

Eye-Hand Coordination: Saccades Are Faster When Accompanied by a Coordinated Arm Movement

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Snyder, Lawrence H., Jeffrey L. Calton, Anthony R. Dickinson, and Bonnie M. Lawrence. Eye-hand coordination: saccades are faster when accompanied by a coordinated arm movement. *J Neurophysiol* 87: 2279–2286, 2002; 10.1152/jn00854.2001. When primates reach for an object, they very often direct an eye movement toward the object as well. This pattern of directing both eye and limb movements to the same object appears to be fundamental to eye-hand coordination. We investigated interactions between saccades and reaching movements in a rhesus monkey model system. The amplitude and peak velocity of isolated eye movements are positively correlated with one another. This relationship is called the main sequence. We now report that the main sequence relationship for saccades is changed during coordinated eye and arm movements. In particular, peak eye velocity is approximately 4% faster for the same size saccade when the saccade is accompanied by a coordinated arm movement. Saccade duration is reduced by an equivalent amount. The main sequence relationship is unperturbed when the arm moves simultaneously but in the opposite direction as the eyes, suggesting that eye and arm movements must be tightly coordinated to produce the effect. Candidate areas mediating this interaction include the posterior parietal cortex and the superior colliculus.

INTRODUCTION

Rapid eye movements, or saccades, show a positive correlation between amplitude and peak velocity, and between amplitude and duration, called the main sequence (Bahill et al. 1975). The main sequence is a feature of both human and nonhuman primate saccades (Fuchs et al. 1985). It is shared by all types of rapid eye movements, including vestibular and optokinetic fast phases (Komatsuzaki et al. 1972; Ron et al. 1972). The stereotyped relationship between movement dynamics and kinematics reflects the fact that the velocity trajectories of rapid eye movements, unlike the movements of other body parts, are not under conscious control. Although we can choose to move our arm either rapidly or slowly, this is not the case for our eyes.

The machine-like quality of rapid eye movements, compared with the more free-form movement of other body parts, reflects the origin of the control signals. The dynamics of somatomotor movements are likely controlled at least in part by the cerebral cortex, where neurons have been identified whose firing rate is

correlated with the velocity and acceleration of arm movements, for example (Johnson et al. 1999; Moran and Schwartz 1999). In contrast, no neural correlates of eye velocity or acceleration have been reported in the cortex (Segraves and Park 1993). The cortex specifies where and when to move (Hanes and Schall 1996), while dynamics are the province of bursting neurons in the superior colliculus and brain stem, probably configured as a feedback controller (Wurtz and Optican 1994). This controller is optimized for moving the eyes rapidly from one target to the next, thereby minimizing the time during which vision is degraded by motion-induced blur. The result is the machine-like behavior of the main sequence.

Under some conditions, however, main sequence characteristics can be altered. Different individuals have different main sequence relationships, and there is variability even within an individual (Bollen et al. 1993). Memory-guided saccades (to remembered targets that are no longer visible), saccades made in the dark, anti-saccades (directed away from a visual target), and auditory saccades (toward an unseen sound source) are generally slower and more variable than visually guided saccades of the same amplitude (Becker and Fuchs 1969; Sharpe et al. 1975; Smit and Van Gisbergen 1987; Zambarbieri et al. 1982). Preventing the head from moving (Collewijn et al. 1992), fatigue (Schmidt et al. 1979), pharmacologic agents (Jurgens et al. 1981; Rothenberg and Selkoe 1981; Rothenberg et al. 1980), and saccade adaptation (Abrams et al. 1992) can all alter main sequence characteristics. These factors all tend to reduce peak eye velocity for a given saccade amplitude.

In the current study, we asked whether coordinated arm movements may affect saccade dynamics in monkeys. Previous work in humans has shown that concurrent arm movements result in faster saccades (Epelboim et al. 1997). Conflicting effects on saccade latencies have been reported (reviewed in Lunenburger et al. 2000). No studies have addressed these issues in monkeys. Until recently, there was little neurophysiological evidence for an effect of arm movements in oculomotor structures. Recently, however, this has changed (Stuphorn et al. 2000; Werner 1993). We now report that, in monkey, concomitant arm movements increase the velocity of saccadic eye movements directed to the same target.

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METHODS

Three rhesus monkeys performed rapid eye movements to peripheral visual targets in the presence or absence of arm movements to those same targets. All procedures conformed to the *Guide for the Care and Use of Laboratory Animals* (ISBN 0-309-05377-3). Each animal was prepared for experiments by attaching a stabilization platform to the head and implanting a scleral search coil under the conjunctiva of one eye (Judge et al. 1980; Robinson 1963). Surgery was performed using isoflurane anesthesia (1–2%). For experiments, the animal was seated in a custom-designed monkey chair (Crist Instruments) that allowed a wide range of arm movement. The head of the animal was securely fixed in a straight-ahead position, aligned with the body. Visual stimuli were projected (Electrohome ECP 3000) onto a vertically oriented touch screen (Keytec, model 1700, 33 × 26 cm) placed approximately 20 cm from the animal. Eye position was recorded with 0.05 deg precision every 2 ms using a field coil system (CNC). Hand position was recorded using the touch screen every 30 ms with a nominal precision of 0.1 mm. The actual precision was limited by the animal's hand posture, which often involved splayed fingers. Stimuli were controlled by custom software.

