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RESEARCH ARTICLE

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Hand-eye coordination for rapid pointing movements

Arm movement direction and distance are specified prior to saccade onset

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Abstract Visually guided arm movements such as reaching or pointing are accompanied by saccadic eye movements that typically begin prior to motion of the arm. In the past, some degree of coupling between the oculomotor and limb motor systems has been demonstrated by assessing the relative onset times of eye and arm movement, and by the demonstration of a gap effect for arm movement reaction times. However, measures of limb movement onset time based on kinematics are affected by factors such as the relatively high inertia of the limb and neuromechanical delays. The goal of the present study was thus to assess the relative timing of rapid eye and arm movements made to visual targets by examining electromyographic (EMG) activity of limb muscles in conjunction with eye and arm position measures. The observation of a positive correlation between eye and limb EMG onset latencies, and the presence of a gap effect for limb EMG onset times (a reduction in reaction time when a temporal gap is introduced between the disappearance of a central fixation point and the appearance of a new target) both support the idea that eye and arm movement initiation are linked. However, limb EMG onset in most cases precedes saccade onset, and the magnitude of EMG activity prior to eye movement is correlated with both the direction and amplitude of the upcoming arm movement. This suggests that, for the rapid movements studied here, arm movement direction and distance are specified prior to the onset of saccades.

Keywords Eye-hand coordination · Saccades · Pointing · Gap effect · Reaction time · Movement planning · Human

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Introduction

Goal-directed arm movements such as reaching or pointing to a visual target are typically accompanied by saccadic eye movements. Several studies have examined the relative timing of eye and hand movements as a way of assessing the potential coupling of the oculomotor and limb motor systems (see Carey 2000 for review). Usually the eyes begin moving toward a target 40–100 ms in advance of hand movement (Angel et al. 1970; Prablanc et al. 1979; Biguer et al. 1982; Jeannerod 1988). In reaction time tasks, onset latencies for the eye and hand tend to be positively correlated on a trial-by-trial basis, suggesting a common source for eye and arm movement initiation (Herman et al. 1981; Fischer and Rogal 1986; Jeannerod 1988; also see Fisk and Goodale 1985). Similarly, a gap effect (a reduction in reaction time when a temporal gap is introduced between the offset of a central fixation point and the appearance of a new target) has been reported for both saccade onset (Saslow 1967; Fischer and Boch 1983; Munoz et al. 2000) and hand movement latency (Herman et al. 1981; Fischer and Rogal 1986; Jeannerod 1988), suggesting a common mechanism of disinhibition that acts both on the oculomotor and limb motor systems (Bekkering et al. 1996; Boulinguez et al. 2001). However, previous studies of eye and arm movements in reaction time tasks have assessed arm movement latencies based on measures of arm position, which is influenced by neuromuscular delays and the relatively high inertia of the limb as compared to the eye. The precise relative timing of efferent signals to the eyes and to the limb therefore remains unclear.

Electromyographic (EMG) recordings of limb muscle activation are more closely related in time to the descending neural drive to the limb motor system and may provide more precise information about the relative timing of eye and limb movement initiation. It is well known that EMG activity for limb muscles begins as much as 100 ms prior to arm movement (Wadman et al. 1980; Karst and Hasan 1991). Taking this into account in combination with the knowledge that, in reaction time tasks, saccades can precede movement of the arm by 40–100 ms, one may hypothesize that arm movement may be initiated simultaneously with, or perhaps in some cases prior to saccade onset. The goal of the present study was thus to test this hypothesis by systematically examining the relative timing of eye and arm movement initiation using EMG recordings of limb muscles in combination with recordings of eye and limb position.

We show that, in agreement with previous work on eye-hand coupling based on positional measures of limb movement initiation, a positive correlation is observed between onset latencies for eye movement and limb EMG activity, and a gap effect is observed for limb EMG onset. More interestingly, however, we demonstrate that the onset of limb EMG activity is not coincident with saccade initiation – rather, in most cases limb EMG onset occurs in advance of eye movement. In addition, an examination of the portion of limb EMG activity occurring prior to a saccade reveals that both the direction and the amplitude of an upcoming arm movement are specified before the onset of eye movement. These findings further refine our knowledge about the relative timing of eye and limb movement initiation and provide novel information about the relative timing of the specification of eye and limb movement parameters by the oculomotor and limb motor systems in reaction time tasks.

Materials and methods

Subjects

Eleven subjects (eight men, three women) between the ages of 21 and 32 years participated in the study. Subjects reported no history of neurological or musculoskeletal disorders. All subjects provided written informed consent. The procedures used in this study were approved by the University of Western Ontario Ethics Review Board.

Apparatus

Figure 1A shows the experimental setup. Subjects were seated in the dark in front of a glass tabletop, with their right arm abducted at the shoulder and supported by custom made air-sleds (One of a Kind) in a horizontal plane containing the shoulder. The effect of the air-sleds, which were connected to a 40-psi compressed air source, was to support the arm against gravity and to reduce friction during movement. Medium-density Temper foam (Kees Goebel Medical) was used to provide a cushion between the arm and the air-sleds, and as a result the arm was suspended about 10 cm above the surface of the glass tabletop. A computer-controlled LCD projector was used to project visual targets onto a virtual plane in front of subjects. Targets were projected onto a back-projection screen, suspended 20 cm above the hand, and were reflected into the view of subjects by a semi-silvered mirror positioned 10 cm below the screen. This resulted in the perception of virtual targets “floating” in the plane of the subject’s hand. A lamp illuminated the area below the mirror, providing subjects with full visual feedback of their arm during the experiment.

