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Afferent Input, Efference Copy, Signal Noise, and Biases in Perception of Joint Angle During Active Versus Passive Elbow Movements

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INTRODUCTION

This study examines the nature and origin of perceptual biases in estimation of transiently sensed positions of the unseen limb experienced during movement, as distinct from static limb positions during stable postures (Bevan et al. 1994; Brown et al. 2003; Cordo et al. 2000, 2002). The perception of limb position during voluntary movements in the absence of vision is thought to rely on a combination of proprioceptive sensory feedback and signals of central origin (Davidson and Wolpert 2005; Desmurget and Grafton 2003; Sabes 2000; Wolpert and Flanagan 2001).

The principal afferent sources of proprioceptive sensory signals are muscle spindles, with secondary contributions from Golgi tendon organs, joint receptors, and cutaneous mechano-receptors (for review, see Gandevia 1996; Matthews 1982; Proske 2006). Spindle primary afferents signal the rate of change of muscle length during movement and static muscle length at rest, whereas spindle secondary afferents mainly signal muscle length (Hagbarth and Vallbo 1969; Hasan 1983; Kakuda and Nagaoka 1998; Matthews and Stein 1969; McCloskey 1973; Prochazka and Gorassini 1998; Prochazka et al. 1977). As a result, signals about the angular position, direction, and speed of single-joint and whole limb movements can be extracted from the activity of small ensembles of spindle afferents located in both agonist and antagonist muscles (Bhushan and Shadmehr 1999; Hwang and Shadmehr 2005; Jones et al. 2001b; Ribot-Ciscar et al. 2002, 2003; Scott and Loeb 1994; Stein et al. 2004).

Proprioceptive signals about limb position and movement are critical for both kinesthetic sensation and control of voluntary movements. Neurological patients with large-diameter sensory fiber neuropathies suffer a devastating deterioration of both functions when deprived of visual input about the limb (Forget and Lamarre 1987; Gordon et al. 1995; Sainburg et al. 1993).

To generate an appropriate motor command, the CNS must have a good estimate of the initial state (position and velocity) of the arm before movement onset to plan the upcoming movement. It must also monitor the arm’s state during the movement to extract error signals for feedback-mediated correction to assure successful completion of the movement and as teaching signals for motor skill acquisition. However, state estimation based solely on afferent input during movement is problematic because of the conduction delays, which can lead to dynamic instability in the feedback control circuit. Theoretical studies propose that an “internal forward model” could reduce the instability problem by using both an efference copy of the outgoing motor command and afferent sensory signals to estimate the current or immediate future state of the limb (Bhushan and Shadmehr 1999; Miall et al. 1993; Scarchilli et al. 1999; Wolpert et al. 1995). According to the theory, as the movement unfolds, efference copy–based predictions about future states of the limb would combine with delayed sensory feedback signals about the most recently sensed actual state of the limb to continuously update the limb state estimate.

Efference copy may also influence kinesthetic sensations. For instance, altered or diminished tactile and kinesthetic sensations during active movements are thought to reflect the effect of efference copies on ascending afferent volleys or on state estimation (Angel and Malenka 1982; Bays et al. 2005; Blakemore et al. 1998; Chapman et al. 1987; Claxton 1975; Shergill et al. 2003; Voss et al. 2006). The perception of final static limb position is often more accurate after active movements than passive movements (Adamovich et al. 1998; Craske and Crawshaw 1975; Lafer et al. 2001; Paillard and Broučon...
Perception of Joint Angle During Movement

Methods

Subjects

Seven right-handed subjects (age, 23–35 yr; 2 males and 5 females) with no known neurological disorders participated in this study. They gave informed consent before their inclusion and were naïve to the objectives of the study. The study was approved by the Human Research Ethics Committee of the Faculté de Médecine, Université de Montréal, and was carried out in accordance with institutional and national ethical standards.

Apparatus

The subjects sat facing a computer screen with their right arm supported in the horizontal plane at shoulder height by a single-joint planar robotic manipulandum (Fig. 1). The axis of rotation of the elbow was centered on the axis of rotation of the manipulandum. A horizontal opaque screen blocked vision of the arm and manipulandum at all times. A potentiometer mounted on the axis of rotation of the manipulandum measured the angular position of the elbow at 0.04° angular resolution. Angular positions were stored every 5 ms during the behavioral trials. The manipulandum was mounted directly onto the shaft of a ShinMaiwa torque motor, which was used to produce passive movements of the subjects’ arm.

