

# Saccadic Output Is Influenced by Limb Kinetics During Eye–Hand Coordination

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**ABSTRACT.** In several recent studies, saccadic eye movements were found to be influenced by concurrent reaching movements. The authors investigated whether that influence originates in limb kinematic or kinetic signals. To dissociate those 2 possibilities, the authors required participants ( $N = 6$ ) to generate pointing movements with a mass that either resisted or assisted limb motion. With practice, participants were able to generate pointing responses with very similar kinematics but whose kinetics varied in a systematic manner. The results showed that saccadic output was altered by the amount of force required to move the arm, consistent with an influence from limb kinetic signals. Because the interaction occurred before the pointing response began, the authors conclude that a predictive signal related to limb kinetics modulates saccadic output during tasks requiring eye–hand coordination.

*Key words:* eye–hand coordination, limb kinematics, limb kinetics, pointing, saccades

To enable an individual to reach toward an object, the central nervous system must determine the spatial location of the object with respect to the observer and transform that information into coordinated motor output of the eyes and hand. Signals generated by the oculomotor system before and during the response have been shown to influence the planning and control of the reaching movement (Henriques & Crawford, 2002; Sailer, Eggert, Ditterich, & Straube, 2000; van Donkelaar, 1997). In other research, the converse interaction has been found: Saccades generated in combination with a reaching movement are initiated more quickly and tend to be more accurate (Lunenburger, Kutz, & Hoffmann, 2000) or to have higher peak velocities and shorter movement durations (Epelboim et al., 1997; Snyder, Calton, Dickinson, & Lawrence, 2002) than do saccades generated in isolation.

Our purpose in the present study was to gain a better understanding of that interaction. In particular, we sought to determine whether the modulation of saccadic output origi-

nates from limb movement kinematic or kinetic signals. Using a mass that either resisted or assisted arm motion, we accomplished that objective by dissociating those two signals. With sufficient practice, participants generated limb movements with similar kinematics but whose kinetic requirement varied widely. The manipulation led to two alternative predictions with regard to the expected influence on saccadic output. In particular, if the pertinent signal is kinematic in origin, then the addition of the mass should have no influence on saccadic output, because the limb kinematics do not change markedly with that manipulation. However, if the pertinent signal is kinetic in origin, then the addition of the resisting mass should increase the influence of the arm movement on saccadic output, and the addition of the assisting mass should decrease that influence.

## Method

### *Participants*

Six naïve individuals (4 men and 2 women, mean age =  $27 \pm 2$  years) participated in the current experiment after giving informed consent. Each participant was free from self-reported neurological impairments affecting ocular or manual control and had normal or corrected-to-normal vision. The local ethics committee had approved the experimental procedures.

### *Apparatus*

The participant was seated in a dimly illuminated room, looking down at targets projected onto a horizontally

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positioned semisilvered mirror. Reaching movements were made to the virtual location of the target on a table positioned underneath the mirror. Visual feedback from the hand was continuously available from illumination of the space underneath the mirror. A WATSMART system (Northern Digital, Inc., Waterloo, Ontario) monitored the motion of the right index finger. We used an infrared corneal reflection device (Skalar IRIS [Skalar Medical BV, Delft, The Netherlands]) to measure eye movements. Both systems were sampled at 200 Hz. We calibrated the eye-movement recording device by having the participant fixate targets at known eccentricities before and at several points in time during data collection. We used a bite bar to stabilize the head. Activity was recorded (Bagnoli-2 EMG system; Delsys, Inc., Boston, MA) in the agonist muscles contributing to right arm movements in a leftward (pectoralis) and rightward (triceps) direction. For that purpose, we attached surface electrodes to the skin overlying each muscle, and the signal was subsequently amplified (1,000 $\times$ ) before storage.

