Saccade Adaptation in Response to Altered Arm Dynamics

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Nanayakkara, Thrishantha and Reza Shadmehr. Saccade adaptation in response to altered arm dynamics. *J Neurophysiol* 90: 4016–4021, 2003; 10.1152/jn.00430.2003. The delays in sensorimotor pathways pose a formidable challenge to the implementation of stable error feedback control, and yet the intact brain has little trouble maintaining limb stability. How is this achieved? One idea is that feedback control depends not only on delayed proprioceptive feedback but also on internal models of limb dynamics. In theory, an internal model allows the brain to predict limb position. Earlier we had found that during reaching, the brain estimates hand position in real-time in a coordinate system that can be used for generating saccades. Here we tested the idea that the estimate of hand position, as expressed through saccades, depends on an internal model that adapts to dynamics of the arm. We focused on the behavior of the eyes as perturbations were applied to the unseen hand. We found that when the hand was perturbed from stable posture with a 100-ms force pulse of random direction and magnitude, a saccade was generated on average at 182 ms postpulse onset to a position that was an unbiased estimate of real-time hand position. To test whether planning of saccades depended on an internal model of arm dynamics, arm dynamics were altered either predictably or unpredictably during the postpulse period. When arm dynamics were predictable, saccade amplitudes changed to reflect the change in the arm's behavior. We suggest that proprioceptive feedback from the arm is integrated into an adaptable internal model that computes an estimate of current hand position in eye-centered coordinates.

INTRODUCTION

When volunteers are asked to visually track their unseen hand during reaching movements, they produce a series of saccades. Although the trajectory of the reach may be stereotypical, timing of saccades is widely distributed. Saccades that are initiated at time t have an endpoint $e(t)$ that roughly predicts hand position $h(t + 195 \text{ ms})$ (Ariff et al. 2002). If the hand is perturbed during the reach with a force pulse that initiates at time t, saccade initiation probability $P(s)$ reaches a minimum at $t + 100$ ms but rises sharply and peaks at $t + 180$ ms. The postperturbation saccades have endpoints $e(t)$ that roughly predict hand position $h(t + 150 \text{ ms})$. Taken together, these results suggest that, during reaching movements, the brain can rely on proprioceptive feedback from the arm to compute a real-time estimate of hand position in a coordinate system appropriate for planning of eye movements.

However, this estimate of hand position cannot depend solely on delayed proprioception. Rather, estimate of hand position likely depends on a neural system that also uses some form of arm efference copy. One possibility is that this neural system contains an internal model of the limb's dynamics. In such a theoretical scenario, efference copy is used as a forcing function that drives an estimate of the limb's state from an initial condition specified by the delayed sensory feedback (Bhushan and Shadmehr 1999; Jordan and Rumelhart 1992; Miall et al. 1993). We have hypothesized that the output of this forward model might be a real-time estimate of hand position in retinocentric coordinates. It is possible that in the posterior parietal cortex, the brain maintains an estimate of both hand position and target position in retinocentric coordinates (Buneo et al. 2002) and uses these estimates to compute a real-time measure of a hand-to-target difference vector (Shadmehr and Wise 2004).

While there are many components of this hypothesis that have yet to be tested, the central idea is that the brain uses an internal model of arm dynamics to transform delayed proprioceptive feedback from the arm into an estimate of current hand position in a coordinate system appropriate for planning of eye movements. If estimates of hand position are to remain accurate, the internal model must adapt when arm dynamics change. Here we test this prediction.

METHODS

We removed visual feedback from the arm, perturbed the hand from a stable posture, and recorded the response in the oculomotor system as well as the hand. We tested the idea that the oculomotor response depended on the dynamics of the arm. Our setup was similar to an earlier experiment (Ariff et al. 2002) and is shown in Fig. 1*A*. Volunteers ($n = 18$, all naïve to the purpose of the experiment) held the handle of a planar robotic arm (Shadmehr and Brashers-Krug 1997) that housed a high-intensity LED at its handle. An opaque screen ($12 \times 10 \times 0.2$ in) was suspended 0.5 cm in the horizontal plane above the handle, and a dark heavy cloth was draped around the screen. This allowed the participants to fixate the LED image, back projected onto the screen, without seeing their arm. We used a real-time hand position indicator (a handle-attached LED) rather than a video display of a cursor to circumvent the inherent delays that are present in the updating of these displays. The delays are plainly visible, at least in our system, when the handle-attached LED and projection of the hand position via cursor are viewed simultaneously.