For some tasks, a separate pointer was mounted above the opaque screen and instrumented with another potentiometer to record its angular position (0.04° angular resolution). Its axis of rotation was aligned with the subjects’ elbow, and its motion was completely independent of the manipulandum. The length of the pointer was such that the end of the pointer traveled along the same spatial arc as the subjects’ hand in the manipulandum under the opaque screen.

Tasks

All subjects performed several variants of a kinesthetic perceptual task in pairs of matching active and passive conditions. They did pairs of matching conditions over 2 consecutive days and different pairs of conditions at more widely separated intervals, often weeks apart. All tasks involved a series of trials comprised of an extension movement of the elbow (test movement) during which they received a sensory cue to memorize their current (target) joint angle, followed by a...
“report” movement during which they attempted to reproduce the remembered angle. Tasks differed in the nature (active vs. passive), speed, and extent of the test movement, in the range of target angles, and in how the subjects reported their elbow angle (Table 1). Several task variants were developed during the course of the study to validate the main findings, by assessing potential sources of perceptual biases in the basic design of the task. Subjects never received knowledge of results of differences between target and reported elbow angles.

Active test movement: slow speed, flexion report (active SF task)

The active SF task and its matching passive SF task were the basic tasks of the study. They established the patterns of errors in elbow angle estimation during unseen active elbow extension movements and during passive movements with the same kinematics.

In the active SF task, subjects performed slow self-paced elbow extensions (test movements) of their unseen arm. To start each trial, the subjects placed their arm in the starting elbow position of 40° flexion between the upper arm and forearm. After holding the starting position for 0.5 s, a green 2.5 × 2.5-cm square appeared at the center of the computer screen to prompt the subjects to start to extend their elbow at a preferred slow speed. Maximum test movement amplitude was full extension (180°), demarcated by a stopper. When the elbow reached a certain angle, the cue changed color from green to blue, accompanied by a brief tone on the PC speakers (Fig. 2). We will refer to this timing signal as the “mnemonic cue” because it instructed the subjects to remember their perceived elbow angle at that moment without stopping the test movement. The mnemonic cue appeared when the extending elbow reached one of eight pseudorandomly selected target angles, from 60 to 165° in 15° increments. The test movement ended when the cue color changed to yellow (report cue), at which time the subjects actively returned their arm directly to the remembered joint angle by flexing their elbow (i.e., flexion report movement). The subjects held that position until the cue turned red, at which time they returned their arm to the start position and waited for the cue to turn green to start the next trial.

Each trial lasted 6–7 s. The subjects practiced this (and all other) tasks until they were confident that they understood the task before we collected experimental data. Typically, subjects required <10 practice trials. Subjects performed the active SF task in blocks of 40 trials. Each block consisted of five replications of each target angle in a randomized-block sequence.

Passive test movement: slow speed, flexion report (passive SF task)

In separate blocks of trials, the robotic manipulandum imposed the test movements while the subjects relaxed their arm muscles. The passive trials reproduced as closely as possible the actual kinematics of the active test movements made by the subjects in the active SF task. To this end, the robotic controller replicated the angular position trajectories of the sequence of test movements recorded during the previous block of trials of the active SF task by applying torques to minimize the error between the recorded and current angular position and velocity at every 5-ms interval. The mnemonic cue appeared when the robot reached the same angular position as in the corresponding trial of the active SF task. The robot reproduced the active test movements up until the time that the elbow reached the angle at which the report cue appeared in the active trials. The torque motor turned off, and the subjects made an active flexion report as in the active SF task. They actively returned their elbow to the starting angle, relaxed their arm muscles, and awaited the start of the next trial.

The passive SF task involved blocks of 40 trials in the identical sequence as the corresponding block of the active SF task. Each subject performed eight alternating blocks of active and passive SF tasks (4 blocks of each task) over two sessions on separate days. The data set was comprised of 20 trials per target angle per active and passive condition (320 trials in total per subject).

Active/passive test movement: slow speed, extension report (SF task)

In two other daily sessions, subjects reported their remembered joint angle with an extension movement (Fig. 2). This condition assessed the influence of two possible confounding factors on elbow angle estimates in the SF task. First, the direction of the report movement was opposite to the test movement in the SF tasks. Second, the time required to remember the elbow angle between the appearance of the mnemonic cue and the end of the report movement was longer in the SF tasks when the mnemonic cue appeared early in the test movement than near the end.