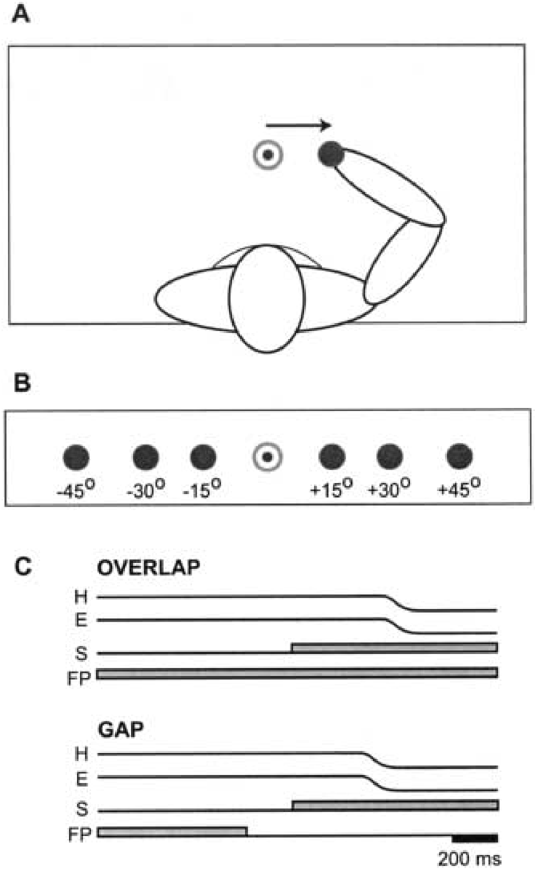

Fig. 1A–C Experimental setup and design. **A** Subjects performed rapid pointing movements in the horizontal plane, to virtual targets projected onto the plane of the hand. A compressed air system supported the arm against gravity and provided for frictionless motion on a glass tabletop. Subjects pointed to a central fixation target with the eyes and the hand and were instructed to “move the eyes and hand as fast as you can” to a peripheral target, located at one of three eccentricities to the left- or right-hand side of the central fixation target. **B** Peripheral movement targets were located 15°, 30°, or 45° on either side of the central fixation point. **C** Subjects performed 120 movements in two experimental conditions. In the overlap condition, the central fixation target (*FP*) remained on throughout the trial. In the gap condition the central fixation target was extinguished 200 ms prior to the appearance of the peripheral target stimulus (*S*). Horizontal hand position (*H*), horizontal eye position (*E*), and EMG signals from arm muscles were recorded

Experimental tasks

Subjects performed rapid pointing movements to visual targets projected in the horizontal plane. In each trial, subjects were instructed to look at and hold their hand stationary at a central fixation target (see Fig. 1A, B). After maintaining this position with their eyes and hand for a period of time between 1,750 and 2,250 ms (randomized across trials), a single peripheral target appeared, either to the left or right of the central target, and at one of three different eccentricities: 15°, 30°, or 45° (see Fig. 1B). These targets corresponded to hand movement distances of 6 cm, 15 cm, and 30 cm, respectively, to the left and right of the central fixation target. The order of target presentations was randomized for each subject. Instructions to subjects were to “move your eyes and your hand as fast as you can to the target, and hold the final position”. No instruction was given about the order or relative timing of eye and hand movements. After holding the final target position for 1,500 ms, the target was extinguished and the next trial began. Subjects were instructed not to make orienting movements to the target with their head, but to hold head position constant throughout each trial. The central fixation target was 5 mm in diameter (1°) and was surrounded by a circle 30 mm (5°) in diameter. The peripheral targets were 30 mm in diameter. There was an interval of 3,000 ms between each successive trial.

Subjects performed movements in two experimental conditions (Fig. 1C). In the overlap condition, the central fixation target remained illuminated throughout the trial. In the gap condition, the central fixation target was extinguished 200 ms before the appearance of the peripheral movement target. In each experimental condition, subjects completed 120 trials. The order of conditions was randomized across subjects. A 5-min rest period was introduced between each experimental condition.

Signal recording

An electromagnetic motion-tracking system (Ascension Technology) was used to record the time-varying position of a receiver with a spatial resolution of 0.5 mm. The receiver (2.6×2.6×2.08 cm) was secured to the distal portion of the index finger using adhesive tape. The position signals were sampled at 140 Hz and stored on a digital computer for off-line analysis. Two additional receivers were attached to the head, using a Velcro headband, and were used to measure horizontal rotations of the head during the experimental task.

EMG activity of limb muscles was recorded using double-differential surface electrodes (Delsys). Each electrode consists of three 1×10 mm parallel silver bars placed 10 mm apart. Electrodes were housed in a compact case containing a ×10 preamplifier. Signals were further amplified ×1,000, analog band-pass filtered between 20 Hz and 450 Hz, and digitally sampled at 1,000 Hz. Recordings were made from shoulder muscles that have mechanical actions resulting in motion of the arm to the left and right, in the horizontal plane (see Fig. 1A). Recordings were made from the posterior head of deltoid, a muscle producing shoulder extension torque (resulting in motion of the arm to the right), and from the clavicular head of pectoralis, a muscle producing shoulder flexion torque, resulting in motion of the arm to the left. In light of the well-documented proximal-to-distal temporal ordering of limb muscle activation (see Discussion), we chose to focus in this study on shoulder rather than elbow muscles, to identify the earliest correlate of limb muscle activity. In two subjects recordings were also made from the anterior head of deltoid (shoulder flexor), sternocostal head of pectoralis (shoulder flexor), short head of biceps (shoulder flexor), and long head of triceps (shoulder extensor). In all cases the patterns of results for triceps long head were the same as for the posterior deltoid, and the results for the anterior deltoid, pectoralis sternocostal head, and biceps short head were the same as for the pectoralis clavicular head (Gribble and Ostry 1999). Electrode placement was verified prior to data collection using a combination of isometric force-production test maneuvers and shoulder flexion and extension movements (Gribble and Ostry 1998, 1999).

Horizontal eye position was recorded using an electro-oculography (EOG) system (Micromedical Technologies) by placing Ag-AgCl skin electrodes at the outer canthi of both eyes. A ground electrode was placed just above the eyebrows in the center of the forehead. To minimize EOG drift, subjects wore the electrodes for approximately 10 min before the start of the experiments. Because we were only interested in measuring saccadic reaction times and in identifying direction errors, we did not attempt to calibrate the EOG signals for absolute eye position. EOG signals were digitally sampled at 1,000 Hz and stored on computer disk for off-line analysis. Signals for eye position, hand position, and EMG signals were temporally synchronized using a 100-MHz clock chip provided on a National Instruments A/D board. Data collection and target presentation were controlled using custom software programmed in LabView (National Instruments).

Data analysis

Hand position and head orientation signals were digitally low-pass filtered at 15 Hz using a second-order Butterworth filter implemented in Matlab (The Mathworks). EMG signals were digitally band-pass filtered between 30 and 300 Hz, full-wave rectified, and then low-pass filtered at 50 Hz. Eye position signals were band-stop filtered at 60 Hz and low-pass filtered at 50 Hz.