Volunteers were instructed that their hand would be perturbed and that the LED image would disappear, but that at all times they should try to look where they think their hand is located. They were also
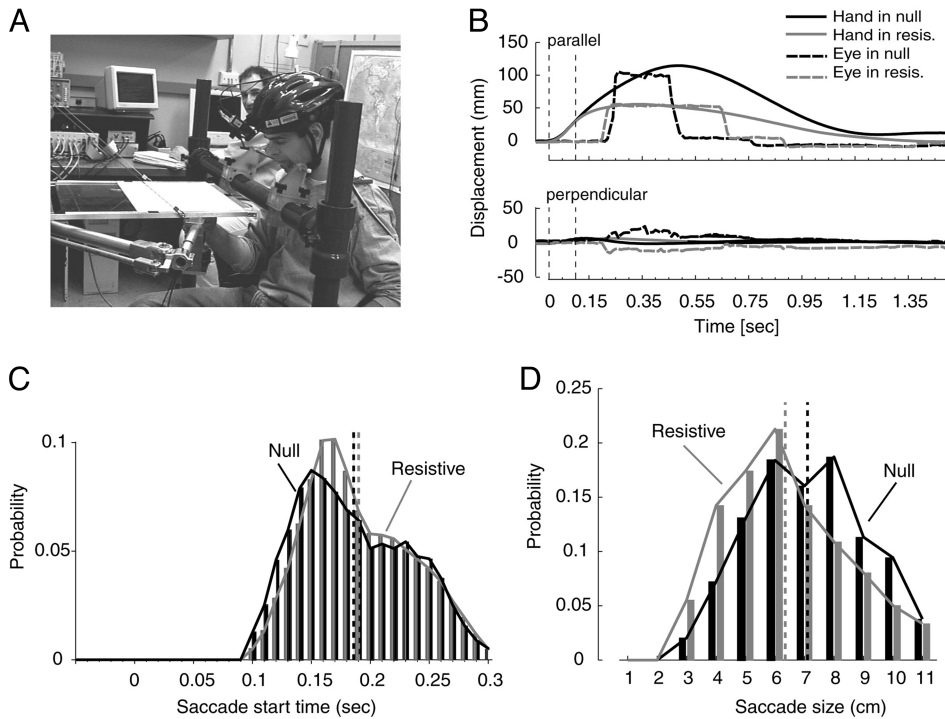
A

B

C

D

FIG. 1. Force pulse (100 ms) of random direction and magnitude perturbed the unseen hand. Hand perturbation was accompanied by a series of saccades. Trials were aligned to pulse onset. Data are for the main subject group, where different arm dynamics were experienced in 2 blocks of trials. *A*: experimental set-up. The subject used a bite-bar. An opaque screen was positioned above the manipulandum to cover subject's hand. A projector was mounted above this screen. A thick drape completely covered the rest of the manipulandum and the subject's arm (not shown). Eye movements were tracked using a camera mounted on the helmet. *B*: example trials in the pulse-null and pulse-resistive conditions. Pulse period is shown by 2 dashed lines. Parallel and perpendicular traces refer to positions of hand and eye as projected onto a vector that pointed from hand origin to hand position at 100 ms (end of the pulse). *C*: probability of saccade initiation times in the pulse-null and pulse-resistive trials. Bin size is 10 ms. Means of the distributions are shown with dashed lines. *D*: probability of saccade size in the pulse-null and pulse-resistive trials. Bin size is 10 mm.

instructed that despite the perturbation, they should try to maintain their hand position at the origin. The JHU Institutional Review Board approved our experimental procedures, and all volunteers signed a consent form.

