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Temporal Shift From Velocity to Position Proprioceptive Feedback Control During Reaching Movements

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¹Department of Bioengineering and ²Department of Kinesiology and Nutrition, University of Illinois at Chicago; ³Department of Physical Medicine and Rehabilitation, Northwestern University; and ⁴Sensory Motor Performance Program, Rehabilitation Institute of Chicago, Chicago, Illinois

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Niu CM, Corcos DM, Shapiro MB. Temporal shift from velocity to position proprioceptive feedback control during reaching movements. *J Neurophysiol* 104: 2512–2522, 2010. First published August 25, 2010; doi:10.1152/jn.00302.2010. Reaching movements to a target usually have stereotypical kinematics. Although this suggests that the desired kinematics of a movement might be planned, does it also mean that deviations from the planned kinematics are corrected by proprioceptive feedback control? To answer this question, we designed a task in which the subjects made center-forward movements to a target while holding the handle of a robot. Subjects were instructed to make movements at a peak velocity of 1 m/s. No further instructions were given with respect to the movement trajectory or the velocity time profile. In randomly chosen trials the robot imposed servo-controlled deviations from the previously computed unperturbed velocity and position time profiles. The duration of the velocity deviations and the magnitude of accumulated position deviations were manipulated. The subjects were instructed to either “Attempt to correct” or “Do not correct” the movement. The responses to the imposed deviations in the surface electromyograms in the elbow and shoulder agonist muscles consisted of an initial burst followed by a sharp decrease in the “Do not correct” condition or by sustained activity in the “Attempt to correct” condition. The timing and magnitude of the initial response burst reflected those of the velocity deviations and were not affected by the instruction. The timing and magnitude of the late response activity reflected position feedback control and were strongly affected by the instruction. We suggest that proprioceptive feedback control is suppressed in the beginning of the movement, then velocity feedback control is activated in the middle of the movement to control a desired velocity, whereas position feedback control is facilitated late in the movement to acquire the final position.

INTRODUCTION

One of the unresolved questions in studies of reaching movements is whether the motor system controls a desired trajectory throughout the movement or whether it controls only task parameters such as final position or instructed movement speed. If a desired trajectory does not exist (Cisek 2005; Kalaska et al. 1998; Todorov and Jordan 2002) then a neural response to perturbations is directed exclusively at achieving the final position. On the other hand, the stereotypical kinematics of reaching movements suggests that a desired trajectory may be planned (Atkeson and Hollerbach 1985; Flanagan and Rao 1995). If the motor system plans a desired trajectory, does it use neural feedback control to correct position or velocity deviations if a movement is unexpectedly perturbed?

The possible concurrent activity of both position and velocity feedback presents a way to answer this question. Consider a reaching arm movement to a target. If external resistance to the arm is unexpectedly increased, the movement becomes slower and the arm position starts lagging behind the expected trajectory. Initially, the position and velocity deviations are of the same sign and both feedback responses will accelerate the movement. The arm will reach the desired velocity sooner than it will “catch up” with the desired position. Once the arm reaches the desired velocity, the position feedback controller should accelerate the arm beyond the desired velocity against the action of the velocity feedback controller. In engineering control applications, the position and velocity feedback gains are tuned to achieve the required response dynamics of the system. It is not clear, however, how neural position and velocity feedback control operate during reaching movements.

We considered two possible cases of feedback control activity: 1) position and velocity feedback control mechanisms are activated simultaneously and act concurrently during the movement and 2) these feedback mechanisms are activated sequentially. In case 1, if both the velocity and position feedback control are activated early in the movement, then the feedback response will reflect the sum of the velocity and position deviations (Fig. 1, “Early position feedback” panel). However, if the position feedback is activated later in the movement when the arm approaches the target, as in case 2, then the feedback response will reflect first the velocity deviation and then position deviation (Fig. 1, “No early position feedback” panel). These possible control schemes were tested using a servo-controlled robot that unexpectedly perturbed the movement trajectory in a small subset of movements. We manipulated the duration and magnitude of the velocity and position deviations from the unperturbed movement trajectory. Analysis of the response in the muscle surface electromyogram (EMG) to the perturbations suggested that an initial part of the response is driven by the velocity feedback with respect to an unperturbed (desired) velocity, whereas the late part of the response is aimed at acquiring the final position. Our results are compatible with previous studies that have suggested that the movement trajectory and final position may be planned and controlled differently (Dizio and Lackner 1995; Ghez et al. 2007; Kurtzer et al. 2005; Sainburg et al. 1999; Scheidt and Ghez 2007) and provide further insight about the organization of neural feedback control during reaching movements.

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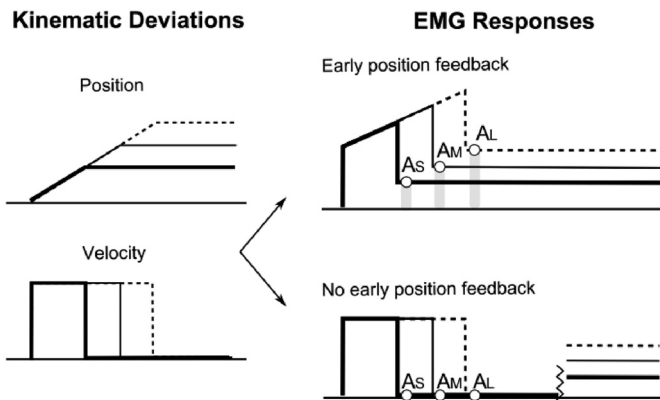


FIG. 1. The rationale for the experimental design. The kinematic deviations applied by a robot will elicit an electromyographic (EMG) response that reflects the activity of the proprioceptive feedback control system. The response to position and velocity deviations is assumed to be additive. If the position feedback is activated early, simultaneously with the velocity feedback, then the response will reflect the sum of the position and velocity deviations and the initial burst will terminate with the tonic level that increases with the magnitude of the small (S), medium (M), or large (L) position deviation (A_S , A_M , and A_L in “Early position feedback” panel). If the position feedback is activated later, then the response will reflect first the velocity deviation and a later tonic activity will reflect the position deviation (“No early position feedback” panel). In this case the response will exhibit a sharp decrease when the velocity deviation returns to zero. The sharp decrease in the response that is delayed with the offset of the velocity deviation will provide evidence for feedback control of a desired velocity time profile during movement. Analysis of the response magnitude after the sharp decrease A_S , A_M , A_L will indicate whether the position feedback control is active at that time.

METHODS

Subjects

Eight neurologically healthy subjects (five males and three females, aged 21–55 yr) participated in the study. All subjects gave informed consent according to a protocol approved by an Institutional Review Board (IRB) of the University of Illinois at Chicago and the IRB of Northwestern University.