<table>
<thead>
<tr>
<th>Test movement</th>
<th>SE</th>
<th>SF</th>
<th>FE</th>
<th>FF</th>
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<th>SF-G</th>
<th>SP-R</th>
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**TABLE 1. Summary of all tasks**

![FIG. 2. Examples of single trial records for SF and FE tasks (Table 1). Solid black lines show joint angle trajectories during active test movement trials. Dashed black lines show joint angle trajectories for corresponding passive test movement trials. Vertical gray lines mark times when color cues appeared. Visual cues were as follows: green, start initial movement (0 on the time axis); blue, remember current (target) joint angle; yellow, report remembered angle; red, end of trial, return to starting position. Horizontal dotted gray line shows reported angle for the passive trial. RE, report error between target angle and reported angle; TA, cue-position time asynchrony: interval between time elbow was at target angle and at reported angle during test movement.](jn.physiology.org)
When the report cue appeared in SE tasks, the subjects returned their arm all the way back to the starting angle before moving it to the remembered angle by an extension report movement. As a result, the test and report movements were in the same direction, and any target angle-dependent biases in memory period duration were reduced. Subjects performed eight alternating blocks of active and passive SE tasks (20 trials per target angle per active and passive condition) over two sessions on separate days (320 trials in total).

Active/passive test movement: fast speed, flexion and extension report (FF and FE tasks, respectively)

In four other sessions, subjects made fast test movements to assess the effect of speed on elbow position estimates (Fig. 2). The report movement speed was the same as in the previous tasks. Subjects performed 20 trials per target angle in each of the active and passive FF (320 trials) and FE (320 trials) tasks.

Active/passive test movement: slow speed, flexion report, short test movement (SF task)

This and the next pair of tasks addressed the potential contribution of any “range effect” to the estimation of elbow angles. The term range effect refers to a commonly observed trend in psychophysical studies for the distribution of the responses of subjects to be narrower than the distribution of experienced conditions, because their responses at the extremes of the range of experienced conditions tend to migrate toward the mean value of the range of conditions (Poulton 1979, 1981). The SF-S task tested the effect of the experienced test movement range on the angle estimates by presenting only the first four target elbow angles (60–105°) and reducing the maximum extent of the test movement to 120°, compared with 180° in the standard tasks. The speed of the test movement (slow) and the direction of the report movement (flexion) were similar to those in the SF task. Subjects performed 20 trials per target angle per active and passive SF-S task (160 trials in total) in one session.

Active/passive test movement: slow speed, flexion report, grouped target angles (SF-G task)

The SF-G task also tested the effect of the range of target angles on elbow angle estimates. In two further sessions, the subjects performed the full 180° test movement at slow speed. However, only the first four target elbow angles (60–105°; group 1) were presented during the first daily session, and only the last four target angles (120–165°; group 2) were presented during the second daily session. The test and report movements were similar to those in the basic SF task. Subjects performed 20 trials per target angle per active and passive SF-G task (320 trials in total).

Active/passive test movement: slow speed, pointer report, remembered angle (SP-R task)

The SP-R task further assessed any confounding factors that may have arisen when the subjects used the same unseen arm to sense and report the remembered elbow angles and to provide a control for the SP-C task. Subjects performed this task in two separate sessions, during which they reported the remembered elbow angle not by moving their arm, but by moving a pointer mounted above the manipulandum. The test movement and the target angles were the same as in the SF task. After completing the test movement, subjects kept their right arm in the fully extended position and used their left arm to move the pointer, positioned initially at the fully extended 180° angle, to an angle matching the remembered elbow joint angle. Subjects performed 20 trials per target angle per active and passive SP-R task (320 trials in total).

Active/passive test movement: slow speed, pointer report, current angle (SP-C task)

The SP-C task resembled the paradigm used by Wolpert et al. (1995). In this task, subjects stopped the test movement as soon as the mnemonic cue appeared (unlike all other tasks in which they continued moving) and kept their arm in that position. Subjects typically stopped the test movement 420–590 ms after the mnemonic cue appeared. They reported their current static elbow angle by moving the pointer with their left arm instead of attempting to reproduce a remembered joint angle. Subjects performed 20 trials per target angle per active and passive SP-C task (320 trials in total) in two daily sessions.

Data collection and analysis

The potentiometer data from the manipulandum and pointer were sampled at 200 Hz and stored on a PC, along with the onset time of all color cues. The stored times of the mnemonic cues verified that the elbow angle at which the cue appeared coincided with the intended target angles.