A trial began with the handle LED on. The origin target was displayed at the center of the screen (with an overhead projector) and the robot brought the subject's hand to the origin. Subject fixated the LED for a random time (0.5–1.5 s), after which the hand was perturbed, the LED was turned off, and a stationary random dot pattern filled the screen (approximately 35 dots/in^2). Each dot was 0.25 mm^2 in size, and its position was randomly selected for each trial. These random dots were intended to work as targets of eye movements. They greatly facilitated the recordings by stabilizing the eyes at the end of a saccade. After an additional random interval (0.5–1.5 s), origin target was extinguished, and a 100-ms force pulse of random magnitude was given to the hand in a randomly selected direction. The range of magnitudes was slightly larger for some directions: 13–17 N for directions 0°, 180°, 90°, 270°, 135°, and 315° versus 10–14 N for directions 45° and 225°. This produced a roughly equal range of magnitudes of hand displacement across directions.

As the perturbation began to displace the hand (encoder resolution of handle position was better than 0.05 mm, and movement initiation was detected using a fixed 0.02 m/s threshold), the handle LED was turned off. The resulting eye and head movements were recorded at 100 Hz using an infrared camera and light source (iView system, SMI; 0.1° tracking resolution, 1° typical gaze position accuracy, 6 ms estimated delay) that was mounted on a helmet that was also tracked (Polhemus). To improve accuracy of the recordings, however, subjects used a bite bar that we had anchored to the floor. Our software provided a near real-time estimate of gaze position. We used this to check calibration of the eye system with respect to hand position before every trial. False starts and/or poor calibration resulted in rejection of that trial and recalibration. End of trial was sensed when the hand remained stationary for 1 s.

To assess whether eye movements were influenced by arm dynamics, we occasionally varied the behavior of the robot immediately after the 100-ms force pulse. We considered two conditions. In pulse-null trials, the robot motors produced no forces after the offset of the force pulse. In pulse-resistive trials, a viscous field that resisted hand's

motion was imposed at the offset of the force pulse [$F = Bv$, where $B = (-20, 0; 0, -20)$ kg/s]. All subjects experienced both conditions. However, in our control group ($n = 8$), the order of the two conditions was random. This made it so that in any given trial one could not predict whether a viscous field would be present or not. In our main group ($n = 10$), the trials were divided in half so that each half contained a consistent field pattern (either null or resistive). Some subjects in this group experienced the pulse-null condition first, while others experienced the pulse-resistive condition first. Each subject performed approximately 150 trials. Subjects never received feedback regarding accuracy of their eye movements.

To assess the effect of perturbations on saccades, an ANOVA was performed with the main effects of postpulse field type (null or resistive), pulse size, and pulse direction.

RESULTS

A 100-ms force pulse of variable magnitude and direction was imposed on the unseen hand. The pulse was followed by either a null field or a viscous field that resisted hand's motion. We begin by presenting the data from the main group where pulse-null and pulse-resistive trials were performed in two separate blocks. The order of the blocks was balanced across subjects.

Trials were aligned to the onset of the pulse. To compare data across various directions of perturbation, for each trial, we projected hand's trajectory along a vector that pointed from the origin to the hand position at pulse offset. Eye position was also projected along this hand-centered vector. The resulting eye and hand trajectories are plotted for a representative trial in Fig. 1*B*. As expected, during the pulse period, hand trajectories did not differ between the pulse-null and pulse-resistive trials. Neither hand displacement nor velocity was significantly different at pulse offset (paired *t*-test, hand velocity at 100 ms, pulse-null and pulse-resistive groups, $P > 0.5$). However, hand trajectories diverged in the postpulse period. We estimated that

the earliest point in time when hand position in the resistive trials significantly diverged from null trials was at $t = 130$ ms.

As the pulse displaced the hand, the oculomotor system responded by generating a sequence of saccades. We focused our analysis on the first saccade. On average, the first saccade was initiated at 182 ms after perturbation onset (pulse-null trials: 181 ± 45 ms; median, 170 ms; pulse-resistive trials: 183 ± 43 ms; median, 170 ms). The histograms of saccade initiation times are plotted for the pulse-null and pulse-resistive trials in Fig. 1*C*. We found that change in arm dynamics had no significant effect on saccade timing (Kolmogorov-Smirnov test of difference in distributions, $P > 0.4$). The *t*-test of distribution of saccade initiation times, pulse-null versus pulse-field trials, and paired *t*-test of within-subject saccade initiation times were not significantly different ($P > 0.5$ in each case). However, change in arm dynamics had a significant effect on saccade amplitudes. The histograms of saccade amplitudes are plotted in Fig. 1*D*. The mean amplitude shifted from 7.1 ± 0.5 cm in the pulse-null trials to 6.3 ± 0.4 cm in the pulse-resistive trials. This difference was highly significant at the distribution level (*t*-test, $P < 0.001$), as well as in terms of within subjects (paired *t*-test, $P < 0.007$).