### *Behavioral Task*

At the beginning of each trial, a central fixation target (a plus sign [+] subtending  $\sim 1^\circ$ ) appeared. The participants were required to align their eyes and hand on that target. The initial hand position was achieved with  $\sim 135^\circ$  elbow angle,  $\sim 30^\circ$ s of shoulder flexion, and slight upper arm abduction. After a variable delay (500–1,500 ms) the central fixation target disappeared and a second target (a circle [o] subtending  $\sim 1^\circ$ ) was presented  $10^\circ$  to the left or right of center to which the participant made coordinated eye and hand movements. Participants achieved the movement to the right by using a combination of upper arm adduction and slight elbow extension, whereas movement to the left was achieved with a combination of upper arm abduction and slight elbow extension. We dissociated the kinematic and kinetic requirements of the reaching task by attaching to the wrist a mass that either resisted or assisted arm motion. In separate blocks of trials, the mass (0.5 kg) was suspended by a cable through a pulley system placed over either the left- or right-hand side of the table. Thus, the arm motion was assisted if the pointing response and mass were in the same direction and was resisted if they were in opposite directions. At the beginning of each block of trials, the participants practiced performing limb movements with the mass. In that way, they were adapted to the altered kinetic requirements of the task by the time the experimental trials were started. In addition to the conditions with the mass, a block of trials without the mass was also collected as well as a block of trials in which only saccades were generated. Ten trials were completed for each of the four conditions, and the order of presentation of each condition was counterbalanced across participants.

### *Data Analysis*

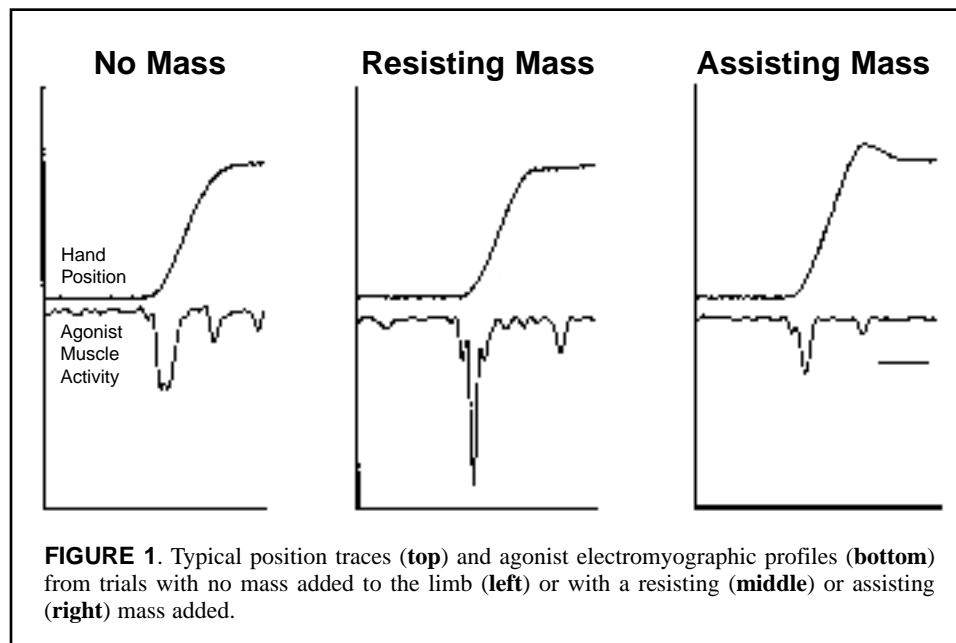
Using velocity–time thresholds for each type of response,

we automatically identified eye and hand movement onsets and offsets; the user could adjust those measures, if necessary, in a graphical interface implemented in MATLAB (MathWorks, Inc., Natick, MA). Movement onsets were defined as the point in time at which eye or hand velocity exceeded 10% of peak velocity. Movement offsets were defined as the moment at which eye or hand velocity fell below 10% of peak velocity. From the onsets and offsets, response latency, amplitude of the primary submovement, movement time, and peak velocity were calculated. With additional measures for the hand movement, we assessed the extent to which participants compensated for any initial inaccuracy in the planning of the pointing response. Those measures included time to peak velocity and percentage of time spent accelerating and decelerating. Finally, the magnitude of the agonist muscle activity was quantified after the electromyographic (EMG) signal was full-wave rectified, smoothed with a fourth-order dual-pass Butterworth filter (cutoff frequency = 50 Hz), and then integrated. The magnitude of the muscle response was calculated as the area under the resulting curve from the user-defined onset to the offset. Those measures were then collapsed across movement direction, and we made statistical comparisons by using one-way repeated measures analyses of variance, with mass condition (no mass, assisting mass, resisting mass) as the independent variable.