For each trial, hand position, eye position, head orientation, and EMG signals were aligned to hand movement onset, which was scored by identifying 5% of the peak tangential velocity of the hand during movement. Similarly the onset of saccades was scored on the basis of 5% of the peak velocity of the eye position signal. The onsets of agonist and antagonist EMG bursts associated with arm movement were scored using an interactive computer program written using Matlab. For each muscle, a threshold was determined based on 3 SDs above the mean EMG signal observed during a 200-ms window before the appearance of the peripheral target (or before the disappearance of the fixation point in the gap condition). The onset of an EMG burst was scored as the point in time when the EMG signal rose above the threshold level. Reaction times were calculated as the time between the appearance of the peripheral target and the onset of the saccade, arm movement and each EMG signal. Data for one subject were discarded due to the inability of the subject to complete the experiment. The analyses reported here are based on data from the ten remaining subjects. Trials in which the EMG bursts could not easily be identified, or in which subjects made a significant movement error (e.g., no motion, or motion in the incorrect direction), or in which head rotation exceeded 5°, were excluded from these analyses. This resulted in setting aside between 4 and 32 trials (out of 240 total) per subject (mean 15.6 trials). Analysis of variance (ANOVA) and Tukey post hoc tests were used to test the statistical reliability of differences between mean onset times and mean presaccadic EMG activity, and *t*-tests were used to test the significance of correlation coefficients (see Results).

Results

Figure 2 shows typical patterns of eye movement, arm movement and arm muscle activity patterns for a single trial in the gap condition. Arm movement onset is indicated by a vertical line (H). In this trial the peripheral target appeared on the left hand side of the central fixation target. Onset time of the target stimulus is indicated by a vertical line (S). As was typical for all subjects in the experiment, saccade onset (indicated by a vertical dashed line over the eye position record) occurred about 30–40 ms prior to the onset of the arm movement. It is clear, however, from the EMG records that the onset of agonist muscle activity, in this case recorded from pectoralis, occurred prior to the onset of eye movement – in this trial about 40 ms before the onset of the saccade. As is typical in rapid arm movement, the delay between the onset of agonist EMG activity and arm movement onset was about 80 ms, and antagonist EMG activity (in this case posterior deltoid) appeared at or just prior to the peak velocity of the arm movement. The orientation of the head in the horizontal plane, shown at the bottom of Fig. 2, was virtually constant across the movement trial.

Limb movements were rapid, averaging between 210 ms and 340 ms in duration across subjects (mean 291 ms, SD 72 ms). There were no differences in movement duration in the gap compared with the overlap

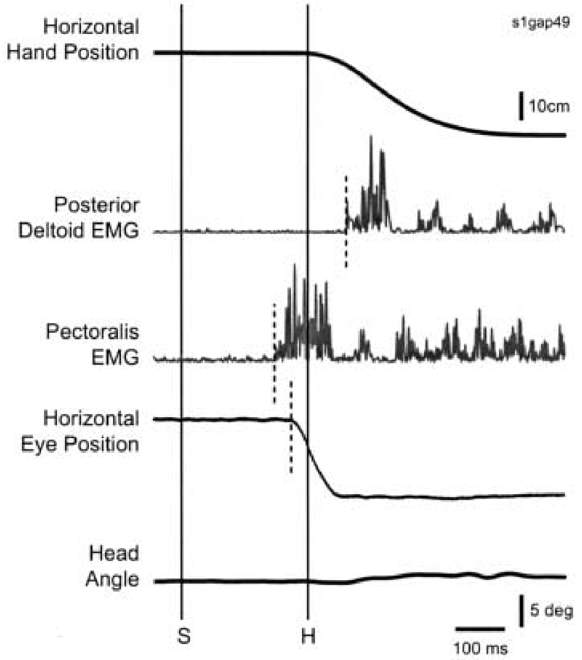

Fig. 2 Typical data from a single trial are shown for one subject. Records are time-aligned to the onset of hand movement (*H*). The appearance of the perhiperal target stimulus is indicated by *S*. Horizontal position of the hand, horizontal eye position, horizontal head orientation, posterior deltoid EMG, and pectoralis EMG are shown over time. Signal changes *downward* correspond to movements to the left and the *upward* direction corresponds to movements to the right. *Vertical dashed lines* indicate the onset of EMG bursts and saccade onset. Note that pectoralis muscle activity precedes the onset of the saccade, which in turn precedes the onset of hand movement

conditions ($P>0.05$). Although there were no explicit instructions regarding accuracy, limb movement errors for all subjects were small. Average endpoint error across subjects ranged from 0.8 cm to 3.3 cm (mean 1.9 cm, SD 0.7 cm). No differences in limb endpoint error were observed in the gap compared with overlap conditions ($P>0.05$). In both the gap and overlap conditions, there was a small but statistically reliable effect of target eccentricity on limb endpoint error for seven of the ten subjects ($P<0.05$), such that endpoint errors were slightly higher for targets farther from the central fixation point. Across subjects, limb endpoint errors for the 45° target were 5%–10% larger than for the 15° target. The mean duration of saccades across subjects ranged from 76 to 92 ms (mean 85 ms, SD 7 ms). No statistically reliable differences in saccade duration were observed in the gap versus overlap condition ($P>0.05$).

Eye-hand coupling and the gap effect

To assess the potential coupling between eye and hand movements, we compared reaction time latencies for eye and hand movement onset, as well as for EMG onset in the gap and overlap conditions. Figure 3 shows distributions of reaction time latencies for a typical subject. Data are shown separately for movements to the left (dark bars) and right (light bars) targets. Data are pooled across the three target eccentricities, and mean reaction time latencies are indicated in each panel. As was typical for all subjects, a significant decrease in saccadic reaction time was observed in the gap condition compared with the overlap condition, for both left and right movements ($P<0.01$ in both cases). A significant gap effect was also observed for hand movement and for the onset of limb

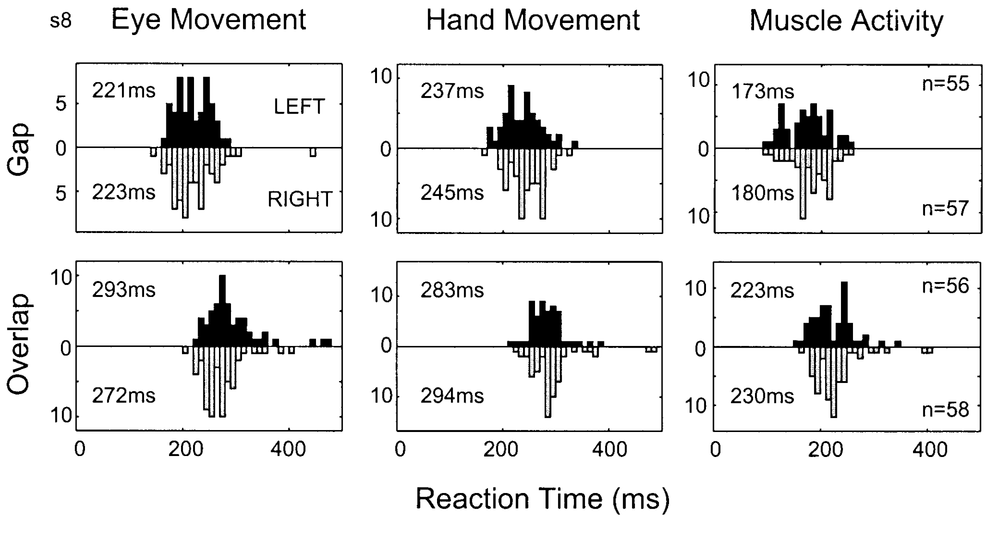

Fig. 3 Typical distributions of reaction times. Reaction time distributions are shown for the onset of eye movement, hand movement, and the onset of EMG activity in shoulder muscles, for a single subject. *Dark bars* indicate reaction times for movements to targets on the left-hand side of the central fixation target, and *light bars* show reaction times for movements to the right. Distributions are shown separately for the gap (*top row*) and overlap (*bottom row*) conditions. Mean reaction times for each distribution are indicated beside each plot