Much of the variance in the distribution of saccade amplitudes is because different pulse magnitudes were accompanied with different saccade sizes. We compared saccade amplitudes (a scalar value representing magnitude of the saccade displacement) in the pulse-null and pulse-resistive conditions using a three-way ANOVA that considered arm dynamics (null or resistive), pulse amplitude, and pulse direction. We found a significant effect of arm dynamics on saccade amplitudes ($F = 51.02$, $P < 0.0001$) and a significant interaction between arm dynamics and pulse amplitude on saccade amplitudes ($F = 2.95$, $P < 0.05$). Therefore a change in arm dynamics during the postpulse period significantly affected amplitudes of postpulse saccades.

These results were observed in trials where, during the postpulse period, the hand was either consistently in a null field or in a resistive field. We performed a control experiment where pulse-null trials and pulse-resistive trials were intermixed. Eye and hand positions for typical trials are shown in Fig. 2*A*. As before, the earliest point in time when hand velocity in the pulse-resistive trials significantly diverged from null trials was at $t = 130$ ms. Similar to the previous experiment, saccade timing did not appear to be affected by arm dynamics. Saccades were initiated on average at 201 ± 39 ms postpulse onset in the pulse-null trials (median, 210 ms) and 200 ± 39 ms postpulse onset in the pulse-resistive trials (median, 200 ms; *t*-test of distributions, $P > 0.5$; paired *t*-test within subjects, $P > 0.1$). However, unlike the previous experiment, saccade amplitudes were not significantly affected by the change in the arm's behavior (Fig. 2*B*). Saccade amplitudes in the pulse-null and pulse-resistive trials had a mean value of 6.1 ± 0.5 and 5.9 ± 0.5 cm, respectively (within-subject paired *t*-test, $P > 0.5$).

We next quantified how well the postpulse saccade predicted hand position in the same trial. If the first saccade was initiated at time t, we compared the endpoint of that saccade with hand position at $h(t + \Delta)$. Using a vector correlation algorithm (Shadmehr and Mussa-Ivaldi 1994), we found that the two positions best correlated at $\Delta = 30$ ms in the pulse-null trials and $\Delta = 10$ ms in the pulse-resistive trials (Fig. 3*A*). At these
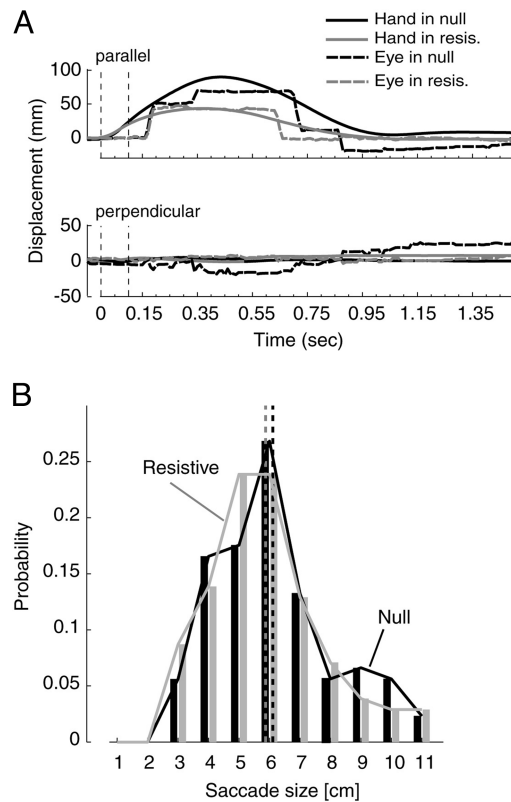

FIG. 2. Eye-hand behavior in a condition where pulse-null and pulse-resistive trials were intermixed. *A*: example trials in the pulse-null and pulse-resistive conditions. Format is the same as in Fig. 1*B*. *B*: probability of saccade size in the pulse-null and pulse-resistive trials. Bin size is 10 mm.

optimum delays, the slopes of linear fits between eye and hand positions were 0.99 in the x component and 1.08 in the y component, with a bias of 1.1 and 6.5 mm, respectively ($r^2 = 0.79$, $P < 0.001$). In the resistive field, the slopes of the linear fits were 0.92 for both x and y components of position, with biases of 1.0 and 2.3 mm, respectively ($r^2 = 0.73$, $P < 0.001$). Therefore saccade endpoints typically predicted approximately 75% of the variance in real-time hand position.