## **Results**

### **Pointing Movements**

The addition of a mass that assisted or resisted motion was effective in dissociating the limb kinematics and kinetics. Typical pointing responses as well as the underlying agonist muscle activity without the mass or with a resisting or assisting mass are shown in Figure 1. In those examples, it is clear that the kinematics of the responses were relatively invariant, whereas their kinetics (as implied by the muscle activity) were greatly modulated. The group means for the primary submovement amplitude, peak velocity, movement time, response latency, and agonist muscle activity are displayed in Figure 2A–E. The first four variables were relatively constant regardless of whether no mass, an assisting mass, or a resisting mass was used. Analyses of variance performed on the data from each of those variables showed no significant effects. It is possible, however, that participants made online corrections for inaccuracies in the initial planning of the pointing response induced by the addition of the mass. If that occurred, it would not necessarily be apparent in our measures of movement amplitude, peak velocity, movement time, or response latency of the primary submovement. To address that issue, we examined the time to peak velocity and the percentage of time accelerating and decelerating. As for the main measures of limb movement, analyses of variance revealed that the mass manipulation also did not affect the additional variables. By contrast, the magnitude of the agonist muscle activity was found to vary significantly, depending upon the kinetic



requirements of the task,  $F(2, 15) = 4.57, p = .028$ . Post hoc Tukey tests demonstrated that the cause of that interaction was the greater agonist muscle activity when there was a resisting mass than when the mass assisted arm motion or when there was no load. Thus, taken together, the data showed that with practice, the participants were able to generate limb movements that had similar kinematics but varied widely in the underlying forces used to move the arm.

### Saccadic Eye Movements

In Figure 3A–D, we present group means for saccade amplitude, peak velocity, movement time, and response latency, respectively, in the three limb movement conditions relative to the condition in which saccades were made in isolation. Analyses of variance revealed significant differences across the conditions only for peak saccade velocity,  $F(2, 15) = 2.59, p = .041$ . Post hoc Tukey tests demonstrated that saccade velocity was greatest when the resisting mass was added to the limb, significantly less when no mass was present, and least when an assisting mass was added. Thus, variations in the kinetic requirements of the pointing response modulated saccade dynamics despite relatively constant limb movement kinematics.