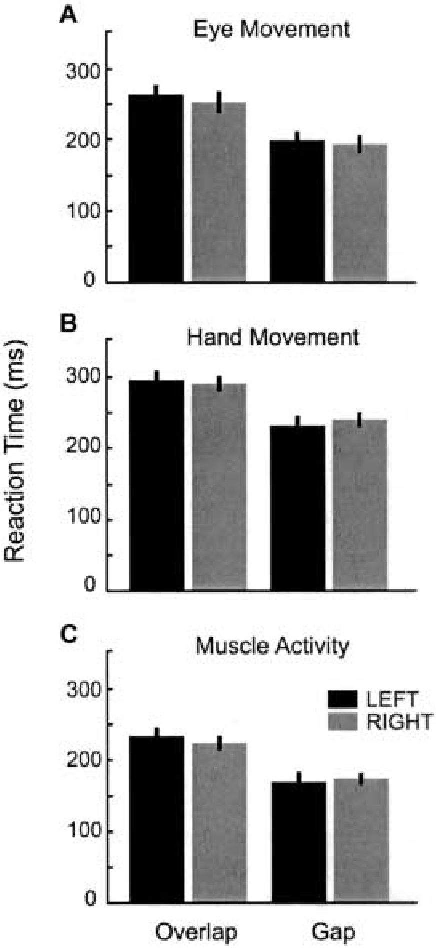

Fig. 4A–C Gap effect for eye movement, hand movement, and muscle activity. Mean reaction times across ten subjects are shown for the onset of eye movement, hand movement, and shoulder muscle activity for movements to the left (*dark bars*) and right (*light bars*), in both the gap and overlap conditions. *Error bars* indicate 1 SE of the mean. Mean reaction time is in all cases higher in the overlap condition as compared to the gap condition

Table 1 ANOVA results for main effect of target condition (Gap vs Overlap), for saccade onset (*Saccade*), arm movement onset (*Arm*), and agonist EMG burst onset (*EMG*). The mean gap effect (the reaction time reduction in gap as compared to overlap condition) is shown for data pooled across target direction and eccentricity

Subject	Saccade	Arm	EMG
1	26 ms $F_{1,\ 221}=30.95$ $P<0.001$	23 ms $F_{1,\ 221}=30.78$ $P<0.001$	24 ms $F_{1,\ 221}=35.07$ $P<0.001$
2	59 ms $F_{1,\ 198}=69.21$ $P<0.001$	52 ms $F_{1,\ 198}=122.73$ $P<0.001$	53 ms $F_{1,\ 198}=154.98$ $P<0.001$
3	89 ms $F_{1,\ 218}=248.83$ $P<0.001$	91 ms $F_{1,\ 218}=403.47$ $P<0.001$	94 ms $F_{1,\ 218}=390.75$ $P<0.001$
5	37 ms $F_{1,\ 223}=61.96$ $P<0.001$	52 ms $F_{1,\ 223}=159.88$ $P<0.001$	46 ms $F_{1,\ 223}=121.97$ $P<0.001$
6	69 ms $F_{1,\ 225}=148.34$ $P<0.001$	51 ms $F_{1,\ 225}=179.93$ $P<0.001$	56 ms $F_{1,\ 225}=206.11$ $P<0.001$
7	62 ms $F_{1,\ 213}=48.73$ $P<0.001$	52 ms $F_{1,\ 213}=176.16$ $P<0.001$	54 ms $F_{1,\ 213}=178.35$ $P<0.001$
8	61 ms $F_{1,\ 215}=110.79$ $P<0.001$	48 ms $F_{1,\ 215}=91.05$ $P<0.001$	50 ms $F_{1,\ 215}=91.17$ $P<0.001$
9	89 ms $F_{1,\ 211}=216.49$ $P<0.001$	95 ms $F_{1,\ 211}=474.1$ $P<0.001$	90 ms $F_{1,\ 211}=424.34$ $P<0.001$
10	66 ms $F_{1,\ 197}=68.99$ $P<0.001$	69 ms $F_{1,\ 197}=130.25$ $P<0.001$	63 ms $F_{1,\ 196}=109.26$ $P<0.001$
11	66 ms $F_{1,\ 213}=33.59$ $P<0.001$	48 ms $F_{1,\ 213}=52.71$ $P<0.001$	49 ms $F_{1,\ 212}=50.96$ $P<0.001$

muscle activity ($P<0.01$ in both cases). For the subject shown in Fig. 3, the mean gap effect for the eye, hand, and muscle activity was 61 ms, 48 ms, and 50 ms, respectively. No reliable differences were observed between reaction times for movements to the left- versus right-hand-side targets.

It is interesting to note that, particularly in the gap condition, reaction time latencies for limb EMG onset were extremely fast, ranging from just under 100 ms to 250 ms (mean: 173 ms for left, 180 ms for right). In addition, although the number of trials is not large ($n=55$ for the subject shown in Fig. 3), it appears, for movements to the left, that there may be a distinct mode of fast EMG onsets in the gap condition. Mean onset of limb EMG in the gap condition was consistently fast across all subjects, ranging from 134 to 207 ms (mean 168 ms, SD 22 ms).

Figure 4 shows mean reaction times across all subjects for eye movement, hand movement, and EMG activity onset, for gap and overlap conditions. Data are shown separately for movements to left and right targets. For eye movement onset, as well as hand movement and EMG activity, reaction times decreased in the gap condition as compared to the overlap condition. To assess the statistical reliability of the gap effect, we conducted a 3-factor ANOVA, condition (gap/overlap) × direction (left/right) × eccentricity (15°,30°,45°), within each subject. All subjects showed a significant main effect of gap/overlap condition on reaction time latency for the eye, hand, and EMG onset ($P<0.01$; see Table 1). The mean magnitude of the gap effect across subjects was 62 ms, 58 ms, and 58 ms for the eye, arm and EMG activity, respectively. In three subjects a small effect of target direction (left/right) was observed for onset latencies, but no consistent pattern was seen across subjects. No effects of target eccentricity on reaction times were observed ($P>0.05$). In addition no statistically reliable differences in the magnitude of the gap effect were seen for eye as compared to arm or EMG onset.

