC drives both pulse generators (Arai et al. 1994; Keller 1979; Van Opstal and Kappen 1993; Waitzman et al. 1988, 1991) and thus cannot exert independent control over component motor error. These models make sharply different predictions if, for a fixed desired displacement vector, the component amplitude produced by one pulse generator is systematically altered. Vectorial comparator models predict strong interactions between the amplitude produced by one pulse generator and the amplitude produced by the other. Independent comparator models predict independence between the component amplitudes.

We tested these predictions by fixing the site of electrical stimulation in the SC while systematically varying the amplitude of one component of oblique stimulation-evoked saccades. Despite the wide variations in the amplitude of one component of these saccades, the amplitude of the orthogonal component remained roughly constant. Vectorial comparator models cannot account for these results. Independent comparator models can.

Underlying assumptions

The validity of this empirical test depends on two assumptions regarding the experimental paradigm. First, the ob-
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observed horizontal and vertical amplitudes of redirected stimulation-evoked saccades must reflect the output of the corresponding pulse generators. Second, the fixed location of the stimulating electrode must lead to a roughly fixed locus of stimulation-induced activity in the SC.

If the changes in component amplitude observed in this paradigm were mediated at a neural stage below the level of the pulse generator and the feedback loop (e.g., at the motoneurons), both classes of models would predict independence between horizontal and vertical amplitude. Therefore we must assume that the horizontal and vertical amplitudes of redirected stimulation-evoked saccades reflect commands from the corresponding pulse generators within the feedback loops. The assumption is justified on the basis of four aspects of the data.

First, to maintain the eyes in eccentric post-saccadic positions, the feed-forward oculomotor integrator (NI in Fig. 1) must provide an orbital position signal to the motoneurons (e.g., Robinson 1975). NI generates this signal by computing the time integral of the pulse generator’s saccadic velocity command, just as the feedback integrator does. Any changes in saccade amplitude produced by altering the output of elements downstream from NI would lead to a mismatch between the final eye position after each saccade and the position specified by NI. If the amplitude effects observed in our paradigm resulted from altering the output of such elements, then there would be systematic mismatches between post-saccadic eye position and the eye position specified by NI. Consequently, after each stimulation-evoked saccade, the eyes would drift rapidly from their post-saccadic position to the position specified by NI with a time constant of ~200 ms (e.g., Cannon and Robinson 1987; Robinson 1970). Such large and systematic drift was not observed after redirected stimulation-evoked saccades (see Fig. 4I). Therefore the effect is mediated by elements upstream from NI.

Second, the instantaneous velocity profiles (see Fig. 4E) and the peak velocity-amplitude relationships (see Fig. 4F) of redirected stimulation-evoked saccades are very similar to those of their visually guided counterparts. Local feedback models typically explain these attributes of saccades in terms of the pulse generator and the feedback loop (e.g., Robinson 1975; Van Gisbergen et al. 1981).

Third, these redirected saccades exhibit appropriate component stretching (Nichols and Sparks 1996). The peak velocity of the smaller component of oblique saccades decreases with increasing amplitude of the orthogonal component, whereas the duration of the smaller component is prolonged so that its amplitude is constant. This reciprocal relationship between peak velocity and duration while amplitude remains constant strongly suggests that the neural basis of this aspect of the phenomenon lies within the feedback loop, at least for the smaller component. Moreover, component stretching in visually guided saccades reflects the discharge of midbrain excitatory burst neurons (King and Fuchs 1979), which are very likely the neural substrate of the vertical pulse generator.

Finally, the overall pattern of amplitude interactions between visually guided and stimulation-evoked saccades in this paradigm strongly suggests an interpretation in terms of the resetting process of the feedback integrator (Nichols and Sparks 1995), as described in METHODS. In simplest terms, the observed amplitude effect demonstrates that the saccadic system has a transient “memory” of the amplitude of the immediately preceding saccade. And because a resettable integrator exhibits precisely that sort of transient memory, it provides a ready account of the phenomenon. If this interpretation is correct, then the effect occurs within the feedback loop by definition.