Data analysis was performed off-line using MatLab 7 (The Mathworks). Elbow movement angular velocity was calculated by differentiation of angular position records and low-pass filtered at 10 Hz with a zero-phase Butterworth digital filter. The target angle was the measured angular position at the time the mnemonic cue appeared in each trial (Fig. 2). The only exception was the SP-C task, in which the target angle was the final static elbow angle after the subjects stopped moving. To calculate the reported elbow angle in each trial, we averaged all samples of elbow angular position after the subject came to a stop during the report phase of that trial (angular velocity < 5% of the peak velocity in that trial). In pointer report tasks (SP-R and SP-C), the angular position of the pointer was used to calculate the reported angle. The report error was calculated by subtracting the target elbow angle from the reported angle. Report error was positive when the subjects overestimated the angle of elbow extension in the direction of the test movement and negative when the subjects underestimated it (Fig. 3). Mean report errors and SD were calculated for each target angle in each task for each subject.

FIG. 3. Example of data from a representative subject. ○, individual active trials; ●, individual passive trials. Solid thick and thin lines connect respective active and passive mean values for each target angle. Dotted diagonal line and gray squares indicate target angles (e.g., 0 error).
During the SP-C task, the target angles formed a continuous distribution of positions at which the subjects stopped their test movements rather than the fixed sets of target angles in all other tasks. To calculate mean report errors in this task, the elbow angles at which the subjects stopped were binned around the eight standard target angles, e.g., all elbow angles that fell between 68 and 83° were grouped into the 75° target bin and the report errors for that group of trials were averaged. Because of the delay needed to respond to the mnemonic cue and halt the movement, none of the subjects were able to stop quickly enough for their final elbow angles to fall within the 60° target angle bin and very few stopped within the next (75°) target angle range. Therefore these two target angles were dropped from the statistical analysis of the SP-C task.

In most tasks, subjects were asked to report their perceived elbow angle at the instant they saw the mnemonic cue. However, one can assume that there was a delay between the onset time of the mnemonic cue and its perception and interpretation by the subjects and a further central delay to associate it with the current sensed elbow angle. During those delays, the arm continued to move. Therefore errors in joint angle estimates of what the subjects perceived as temporally synchronous events may have actually resulted from temporally asynchronous perceptual and cognitive processes. To assess the possible effect of those delays, we converted the reported spatial errors into temporal errors by measuring the difference between the onset time of the mnemonic cue and the actual time at which the elbow was at the angle the subjects reported it to be when they detected the cue during the test movement (Fig. 2, SF). We called this measure the “cue-position time asynchrony.” A positive value meant that it took a certain period of time after cue presentation for the elbow to arrive at the position the subjects reported. This could reflect central processing delays. In contrast, a negative asynchrony value meant that the subjects reported an elbow angle that they had already passed by before the cue appeared. This could result from such factors asafferent feedback delays.

Statistical analysis was done using SYSTAT 11 (SPSS). Four repeated-measures ANOVA tests (tests 1–4) were applied to the report errors from individual trials of all tasks, all subjects pooled together. Test 1 included data from four tasks (SE, SF, FE, and FF) and consisted of four within-subject factors: angle (target angles 60–165°, 8 levels), type (active or passive, 2 levels), speed (fast or slow test movement, 2 levels), and report (flexion or extension report movement, 2 levels). Test 2 included data from three control tasks (SF, SF-G, and SP-R) and consisted of three within-subject factors: angle (target angles 60–165°, 8 levels), type (active or passive, 2 levels), and task (3 levels). Tests 3 and 4 were similar to test 2 and compared the errors in SP-C and SF-S tasks, respectively, against the errors in the SF task. These tasks were analyzed separately because they included smaller numbers of target angles. Test 3 had only six levels for the angle factor (90–165° target angles) because subjects were not able to stop close to the 60 and 75° target angles in the SP-C task. Test 4 had only four levels of the angle factor (target angles 60–105°) because of the shorter test movement in the SF-S task.

RESULTS

Overall performance

After the practice trials, the velocity profiles of each subject’s test movements became stereotyped and consistent in each task. The mean test movement velocities across all target angles ranged from 31 to 97°/s in the SF and SE tasks and 152 to 270°/s in the FF and FE tasks. The mean durations of the test movements ranged across subjects from 1.9 to 4.4 s in the slow tasks and 0.6 to 2.2 s in the fast tasks. The time-course of the actively performed and passively reproduced slow test movements were generally very similar (Fig. 2). Occasionally, there was a discrepancy in the kinematics of a pair of active and passive test movements, possibly because the subject inadvertently intervened to actively assist or resist the passive movement. Those trials were not included in the analysis. Several subjects spontaneously remarked that the passive tasks were easier to perform than the active tasks because they did not have to attend to the green start cue and make the test movements themselves. This provided further indirect evidence that they generally complied with the instructions to relax and let the manipulandum make the passive test movements.