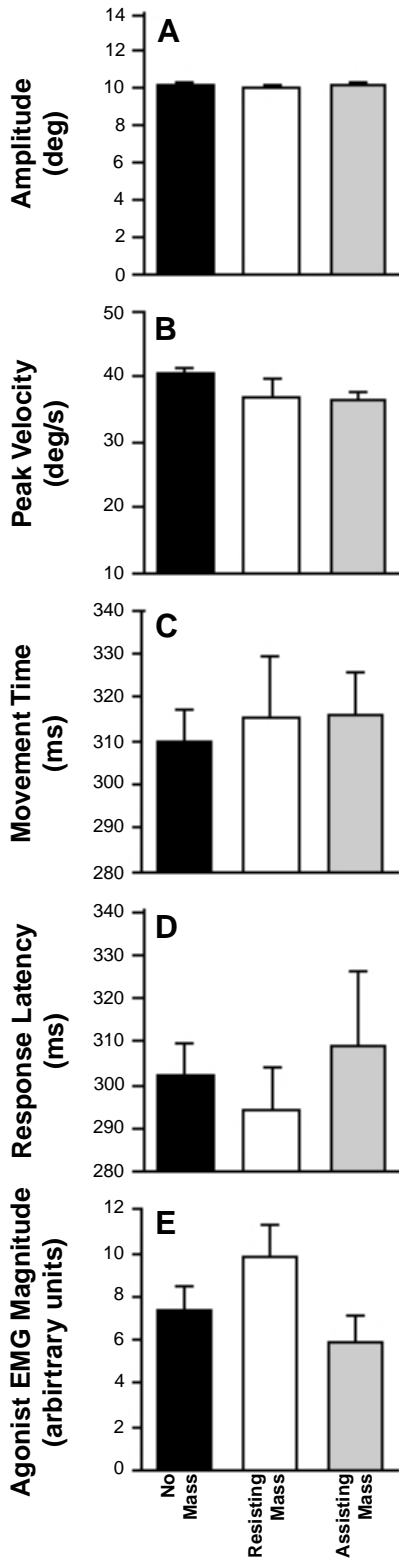
### Eye–Hand Relationship

In addition to the group analysis, we examined the relation between limb kinetics and peak saccade velocity within each individual on a trial-to-trial basis. We plotted the magnitude of the peak saccade velocity in each trial of the three limb movement conditions relative to the average peak velocity for saccades generated in isolation against the magnitude of the agonist muscle activity in the same trials relative to the average of the muscle activity in the condition with no load. The resulting scatterplot for a single participant is displayed in Figure 4A. Clearly, trials with

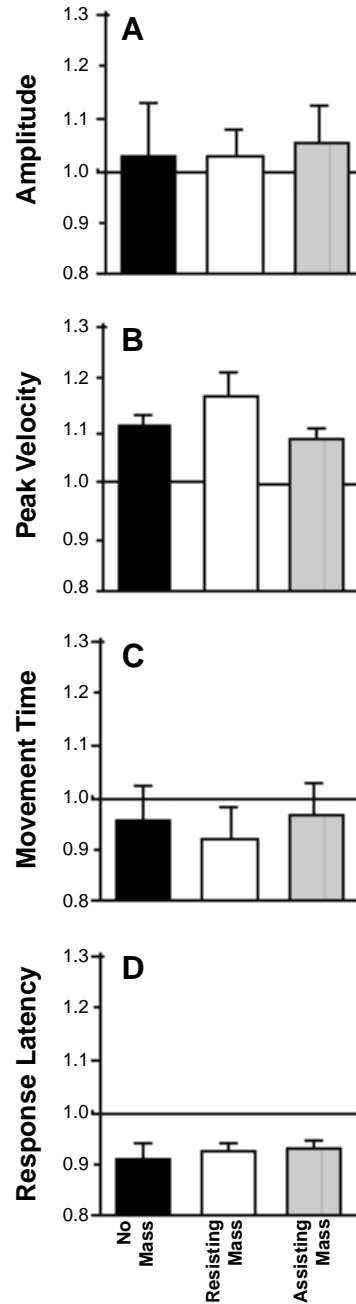
greater agonist muscle activity also tended to have larger peak saccade velocities. By contrast, when the relative peak arm and saccadic velocities were plotted against each other for the same trials, the relationship was no longer present (Figure 4B). The correlation coefficients for the agonist muscle activity–saccade velocity relationship ranged from .56 to .87 for each of the participants tested in that paradigm; whereas for the arm velocity–saccade velocity relationship, the correlation coefficients ranged from .008 to .150. We achieved a more stringent test of the greater influence of limb kinetics on saccadic output by directly comparing the affect on saccade velocity of the same relative change in agonist muscle activity and peak arm velocity. Across participants, peak arm velocity increased ~1.6 times from the slowest 10 trials within a session to the fastest 10 trials. Peak saccade velocity during those two sets of trials changed by an average of 3%. By contrast, an increase of ~1.6 times in agonist muscle activity was associated with an 18% increase in peak saccade velocity. The difference in percentage change in peak saccade velocity was significant ( $t$  test,  $p < .05$ ). Taken together, those results suggest that the limb movement signal that modulates saccade dynamics carries kinetic rather than kinematic information.