Therefore, if the amplitude effect is to be explained without invoking the feedback loop and the pulse generator, we must also explain the peak velocity-amplitude relationship, component stretching, the shape of the instantaneous velocity profiles, and the absence of postsaccadic drift without invoking the pulse generator and the feedback loop. The authors are unaware of any local feedback model that satisfies those requirements. Certainly the models under consideration do not. Therefore it is reasonable to assume that the amplitude effects, as well as the other aspects of the data, reflect the output of the pulse generators within the feedback loops.

**Fig. 6.** Two additional data sets (T06JN.95 and S27AU.95) that exhibit another type of deviation from the prediction of the independent comparator model. A: vertical amplitude vs. horizontal amplitude for saccades evoked by stimulation at a single collicular site. Open circles represent control stimulation-evoked saccades; filled circles represent stimulation-evoked saccades that immediately followed vertical visually guided saccades. B: same phenomenon depicted in A, but for a horizontal data set obtained from a different collicular stimulation site.
LOCUS OF COLICULAR ACTIVITY Although both the site and the parameters of electrical stimulation were fixed for each experimental session, it is theoretically possible that the locus of stimulation-induced collicular activity was not constant. Both independent and vectorial comparator models could account for our data if, for each stimulation-evoked saccade, the effective locus were shifted to the exact site in the SC representing the saccade vector actually observed. Therefore we must ask whether residual effects from visually guided saccades could have produced such shifts in the effective locus from one stimulation-evoked saccade to the next. Two previously reported phenomena suggest ways that the spatial distribution (and thus, the effective locus) of collicular activity might be shifted during stimulation-evoked saccades.

First, if low level collicular activity persists for a brief period after visually guided saccades (Mays and Sparks 1980; Waitzman et al. 1991), vector averaging (Gilmcher and Sparks 1993; Robinson 1972; Schiller and Sandell 1983; Sparks and Mays 1983) could occur between activity at the site encoding the metrics of the visually guided saccade and stimulation-induced activity at the site of the electrode tip. During stimulation-evoked saccades, if vector averaging were to shift the effective locus away from the site of the electrode tip to the precise position in the collicular map that normally specifies the actual metrics of the saccade, then the vectorial comparator model could account for the metrics of those stimulation-evoked saccades. However, vector averaging in our paradigm will tend to shift the effective locus away from, not toward, the appropriate locus. For example, suppose stimulation is applied at a collicular site specifying a saccade up and to the right immediately after a downward visually guided saccade. Vector averaging predicts that both the vertical and the horizontal amplitudes of the stimulation-evoked saccade should be reduced. However, under these conditions, the vertical amplitude would increase and the horizontal amplitude would remain unchanged. Therefore, although weak averaging may occur during stimulation-evoked saccades, it cannot account for the metrics of these redirected saccades in our paradigm.

Alternatively, cells that discharge for the initial downward movement in the example just given could become refractory or less excitable during the subsequent stimulation-evoked saccade. From a vector averaging perspective, reduced excitability in cells that normally would have responded to electrical stimulation could also shift the effective locus during stimulation-evoked saccades. Such shifts would be opposite (Lee et al. 1988) to those produced by elevated activity at the same position in the map. Three arguments make this explanation of the results implausible. First, it predicts amplitude effects on both components of stimulation-evoked saccades, when in fact, the amplitude of one component was unchanged. Second, the metrics of the visually guided saccade often differed widely from those specified by the stimulation site. Therefore the active population for the visually guided saccade and the active population for the control stimulation-evoked saccade often were largely nonoverlapping. For collicular cells that would not normally have responded during stimulation, reduced excitability should have no effect on the metrics of the saccade. Finally, the overall pattern of amplitude effects should be similar to those produced when a subset of the active population is inactivated by focal injection of lidocaine into the collicular map (Lee et al. 1988). Yet, such a pattern was not observed (see also, Nichols and Sparks 1995).