To represent the effect of arm dynamics on saccade planning, we considered $\Delta = 20$ ms as a rough estimate of the best correspondence between saccade endpoint and hand position. For each saccade at time t, we computed the corresponding hand position at $t + 20$ ms. The distributions of hand positions in the pulse-null and pulse-resistive trials for block and intermixed trials are shown in Fig. 3, *B* and *C*. In block trials, hand displacement at $t + 20$ ms was reduced from 6.5 ± 0.5 cm in the pulse-null trials to 5.6 ± 0.6 cm in the pulse-resistive trials ($P < 0.001$). Similarly, in the intermixed trials, hand displacement was reduced from 6.3 ± 0.5 to 4.9 ± 0.6 cm ($P < 0.001$). Therefore while in both the block and intermixed trials, hand position near saccade initiation time was significantly affected by the altered dynamics, a significant change in saccade amplitudes was observed only in the block trials.

Much of the variance in these distributions is because hand displacement depends on direction of the force pulse. To account for this variance, we binned hand and eye positions for each pulse direction. The averaged values are shown in Fig. 3, *B* and *C,* for the block trials and for the intermixed trials, respectively. In both the block and intermixed designs, hand
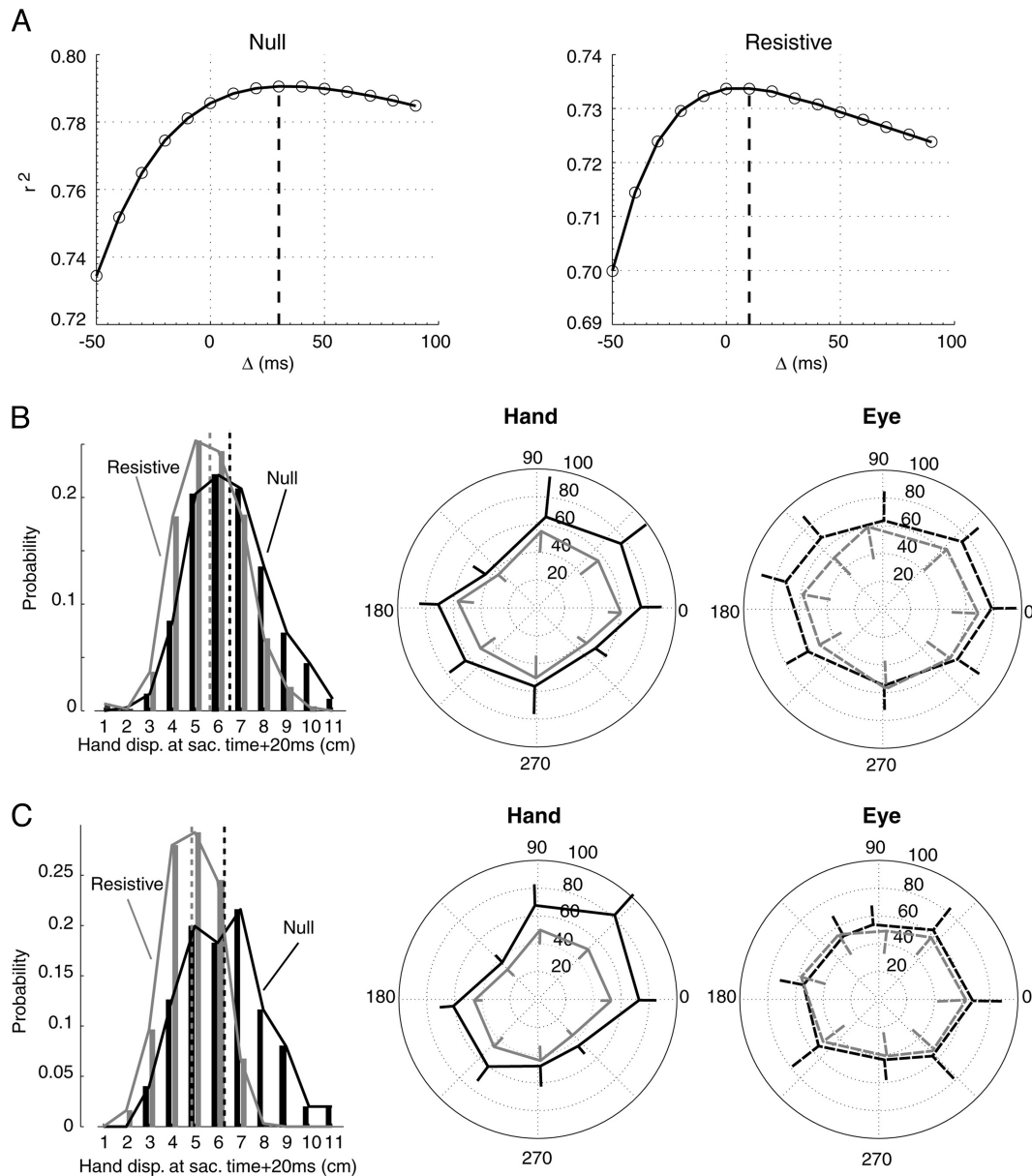
FIG. 3. Saccade adaptation to predictable change in arm dynamics. *A*: for saccades initiated at time *t*, eye position at end of saccade was correlated with hand position at time *t* + Δ. Squared correlation coefficients are plotted in the pulse-null and pulse-resistive trials. *B*: effect of blocked presentation of altered arm dynamics on saccade and hand positions. *Left*: probability of hand displacement at saccade initiation time t + 20 ms in pulse-null trials and pulse-resistive trials. *Center*: mean ± SD of hand displacement in each direction of perturbation in the pulse-null and pulse-resistive trials. *Right*: mean ± SD eye position. *C*: effect of intermixed presentation of altered arm dynamics on saccade and hand positions.