### Discussion

Numerous times during the course of a day we direct our eyes and hands to objects of interest. The coordination that is observed appears to be the result of an exchange of information between those two motor systems at several different brain sites. Research reported in a growing body of literature has clearly demonstrated that signals related to eye position and motion influence the concurrently produced limb movement (e.g., Henriques & Crawford, 2002; Miall & Reckess, 2002; Sailer et al., 2000; van Donkelaar, 1997; Vercher, Magenes, Prablanc, & Gauthier, 1994). Other researchers

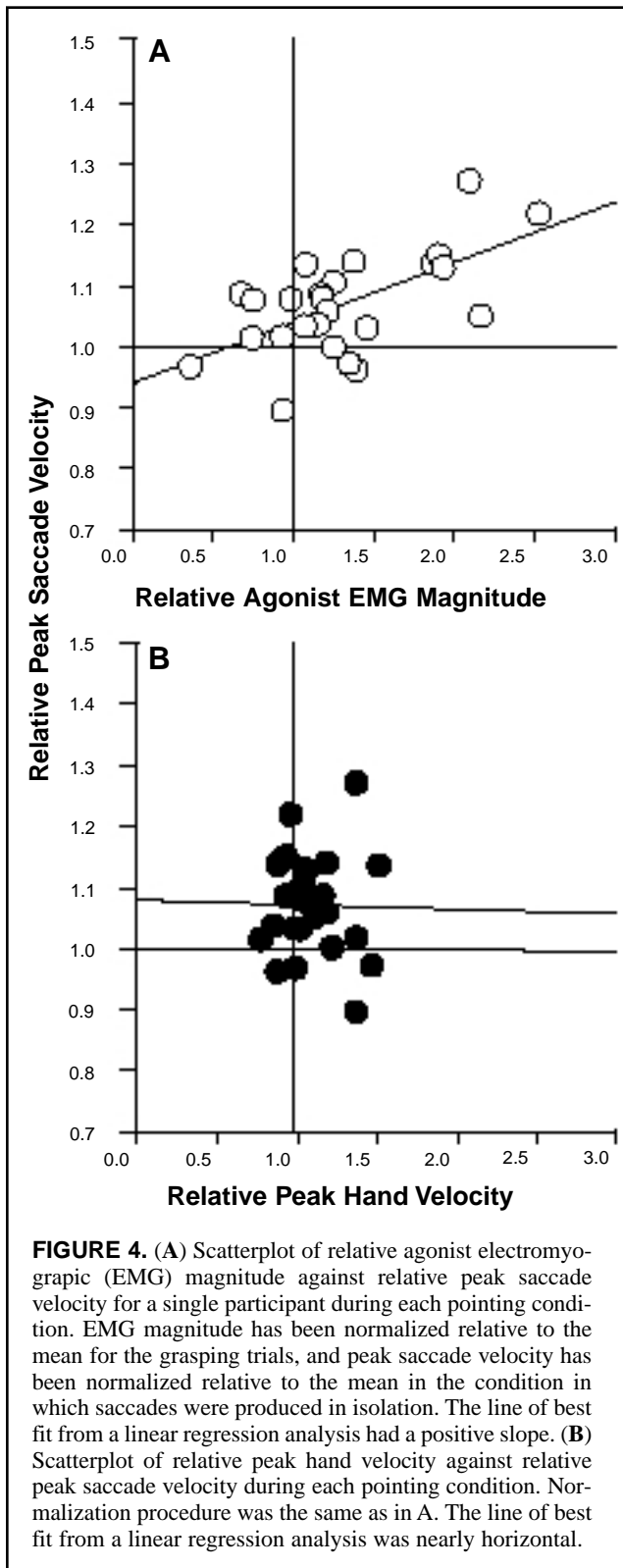


**FIGURE 2.** Group averages for hand movement amplitude (A), peak velocity (B), movement time (C), response latency (D), and integrated agonist electromyographic (EMG) magnitude (E) in the no mass (solid bar), resisting mass (white bar), and assisting mass (light gray bar) conditions. Error bars = 1 interparticipant standard error.