Three behavioral paradigms were used (Fig. 1). Two animals were tested using two visually guided saccade tasks, and a third animal was tested using a memory-guided saccade task.

1) *Visually guided movements: cue-target trials.* In these trials, animals were instructed in advance as to the movement type (eye,

arm, or coordinated eye and arm), but not the location of the target. Animals initially fixated and touched a central blue target in an otherwise dark room. After 500 ms, the target turned red, green, or white, instructing the preparation of an eye, arm, or combined movement, respectively. After a delay of 600–1200 ms, a blue peripheral target appeared at one of eight radially symmetric locations, 20 deg from the fovea. The animal was allowed to move as soon as it had received the second instruction (target location) and was rewarded for acquiring the target as previously instructed.

2) *Visually guided movements: target-cue trials.* In these trials, animals were instructed in advance as to the target location, but not the type of movement to make. Animals initially fixated and touched a central blue target in an otherwise dark room. After 500 ms, a blue peripheral target appeared 20 deg from the fovea at one of eight radially symmetric locations. After a delay of 600–1200 ms, the fixation point changed from blue to red, green, or white, instructing the animal to acquire the visible peripheral target using an eye movement, arm movement, or combined eye and arm movement. Once again, the animal was allowed to move as soon as it had received the second instruction (movement type) and was rewarded for acquiring the target consistent with that instruction. All three types of target-cue trials (eye, arm, and combined eye plus arm) were presented in random order and interspersed with all three types of cue-target trials.

3) *Memory-guided movements.* In these trials, animals were instructed as to both the target location and the type of movement well in advance of movement execution. After 750 ms of central fixation and touch, a red or green peripheral target appeared for 150 ms. This target instructed both the type of movement (eye or arm) and the target location for that movement. After another 1–1.5 s, the fixation was extinguished and the animal was rewarded for making the appropriate movement to the remembered target location.

On one-half of memory-guided movement trials, animals were required to make both an eye and an arm movement in either the same or the opposite directions. On these trials a complementary-colored second target appeared for 150 ms, 80 ms after the offset of the first target. The second target appeared at the same location as the first target (instructing eye and arm movements in the same direction) or on the opposite side of the fovea (instructing eye and arm movements in opposite directions). All four types of memory-guided trials (eye only, arm only, coordinated eye and arm, disjunctive eye and arm) were randomly interleaved.

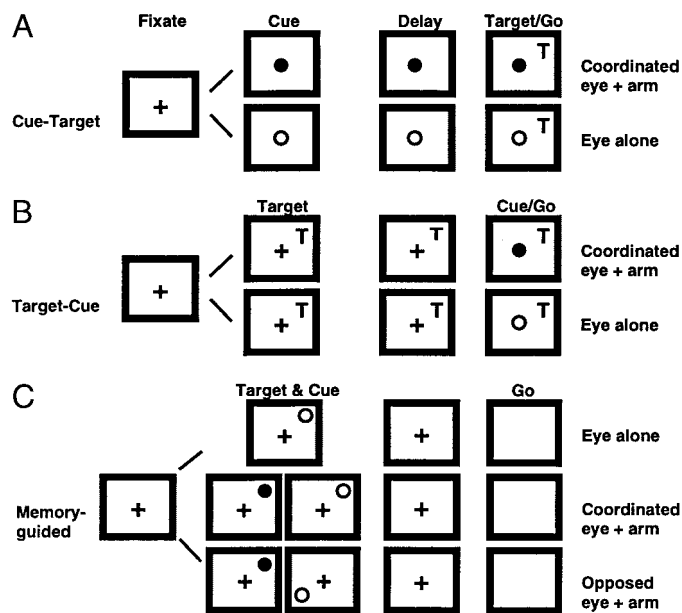


FIG. 1. The three paradigms used in this study are presented schematically. The first two were designed to allow comparisons of eye movements made with and without accompanying arm movements to the same target. On cue-target trials (A), animals were first instructed, by the color of a foveal cue (with the two colors represented here by filled and hollow symbols), what type of movement to plan: coordinated reach and saccade (“eye + arm”) or saccade alone (“eye”). (Reach alone trials are not illustrated.) They were then rewarded for executing that movement to a peripheral target when it appeared 1–1.6 s later. Target-cue trials (B) were identical, but the order of presentation of the cue and the target were reversed. On memory-guided trials (C), the type of movement was instructed by the color of the peripheral target. A single red or green target instructed an eye or arm movement (*top row*). A red and a green target appearing sequentially at the same location instructed a coordinated eye plus arm trial (*middle row*), while a red and a green target appearing sequentially but on opposite sides of the fovea instructed eye and arm movements in opposite directions (*bottom row*). On memory-guided trials the targets then disappeared and a 1- to 1.5-s delay ensued. Animals were rewarded for making the appropriate memory-guided movements once the fixation target disappeared.