Relative timing of eye and hand movements

To assess the potential coupling between movement initiation for the eye and the arm, we examined the trial-

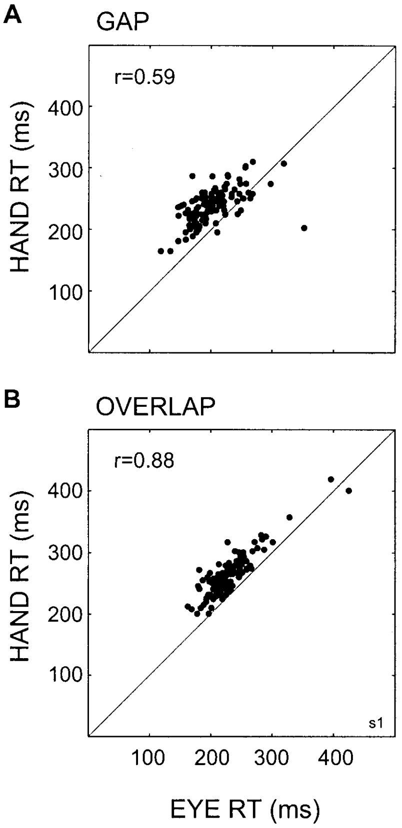

Fig. 5A, B Coordination of reaction times for the eyes and hand. Reaction times for the onset of hand motion are plotted as a function of eye movement reaction time in the gap (*top*) and overlap (*bottom*) conditions. Data shown are for a single typical subject. Reaction times for hand movement lag those for eye movement onset, but are strongly correlated to saccade onset on a trial-by-trial basis. Correlation coefficients are shown in each plot

to-trial relationship between saccadic reaction time and onset times for hand movement and EMG activity. Figure 5 shows hand movement reaction time plotted as a function of saccadic reaction time in both the gap (Fig. 5A) and the overlap (Fig. 5B) conditions, for a single typical subject. Data are pooled across target direction and eccentricity. In both gap and overlap conditions, a relationship exists between eye movement and hand movement onset times – longer saccadic reaction times are associated with longer hand reaction times (gap r=0.59; overlap r=0.88; P<0.01 in both cases). In addition Fig. 5B demonstrates the tendency of saccade onset to precede motion of the hand.

A similar analysis is shown for the same subject in Fig. 6, in which we plot the onset time of agonist EMG activity in limb muscles as a function of saccadic reaction time. A strong relationship is observed between eye movement onset and the appearance of muscle activity (gap r=0.54; overlap r=0.87; P<0.01 in both cases). A full listing of the correlation coefficients for eye-hand and eye-EMG reaction time latencies is given for each subject in Table 2. Significant correlations were observed for both eye-hand and eye-EMG reaction times (P<0.01 for all subjects). Although in some subjects a statistically significant difference was seen in the correlations for gap versus overlap conditions (e.g., for the subject shown in Fig. 6), no consistent pattern was seen across all subjects. Figure 6 also shows the tendency for EMG onset to

Table 2 Correlation coefficients for trial-to-trial relationship of saccade reaction time to arm movement reaction time (*Eye-Hand*) and agonist EMG burst reaction time (*Eye-EMG*). Correlations are shown separately for the overlap and gap conditions

Subject	Gap		Overlap	
	Eye-Hand	Eye-EMG	Eye-Hand	Eye-EMG
1	0.59	0.54	0.88	0.87
2	0.22	0.22	0.40	0.30
3	0.52	0.42	0.68	0.68
5	0.55	0.55	0.60	0.62
6	0.68	0.62	0.81	0.81
7	0.43	0.29	0.42	0.41
8	0.54	0.53	0.50	0.53
9	0.27	0.31	0.41	0.36
10	0.25	0.30	0.43	0.50
11	0.53	0.61	0.41	0.57

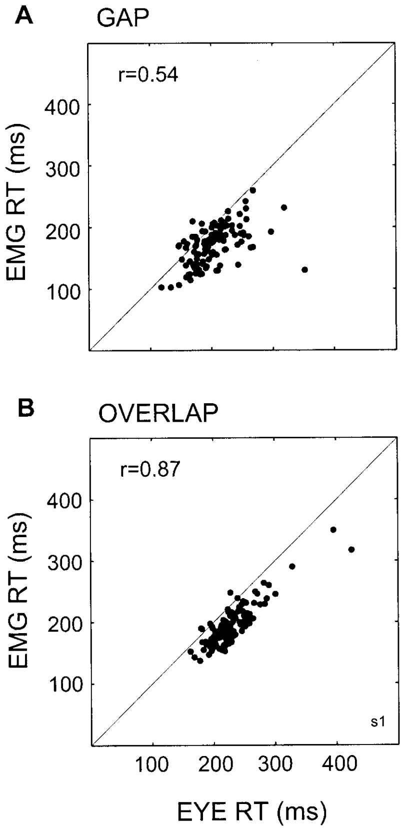

Fig. 6A, B Coordination of reaction times for onset of eye movement and muscle activity. Reaction times for the onset of agonist shoulder muscle activity are plotted as a function of eye movement onset, for the gap (*top*) and overlap (*bottom*) conditions. Data shown are for a single typical subject. Muscle activity onset times are strongly related on a trial-by-trial basis to saccade onset times. In contrast to hand movement onset times, muscle activity tends to precede eye movements