**FIGURE 3.** Relative group averages for saccade amplitude (A), peak velocity (B), movement time (C), and response latency (D) in the no mass (solid bar), resisting mass (white bar), and assisting mass (light gray bar) conditions. Each variable is plotted in the three conditions with pointing relative to the average in the condition in which saccades were produced in isolation (horizontal line). Error bars = 1 interparticipant standard error.

have examined the converse interaction: that which limb movement signals have on the planning and generation of eye movements. That influence has been explored in detail in the context of pursuit tracking, and the results of those studies have demonstrated that smooth pursuit eye movements are



improved (i.e., have a shorter reaction time, higher gain, and fewer saccadic interruptions) when the hand also tracks the target or is the target itself (e.g., Mather & Lackner, 1981; Steinbach & Held, 1968). The fact that those effects are also observed in deafferented patients suggests that the pertinent

limb movement signal is an efference copy of the motor command rather than proprioceptive feedback from the arm itself (Vercher et al., 1996).

In several more recent studies, that interaction has also been found to occur during discrete eye and limb movements to targets that change position abruptly. In particular, saccades generated in combination with a reaching movement to a single-step target displacement are initiated more quickly and tend to be more accurate (Lunenburger et al., 2000) or to have higher peak velocities and shorter movement durations (Epelboim et al., 1997; Snyder et al., 2002) than do saccades generated in isolation. Moreover, those effects do not result from the mere presence of a limb movement: If the reach response is in the direction opposite to the saccade, then the modulation of saccadic output is no longer apparent (Lunenburger et al.; Snyder et al.). Thus, by including a limb movement in the response, one may be able to alter the initial planning of the saccade as well as the characteristics of the main sequence itself.

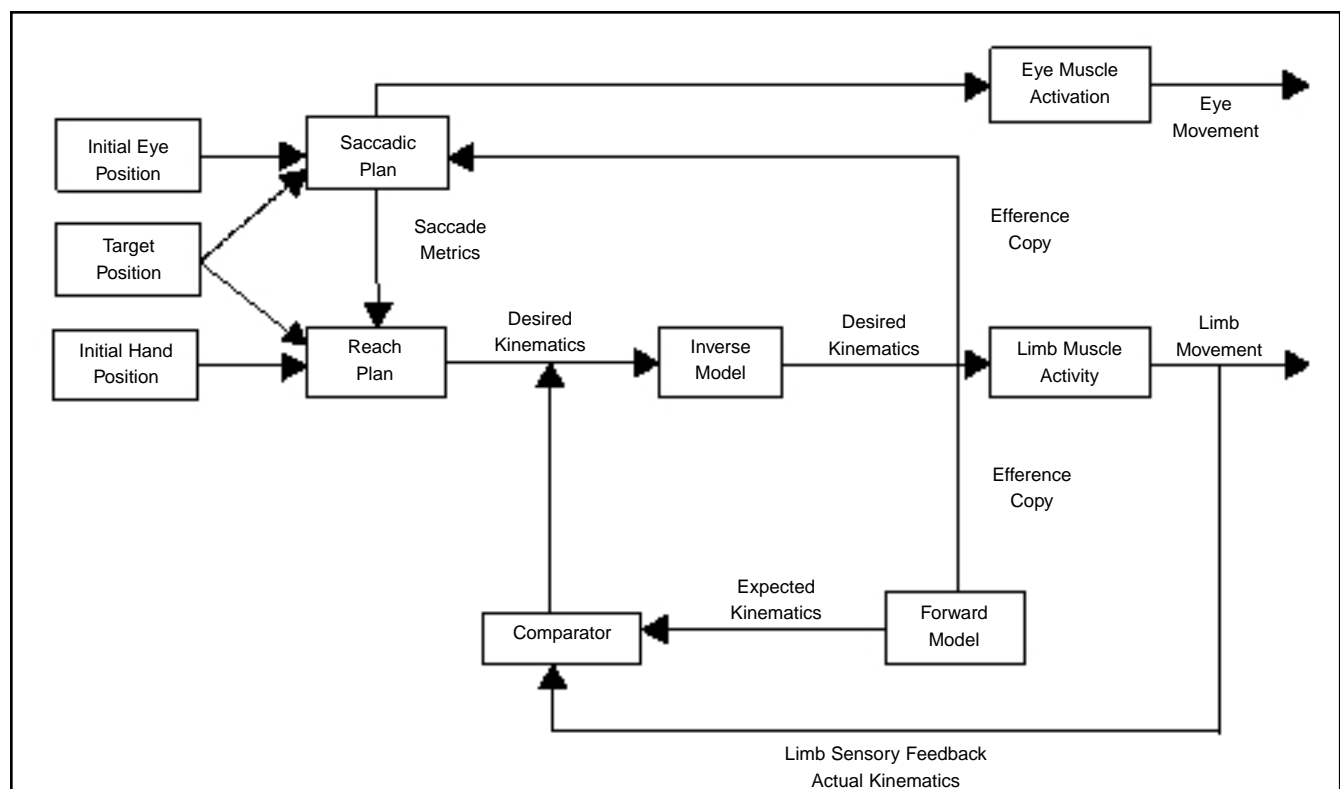
Our purpose in the present experiments was to gain a better understanding of the nature of that interaction. Our main finding was that the modulating effect of hand movements on saccadic output appears to be related to the kinetic requirements of the pointing task rather than the resultant kinematics. In particular, when the limb movement kinetics and kinematics were dissociated with a load manipulation, saccadic output varied with the force required to move the limb, rather than with the resulting pointing velocity. One could argue that although our manipulation did indeed directly influence the kinetic requirements of the task, it only indirectly controlled for the kinematic requirements. Ideally, one should have a control condition in which the kinematics are allowed to vary while the kinetics are held constant to truly demonstrate that kinetics are solely responsible for the effects on saccadic output. Although we did not complete such a control condition, similar experiments have been carried out addressing the issue of interlimb (as opposed to intereffector) coordination. In those experiments, the investigators independently manipulated velocity and net torque of one limb to yield a true dissociation between kinetics and kinematics, and they demonstrated that only kinetics affected the movement of the opposite limb in a time-dependent manner (Walter & Swinnen, 1990a, 1990b). Furthermore, the fact that the influence was noted even during the pre-movement build up of electromyographic activity implies that it did not result simply from crosstalk between the limbs during execution (Swinnen, Young, Walter, & Serrien, 1991). Thus, for interlimb coordination, kinetics appear to be significantly more influential than kinematics. It seems probable that the same may hold for eye-hand coordination.