General methods

All targets were 1.6×1.6 deg squares. Initial eye fixation requirements were typically ± 2.5 deg from the target center. Once eye fixation was achieved, the eyes were constrained to remain within 3 deg of their original position. Initial arm “fixation” requirements were typically ± 5 deg from the target center, and the arm was constrained to remain within 2 deg of its original position. Peripheral target acquisition was defined as a movement to within 3.5 deg (eye) or 6 deg (arm) of a visible target, or to within 7.5 deg (eye) or 8.5 deg (arm) of a remembered target. Animals were allowed ample time for this movement (800–1200 ms, depending on trial type). Peripheral targets were seldom obscured by an animal's arm, since such occlusion would have prevented the animal from succeeding in the task. Once the peripheral target was acquired, the window requirements were relaxed an additional 1–2 deg and the animal was required to hold that position for another 300 (memory-guided movements) or 400 ms (visually guided movements). It is important to note that the uninvolved body part (eyes on arm movement trials, arm on eye movement trials) continued to be under the same drift constraint (< 3 and 2 deg of drift for the eyes and arm, respectively) until the end of the trial. Trials in which errors occurred were immediately aborted and a 1–2 s time out ensued. Data were collected from each animal during 70–80 daily sessions.

Data analysis

Analysis was focused on saccadic eye movements. Arm position was recorded with low temporal resolution, and therefore, detailed results from arm-only and combined arm and eye trials are not reported. Saccades were detected using custom software routines. Instantaneous velocity was computed using a five-point difference filter, which was then averaged over six adjacent points to detect peak velocity. Saccade start and finish were defined to be the times at which velocity (computed using a simple 3-point difference filter; Bahill et al. 1982) first rose above 30 deg/s and dropped below 24 deg/s, respectively. Saccade amplitude and duration were based on these start and finish points.

To visualize eye-movement trajectories in the presence and absence of arm movements, trials were first sorted by animal, trial type, and direction. Next, each eye position trajectory was aligned on the time of peak velocity, offset so that eye position from 200 to 100 ms prior to peak velocity was equal to zero and then smoothed using a 73-point low-pass filter with a -3 dB point at 46 Hz. For Fig. 2 only, velocity traces were obtained by differentiating each smoothed eye position trace with a single point difference filter with a step size of 6 ms. Single trials were then averaged together to generate mean position and velocity trajectories. To eliminate any systematic differences in saccade amplitude resulting from the presence or absence of arm movements, saccades were used only if they lay within a narrow band of amplitude (± 0.5 deg). Saccades both with and without accompanying arm movements had to fall within this amplitude band, but the band itself differed for each monkey, saccade direction, and behavioral paradigm. The amplitudes of downward movements were particularly variable, and no band included more than four to five; so downward movements were excluded from this analysis (but not from subsequent analyses). The resulting number of saccades per monkey, trial type, and direction ranged from 11 to 59, with a mean of 36.

A second analysis was performed to compare peak eye velocities and durations. In this analysis, saccades were not limited to a narrow band of amplitudes. To eliminate anomalous movements in an objective manner, any movements lying more than 3 SDs from the mean peak velocity, duration, or amplitude were discarded. In a normal distribution, one would expect that approximately 1–3% of the data would be eliminated, depending on the degree of correlation between the three variables. Of 4421 saccades from the first animal, 149 (3.5%) were eliminated. Of 11,380 saccades from M2, 206 (1.8%) were eliminated. Of 1620 saccades from M3, 40 (1.9%) were eliminated. Saccades with latencies < 100 ms were also eliminated [38 (1%) from M1, 13 (0.1%) from M2, and 5 (0.3%) from M3].

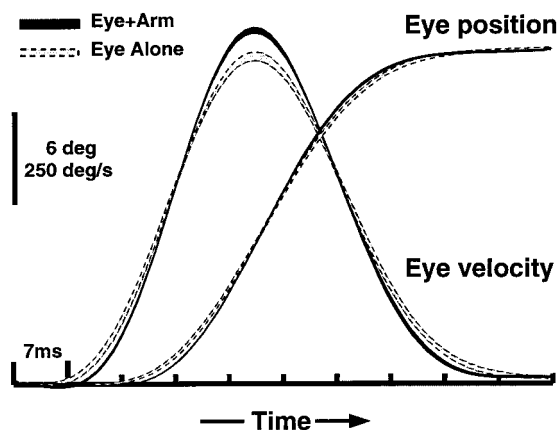


FIG. 2. Mean eye position and velocity traces for selected horizontal saccades made with (solid; $n = 26$) and without (dashed; $n = 19$) coordinated arm movements. Saccades are selected to be equal amplitude (between 22 and 23 deg). Traces are \pm SE. Traces are aligned on peak eye velocity. Because of this, earlier acceleration does not imply shorter saccadic latency.

A final analysis was performed to compensate for any incidental differences in saccade amplitude on trials with and without arm movements. Differences in mean peak eye speed of saccades with and without accompanying arm movements were plotted as a function of the difference in mean saccade amplitude. Approximating the *local* amplitude-velocity relationship as a straight line, we could fit the data to a straight line (using least-squares linear regression). The intersection of this line with the y -axis would provide the estimated difference in peak eye velocity when the difference in saccade amplitude was zero. To construct this straight line, we used the mean values of amplitude and velocity obtained from the eight different target directions and the two different visually guided saccade trial types. We also performed a variation on this analysis. Regression lines were fit to data obtained from each individual saccade, and then this fit was used to calculate the theoretical peak velocities for saccades, of the same size, with and without an arm movement. The actual size used was the mean of all the saccades recorded, including both those made with and those made without coordinated arm movements. The results of this analysis were consistent with the results using regression on groups of saccades and are therefore not reported.