Apparatus

The subjects were seated comfortably in a chair set in front of a haptic robot (HapticMASTER, FCS Control Systems) (Fig. 2A). The robot simulated a horizontal surface with minimal friction passing through the center of rotation of the shoulder. The seated subjects made forward reaching movements on the simulated surface with the right arm. The arm was supported against gravity by a sling attached to the ceiling (not illustrated). A computer monitor positioned in front of the subject displayed the hand position as a cursor registered to the handle of the robot, the initial position, and the target. The cursor (current hand position), initial position, and target were displayed as spheres. The diameter of the spheres indicating the initial position and the hand position corresponded to 0.02 m distance on the plane of the movement; the diameter of the target sphere corresponded to a 0.05 m distance on the plane of movement. To prevent vision-based corrections (Franklin and Wolpert 2008) the cursor was extinguished when movement velocity was >0.01 m/s. The subjects were asked to keep fixating on the monitor (positioned to the right of the robot) so the moving arm was in the subject’s peripheral field of view. The monitor was positioned about 5 ft in front of the subject and the center of the screen was about 1.5 ft to the right of the robot so that the subject’s head was turned about 15° when looking straight at the center of the screen. Although we cannot rule out the possible contribution of peripheral vision to the feedback response to the initial slowing of the arm movement, we do not think that the peripheral vision of the arm

affected the response to the subsequent changes in the kinematic deviations later in the movement.

The position and velocity of the handle were digitized by the HapticMASTER at 2,500 Hz. The surface muscle EMGs were recorded from the biceps brachii, brachioradialis, triceps brachii (lateral and long heads), pectoralis, anterior deltoid, and posterior deltoid. The EMGs were recorded using a Bagnoli system (Delsys, gain 1,000, built-in band-pass filter 20–450 Hz). The elbow angle was also recorded using a goniometer (Delsys). The EMGs and the goniometer signals were digitized at 1,250 Hz (National Instruments, 16-bit resolution A/D card). All digitized signals were resampled down to 1,000 Hz for off-line processing. The EMG signals were digitally full-wave rectified and then low-pass filtered with a second-order dual-pass Butterworth filter with a 50-Hz cutoff frequency.

Servo-controlled kinematic deviation

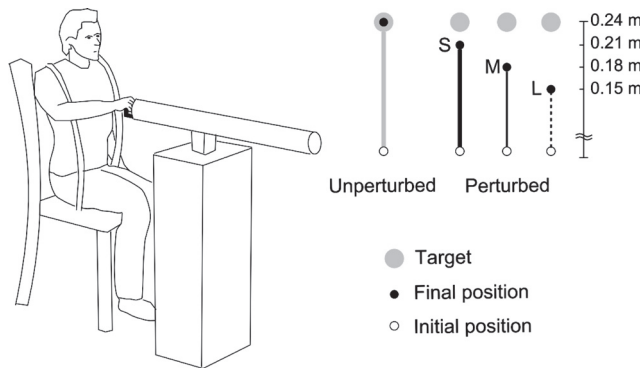
Proprioceptive feedback control during movement can be tested by unexpectedly altering the movement and analyzing the resulting changes in the EMGs. In most previous studies that have investigated the role of reflexes in movement, the movement was unexpectedly perturbed by a brief torque pulse (e.g., Brown and Cooke 1981; Hallett et al. 1975; Koshland and Hasan 2000). The advantage of applying a torque pulse is that the magnitude and duration of the pulse can be accurately controlled. However, a torque pulse of the same magnitude and duration will elicit different kinematic deviations from the unperturbed movement in different subjects and in different conditions, resulting in substantial variability of the perturbed trajectory (discussed in Shapiro et al. 2009). Therefore to reduce variability of the kinematic deviations in the perturbed movements we used servo control to guide the robot along a precomputed trajectory (Fig. 2B).

Control of the duration and magnitude of the kinematic deviations was implemented as follows. First, a series of unperturbed movements with the desired kinematics were recorded and averaged to obtain the baseline position and velocity. Next, a short, medium, or long velocity deviation was subtracted from the velocity baseline to obtain the template time profile for a corresponding perturbed movement. The template was used to servo control the robot once the perturbation was triggered early in the movement. The perturbed movement was made slower than the unperturbed movement for the duration of the velocity deviation and then the arm was accelerated so that the velocity returned to the unperturbed time profile. We adjusted the template so that the perturbed velocity exceeded the unperturbed velocity after the end of the velocity deviation. This ensured that the offset of the velocity deviation (V_{OFF}) is well controlled, even if the unperturbed velocity in some subjects was faster than the template velocity profile. Servo control of the duration of the velocity deviation meant that the magnitude of the accumulated position deviation was controlled as well. Thus the short, medium, or long duration of the velocity deviation corresponded to a small, medium, or large position deviation (Fig. 2B; see “Position deviation” and “Velocity deviation”).

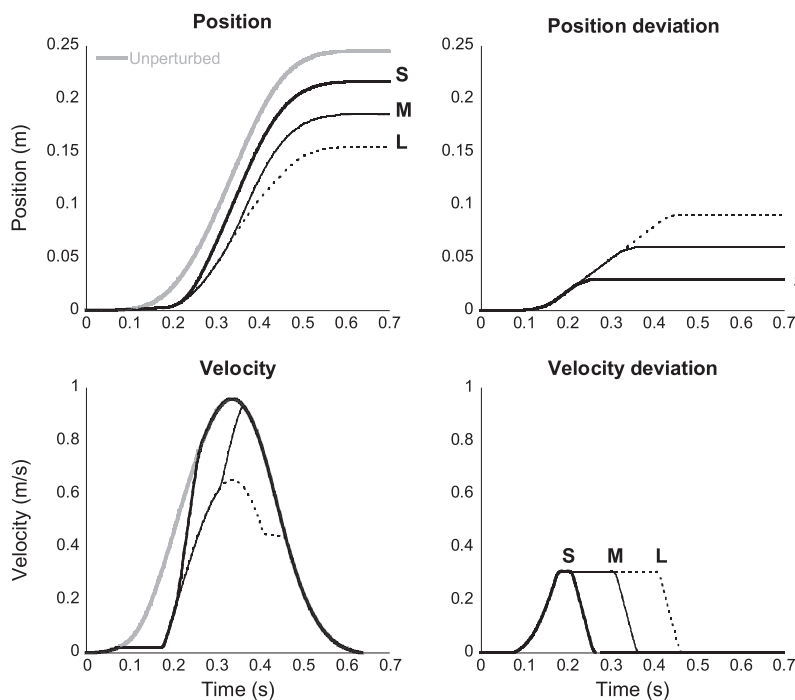
Tasks

The subjects were instructed to make forward reaching movements to a target. The movement distance was 0.24 m and the desired peak velocity was 1 m/s. The protocol included three perturbation conditions and two instruction conditions: “Do not correct” and “Attempt to correct.” The rationale for using two different instructions was as follows. It has been well documented that the magnitude of late components of the EMG responses to perturbations in postural tasks depends on the instruction to the subject (Crago et al. 1976; Everts and Tanji 1974; Hammond 1956; Pruszynski et al. 2008). It can also be predicted that the magnitude of the EMG response during movement may depend on the instruction because the latter affects the cost assigned to movement errors (Todorov 2004). We tested this prediction by comparing the EMG responses in the two test series of

A. Experimental setup



B. Kinematics templates



movements made under the instruction “Do not correct your movement if the robot feels different” or “Attempt to correct your movement if the robot feels different.” The movement sequence included a practice series of 100 trials followed by the 150 test series under each instruction condition. The order of the “Do not correct” and “Attempt to correct” instruction conditions was randomized across subjects.