Most interesting, we did not find a consistent effect on saccadic reaction times without load manipulation, as has been demonstrated previously (Lunenburger et al., 2000). Although saccadic latencies were reduced by ~10%, the

reduction did not reach statistical significance. A similar absence of effect was apparent in the studies by Epelboim et al. (1997) and Snyder et al. (2002). By contrast, Lunenburger et al. (2000) did not observe any influence of the limb movement on saccade dynamics. It is unclear why those differences across studies would arise. It is possible that the experimental task and setup were sufficiently different to result in the observed behavioral alterations. In all cases, however, the outcome for the participant was that the eyes arrived at the target sooner when a limb movement was also made. Thus, the effects were similar functionally. Most important, those effects on saccade latency and dynamics very likely occur at different levels in the brain. In particular, whereas saccade latency is thought to be mainly influenced by higher level processes implemented in areas such as the lateral intraparietal area (Li, Mazzoni, & Andersen, 1999) and the frontal eye fields (Schall & Thompson, 1999), saccade dynamics are generally assumed to be under lower level control via the superior colliculus and oculomotor brainstem structures (Moschovakis & Highstein, 1994). Thus, the results of the

different experiments published to date on this issue imply that the influence of limb movements on saccades can occur at both cortical and subcortical sites. Future single-unit neurophysiological and human brain imaging studies should shed more light on how that interaction is carried out in the brain.