In summary, vectorial comparator models can explain our results only if, despite the fixed site and parameters of stimulation, the effective locus of stimulation-induced activity were shifted to the exact location in the collicular motor map that normally codes the metrics of the redirected stimulation-evoked saccade. In light of the preceding arguments, we conclude that the locus of collicular activity did not vary in the systematic way required by vectorial comparator models, and that the locus was roughly constant for stimulation-evoked saccades. Consequently, the vectorial desired displacement signal and the locus of the putative vectorial comparator were essentially constant from one stimulation-evoked saccade to the next.

Vectorial comparator models

The concept of a vectorial comparator for controlling the amplitudes of oblique saccades has been proposed repeatedly (Arai et al. 1994; Keller 1979; Tweed and Vilis 1985; Van Opstal and Kappen 1993; Waitzman et al. 1988, 1991). Waitzman et al. (1988, 1991) presented a very simplified schematic of a model in which a single vectorial dynamic motor error signal is encoded by the level of activity at a single collicular locus even during oblique saccades. Arai et al. (1994) proposed a detailed vectorial comparator model very similar to the model in Fig. 1B. Output neurons at each collicular locus receive input from a desired displacement reference signal, also encoded by the locus of activity in the map. These output cells receive feedback from both horizontal and vertical displacement integrators. The resulting vectorial dynamic motor error signal is decomposed according to a site-specific ratio to provide input to both horizontal and vertical pulse generators downstream.

Van Opstal and Kappen (1993) proposed a model that, unlike the vectorial comparator model in Fig. 1B, merges comparison, feedback integration, and pulse generation into a single vectorial locus in the SC for each saccade. But ascribing these other functions to the vectorial locus does not alter the predictions described in the INTRODUCTION and METHODS. The model still does not permit independent control of horizontal and vertical amplitude during oblique saccades. In fact, Van Opstal and Kappen (1993) argued that their model is mathematically equivalent to models that separate the functions of integration and pulse generation from the locus of the vectorial comparator. Tweed and Vilis (1985) also proposed a vectorial comparator but placed it downstream from the SC in an array of pontine long lead burst neurons (LLBNs). In their model, each locus in the array acts as the comparator for a different saccade vector. The locus of activity in the SC represents desired displacement and automatically activates the appropriate comparator locus in the LLBN array.

Because these vectorial comparator models predict strong interactions between component amplitudes in the present experimental paradigm, none can account for our results. They fail because they exert feedback control in only one dimension (vectorial motor error) rather than in two independent dimensions (horizontal and vertical motor error). In principle, this limitation might be surmounted if vectorial
models were modified to exert independent control over both vectorial amplitude and direction (i.e., in polar coordinates). Because the location of the active comparator in the collicular map determines the direction of vectorial motor error in these models (Van Opstal and Kappen 1993), feedback concerning errors in direction would have to shift the locus of activity by just the proper amount to drive the eyes in the compensatory direction (for related arguments, see Becker and Jürgens 1990). To account for the dramatic changes in direction of stimulation-evoked saccades in the present paradigm, the saccadic controller would have to "mistake" the direction of the initial visually guided saccade as a direction error at the beginning of the stimulation-evoked saccade. To compensate for the error, synaptic mechanisms would have to override direct stimulation-induced excitation near the electrode tip and shift the active site to an entirely different location in the collicular map. Even if such mechanisms existed for direction control during visually guided saccades, it seems likely that they would be severely disrupted by the fixed site of electrical stimulation. In any case, as they stand, models that propose dynamic feedback control over vectorial motor error but not over direction (Arai et al. 1994; Keller 1979; Van Opstal and Kappen 1993; Waitzman et al. 1988, 1991) do not survive the present experimental test.