Three perturbation conditions were interspersed in each 150 trial test series: S condition introduced a small magnitude position deviation (0.03 m) and a short velocity deviation (70 ms); M condition introduced a medium magnitude position deviation (0.06 m) and a medium duration velocity deviation (200 ms); and L condition introduced a large magnitude position deviation (0.09 m) and a long duration velocity deviation (>350 ms) (Fig. 2B). In all conditions, the perturbation was triggered close to the movement onset on a 0.02 m/s velocity threshold. This occurred at 0.078 ± 0.008 s (mean \pm SD) from the earliest onset of the muscle EMGs that initiated the movement (triceps lateralis). After the perturbation had been triggered, the servo control was maintained for the entire movement duration. The perturbations were applied in 30 randomly chosen trials in each of the test series. Among the 30 perturbed trials, there were 10 condition S trials, 10 condition M trials, and 10 condition L trials, randomly mixed. In

each trial, the robot first brought the arm to the initial position and locked for 0.2 s. Then the robot unlocked to allow free movement while the subject kept the arm at the initial position for another 0.2 s. At this point a “Go” beep instructed the subject to move and the cursor was extinguished when the movement velocity exceeded 0.01 m/s. The perturbed trials ended when the robot reached a precomputed final position. In the unperturbed trials, once the subject reached the target and remained within the target for ≥ 0.2 s the target changed color and the robot was locked in place. Then the robot returned the arm to the initial position. After each unperturbed trial, a slider on a horizontal bar on the screen indicated the peak velocity (PkV). The span of the bar corresponded to PkV within a range of 0.8–1.2 m/s. After the perturbed trials the bar indicator of PkV was not displayed.

each trial, the robot first brought the arm to the initial position and locked for 0.2 s. Then the robot unlocked to allow free movement while the subject kept the arm at the initial position for another 0.2 s. At this point a “Go” beep instructed the subject to move and the cursor was extinguished when the movement velocity exceeded 0.01 m/s. The perturbed trials ended when the robot reached a precomputed final position. In the unperturbed trials, once the subject reached the target and remained within the target for ≥ 0.2 s the target changed color and the robot was locked in place. Then the robot returned the arm to the initial position. After each unperturbed trial, a slider on a horizontal bar on the screen indicated the peak velocity (PkV). The span of the bar corresponded to PkV within a range of 0.8–1.2 m/s. After the perturbed trials the bar indicator of PkV was not displayed.

Data analysis

The EMG responses and kinematic deviations were calculated as the difference between the averaged time series in the sets of perturbed and unperturbed trials for six experimental conditions (3 deviations \times 2 instructions). The difference between the perturbed and unperturbed positions is referred to as the *position deviation*; the

difference between the perturbed and unperturbed velocities during the initial interval of lower velocity (up to the point when it reached again the unperturbed velocity) is referred to as the *velocity deviation*. Although the unperturbed movements were not constrained, the averaged unperturbed trajectories were very close to a straight line. The perturbed movements were constrained to a straight line, so the imposed deviations in the lateral direction were negligible compared with the deviations in the forward direction. Therefore we analyzed the deviations only in the forward direction, as shown in Fig. 2A.

The responses were reliably detected in the triceps lateralis (TRIC), triceps longus (TricL), pectoralis (PEC), and anterior deltoid (AD). These muscles produced initial accelerations at the elbow and shoulder joints and were considered agonists. The response in the “Do not correct” series consisted of a pronounced burst followed by an interval of tonic activity. In the S and M conditions, the burst and tonic components of the response were often separated by a period where the EMG activity in the perturbed movement returned to the unperturbed level before increasing again close to the end of the movement (Fig. 3A, *iii*). Analysis of the timing of the response burst was done using measures of its onset (R_{ON}) and offset (R_{OFF}). First, data for each movement trial were aligned on the movement onset ($t = 0$), defined as the time when the TRIC EMG increased 3SDs above the baseline activity. The baseline activity was calculated as the average EMG within 0–100 ms after the “GO” signal. Second, for each condition and each muscle, the sets of time series from the unperturbed and perturbed trials were compared at every sample point using

the Welch–Satterthwaite t -test (Shapiro et al. 2002). This procedure yielded a time series of P values. The EMGs in the unperturbed and perturbed movements were considered significantly different when P remained <0.05 for ≥ 10 ms. The earliest time of the significant difference between the EMGs was considered R_{ON} . The offset of the response burst R_{OFF} was determined as the time when the response magnitude first decreased to 20% of its peak. The 20% threshold was chosen because it allowed us to reliably determine the R_{OFF} across subjects in the “Do not correct” condition. The response in the “Attempt to correct” condition did not exhibit a well-defined burst (Fig. 3B, *iv*), so R_{OFF} was not analyzed for this condition. The amplitude measures included the initial part of the response burst (A_1) within 0–50 ms after R_{ON} ; the response (A_2) at the end of the velocity deviation within 25–75 ms after V_{OFF} ; the tonic component of the response (A_3) within the time interval 500–700 ms from the movement onset. The values of A_1 , A_2 , and A_3 were calculated as the average response levels within the corresponding time intervals (indicated by the shaded areas in Fig. 3B, *iii* and *iv*). To allow comparison across the subjects, for each of the agonist muscles, the values of A_1 , A_2 , and A_3 were divided by the average EMG level in the unperturbed movement within 100–300 ms from the movement onset. Thus the measures of response amplitude were expressed as a fraction of the average magnitude of the main agonist burst in the unperturbed movement.

For the kinematic signals, the timing measures included the onset (V_{ON}) and offset (V_{OFF}) of the velocity deviation. The onset V_{ON} was