displacement was significantly smaller in the pulse-null trials versus the pulse-resistive trials. However, as we noted earlier, only in the block trials did the corresponding eye positions also change significantly.

We found that in the intermixed trials, hand displacements were on average smaller than the displacements recorded in the block trials. This suggests that in the intermixed trials, the arm was somewhat stiffer because the same perturbations displaced the hand by a smaller amount. However, note that the change in hand position in the intermixed trials (1.4 cm) was actually larger than the change in the block trials (0.9 cm; Fig. 3, *B* and *C*). Despite this, saccade amplitudes did not change significantly.

While saccade amplitudes changed with persistent changes in arm dynamics, results in Fig. 3*B* show that the anisotropy of hand displacements was not reflected in the saccades. This is particularly evident in the directions of 315° and 135°. For example, when the force pulse displaced the hand along 135°, the brain estimated the hand to go much farther than it actually went. Also note the large errors in saccade endpoints in the direction perpendicular to hand displacement along direction 180°. When the pulse displaced the hand along 180°, estimate of hand position was off by approximately 12°. Using a four-link model of a subject's arm and the robotic arm (Shadmehr and Brashers-Krug 1997), we found that the inertia matrix of the coupled system had its primary Eigen vector along 150°.

This suggests that at least some of this error between eyes and the hand may be due to the anisotropy of arm-robot dynamics. Apparently, this anisotropy was not accurately accounted for in predicting the effects of force pulses on hand displacement and the amount of training was not sufficient to allow for adaptation to this altered dynamics.

DISCUSSION

We reported earlier that the brain's estimate of current hand position during unseen voluntary movements was not a delayed version of proprioception. Rather, when this estimate was expressed through eye movements, saccades typically led hand position by approximately 180 ms (Ariff et al. 2002). We hypothesized that this estimate of future hand position was due to a system that incorporated proprioceptive feedback and efferent copy through an internal model of the dynamics of the arm. Here we tested the idea that the internal model adapted to the changed dynamics of the arm. Our focus was on involuntary movements where efferent copy should play a minor role. We perturbed the unseen hand from stable posture with a brief (100 ms) force pulse vector of random magnitude and direction and varied the postpulse dynamics of the arm with either a "null" field or a resistive field. The altered arm dynamics resulted in a significant change in hand position at no earlier than 130 ms postpulse onset. The oculomotor system responded to the pulse with a saccade at approximately 180 ms. While saccade timing did not vary with changes in arm dynamics, saccade amplitudes changed when arm dynamics changed from null to resistive. However, saccade adaptation occurred only when the change in arm dynamics was predictable.