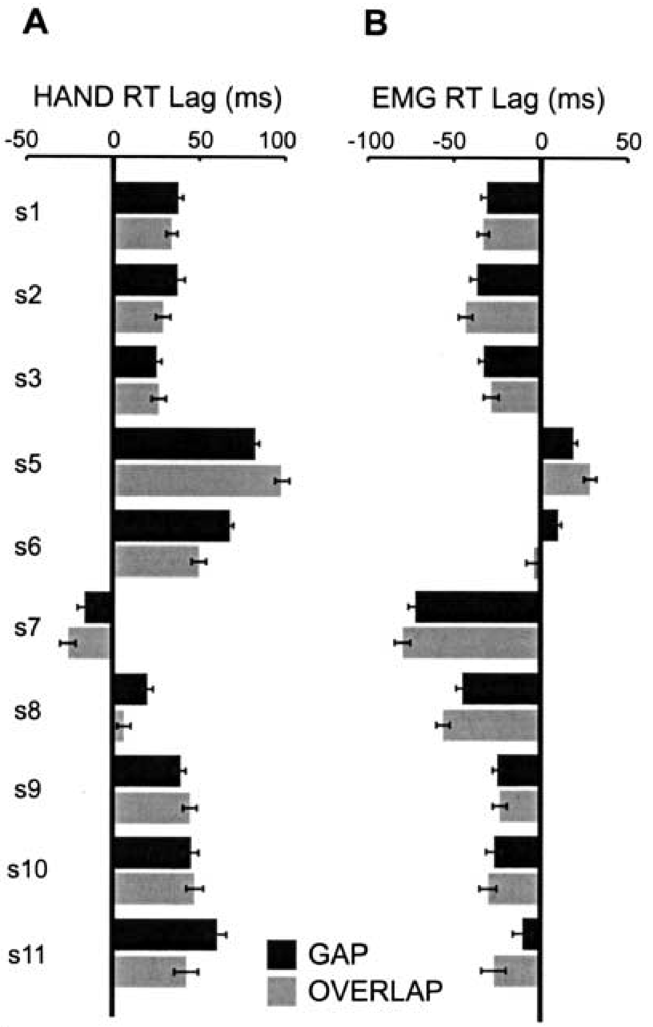

Fig. 7A, B Reaction time differences for eye, hand, and muscle activity. Mean difference in reaction time for hand versus eye movement onset (*left*) and EMG versus eye movement onset (*right*) are shown for ten subjects, in the gap (*dark bars*) and overlap (*light bars*) conditions. *Error bars* indicate 1 SE of the mean. For all subjects but one, eye movements tended to precede the onset of hand motion by 40–100 ms (mean across subjects, 39.5 ms for gap and 35.1 ms for overlap conditions). In contrast muscle activity tended to precede the onset of eye movements by 20–80 ms (mean across subjects, 24.9 ms for gap and 29.4 ms for overlap)

precede the onset of saccades, even for the fastest responses.

In Fig. 7 we show the mean relative timing delays between the eye and hand, and the eye and limb muscle activity for all ten subjects. Figure 7A shows the mean difference in time between saccade onset and hand movement onset, for each subject in the gap (dark bars) and overlap (light bars) conditions. Hand-eye lag times across subjects varied between –26 ms (hand preceding saccade) and +97 ms (saccade preceding hand movement). For all subjects (except subject 7, and subject 8 in the overlap condition), the hand movement onset significantly lagged the saccade onset ($P<0.01$). The mean onset time differences across subjects were +39.5 ms (gap) and +35.1 ms (overlap). Figure 7B shows the mean time between saccade onset and the appearance of agonist limb EMG activity (pectoralis activity for movements to the left, and posterior deltoid activity for movements to the right). For all subjects (except subjects 5 and 6), EMG activity onset significantly preceded saccade onset ($P<0.01$). Mean lag times ranged from –80 ms (EMG preceding saccade) to +28 ms (saccade preceding EMG). Means across subjects were –24.9 ms (gap) and –29.4 ms (overlap). Although in some individual subjects small differences in mean lag times were observed in the gap versus overlap conditions (e.g., subject 11), no consistent pattern was seen across subjects.

Table 3 Number of trials in which the onset of agonist limb EMG preceded saccade onset, in the gap and overlap conditions. The data are also given as the proportion of the total number of trials in each condition (120 trials)

Subject	Gap	Overlap
1	100 83%	115 96%
2	79 66%	92 77%
3	94 78%	92 77%
5	23 19%	22 18%
6	41 34%	62 52%
7	104 87%	116 97%
8	105 88%	111 93%
9	77 64%	76 63%
10	71 59%	81 68%
11	53 44%	67 56%

Limb movement parameters specified prior to saccade onset

To assess the kinds of information about the upcoming arm movement that may be specified prior to saccades, we examined for each subject the subset of trials in which agonist limb muscle EMG activity onset preceded eye movement onset. This subset corresponded to a mean across subjects of 62% (gap) and 70% (overlap) of the total number of trials recorded. Table 3 gives the specific number of trials examined for each subject in the gap and overlap conditions.

We first assessed the extent to which limb movement direction is specified in limb EMG signals prior to saccade onset. The alternative is that the observed presaccadic EMG activity may be nondirectional in nature, for example as would be expected if it were associated with a general increase in cocontraction level. To test this possibility, the mean EMG activity in each muscle was computed for each trial over a window of

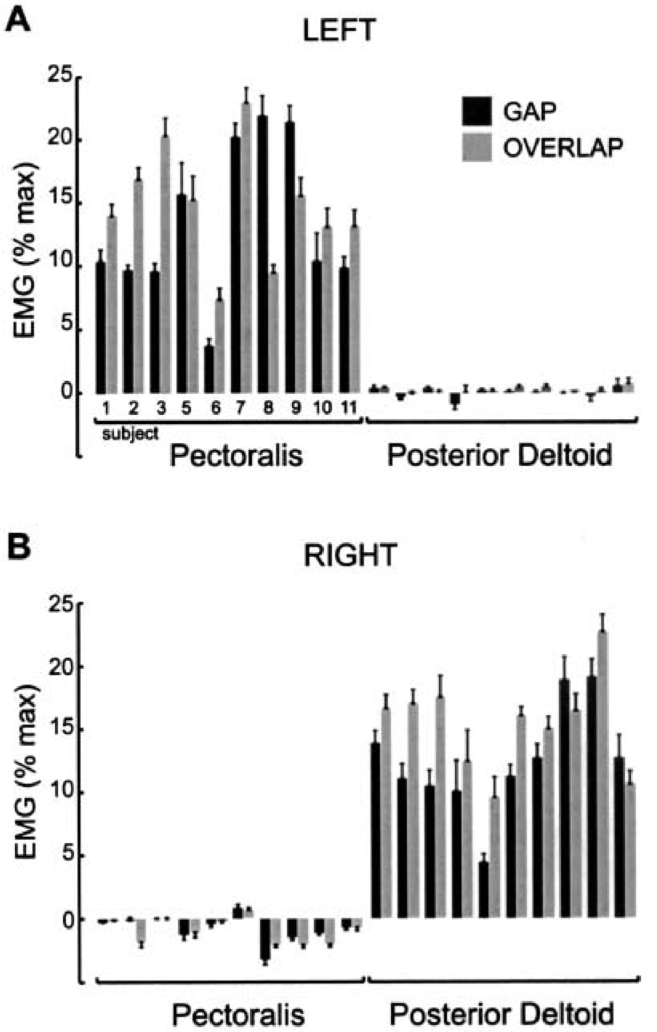

Fig. 8A, B Arm movement direction is specified prior to saccade onset. Mean muscle activity between EMG burst onset and saccade onset is shown for those movements in which muscle activity preceded saccade onset. Data for pectoralis and deltoid are shown separately for movements to the left (*top*) and right (*bottom*) of the central fixation target, for the gap (*dark bars*) and overlap (*light bars*) conditions. Mean data are shown for all ten subjects (from *left* to *right*, s1, s2, s3, s5, s6, s7, s8, s9, s10, s11); *error bars* indicate 1 SE. For movements to the left, average muscle activity prior to saccade onset in pectoralis (a shoulder flexor that produces arm movement toward the left) was significantly higher than in posterior deltoid (a shoulder extensor producing limb motion to the right), which was relatively silent. Similarly for movements to the right, mean deltoid muscle activity prior to saccade onset was significantly higher than in pectoralis, which was relatively silent