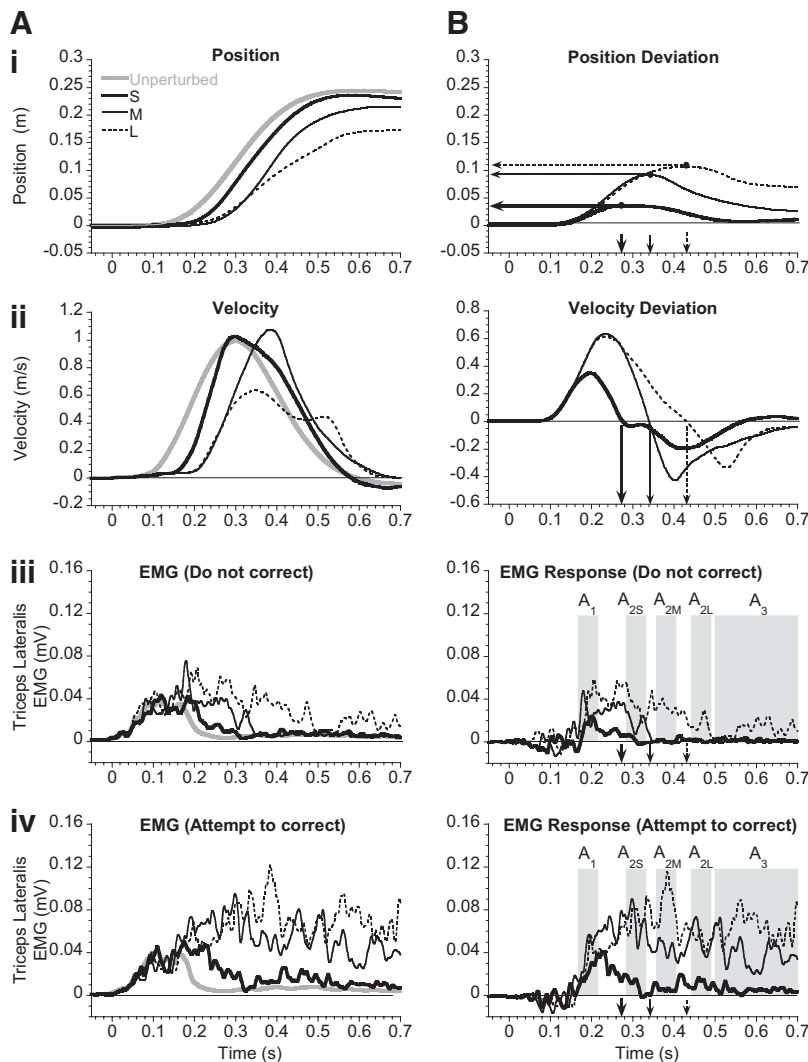


FIG. 3. A: the hand kinematics and triceps lateralis (TRIC) EMG for one representative subject. B: the kinematic deviations and EMG responses (difference between the EMG in the perturbed and unperturbed movements) in the 2 instruction conditions. As expected, the S, M, and L perturbation conditions produced the velocity deviations that crossed zero at the progressively later times (arrows in *ii*); the peaks in the position deviations increased with the duration of the velocity deviation (arrows in *i*). Since the perturbation conditions were triggered on the same velocity threshold and were randomly interspersed, the onset of EMG response was not significantly affected by the perturbation (main effect $P > 0.5$ for each muscle, 2-way ANOVA). The response onset also was not significantly affected by the instruction (main effect TRIC $P = 0.47$; triceps longus [TricL] $P = 0.15$; anterior deltoid [AD] $P = 0.57$; pectoralis [PEC] $P = 0.37$). The shape of the response, however, was different in the movements made under the 2 instructions. In the “Do not correct” condition, the response in the perturbed movements sharply decreased or even transiently terminated close to the offset of the velocity deviation (arrows in *iii*). In movements made under the instruction “Attempt to correct” the response did not exhibit a sharp decrease; the late sustained activity increased with the magnitude of the position deviation in the S, M, and L conditions (*iv*).

determined as the time of the earliest significant difference between the perturbed and unperturbed velocities; V_{OFF} was determined as the time when the velocity deviation crossed zero for the first time.

Statistics

In the “Do not correct” test series of movements, a one-way repeated-measures ANOVA was used to test the effect of the perturbation condition (S, M, L) on the offset of the response burst (R_{OFF}). The relation between the R_{OFF} and V_{OFF} was also analyzed using mixed-model regression as follows

$$R_{OFF}^i = \alpha_j + \beta_j V_{OFF}^i + \varepsilon_i \quad (J)$$

where $i = 1, 2, \dots, 24$ for 8 subjects and 3 conditions. The independent variable V_{OFF}^i is the offset of the velocity deviation for each subject in each condition. Mixed-model regression analysis allows individual subjects to have different intercepts ($\alpha_j, j = 1, \dots, 8$) and different slopes (β_j), as long as the individual intercepts and slopes are normally distributed. This technique enabled us to account for the variability across individual subjects (Shapiro et al. 2009). This analysis was done for “Do not correct” instruction only.

The effects of instruction condition (“Do not correct”; “Attempt to correct”) and perturbation (S, M, L) on the response magnitude A_1, A_2, A_3 were tested using a two-way repeated-measures ANOVA. All the values of A_1, A_2, A_3 were cubic-root transformed to ensure homoscedasticity. Post hoc analyses were done using Tukey’s honestly significant difference (HSD) test.

RESULTS

Kinematic deviations

The time profiles of the position and velocity of the hand in the “Do not correct” condition for one representative subject are shown in Fig. 3A. The kinematics of the unperturbed movements were similar in movements made under the “Do not correct” and “Attempt to correct” test series (data not shown), which suggests that the instruction of how to react to possible perturbations did not affect the planning of movement kinematics. The servo-controlled kinematics of perturbed movements were similar in the two instruction conditions because the perturbed movements were completely constrained by the robot. As expected, the offset V_{OFF} of the velocity deviation was delayed in the S, M, and L conditions (Fig. 3B, arrows in *ii*). Since the perturbations were triggered on the same velocity threshold, the onset of the velocity deviation V_{ON} occurred at similar times across the conditions. Therefore the offset and duration of the velocity deviations were uniquely related and will be referred to interchangeably, depending on the context. The peak in the position deviation increased with the duration of the velocity deviation in conditions S, M, and L (Fig. 3B*i*). After the peak, the position deviation somewhat decreased but was maintained by the robot until the end of the movement.

Although our experimental manipulation was based on kinematic deviations of the hand in Cartesian space, the muscle proprioceptors convey information of movement about the joints. Therefore we analyzed the kinematics of the elbow and shoulder joints (Supplemental material).¹ Overall, the timing and sign of the angular kinematic deviations were similar to the hand kinematic deviations and in the following analysis we focused on the hand kinematics.

EMG response exhibits early burst and late tonic activity

The EMG responses were similar in the shoulder and elbow agonist muscles. The elbow joint was extending while the shoulder joint was flexing during the movement, so the elbow extensors TRIC and TricL and the shoulder flexors PEC and AD acted as the agonist muscles that produced an initial acceleration. The EMGs in these four muscles showed a consistent increase in response to the initial lower velocity in the perturbed movement. In contrast, the EMG responses in the biceps brachii, brachioradialis, and posterior deltoid were either inconsistent or completely absent, likely because the perturbations were elicited by initially increasing the robot resistance. Therefore all the subsequent analyses were done on the responses in the agonist muscles.

The response onset was not significantly affected by the instruction [main effect TRIC $F_{(1,7)} = 0.59, P = 0.47$; TricL $F_{(1,7)} = 2.63, P = 0.15$; AD $F_{(1,7)} = 0.35, P = 0.57$; PEC $F_{(1,7)} = 0.93, P = 0.37$]. However, the shape of the response depended on the instruction. In the “Do not correct” condition, the response exhibited a burstlike increase in activation that was often followed by sustained activity, especially in the L perturbation condition (Fig. 3, A and B, *iii*). These two components will be referred to as the “response burst” and the “tonic response.” As can be seen in Fig. 3, the response burst was prolonged with an increase in the duration of the velocity deviation. As expected, the response onset (R_{ON}) appeared at the same time in all conditions because of the same onset of the velocity deviation, so the burst duration and offset were uniquely related and will be referred to interchangeably, depending on the context, similar to that of the velocity deviation as described earlier in *Kinematic deviations*. In contrast, in the “Attempt to correct” condition the response did not exhibit a sharp decrease and could not be unambiguously separated into the burst and tonic components (Fig. 3, A and B, *iv*), so analysis of the burst duration in the following text was done only for the condition “Do not correct.”