RESULTS

Animals moved to a visible peripheral target in one of eight different directions. On interleaved trials, the animals were instructed to move either the eye alone, the eye and the arm together, or the arm alone. At the start of each trial, animals pointed to and fixated the same central fixation target. On eye alone trials, the arm remained at the fixation target. On eye plus arm trials, eyes and arm moved to the same target. Animals performed reliably, at success rates often exceeding 90%. On combined eye and arm movement trials, arm movement onset followed eye movement onset by 50–100 ms, depending on the direction and the particular behavioral paradigm. We compared the speed of saccades made with and without accompanying arm movements. Data from arm alone trials are not included in this report.

Figure 2 shows the average time course of horizontal eye position and eye velocity for saccades made by M1 to a target 20 deg to the right. The saccades whose mean trajectory is shown in black were accompanied by coordinated arm movements to the same target, while the saccades whose mean trajectory is shown in gray were from interleaved trials without arm movements. To eliminate any possible effects of arm movement on saccade size, only data from saccades with an amplitude between 22.0 and 23.0 deg are included. Mean peak eye velocity is slightly larger when the saccade is accompanied by a coordinated arm movement (mean \pm SD of 19 saccades: 983 ± 48 deg/s) than when the saccade is performed alone (26 saccades: 910 ± 52 deg/s). The increase in speed (73 deg/s, or 8.0%; $P < 0.0001$) is apparent both in the velocity trace, where black traces are larger than gray, and in the position trace, where black traces are steeper than gray.

Mean saccade duration is reduced when the saccade is accompanied by an arm movement (86 vs. 93 ms, a reduction of 7.5%). This can be seen by the fact that the gray velocity trace deviates from zero slightly sooner than the black trace, and returns to zero slightly later. Notice that the shape of the mean trajectories are otherwise similar; it is not the case that the change in saccades in the presence of arm movements are distorted or asymmetric compared with saccades in the absence of arm movements.

Eye position was measured by setting up a magnetic field,

which induced a current in a loop of wire implanted in the eye (Robinson 1963). Changing the position of the arm movement inside or near this field would be expected to distort the field. This distortion could in turn distort eye position readings. The distortion might be particularly strong when the arm is actually moving. However, it is unlikely that such an artifact is responsible for the effect we have observed. The effect was consistent across all eight different directions of saccades (e.g., Fig. 3). An artifactual distortion would be likely to have opposite effects for movements in opposite directions. Furthermore, since the arm movements had longer latencies than the eye movements (data not shown), we would expect that artifactual distortions due to arm movement would be more pronounced later in the saccade trajectory. Instead, there were symmetric effects on the accelerating and decelerating portions of the saccade trajectory (Fig. 2).

To determine whether arm movements systematically speed up saccades, we compared peak eye speed achieved by saccades accompanied or unaccompanied by arm movements (Fig. 3). For each monkey, direction, and trial type, we plotted mean peak velocity from saccades with arm movements (ordinate) against mean peak velocity from saccades without arm movements (abscissa). There were only eight different targets, but 16 data points are shown because we collected two independent data sets per target (target-cue and cue-target trials; see METHODS). The dashed diagonal line represents the null hypothesis of no effect of arm movement on saccade velocity. Most points lie above this line (11 of 16 for M1, and 15 of 16 for M2), representing cases in which eye velocity was faster in the presence of a coordinated arm movement. The difference was significant in 19 of 32 cases ($P < 0.05$); in all but one of these cases, eye speed was faster in the presence of an arm movement.

Faster peak velocities might be expected if eye movements are larger when accompanied by an arm movement. This was not the case, however. In M1, the average saccade made with an arm movement was 0.2 deg smaller than the average isolated saccade. On the basis of main sequence behavior alone, this would predict *slower* peak velocities for compound movements. In M2, saccades amplitude differed on average by only 0.01 deg, or approximately 0.1%, an amount that is much too

Peak saccade velocity with and without coordinated arm movement

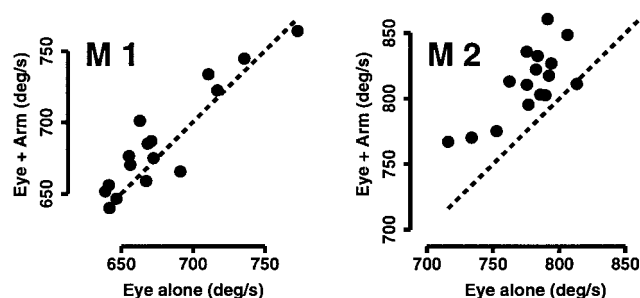


FIG. 3. Peak saccade velocity was higher with coordinated arm movements (ordinate) than without (abscissa). Each point represents the mean of ≥ 92 saccades in a single direction. For horizontal, vertical, and oblique targets, horizontal, vertical, and tangential velocity is plotted, respectively. The dotted line represents the null hypothesis of no effect of arm movements on peak eye velocity. Most points fall above the line. However, possible systematic differences in saccade amplitude are not taken into account (see Figs. 4 and 5).