In the FF and FE tasks, the inertia of the forearm often caused a small lag at the start of the passive test movements compared with the active movements. To compensate, the motor controller had to generate a large enough torque to cause the passive movement to catch up with the recorded active motion. As a result, the peak velocity of the fast passive test movements tended to be slightly greater and later than in the corresponding fast active movements.

The single-trial values and the means of the remembered elbow angles reported by a representative subject for each target angle in the SF, SE, FF, and FE tasks are shown in Fig. 3. This subject displayed the trends seen in all subjects. First, reported angles tended to increase systematically as a function of actual target angles in all tasks, indicating that subjects always had a sense of current angular position throughout the test movement. Second, all subjects showed a systematic trend for overestimation of elbow angle (positive report errors) early in the test movement and underestimation (negative report errors) near the end of the test movement. Third, this error bias was generally greater for passive-movement trials than for active-movement trials, resulting in particular in a greater overestimation of early target angles in the passive tasks. Figure 4 shows the mean and SD of the report errors, obtained by subtracting the target angle from the reported angle, pooled across subjects. The psychophysical function describing the errors in reported estimates of elbow angle during an elbow extension movement had an approximately linear form and

![Report errors from individual trials of all tasks, all subjects pooled together. Test 1 included data from four tasks (SE, SF, FE, and FF) and consisted of four within-subject factors: angle (target angles 60–165°, 8 levels), type (active or passive, 2 levels), speed (fast or slow test movement, 2 levels), and report (flexion or extension report movement, 2 levels). Test 2 included data from three control tasks (SF, SF-G, and SP-R) and consisted of three within-subject factors: angle (target angles 60–165°, 8 levels), type (active or passive, 2 levels), and task (3 levels). Tests 3 and 4 were similar to test 2 and compared the errors in SP-C and SF-S tasks, respectively, against the errors in the SF task. These tasks were analyzed separately because they included smaller numbers of target angles. Test 3 had only six levels for the angle factor (90–165° target angles) because subjects were not able to stop close to the 60 and 75° target angles in the SP-C task. Test 4 had only four levels of the angle factor (target angles 60–105°) because of the shorter test movement in the SF-S task.](https://www.jn.org/content/98/3/1144/F2.large.jpg)
negative slope that was consistently steeper in all passive task conditions. Contrary to the working hypothesis, the subjects showed no evidence of a reduction in initial overestimation during passive elbow movements. Intertrial variability also tended to be somewhat greater for fast test movements, as indicated by the SD bars (Fig. 4).

ANOVA test 1 (see methods) showed highly significant main effects for all factors ($P < 0.001$). However, significant two-way interactions also arose between all factors, which confound the interpretation of the main effects and are discussed in more detail below. Some two-way and all three-way and four-way interaction effects were not statistically significant (type/report: $P = 0.360$, speed/report: $P = 0.376$, angle/type/speed: $P = 0.816$, angle/type/report: $P = 0.146$, angle/speed/report: $P = 0.392$, type/speed/report: $P = 0.584$, angle/type/speed/report: $P = 0.267$).

Active versus passive test movement

Mean report errors were larger in passive trials than in active trials, but this difference was not uniform across target angles and tasks (Figs. 4 and 5A). Consequently, in addition to the significant main effects for angle and type factors, there was a significant two-way interaction between them ($P < 0.001$). Subjects systematically showed greater overestimation of elbow angle in the early part of passive movements compared with corresponding active movements (Fig. 5A).

Speed of test movement

Errors in elbow angle estimates were significantly larger in fast test-movement trials compared with slow test-movement trials (Figs. 4 and 5B). Significantly larger overestimates occurred for target angles in the first part of the fast test movements compared with slow test movements (significant interaction between speed and angle factors: $P < 0.001$). The difference between active and passive report errors also changed at different speeds of the test movement (significant interaction between speed and type factors: $P < 0.001$). These findings raised the possibility that all reported trends were speed-related. To assess this possibility, we examined the dependence of target angle estimates on the kinematics of test movements in more detail.