Independent comparator models

A number of detailed two-dimensional models have been proposed in which the horizontal and vertical amplitudes of oblique saccades are under independent feedback control (Becker and Jürgens 1990; Grossman and Robinson 1988; Scudder 1988). For the purposes of this report, the generic independent comparator model depicted in Fig. 1A captures the essential features of these models. Electrical stimulation at a fixed collicular locus evokes a fixed vectorial desired displacement signal. That vectorial reference signal, encoded by the location of stimulation-induced activity in the collicular motor map, is then decomposed into separate horizontal and vertical reference signals to provide input to independent component comparators. Once the vectorial reference signal is decomposed, two separate controllers reduce horizontal and vertical dynamic motor error to zero independently. Although horizontal and vertical peak velocity and duration during oblique saccades are not controlled independently (see Component stretching), the independent representations of horizontal and vertical dynamic motor error ensure that component amplitudes are controlled independently.

How can the model in Fig. 1A account for the present data? Because the site of collicular stimulation is fixed from one stimulation-evoked saccade to the next, the horizontal and vertical desired displacement signals will be fixed, as well. Once horizontal and vertical desired displacement signals are specified, there is no further opportunity for interaction between horizontal and vertical motor error signals. Again, consider a collicular locus that encodes an upward and rightward desired displacement. Stimulation at this locus yields a rightward desired displacement signal for the horizontal comparator and an upward desired displacement signal for the vertical comparator. If stimulation immediately follows a rightward visually guided saccade, then residual value on the horizontal displacement integrator will be subtracted at the horizontal comparator from the rightward desired displacement signal evoked by collicular stimulation. Thus the rightward amplitude of the stimulation-evoked saccade will be reduced in proportion to the amplitude of the preceding saccade. But residual value on the horizontal displacement integrator can have no effect on the dynamic motor error signal at the vertical comparator. Therefore vertical amplitude will be uninfluenced by the horizontal visually guided saccade. Even if the amplitude effect on the horizontal component is due to a temporary change in the amplitude-gain of horizontal pulse generator (see Methods), vertical dynamic motor error will still be reduced to zero independently. Thus models that control horizontal and vertical dynamic motor error independently can readily account for the present data.

**Deviations from predictions of the independent comparator model**

As described in Results, we observed two apparent deviations from the predictions of the independent comparator model. One type is illustrated in Fig. 6A. In that data set, horizontal amplitude was constant across a wide range of vertical amplitudes (filled circles), but it was smaller than the horizontal amplitude of the control stimulation-evoked saccades (open circles). Although this small effect is not directly inconsistent with independent comparator models, it implies that there is a secondary amplitude effect on stimulation-evoked saccades in this paradigm. To account for this phenomenon, we invoke vector averaging between residual collicular activity from the visually guided saccade and stimulation-induced activity. As stated earlier, such averaging cannot account for the systematic amplitude effect observed in the present study. However, the amplitude effect might be superimposed on weak averaging in some data sets. In the data set in Fig. 6A, for example, all the initial visually guided saccades (not shown) had horizontal amplitudes close to zero. If there were weak vector averaging between residual activity from each visually guided saccade and stimulated activity during the stimulation-evoked saccade, the effective horizontal desired displacement would be uniformly reduced. Consequently, the horizontal amplitude of the stimulation-evoked saccades would be uniformly reduced relative to the horizontal amplitude of the control stimulation-evoked saccades. Any weak averaging between the variable vertical amplitude of visually guided saccades and the vertical amplitude of stimulation-evoked saccades would be thoroughly masked by the much more pronounced amplitude effect on the vertical component.

In a second type of deviation from the predictions of the independent comparator model, there were minor interactions between component amplitudes of stimulation-evoked saccades in some data sets. In the data set in Fig. 5A, for example, as the horizontal amplitude of stimulation-evoked saccades (filled circles) was reduced from the horizontal amplitude normally produced by the stimulation site (open circles), the amplitude of the vertical component was slightly reduced, as well. However, when the horizontal amplitude was increased, there was no corresponding change in the vertical amplitude. In Fig. 5B, as vertical amplitude is increased above the vertical amplitude for the control saccades (open circles), horizontal amplitude is slightly re-
duced. The magnitude and form of these interactions never approached the predictions of vectorial comparator models. In Fig. 5B, for example, horizontal amplitude is reduced by perhaps 2°, whereas vertical amplitude varies over a range of ~20° (an order of magnitude difference). Nonetheless, the interaction is not strictly consistent with the predictions of the independent comparator model.