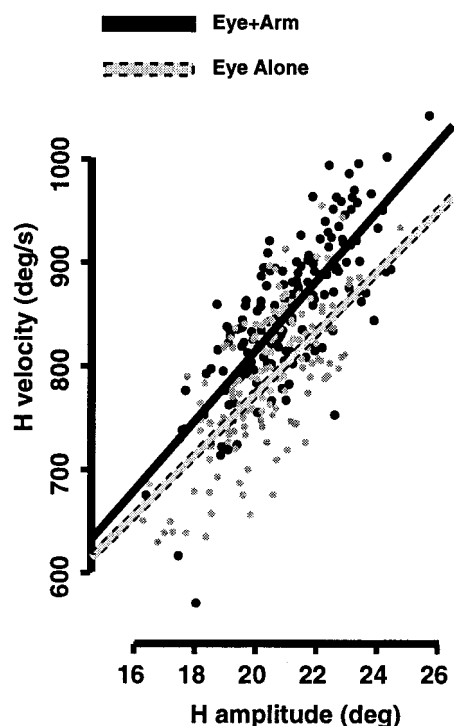


FIG. 4. Peak horizontal eye velocity as a function of horizontal saccade amplitude for saccades made to a target 20 deg to the right (M1). For legibility, only every fourth saccade is shown. Mean peak eye velocity is higher for coordinated saccades (filled; 845 deg/s) than isolated saccades (hollow; 779 deg/s). Linear regression lines confirm that velocity is faster for coordinated movements even when saccade amplitude is taken into account (solid lines).

small to explain the mean difference in observed eye velocity of approximately 50 deg/s or approximately 5%.

To look more directly at the velocity-amplitude relationships, we constructed main sequence plots. Figure 4 shows peak velocity versus amplitude for rightward saccades from M1 performed with and without coordinated arm movements. A linear regression on the data reveals slopes of 33.7 versus 29.3 deg/s per deg, respectively. (We use a linear regression rather than an exponential fit because, in a narrow operating range, the main sequence relationship can be approximated as a straight line.) The difference in slope is statistically significant ($P < 0.01$). For two animals, eight target directions, and two stimulus conditions (target-cue and cue-target trials; see METHODS), the slope of the regression line for coordinated movement was greater than the slope for an isolated saccade in 25 of the 32 conditions. The difference was significant in 10 of these 25 conditions; there was never a significant decrease in slope.

A recent study shows that data collected from saccades directed to a single target does not necessarily predict the main sequence relationship (Quaia et al. 2000). In this study, the slope of the velocity-amplitude relationship under these circumstances was approximately two-thirds of the true main sequence slope. Therefore our Fig. 4 cannot be taken as an illustration of the actual main sequence. Instead what the data show is that, for any given amplitude eye movement, peak saccade velocity is greater when accompanied by an arm movement. We undertook an additional analysis to amplify this point.

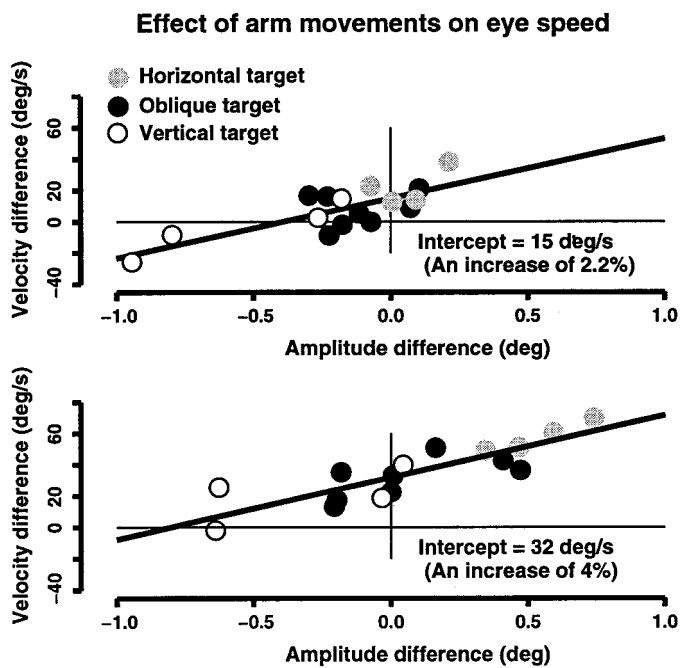


FIG. 5. The difference in peak saccade velocity, for saccades with and without accompanying arm movements, is plotted as a function of the difference in saccade amplitude. The main sequence relationship predicts a monotonically increasing function, which in a local neighborhood can be approximated as linear. Regression lines are fit using a least-squares algorithm and have high correlation coefficients (0.78 and 0.85 for M1 and M2, respectively). The fact that the Y intercept falls above zero indicates that saccades with arm movements are faster than those without, irrespective of differences in saccade amplitude. Each point represents the mean of 92–428 saccades to a single target. Points are coded by saccade direction: horizontal, vertical, or oblique; horizontal, vertical, and tangential velocities are shown. Similar data were obtained using either the pure horizontal or the pure vertical components of the oblique saccades. Horizontal saccades to the same target were larger in amplitude when accompanied by an arm movement. Vertical saccades were smaller and oblique saccades were intermediate. The standard errors of the velocity differences range from 3.1 to 10.3 deg/s, with median values of 5.9 and 3.9 deg/s for M1 and M2, respectively. The standard error of the amplitude differences range from 0.06 to 0.18, with medians of 0.13 and 0.08 for M1 and M2.