Saccades that were initiated at time t best predicted hand position at $t + 20$ ms. Therefore saccade planning could not rely solely on a delayed estimate of hand position derived from proprioceptive feedback. One possibility is that this feedback included not just delayed position and velocity of the arm but also a measure of the force that was imposed on the hand. If force feedback is integrated through an internal model of the arm's dynamics, one could estimate position of the hand slightly beyond the value sensed through proprioception. This might account for the observation that, while saccade endpoints did not lag behind hand position, they also did not lead them. To remain accurate in its estimation of hand position, the internal model would need to adapt when the arm's dynamics are changed. To test for this, we varied postpulse arm dynamics in either a block design where dynamics were predictably altered or an intermixed design where dynamics were random. If proprioceptive feedback was sufficient to allow for state estimation, the saccades should have changed their amplitude in both conditions. We observed significant changes in saccade amplitudes only when changes in arm dynamics were predictable. This would imply that the estimate of current hand position, as expressed through saccades, depends on both feedback and an internal model of arm dynamics.

In contrast, previously we had observed that when the hand was voluntarily reaching a target, saccades predicted hand position approximately 180 ms in the future (Ariff et al. 2002). While in voluntary reaching, estimate of hand position can rely on both proprioceptive feedback and efference copy, in the current task, the early component of hand movement is entirely a result of an externally imposed random force pulse, and therefore efference copy cannot play a significant role in estimating hand position. The fact that without efference copy the eyes cannot predict future hand position is in line with the hypothesis that the brain's estimate of current hand position during voluntary movements, as measured through behavior of the eyes, relies on arm efference copy.

A candidate for the neural system that maintains a real-time estimate of hand position is the posterior parietal cortex (PPC) (Wolpert et al. 1998). In the PPC, neurons tend to encode location of a saccade target in retinocentric coordinates (Andersen et al. 1985). However, when the eyes move, this map is updated (Duhamel et al. 1992). Current evidence suggests that, while this remapping depends on proprioceptive feedback, it also depends strongly on a copy of motor commands to the eye muscles (Sommer and Wurtz 2002). Therefore efference copy of oculomotor commands is used by the brain to predict the current location of saccade targets in retinocentric coordinates. In the dorsal aspects of area 5 and the parietal reach region, neurons are also sensitive to hand position, and the coding of this variable is again in retinocentric coordinates (Buneo et al. 2002). Based on our results, we would predict that the representation of hand position in this region is not merely a delayed mapping of proprioception to retinocentric coordinates, but an internal model that maintains a real-time estimate of hand position. Efferent copy during reaching should produce a remapping, and perturbations to the hand should produce a remapping. In both cases, the remapping should be a prediction that is based on an internal model of arm dynamics. The internal model is sensitive to dynamics of the arm and can adapt. Because the real-time estimate of hand position is in retinocentric coordinates, it allows the brain to direct the eyes to the estimated location of the hand.

However, this estimate of current hand position appeared to have distinct biases for certain class of perturbations. Force pulses that displaced the hand at 135° resulted in saccades that consistently overestimated hand position. Similarly, force pulses at 180° resulted in saccades that were biased by approximately 12°. The source of this bias is unclear to us but may involve two factors. First, the interaction between the human and robot arms distorts the human arm's inertia matrix. An incomplete adaptation to the inertial properties of the robot can account for some of the bias. Second, the precision of proprioception is not uniform across directions of perturbations. Earlier work found that hand localization in the radial direction with respect to the shoulder was more precise than localization in the azimuthal direction (van Beers et al. 1998). We also found that localization along the radial direction (e.g., 90° perturbations) had less bias than other directions. However, if the brain were to use this biased estimate to generate a voluntary movement after the perturbation, that movement should have errors that are a reflection of the bias. This remains to be tested.

DISCLOSURES

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