Response burst is generated by the velocity deviation but not the position deviation

The response burst was prolonged with the duration of the velocity deviation (Fig. 4). A one-way repeated-measures ANOVA showed a significant main effect of the perturbation condition on R_{OFF} for all four agonist muscles [TRIC $F_{(2,14)} = 48.0, P < 0.0001$; TricL $F_{(2,14)} = 11.1, P < 0.01$; AD $F_{(2,14)} = 5.5, P < 0.05$; PEC $F_{(2,14)} = 6.7, P < 0.01$]. The ANOVA results were supported by a mixed-model regression analysis of the R_{OFF} and V_{OFF} (Fig. 4B). The slope β (the overall effect of individual slopes β_j) was significant for the four agonist muscles [TRIC $\beta = 0.77, F_{(1,15)} = 46.2, P < 0.0001$; TricL $\beta = 0.71, F_{(1,15)} = 46.2, P < 0.01$; AD $\beta = 0.77, F_{(1,15)} = 10.96, P < 0.01$; PEC $\beta = 0.34, F_{(1,15)} = 6.86, P = 0.02$], which indicates that the response burst was prolonged proportionally to the offset of the velocity deviation.

We also considered whether the duration of the feedback burst is related to higher derivatives, such as acceleration deviation. Since the perturbations were designed such that the velocity deviation reached its plateau at the same time in all conditions (Fig. 2B, “Velocity deviation” has the same height in the S, M, and L conditions reached at about 150 ms), the

¹ The online version of this article contains supplemental data.

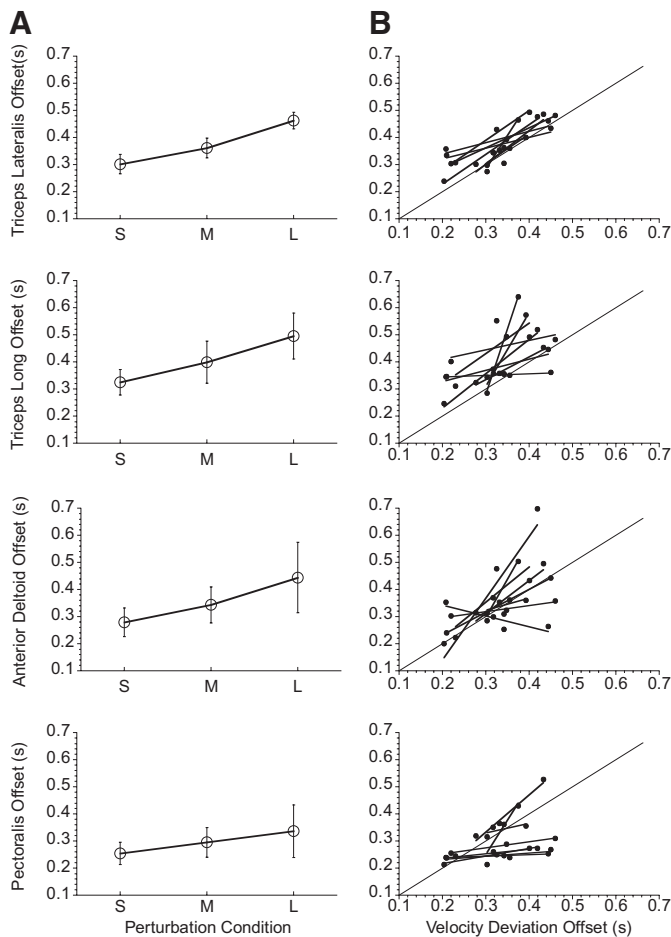


FIG. 4. A: the offsets of the response burst in condition S, M, and L. The burst offset was delayed with an increase in the velocity deviation. B: the burst offset was significantly correlated with the offset of the velocity deviations. Moreover, the difference between the offsets of the response burst and the velocity deviations across the conditions and across the subjects was within (mean \pm SD) 0.042 ± 0.048 s for TRIC; 0.072 ± 0.084 s for TricL; 0.022 ± 0.092 s for AD, and 0.038 ± 0.083 s for PEC. These results suggest that the response burst was driven by the deviations from a desired velocity time profile.

initial acceleration deviation was expected to return to zero at the same time. This was indeed the case for the M and L conditions (Fig. 5). Although the initial M and L acceleration deviations returned to zero at the same time, unlike that of the corresponding velocity deviations, the response burst was delayed in the L compared with the M condition (Fig. 5, dashed and thin arrows). This suggests that the response burst was predominantly driven by the velocity deviation.

Another possible source of sensory feedback control is input provided by nonmuscle receptors (Gandevia et al. 2002), such as Golgi tendon organs or tactile receptors of the hand. In particular, pressure cues from the robot handle can be used to detect the perturbed trial and trigger the response. It is less clear how the tactile feedback contributes to the response in the middle of the movement. We considered whether the changes in the force applied to the robot handle could be related to the response burst. We calculated the difference between the perturbed and unperturbed movements in the forward component of force applied to the handle (Fig. 6). The initial force difference changed sign considerably later than offset of the

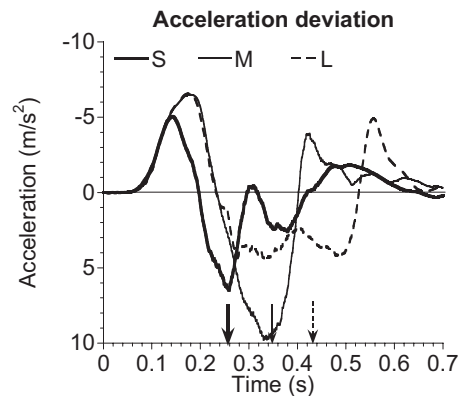


FIG. 5. Acceleration deviations in perturbation conditions S, M, and L. The acceleration deviations first crossed zero at the same time in the conditions M and L, whereas the response burst in the L condition terminated later than in the M condition (the arrows indicate the time of termination of the response burst R_{OFF} in the S, M, and L conditions). Averaged data for one subject are shown (same subject as in Figs. 3 and 4).

response burst in the conditions S and M and did not change sign at all in condition L (Fig. 6, burst offset is marked by arrows). Thus the burst offset could not be related to the change of sign of the force difference, unlike that of the