The effect of a coordinated arm movement on saccade parameters varied with target direction and trial type. We asked whether there was a consistent relationship between the effect on saccade amplitude and the effect on peak velocity. For each target direction and trial type, we calculated the mean difference in each parameter for saccades made with and without arm movements and then plotted the effect on saccade peak velocity as a function of the effect on saccade amplitude (Fig. 5). The position along the abscissa represents the difference in saccade amplitude (combined eye and arm minus eye alone) and position along the ordinate shows the difference in peak velocity. This analysis revealed a consistent relationship: the larger the effect that arm movement had on saccade amplitude, the larger the effect was on saccade velocity. An increase in peak velocity was observed even when no difference in saccade amplitude was observed (data points close to $x = 0$). The effect is systematic: all data points lie close to a line with a slope of approximately 30 deg/s per deg. A regression line through all the data intercepts the y-axis at 15 and 32 deg/s, respectively, for M1 and M2. These intercepts correspond to increases in peak eye speed, in the presence of coordinated arm movement, of 2.2 and 4.0%, respectively.

Figure 5 reveals that much of the scatter seen in Fig. 3 was due to the tendency for horizontal eye movements to be larger in the presence of an arm movement and for vertical eye movements to be smaller. Once this effect is accounted for, saccades in all directions are affected by coordinated arm movements in a very similar manner, that is, data points obtained using horizontal, oblique, and vertical target directions show a common relationship between velocity and amplitude. This is especially clear in M2, where the amplitude differences are sufficiently large to be confident that all the data points lie on the same regression line (Fig. 5).

Figure 2 showed that, for rightward saccades, the presence of a coordinated arm movement not only resulted in increased peak velocity but also in decreased saccade duration. This effect on duration was not unique to rightward saccades. An analysis identical to that of Fig. 5 reveals a mean drop in duration of 4.0 and 3.9%, respectively, in saccades from M1 and M2 (data not shown).

Eye movements are known to be slower when subjects are drowsy or otherwise in a reduced state of alertness. Might the requirement to move the arm in addition to the eyes result in increased vigilance or alertness, thus explaining the increased eye velocity seen during coordinated movement trials? We do not think this a likely explanation for the following reasons. The two types of trials (eye plus arm and eye alone) were interleaved, and so variations in vigilance would need to occur on a time scale of 1–2 s. Thus on an eye movement alone trial, animals might relax and become less alert, while on combined movement trials the reverse might occur. However, on cue-target trials animals had 600–1200 ms of warning as to the type of movement to make, while on target-cue trials there was no warning—movements occurred as soon as the trial type was indicated. If trial-by-trial changes in alertness are responsible for enhanced velocity on eye plus arm trials, then we would expect this enhancement to be large on cue-target trials and small or nonexistent on target-cue trials.

To test these predictions, we split up the data points in Fig. 5 between those in which the animals had 600- to 1200-ms advance notice as to whether an arm movement was required (cue-target trials) and those in which there was no notice (target-cue trials). The absence of advance notice did not diminish the effect. With no warning, coordinated arm movements resulted in an increase in peak velocity of 2.5 and 3.7% (M1 and M2, respectively), while with advance warning, the corresponding values were 1.8 and 4.3%. The fact that the advance warning of the requirement for an arm movement did not produce a systematic increase in peak saccade velocity rules out rapid changes in vigilance as the cause of the effect.

We have argued that a coordinated arm movement is responsible for the increase in eye velocity, but have not yet considered whether an arm movement unrelated to the eye movement might have a similar effect. Figure 6 shows data from a third animal, tested in a memory saccade paradigm in which the arm movement was either coordinated with (black) or directed opposite to (gray) the eye movement. Memory saccades are generally slower than visually guided saccades, and there is more variability in their main sequence characteristics. Despite these differences, a coordinated arm movement has exactly the same effect on memory-guided saccades as was seen with visually guided saccades in the other two animals: peak saccade velocity is increased by 5.4% (greater than zero with $P <$

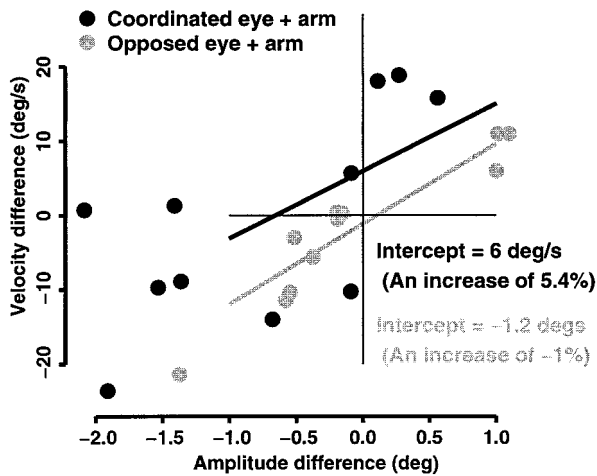


FIG. 6. Comparison of memory-guided saccades accompanied by coordinated or uncoordinated arm movements. Format as in Fig. 5. When the eye and arm are directed to the same target (filled points, solid regression line), the arm movement results in a 5.4% increase in peak eye speed. When the eye and arm are directed to targets in opposite directions, arm movement results in a 1.0% decrease in eye speed. This indicates that only coordinated arm movements increase eye speed.