How can these aspects of the data be explained? Even if horizontal and vertical dynamic motor error are reduced to zero independently, there are still common influences over the amplitudes both components. Consider two possibilities. First, because the desired displacement signals for the component controllers are derived from a common vectorial representation in the SC, any manipulation that influences vectorial desired displacement at that level could influence both the horizontal and vertical amplitudes of oblique saccades. Second, a single pool of omnipause cells in the pontine reticular formation (Keller 1974) appear to inhibit both horizontal and vertical pulse generators (for a recent review, Moscovakis and Hightstein 1994). Indeed, stimulation-evoked pause cell activity can interrupt saccades in midflight (Keller 1977, Keller and Edelman 1994; King and Fuchs 1977) and many local feedback models (e.g., Van Gisbergen et al. 1981) require a continuous signal from the pulse generators to “latch” the pause cells off during saccades. Therefore pause cell activity can exert common influences over the durations, and consequently the amplitudes, of both components of oblique saccades. For example the interaction between components in Fig. 5A can be explained if reduced activity in the horizontal pulse generator leads to a premature failure of the latch on the pause cells, thus truncating vertical amplitude, as well.

Component stretching

Although the evidence presented in this report is consistent with models that postulate independent feedback control over the component amplitudes of oblique saccades, it is an empirical fact that the component peak velocities and durations during oblique saccades are not controlled independently (in cat: Evinger et al. 1981; Guitton and Mandl 1980; in monkey: King et al. 1986; Van Gisbergen et al. 1985; in human: Becker and Jürgens 1990). Instead, the peak velocity of the smaller component is reduced from what it would be for a purely horizontal or vertical saccade of the same amplitude, and the duration of the smaller component is prolonged to match more closely the duration of the larger component. Thus the ratio of horizontal and vertical velocities seems to be adjusted to produce roughly straight saccades.

Two competing accounts of component stretching have been proposed. In cross-coupling models, horizontal and vertical controllers like those in Fig. 1A interact downstream from the SC in order to achieve component stretching (Becker and Jürgens 1990; Grossman and Robinson 1988). In common source models, the SC provides a common velocity signal from which the appropriate ratio of horizontal and vertical velocity signals is derived (Smit et al. 1990; Sparks and Mays 1990; Van Gisbergen and Van Opstal 1989; Van Opstal and Kappen 1993). Independent comparator models incorporating both the cross-coupling approach (Becker and Jürgens 1990; Grossman and Robinson 1988) and the common source approach (Nichols and Sparks 1996) have been proposed. Furthermore, vectorial comparator models incorporating both the common source (Van Opstal and Kappen 1993) and the cross-coupling (Arai et al. 1994) approaches have also been proposed. Therefore these two issues in saccadic control must be addressed separately. However, the same experimental paradigm used here has been used in a previous report to investigate the neural basis of component stretching (Nichols and Sparks 1996). The results of that study are clearly inconsistent with common source models, but are consistent with cross-coupling models.

Conclusions

Numerous modifications and extensions of Robinson's original feedback model of saccadic control (Robinson 1975) have been proposed. Most of these models remain viable, because they have rarely faced clear empirical tests. This wide proliferation of viable models has made it more difficult to design and interpret experiments aimed at further elucidating the neural basis of saccadic control. Experiments that reduce the number of competing models could greatly facilitate progress in this area of research. Toward that end, we have tested sharply differing predictions of competing models for controlling saccade accuracy in two dimensions. By systematically altering the state of putative horizontal and vertical feedback integrators, we have shown that the horizontal and vertical amplitudes of oblique saccades can be controlled independently. We conclude that future studies should focus on mechanisms and models that exert independent control over component amplitudes.

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