During most eye–hand coordination tasks, the eye movement is initiated before the hand movement (e.g., Abrams, Meyer, & Kornblum, 1990; Bekkering, Adam, Kingma, Huson, & Whiting, 1994), and that was also true in the present study. How is it possible, then, for signals from the limb motor system to influence saccade planning prior to an overt response? For that to occur, an efference copy signal related to the upcoming limb movement must have access to and modulate the planning occurring within the saccadic system. Current theoretical models of limb movement control generally include such predictive efference copy signals (e.g., Desmurget & Grafton, 2000). Moreover, those signals are thought to carry information related to the desired kinetics, because an inverse model of the effector transforms the limb movement plan before it is sent to the muscles (Figure 5). To



**FIGURE 5.** Processing schema for the interaction between a model of arm movement control with the saccadic system. Saccadic and reaching movements are initially planned on the basis of information about the initial position of the relevant effector and the target position. Signals related to saccade metrics influence the reach plan (van Donkelaar, 1997). The reach plan itself reflects the desired kinematics of the limb movement response. For the plan to be appropriate for muscle activation, the motor system transforms it into the desired kinetics by using an inverse model of the effector. An efference copy of the desired kinetics is subsequently transformed into a signal related to the expected kinematics by a forward model of the effector. That signal can then be compared with the actual kinematics that are produced, and any changes that are required to the ongoing motor response can be quickly accommodated. The results from the current experiment demonstrated that the efference copy signal related to desired limb kinetics also influences the planning of the saccadic output.

contribute to the control of the limb movement, the motor system uses a forward model of the effector to transform the efference copy signal related to desired kinetics back to a signal related to the expected kinematics. That signal can then be compared with the actual kinematics that result during the limb movement, and any discrepancy can be rapidly corrected in an updated motor plan.

On the basis of the results from the current experiment, we suggest that the efference copy signal related to desired kinetics also interacts with the saccadic planning process. Furthermore, because saccadic onset (and on some trials, saccade termination) occurred before limb movement onset, the signal must be predictive in nature. The interaction occurred because participants knew before a block of trials that a combined eye and hand movement response would be required, and thus they could anticipate the fact that reach planning would occur. Presumably, if the trials were randomized such that the participant did not know until the peripheral target appeared which type of response to produce, the influence of the limb kinetic signals on saccadic planning would be reduced. Clearly, sensory feedback arising from limb movement plays only a minor role, if any, in that effect. Scarchilli and colleagues (Scarchilli & Vercher 1999; Scarchilli, Vercher, Gauthier, & Cole, 1999) reached a similar conclusion regarding the changes that occur in smooth pursuit during coordinated tracking movements of the eye and hand. There are, however, other situations in which sensory feedback from the limb very likely contributes. For example, Ariff, Donchin, Nanayakkara, and Shadmehr (2002) have recently demonstrated that the saccadic system can predict the future position of the unseen moving hand. Because of the nature of their task (long movement duration [ $\sim 800$  ms] and an explicit instruction to look at the position of the hand as it moved), Ariff and colleagues suggested that both efference copy and sensory feedback are used in the forward model to predict the future state of the system and that the prediction is adopted by the oculomotor system to plan and generate saccades with appropriate timing and metrics. Thus, it appears that an efference copy signal related to both limb kinetics and sensory feedback generated during limb movement can contribute to the modulation of saccadic output in a task-dependent manner.

### Conclusion

By dissociating limb kinematics and kinetics, we have shown that saccade dynamics are more affected by limb movement signals related to the kinetics than by those related to the kinematics during a task requiring eye-hand coordination. Because the limb movement occurred after the saccade, the implication is that the signal must be predictive in nature. Such predictive limb kinetic signals are a feature of current models of limb movement control. Neurophysiological and human brain imaging studies should be carried out in the future to enable us to gain a better understanding of the neural mechanisms underlying this interaction.

### ACKNOWLEDGMENTS

We thank Bas Neggers, Digby Elliott, and Charles Walter for their helpful comments on this experiment. This work was partially supported by grants from the National Science Foundation (BCS-9982019 and BCS-0121916).

### NOTE

Portions of this work have been published in abstract form (van Donkelaar, Siu, & Walterschied, 2002).

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*Submitted February 20, 2003*

*Revised June 6, 2003*

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