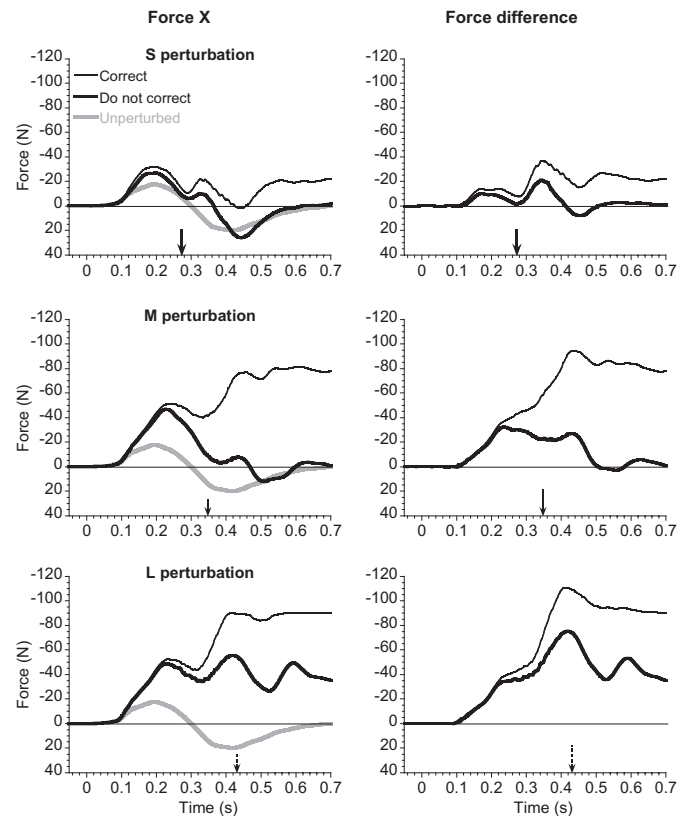


FIG. 6. The force measured at the handle in the forward direction (left column) and the force deviations (right column) in the S, M, and L perturbation conditions in the “Do not correct” and “Attempt to correct” instruction conditions. The arrows indicate the time of termination of the response burst. The R_{OFF} could not be systematically related to the specific events in the force deviation traces. Comparison of the force deviations in the 2 instruction conditions (thick and thin lines) support our conclusion that instruction does not affect the initial part of the response (prior to ~ 0.2 s), which is apparently driven by the velocity deviation. Averaged data for one subject are shown (same subject as in Figs. 3 and 4).

velocity deviation. This suggests that the force or tactile pressure feedback did not determine the duration of the response burst. Overall, the close relation between the offsets of the velocity deviation and response burst suggests that the burst reflected activity of a velocity feedback controller driven by deviations from the desired velocity.

Position feedback does not contribute to the response burst in the “Do not correct” condition

The response burst may be elicited by both position and velocity deviations. A possible contribution of the position feedback component was analyzed at the time when the velocity deviation was reduced to zero at V_{OFF} (the A_2 intervals in Fig. 3B, iii and iv). The A_2 amplitude showed an interaction between the instruction and perturbation conditions (Fig. 7). Therefore we used pairwise S–M and M–L post hoc comparisons for each instruction condition to test whether A_2 was affected by an increase in the magnitude of position deviation. In the “Do not correct” condition, A_2 was not significantly affected by the magnitude of the position deviation in any of the four muscles. In the “Attempt to correct” condition, A_2 in the shoulder muscles did not significantly increase between S–M or M–L conditions. In the elbow muscles A_2 increased between the S–M conditions (TRIC $P = 0.048$; TricL $P = 0.003$), but its further increase was not significant between the M–L conditions (TRIC $P = 0.16$; TricL $P = 0.26$). Thus the position feedback control may have contributed to the response

burst only if the subject was instructed to correct movement errors.

In summary, the analyses of onset and duration of the response burst and its magnitude at the end of the velocity deviation suggest that the motor system uses proprioceptive feedback control to correct deviations from the expected velocity, but not position, in the middle of the movement. Analysis of the effect of instruction on A_1 , A_2 , and A_3 will show that the contribution of position feedback becomes increasingly more pronounced as the limb approaches the target.

Instruction affects the late tonic component of the response but not the early burst

The effect of instruction on the values of A_1 , A_2 , and A_3 is illustrated in Fig. 7. The instruction “Attempt to correct” did not affect the initial burst magnitude A_1 in any of the four muscles. The effect of instruction became pronounced as the movement progressed toward the target, as revealed by A_2 and especially by A_3 measures. Since A_2 showed an interaction between the perturbation and instruction conditions, we tested the effect of instruction for each of the S, M, and L conditions. In the S condition, the instruction “Attempt to correct” did not result in a significant increase of A_2 in any of the four muscles ($P > 0.98$ for each muscle, Tukey’s HSD test). In the M condition, the instruction “Attempt to correct” produced a significant increase of A_2 in the elbow agonists only and in the L condition an increase in A_2 was significant for all four