0.05). When the arm moves in the opposite direction, however, there is neither a significant increase nor a significant decrease compared with the eye-alone condition ($P > 0.25$). Thus a coordinated arm movement is required to obtain the effect. Note that these data further rule out the possibility that the requirement to move the arm increases the animal's state of alertness and thereby increases saccade velocity. An oppositely directed arm movement should have a similar effect on alertness as a coordinated movement, and yet it fails to increase peak saccade velocity.

A final possible artifact that might affect peak saccade velocity is the two-dimensional saccade trajectory. If horizontal saccades, for example, contain larger vertical deviations in the eye alone condition than in the eye plus arm condition, then component stretching might result in faster eye movements in the eye plus arm condition (King et al. 1986). We therefore measured the change in eye position perpendicular to the direction of motion in saccades to horizontal and vertical targets. In 11 of 16 cases, this component was diminished in the eye plus arm condition. However, there was no consistent relationship between the extent of this reduction and the increase in eye velocity.

Finally, we tested the effect of coordinated arm movement on saccade latency. We found that coordinated arm movement added a long, late tail to the saccade latency distribution (Fig. 7). The median saccade latency was minimally affected by arm movement: 8-ms delay and 2-ms advance in M1 and M2, respectively, when the type of movement was known well in advance (cue-target trials), and 6 and 18 ms delay when the type of movement was presented without warning (target-cue trials). In contrast, the 90th percentile latency was greatly increased in the presence of an arm movement: 39- and 16-ms delay (M1 and M2, cue-target trials) and 136 and 33 ms (M1 and M2, target-cue trials).

Coordinated arm movements in humans can result in either speeded or slowed reaction times (e.g., Lunenburger et al. 2000; Neggers and Bekkering 2000). Apparently, the specifics

of the eye-hand task can influence saccadic latency (Johansson et al. 2001). Our results showing slowing of only a subset of saccades is likely to reflect both task and species differences. In contrast to the variable effects on saccade latency, eye-hand coordination appears to consistently increase peak saccade velocity, with similar effects in humans and monkeys, and similar effects in visually guided as well as memory-guided tasks.

If increased saccade velocity on combined eye-arm trials was a result of increased overall alertness or attention, then we would expect to see faster saccadic reaction times on these trials as well. The fact that this was not the case is further evidence against a role of attention in mediating the difference in eye velocity.

We have shown that a coordinated arm movement results in higher peak saccade velocities. In addition, coordinated arm movements sometimes prolong saccade latency (Fig. 7; also Johansson et al. 2001; Neggers and Bekkering 2000). These findings could be related to one another: as with smooth pursuit movements, a saccade whose onset is delayed might, when finally released, show unusually fast dynamics (Lisberger and Westbrook 1985). If true, this would mean that faster saccades are a consequence of longer saccade latencies, and thus, an indirect rather than direct consequence of eye-hand coordination. To test this idea, we calculated whether the effect of a coordinated arm movement was greater for long- compared with short-latency saccades.

Coordinated arm movement caused saccades with latencies less than the median to increase in peak velocity by 2.4 and 4.3% (M1 and M2, respectively). For saccades with latencies greater than the median, the corresponding values were 1.7 and 3.6%. We conclude that the tendency for a combined arm movement to increase the latency of saccades does not account for the increased peak eye velocity. In fact, one animal showed just the reverse effect: peak velocity was inversely correlated

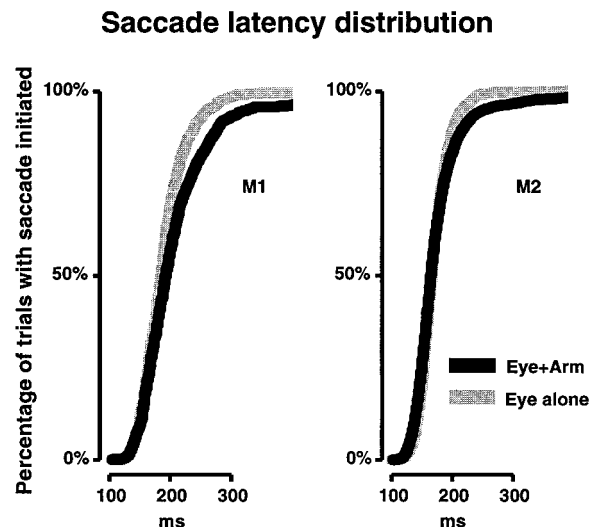


FIG. 7. Cumulative histogram of saccade latencies with and without coordinated arm movements. The abscissa shows time from target onset; the ordinate shows the cumulative percentage of trials in which the saccade had been initiated. The distribution of latencies for coordinated and isolated saccades are similar, except that coordinated saccades have a long tail of slow latencies, indicated by the gap at the top right of each figure. The latencies of downward saccades in M1 were significantly longer than all other saccade latencies; those data are removed from this analysis.

with saccade latency (-0.02 and -0.13 deg/s per ms for M1 and M2, respectively; $P < 0.05$ for M2).