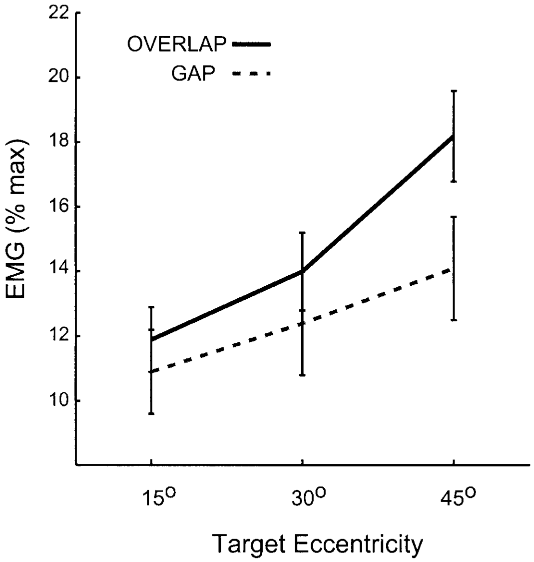

Fig. 9 Arm movement distance is specified prior to saccade onset. Mean agonist muscle activity prior to saccade onset is shown for movements in which the onset of EMG activity preceded the onset of eye movements. Mean data across ten subjects are shown, combined for movements to the left (pectoralis EMG) and right (posterior deltoid EMG). Mean EMG activity is plotted as a function of target eccentricity. In both gap (*dashed line*) and overlap (*solid line*) conditions, mean agonist EMG activity prior to saccade onset is scaled in proportion to target eccentricity and hence the distance of the upcoming armmovement

time beginning at the agonist EMG onset (pectoralis for movements to the left, and posterior deltoid for movements to the right), and ending at the onset of the saccade. Means were taken after first subtracting the baseline activity of each muscle, computed over a 100-ms window before the appearance of the peripheral target, and then normalizing the remaining EMG activity to the maximum value observed in each muscle, over the course of the entire experiment. These normalizations enabled us to make comparisons between muscles and across subjects and were carried out separately for each subject. Data were pooled across the three target eccentricities.

Figure 8 shows the mean presaccadic EMG activity for each muscle in both gap (dark bars) and overlap (light bars) conditions, for each of the ten subjects. It can be seen that, for movements to the left (Fig. 8A), presaccadic activity in pectoralis is significantly higher than activity in posterior deltoid (P<0.01 for all subjects), which is no different from baseline levels (P>0.01 for all subjects). Note that negative values indicate that muscle activity is reduced relative to the baseline. Similarly, for movements to the right (Fig. 8B), presaccadic EMG activity in posterior deltoid is significantly higher than activity in pectoralis (P<0.01 for all subjects), which is no higher than baseline (P>0.01 for all subjects except subject 7, who shows a very small but reliable increase relative to baseline) and, in many cases, lower than baseline (P<0.01 for subjects 2, 5, 8, 9, 10). This presaccadic modulation of EMG activity in the muscle appropriate for generating limb movement in each target direction suggests that target direction is specified in descending neural commands to limb muscles prior to the onset of eye movements.

We also examined whether there is evidence that target eccentricity (and hence upcoming limb movement distance) is specified prior to saccades. Mean presaccadic EMG activity in the agonist muscle (pectoralis for left movements and posterior deltoid for movements to the right) was computed separately for each target eccentricity and pooled over target direction. These data, averaged across subjects, are shown in Fig. 9. For both gap (dashed line) and overlap (solid line) conditions, there was a significant increase in mean presaccadic agonist EMG activity as a function of the eccentricity of the target – and hence the distance of the upcoming arm movement ($P<0.01$ for overlap, $P<0.05$ for gap). This suggests that information about the amplitude of the upcoming limb movement is specified in neural control signals to limb muscles before the initiation of the saccade.

Discussion

To assess the nature of the coupling between eye and hand movements, we recorded EMG activity of limb muscles in conjunction with recordings of eye and hand position during rapid pointing movements to visual targets. We demonstrate a gap effect for limb muscle EMG onset which is similar to that for saccades, supporting the idea that the oculomotor and limb motor systems are influenced by a common neural pathway for disinhibition. We show a tight trial-to-trial coupling between saccadic reaction times and arm movement and EMG activity onset times, supporting the idea that neural control signals underlying movement initiation for the eye and arm are linked. The most interesting findings, however, are related to the relative timing of eye and arm movement initiation. We demonstrate that, for the rapid movements studied here, the onset of limb muscle EMG preceded saccade onset for most trials. Even if one takes into account the neuromuscular delay associated with eye EMG (e.g., 7 ms; Biguer et al. 1982), our results imply that descending neural commands for limb movement initiation are specified in advance of saccade onset. Moreover in these movements both the direction and the distance of the upcoming arm movements were specified in advance of the onset of eye movement. These findings have important implications for theories of how the oculomotor and limb motor systems are organized for rapid movements to visual stimuli.

Our finding that shoulder EMG onset precedes saccade onset extends the earlier work of Biguer et al. (1982), who examined elbow muscle activity patterns during a pointing task to visual targets. The authors report that, for targets distant from a central fixation point, elbow muscle EMG onset co-occurred with or slightly preceded the onset of eye movement, and suggested that neural control signals for movement initiation may be specified for the oculomotor and limb motor systems simultaneously. Many previous reports have demonstrated a proximal-to-distal temporal ordering of corticomotoneuronal discharge and corresponding limb muscle activation patterns (Wadman et al. 1980; Murphy et al. 1985; Karst and Hasan 1991; Scott 1997; Gribble and Ostry 1999). Thus in the present study shoulder muscles were examined rather than elbow muscles, in an attempt to identify an earlier neural correlate of descending commands to the limb.