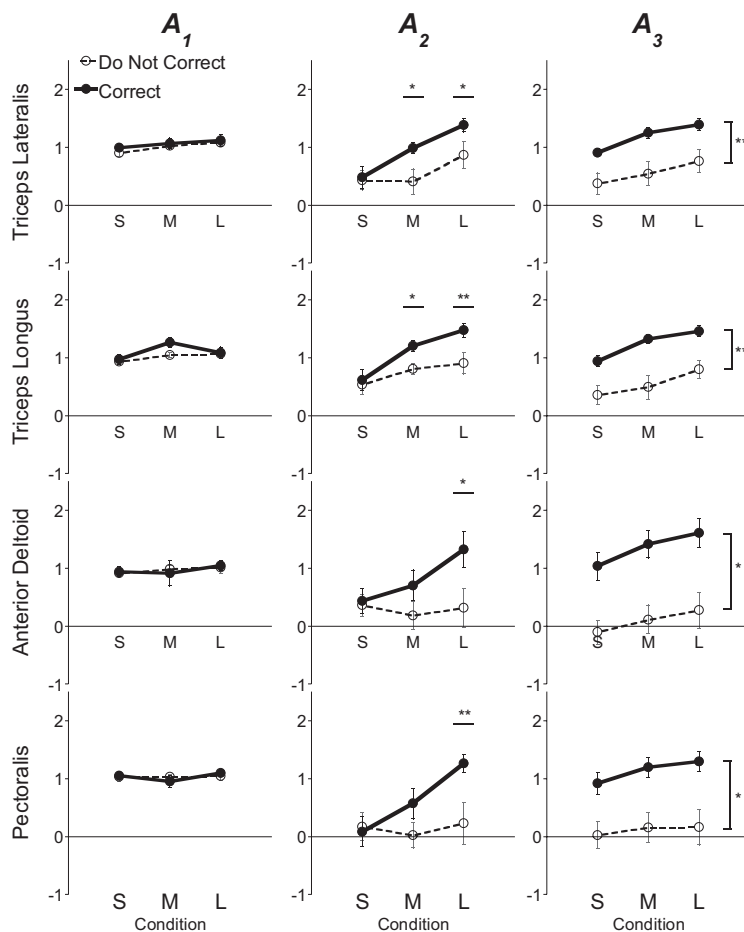


FIG. 7. The effects of the instruction and perturbation conditions on the response magnitude (EMG normalized and cubic-root transformed, mean and SE bars) in the 4 agonist muscles for all subjects. A_1 characterizes the initial part of the response; A_2 was evaluated at the end of the velocity deviation that was prolonged in the S, M, and L conditions; A_3 was evaluated at the end of the movement. The instruction did not significantly affect A_1 [main effect for TRIC $F_{(1,7)} = 2.3$, $P = 0.17$; TricL $F_{(1,7)} = 3.3$, $P = 0.11$; AD $P = 0.96$; PEC $P = 0.95$]. The response A_2 exhibited an interaction between the instruction and perturbation conditions [TRIC $F_{(2,14)} = 3.56$, $P = 0.056$; TricL $F_{(2,14)} = 4.33$, $P = 0.034$; AD $F_{(2,14)} = 3.40$, $P = 0.063$; PEC $F_{(2,14)} = 5.38$, $P = 0.018$]. The A_2 increased at the end of M velocity deviation in the elbow muscles (TRIC $*P = 0.02$; TricL $*P = 0.048$, Tukey HSD test) and in L velocity deviations in all 4 muscles (TRIC $*P = 0.044$; TricL $**P < 0.01$, AD $*P = 0.015$; PEC $**P < 0.01$, Tukey HSD test). The response A_3 increased in all muscles if the subject was instructed to correct movement errors [instruction main effect TRIC $F_{(1,7)} = 13.6$, $**P < 0.01$; TricL $F_{(1,7)} = 13.4$, $**P < 0.01$; AD $F_{(1,7)} = 9.1$, $*P = 0.02$; PEC $F_{(1,7)} = 7.5$, $*P = 0.03$]. The data suggest that the position feedback control is activated late in the movement and is strongly affected by the instruction to the subject.

muscles. It is possible that the instruction “Attempt to correct” resulted in a stronger response only when the stimulus (i.e., velocity deviation) was relatively long. However, the effect of instruction may be determined by the time from the movement onset per se, so the instruction “Attempt to correct” had a pronounced effect only on the later parts of the response. Note that the A_2 was measured at the end of the velocity deviation that occurred at different times from the movement onset in the S, M, and L conditions. Then, A_2 may have increased in L but not in S condition because it was evaluated within a later time interval. In contrast, the A_3 was evaluated close to the end of the movement in all conditions and it exhibited a pronounced increase in all four muscles if the subject was instructed to attempt to correct movement errors. The value of A_3 also progressively increased with the magnitude of the position deviation (perturbation main effect $P < 0.01$ for each muscle). Overall, the temporal evolution of the effects of instruction and perturbation on A_1 , A_2 , and A_3 may reflect a gradual shift from velocity feedback control in the middle of the movement to position control later in the movement.

DISCUSSION

We have found that the EMG responses to kinematic deviations during reaching movements consist of at least two distinct feedback mechanisms. The response in the middle of the movement was generated by the velocity feedback control that corrected deviations from a desired velocity. The late part of the response was generated by position feedback control. The onset and initial magnitude of the response were not affected by the instruction “Do not correct” or “Attempt to correct,” whereas the magnitude of the late part strongly increased when the subject was instructed to correct movement errors. These results suggest that the previously proposed views that the motor system either controls desired movement kinematics or controls only the task parameter (i.e., final position) may not be mutually exclusive but may apply to the different phases of the movement. In particular, the velocity feedback control in the middle of the movement corrects deviations from a desired velocity even if the task does not explicitly require doing so. On the other hand, the activity of position feedback control progressively increased toward the end of the movement, as explicitly required by the task and instruction.

Velocity feedback control in the middle of the movement

It is not clear why proprioceptive feedback in the middle of the movement acts to correct deviations from a desired (unperturbed) velocity time profile that is not explicitly required by the task. Although overall movement speed is a high-level task parameter (Churchland et al. 2006) in any reaching task, only the PkV and accuracy of the final position were explicit task parameters in our study. These two variables are independent and temporally separated, so it could be expected that the motor system corrects errors in peak velocity and final position. Since the perturbed velocity reached instructed PkV later than expected in condition M and never reached it in condition L (Fig. 3A, *ii*), it could be predicted that the velocity feedback control maintains an increased activation of the agonist muscles that accelerate the movement until the perturbed velocity

reaches the PkV. This was not observed, so the response burst in the agonist muscles sharply decreased (Fig. 3B, *iii*) close to the time when the perturbed velocity exceeded the unperturbed velocity (Fig. 4). Thus the feedback control corrected deviations from the expected velocity time profile, even though the instructed PkV may not have been reached, and the movement position was still lagging behind that of the unperturbed movement. To use proprioceptive feedback to control a desired velocity the reference velocity signal has to be available and there is evidence that movement velocity is strongly represented in the cortex (Ashe and Georgopoulos 1994; Moran and Schwartz 1999; Paninski et al. 2004; Schwartz and Moran 2000) and cerebellum (Ebner 1998; Roitman et al. 2009).

We found that the velocity feedback control in the middle of the movement cannot be changed by a direct instruction. This complements a previous result that the subjects could not voluntarily switch between the motor programs acquired after adapting to the two novel force fields when those fields were later presented in an alternating sequence, even when the subjects were informed which field would be presented next (Karniel and Mussa-Ivaldi 2002). However, the subjects are able to switch between the different force environments when presented with a contextual visual cue (Cothros et al. 2009). The movement context can also alter proprioceptive feedback control. It has been found that the earliest onset of feedback corrections to unexpected perturbations is delayed when the planned movement is slower (David et al. 2009) or is made against a heavier load or over a longer distance (Shapiro et al. 2004); the sign of the response—i.e., increase or decrease in the muscle EMGs—is different if the subject expects an inertial load or a viscous load (Shapiro et al. 2009) or catches a ball (Lacquaniti et al. 1991).

Position feedback control late in the movement

One of the goals of this experiment was to dissociate position and velocity feedback control during movement. For movements in the “Do not correct” condition, we found no evidence of position feedback control in the middle of the movement because an increase in the position deviation did not significantly affect the response magnitude A_2 (Fig. 7). The value of A_2 increased with the position deviation only when the subject was instructed to correct movement errors. This suggests that the position feedback was not active until the end of the L velocity deviation in the “Do not correct” condition and was facilitated somewhat before the end of the M velocity deviation in the “Attempt to correct” condition. The delayed activation of the position feedback control supports the simulation results of Scheidt and Ghez (2007) who studied the transfer of learning between the reaching and “slicing” movement tasks made in a visually rotated environment. In the reaching movement task, the subjects had to stop at the target, whereas in the “slicing” movement task the subjects made a continuous movement forward and back. The transfer of learning was limited, especially the final position that was not adapted after the subjects learned to make “slicing” movements in the rotated environment. The authors were able to simulate their results by introducing an end-position controller that is activated later in the movement.

Interestingly, it has been suggested that in visually guided movements, visual feedback control combines both motion and

position feedback (Saunders and Knill 2004). In that study, a cursor indicating the position of the subject's fingertip was available throughout the movement. Thus the CNS may use concurrent feedback control of motion and position when visual feedback of the moving hand is available (Saunders and Knill 2004). Our finding that position feedback is activated after the velocity feedback control suggests that the proprioceptive feedback control operates differently from visual feedback in reaching movements that are not visually guided.