DISCUSSION

We found that, in monkeys performing overtrained eye and arm movements, the main sequence characteristics of saccades are changed when a coordinated arm movement accompanies the saccade. This is surprising, since main sequence characteristics are robust (Bahill et al. 1975). In particular, a coordinated arm movement caused peak eye velocity to increase by approximately 4% and duration to drop by approximately 4%. This effect occurred in three animals, in both visually guided and memory-guided saccades. The effect was absent when arm movements were directed opposite to the target to which the saccade was directed. Finally, the effect does not appear to have been mediated by a modulation in attentional state related to the arm movement.

A similar finding was previously reported in humans by Epelboim et al. (1997). In that study, subjects either looked at, or looked at and tapped, a sequence of targets. The main sequence of gaze movements was altered in the presence of coordinated tapping movements, resulting in 10–20% increase in peak gaze speed for a 20 deg movement. An increase in eye-in-head speed was responsible for about one-half of the total effect (5–10%). The effects in the monkeys (4%) is surprisingly similar, given the differences in species (human versus monkey) and task (sequential tapping versus ballistic center-out movements; head free to move versus head-fixed). The similarity in the results suggests that overtraining does not substantially reduce the effect and that task differences have at best a minor influence on the effect.

What is the explanation for this small but consistent change in saccade main sequence characteristics? If we are about to grasp or otherwise manipulate an object, there is certainly an advantage in foveating the object first. The fovea provides higher resolution information, and this in turn would aid in preshaping the hand for contact. In addition, foveation is likely to provide improved localization information suitable for generating on-line corrections of the arm movement trajectory. Yet a 4% reduction in saccadic movement time is unlikely to provide much of an advantage in this regard. Furthermore, rapid saccades are valuable in even the absence of concurrent arm movements. Thus from a teleological point of view, the fact that a particular saccadic target is also the goal of an arm movement does not necessarily suggest that the eye movement ought to be faster. From a mechanistic point of view, however, there are several likely explanations for the effect.

The fact that eye movements precede arm movements by 50–100 ms implicates a central rather than peripheral (i.e., proprioceptive) source for the effect of coordinated arm movements on saccade dynamics. EMG activity precedes actual arm movement, and this could result in tension in the muscles which might then be sensed by Golgi tendon organs, for example, prior to the start of arm movement. However, the effect of a coordinated arm movement was apparent in the eye trajectory very early on (Fig. 2), making it highly unlikely that proprioceptive signals could travel to the eye movement centers and influence dynamics in time to produce the effects we have observed. Instead, a central mechanism must be at play.

We believe that increased eye speed reflects a direct effect of

the coordinated arm movement. Epelboim et al. (1997) suggest that a change in eye-head coordination, that is, a change in VOR gain, may mediate the effect of a coordinated arm movement. Our experiments show that this indirect mechanism cannot be the sole explanation, however, since we observed faster saccades even though the head was not allowed to move.

Another explanation which posits an indirect effect of coordinated arm movement on eye velocity is that coordinated movement might result in longer saccadic latencies, and saccade-specific mechanisms react to this delay by generating a trajectory with increased velocity. However, the absence of a positive correlation between saccade latency and peak velocity rules out this explanation. Finally, one could argue that without concurrent arm movements, subjects are less attentive, and that this results in a nonspecific effect on eye velocity (Schmidt et al. 1979). The fact that trials with and without arm movements were interleaved, as well as the fact that saccadic latencies on eye-arm trials were not increased, provides evidence against this explanation. These arguments against indirect effects support the hypothesis that specific circuits in the CNS mediate a direct effect of concurrent arm movements on saccade trajectories. Where might such circuits lie?

In the parietal cortex, there appear to be separate areas coding targets for upcoming eye and arm movements: the lateral intraparietal area (LIP) and the parietal reach region (PRR), respectively (Snyder et al. 1997). However, the segregation is incomplete, with cross talk between areas (Snyder et al. 2000). Targets for eye movements are represented, albeit to a small degree, in PRR, and arm movement targets are represented, to a slightly greater degree, in LIP. It is possible that a stimulus that is a target for both an eye and an arm movement might be associated with a more robust representation in LIP than a stimulus that is the target for an eye movement alone. In this case, it is in turn possible that a more robust representation in LIP might lead to faster saccade dynamics. However, there is no data to support the notion that activity levels in LIP modulate saccade dynamics.

A stronger case can be made for a mechanism based on arm movement cells in the superior colliculus (Stuphorn et al. 2000; Werner 1993). Cells in the intermediate and deep collicular layers burst with saccadic eye movements and are related to saccade dynamics, but a subset of neurons has recently been described that are active during arm movements. A projection of even a small percentage of these arm movement neurons to the brain stem saccade generators might provide the extra drive required to boost peak eye velocity by several percentages, and internal feedback loops could then act to drop duration by a compensatory amount.

An important remaining question is whether the increase in peak eye velocity depends on a common arm and eye movement trajectory, or whether a common target would suffice. This question can be addressed by varying the starting point of the arm. The resulting data will further constrain the characteristics of the neural population responsible for the effect. For example, cells in LIP, which code target location on the retina, might mediate an effect that depends on a common target location, but not an effect that depends on a common trajectory. In SC there appear to be both arm movement cells whose activity depends primarily on eye position and arm movement cells whose activity depends primarily on initial arm position (Stuphorn et al. 2000). The former might mediate a common

target effect, while the latter might mediate a common trajectory effect.

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