In the present study the fastest limb agonist EMG onset reaction times were very rapid, in the range of 110 ms–130 ms after the appearance of the peripheral target, and in some subjects (see Fig. 3) there was a suggestion of a distinct mode of fast EMG onset times (although due to the small number of trials in the present study, this possibility could not be assessed quantitatively). Reaction times in this range have been observed for saccades in a gap task and represent a distinct mode of "express saccades," with latencies in the range of the minimal time required for sensory-motor transformation (Fischer and Boch 1983; Fischer et al. 1993). It may be noted that, while reduced saccadic latencies associated with the "express mode" tend to be more prevalent in a gap task, a gap does not guarantee that express saccades will be produced; the occurrence of express saccades depends on other factors such as predictability in the location and timing of the target (see Munoz et al. 2000 for review). The present data suggest a possible express mode for limb movements – one that may only be revealed by examining limb EMG activity. Further studies with a larger number of movement trials are being undertaken in order to rigorously assess this possibility.

A gap effect (a reduction in reaction time associated with a temporal gap between the disappearance of a central fixation point and a peripheral target) has long been demonstrated for saccades (Saslow 1967), and also more recently for arm movement reaction times (Bekkering et al. 1996; Boulinguez et al. 2001). In the present study we demonstrate a gap effect for limb muscle EMG onset times as well. This is perhaps not surprising, since EMG activity may be related to an upcoming arm movement. However, in conjunction with the observation that limb EMG activity onset precedes saccade onset, our findings suggest that the gap effect for arm movement is not dependent on the prior initiation of a saccade. In other words, the present results support a parallel rather than serial organization of the neural pathways for disinhibition in the oculomotor and limb motor systems (Bekkering et al. 1996; Munoz et al. 2000).

Both brainstem and cortical neural pathways have been implicated in the coordination of eye and arm movements to visual targets. Evidence has been reported that the superior colliculus (SC), a brainstem structure known to be involved in orienting movements of the eyes and head (for review, see Sparks and Hartwich-Young 1989), is involved in the production of visually guided limb movements as well. Subpopulations of neurons in the primate SC have been shown to be related to arm movements to visual targets, in the absence of movements of the eyes. These SC "reach neurons" begin to discharge either with the onset of limb movement, during movement, or in many cases well before the onset of limb movement and the earliest sign of associated limb EMG activity (Werner 1993; Werner et al. 1997a, 1997b). In addition some of these SC reach neurons show graded changes in activity with movement direction (Werner 1993), and discharge patterns that are similar in time course to trunk and shoulder muscle EMG activity underlying limb motion, often with mono- or biphasic excitatory bursts of activity (Werner et al. 1997a). This brainstem neural circuitry for transforming sensory inputs into motor commands for the eye, head, and limb may underlie the movements studied in the present paper. A clear avenue for future study is thus to examine the activity of reach-related SC neurons during combined rapid eye and arm movements, and in particular to compare the relative timing of the activity of reach-related and saccade-related SC neurons.

Regions of the posterior parietal cortex (PPC), have also been implicated in the coordination of eye and limb movements. Recent work by Andersen and colleagues has suggested that PPC neurons are involved in combining sensory signals from different modalities and planning movements of the eyes and limbs (Andersen et al. 1998; Snyder et al. 2000). Two areas within PPC have been identified which are hypothesized to code primarily eye movements (lateral intraparietal area LIP) and reaching movements (parietal reach region PRR). It has been proposed that neurons in these areas, through gain modulations by eye and body position signals, code eye and arm movements in multiple coordinate frames (e.g., eye, arm, body) simultaneously (Andersen et al. 1998). Cortical areas more directly related to the production of limb movements such as primary and premotor cortices have also been proposed as candidates for eye-hand coordination. Neurons in primate dorsal premotor cortex and in human primary and premotor cortices modulate their activity with eye and gaze position, suggesting a role for these areas in the integration of eye/gaze information and neural commands to the limb (Boussaoud 1995; Mushiake et al. 1997; Boussaoud et al. 1998; Boussaoud and Bremmer 1999; Jouffrais and Boussaoud 1999). In addition, Goldberg and colleagues have reported a predictive remapping of visual receptive fields in neurons in posterior parietal cortex (Duhamel et al. 1992), frontal eye field (Umeno and Goldberg 1997), and superior colliculus (Walker et al. 1995). These early signals related to upcoming eye movements could conceivably be used to initiate voluntary arm movements.

While the findings summarized above suggest that eye and/or gaze position information may in some circumstances affect the pattern of limb motor commands, it is conceivable that other mechanisms may underlie the present results. For example, in the present task, information about the position of a visual target on the retina may be used to determine the form of neural control signals to the limb. A rapid mechanism for programming limb movements to nonfoveated visual targets may be supported by more direct pathways from visual cortical areas to premotor and primary motor cortical areas controlling limb movements (see Porter and Lemon 1995; Wise et al. 1997, for reviews). For example, neuroanatomical tracing studies have shown that dorsal premotor cortex receives direct inputs from the parieto-occipital area, which in turn receives direct inputs from primary visual cortex (Tanne et al. 1995).

The present findings suggest that, in the rapid movement task studied here, cortical systems subserving arm movements are well informed about target location prior to saccade onset. This does not mean, however, that terminal feedback from oculomotor systems is of no use – this information presumably may be used on a trial-to-trial basis to make adjustments to arm motor commands in response to terminal errors from previous trials. Indeed, an interesting question is the extent to which the present findings may be affected by learning or by prior knowledge of, or experience with the set of possible target locations. Another direction for future study may be the examination of the precision of the directional coding of arm movements prior to saccades, and its possible dependence on factors such as practice and the number of potential targets.

We may also consider the generality of the present findings, which may depend on task parameters. In the task studied here, subjects were instructed to move as fast as possible, with no instruction given about spatial accuracy. There is evidence that, when an extremely high degree of spatial accuracy is crucial to the successful completion of the task, the relative timing of eye and arm movements is quite different. For example, in a task in which subjects were required to grasp and manipulate small objects with the fingers, eye and head movements were made toward an upcoming grasp point and preceded the onset of reaching movements to the same locations by several hundred milliseconds (Johansson et al. 2001). In the context of this task, the authors propose that gaze position informs the limb motor system about the position of upcoming grasp points and hence the direction in which to move the arm. For more rapid pointing tasks, however, subjects can perform accurate arm movements even when the target is not foveated (Crawford et al. 2000). In such a task, pointing error tends to vary with the eccentricity of targets (Henriques and Crawford 2000). It remains an interesting question whether the relative timing of saccades and limb EMG activity reported in the present study might be modulated with the degree of spatial accuracy required of the subjects during a reaching or pointing task. In addition, in the present study the total possible number of targets was relatively small (6). It is possible that, with a larger number of targets or a random set of target positions, eye position and/or gaze information may be required in order to generate appropriate neural commands to the limb motor system.

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