Implications for the models of control of reaching movement

If feedback gains are adjusted depending on the cost of movement errors (Todorov and Jordan 2002), it could be expected that the response may be absent in movements made under the "Do not correct" instruction and the response magnitude should have increased in the "Attempt to correct" condition. Neither of these two predictions was confirmed for the initial part of the response (A_1 in Fig. 7). On the other hand, an increase in the response magnitude in the "Attempt to correct" condition became more pronounced later in the movement (A_3 in Fig. 7), as can be predicted by the optimal feedback control model (Todorov 2004). Given that the optimal feedback control model is flexible, it is possible that the weights of the different cost terms can be adjusted to fit the data. This highlights the necessity of further studies that can provide an experimental basis for choosing the parameters in this model. It should be noted that our reasoning is based on the responses with respect to the hypothesized kinematic time profiles, whereas the control signal in the optimal feedback control model is based on the difference between the current and final position as well as current and zero velocity [damping term in equation for $u(t)$ in Liu and Todorov (2007)].

Our results contradict some predictions of the *lambda* model of equilibrium point control (Feldman 1966, 1986; Latash 1993). According to the *lambda* model, posture is controlled by setting stretch reflex thresholds for the muscles by descending input to the alpha motoneuron pool (Asatryan and Feldman 1965; Feldman and Orlovsky 1972) that define reference limb configuration (Feldman and Levin 1995). It was further hypothesized that movement is produced by a shift in the reference limb configuration (Feldman and Levin 1995). In this case, a shift in the stretch reflex thresholds results in muscle activation due to the stretch reflexes acting as position and velocity feedback control. However, previous experiments demonstrated that the EMG responses to perturbations delivered in the beginning of the movement are centrally suppressed (Brown and Cooke 1981; David et al. 2009; Hallett and Marsden 1979; Hayashi et al. 1990; Shapiro et al. 2002, 2004, 2009). Moreover, in our present experiment the movement kinematics were different in the perturbed and unperturbed movements and, according to the *lambda* model, the differences in the EMGs in the perturbed and unperturbed movements should have reflected both the velocity and position feedback control at all times. This was not the case. Thus our data do not support the hypothesis that movement is produced by a shift in the reference configuration. However, our results do not contradict the idea that the CNS controls static position of the limb by centrally adjusting stretch reflex thresholds. It is possible that as the reference configuration transitions from the initial to the final posture, the corresponding stretch reflexes

are suppressed and the feedforward and feedback control components of muscle activation are generated independently from the changes in the reference configuration. When the final reference configuration (i.e., centrally reset stretch reflex thresholds) emerges close to the end of the movement it contributes to the feedback control with respect to the final position.

Proprioceptive feedback control may be independent from conscious perception

It could be argued that conscious perception of velocity and/or position deviation during movement affects the response. Sittig and colleagues (1985) showed that vibration affected perception of position and velocity in different ways and further suggested that position perception dominates the control of slow movements, whereas velocity perception dominates the control of fast movements (Sittig et al. 1987). Since the movements in the present study were fast, the subject's ability to consciously correct velocity deviations could affect the response. However, this argument alone cannot explain our results. In the S perturbed movements, the response magnitude in the "Attempt to correct" condition, compared with "Do not correct" condition, did not increase in the middle of the movement and increased only late in the movement (compare A_2 and A_3 for the S condition in Fig. 7). This suggests that the perception of the velocity deviation did not determine the response burst, whereas the perception of the position deviation could affect the late part of the response. Our results point to an interaction of the conscious "set" and temporal order of the feedback control processes.

We do not have a definitive answer to the question of how the subjects consciously perceived the perturbation in our experiment because we did not assess it systematically, although we asked the subjects after the first couple of perturbed trials how they would describe the perturbation. The perturbation was perceived as an increased resistance before the robot "got stuck." The subjects gave no indication that they were able to consciously detect finer details of the kinematic deviations from the unperturbed (expected) trajectories. Although the subjects consciously reported the increased resistance, presumably on the basis of the pressure and force receptors, the timing and magnitude of the responses suggest that the neural feedback was based on the kinematic deviations sensed by muscle proprioceptors. In general, this observation points to a dissociation between conscious perception, as tested in matching kinematics paradigms (Djupsjobacka and Domkin 2005; Goble and Brown 2007, 2009; Kerr and Worringham 2002), and proprioceptive feedback control during movement that operates on a fast timescale independent of conscious perception.

Neurophysiological mechanisms of the proprioceptive feedback control

It is interesting to compare the effect of instruction on the magnitude of EMG responses during movement and in the maintenance of static posture. It has been well documented that in postural tasks, the magnitude of the long-latency latency reflex can be modified or even completely abolished by an explicit instruction (Hammond 1956) or by a task that implic-

itly required the subject to resist or assist the perturbation (Evarts and Tanji 1974; Lewis et al. 2006; Pruszynski et al. 2008; Shemmell et al. 2009). In our experiment, the response latency from the perturbation onset was consistent across the conditions for each subject, but ranged from 0.057 to 0.233 s across the subjects and it could be argued that responses were generated by long-loop and possibly transcortical pathways (Day et al. 1991; de Graaf et al. 2009; MacKinnon et al. 2000; Suminski et al. 2007). In this case the value of A_1 should have been affected by the instruction. It was not and this result is compatible with another hypothesis that at least the initial part of the EMG response to perturbations during fast reaching movement is mediated by the spinal pathways (Shapiro et al. 2002). The feedback gains and thresholds of the spinal feedback pathways might be governed by a descending input, similar to a "volitional set" proposed by Gottlieb (1996). The observed long latency of the response can be explained by a hypothesized central suppression of the proprioceptive feedback control in the beginning of the movement (Brown and Cooke 1981; Hallett et al. 1975; Hayashi et al. 1990; Shapiro et al. 2004; Soechting et al. 1981). The feedback control may be hierarchically organized such that the proprioceptive velocity and position feedback control are realized by a low-level, possibly spinal, controller, whereas a higher-level controller provides the reference signals and modulates the gains of the feedback loops. The descending sequential facilitation of the gains of velocity and then the position feedback are compatible with the results of Wang and colleagues (2007) who studied representation of position and velocity of reaching movement in motor cortex. They found that relative weights of the velocity and position signals change during movement, with saliency of position representation decreasing at the beginning of the movement and gradually increasing by the end of the movement (Wang et al. 2007).

Conclusion

In summary, we suggest that the feedback control of reaching movement consists of three phases: 1) the feedback corrections are suppressed in the beginning of the movement; 2) in the middle of the movement the velocity feedback is activated to control a desired velocity; and 3) later in the movement, the position feedback is activated. The feedback control in the beginning or middle of the movement is not affected by a direct instruction to the subject, whereas the position feedback at the end of the movement strongly increases with the subject's intent to correct movement errors.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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