Figure 6 shows the mean angular velocity of elbow movements at each target angle in the four main tasks. In the SF and SE tasks, elbow rotation velocity tended to be highest for the 75 and 90° target angles and gradually decreased for the remainder of the test movement. Mean angular velocities were virtually identical at all target angles for active and passive SF and SE test movements (Fig. 6). The robot was somewhat less successful in replicating the kinematics of the active fast test movements during the passive fast conditions. Passive joint rotations were slightly slower at the 60 and 75° target angles and faster at all subsequent target angles as the robot exerted more torque to correct for the initial lag in joint kinematics in passive trials compared with the active trials it was attempting to replicate. As a result, peak joint velocities occurred at the 90 and 115° angles for the fast active trials and at 115 and 130° angles for the fast passive trials. However, report errors tended to be smallest at those target angles, both in the FF and FE tasks, as well as in the SF and SE tasks (Figs. 2 and 3), so that the amplitudes of report errors at different target angles did not parallel the speed profiles in different tasks.

Nevertheless, further analysis revealed a strong velocity-dependent effect on report errors for many target angles, whose nature was also strongly dependent on where the target angle was located in the test movement (Fig. 7). Trials for each target angle were pooled across slow and fast movement tasks, and binned according to the elbow velocity. Most trials with velocities $<100°/s$ at a given target angle came from slow tasks, whereas most trials with velocities $>100°/s$ occurred in fast tasks (cf. Fig. 6), but there was some overlap at all target angles. For the 60 and 75° target angles, report error size tended to be fairly constant for slow-velocity movements but increased rapidly as velocity increased (Fig. 7A). Overestimation errors rose more rapidly for a given velocity during passive movements than active movements. The slope of this
Direction of report movement

Positive report errors were significantly larger and negative report errors were nonsignificantly smaller during extension-report trials compared with flexion-report trials (SE/FE vs. SF/FF; Fig. 4; significant 2-way interaction between angle and report factors: \( P < 0.001 \)). This shows that reports of remembered elbow angles with extension movements shifted the errors in angle estimates slightly toward overestimation (Figs. 4 and 5C).

The peak velocities of flexion report movements decreased from 133 ± 29 to 62 ± 8\% for target angles 60–165°, respectively, but the peak velocities of extension report movements increased from 89 ± 16 to 148 ± 15\% for the same target angles. These trends show that longer report movements had larger peak velocities and that flexion and extension report movements of similar amplitudes were performed with similar speeds. Despite the reversal in the values of peak velocities associated with different target angles during flexion and ex-

Cue-position time asynchrony

The range and intertrial variability of asynchrony values were much larger during slow movements than fast movements. The mean cue position time asynchrony values during slow test movements were initially positive, ranging 0.27 ± 0.12, 0.20 ± 0.16, 0.19 ± 0.21, and 0.08 ± 0.21 s (±SD) for target angles 60–105°, respectively. During fast test movements, they were 0.13 ± 0.09, 0.10 ± 0.08, 0.06 ± 0.08, and 0.04 ± 0.08 s for the same target angles. The for the 120–165° target angles, the cue position time asynchrony values became negative: −0.07 ± 0.32, −0.14 ± 0.30, −0.23 ± 0.31, and −0.44 ± 0.32 s, respectively, during slow test movements, and 0.02 ± 0.07, −0.02 ± 0.07, −0.05 ± 0.07, and −0.11 ± 0.08 s, respectively, during fast test movements. These values show that the cue position time asynchrony was not constant at different movement speeds or at different times in the trial. Note that any asynchrony value more positive than about −0.03 s is shorter than any proprioceptive feedback delay, whereas values more negative than −0.1 or −0.2 s would seem to be too long to be explained by feedback delays.

FIG. 6. Mean elbow angular velocity at each target angle during SF, SE, FF, and FE tasks, pooled across all subjects. Plots show mean ± SD.

FIG. 7. Relationship between report errors and elbow angular velocity at each target angle during SF, SE, FF, and FE tasks. A: report errors at target angles 60 (diamonds), 75 (circles), 90 (squares), and 105° (triangles); B: report errors at target angles 120 (diamonds), 135 (circles), 150 (squares), and 165° (triangles). Active trials are shown by solid lines with filled symbols (A60–A165); passive trials are shown by dashed lines with open symbols (P60–P165). Symbols represent means ± SE for each target angle.
tension report movements, there was no reversal in error trends.

**Pointer report**

Elbow angle errors reported using a pointer (SP-R task; Fig. 8) showed very similar trends to those made with the subjects’ arm (SF task; Fig. 4). However, all effects within ANOVA test 2 were statistically significant, because subjects tended to show larger initial overestimates and later underestimates with pointer reports (angle and type: \( P < 0.001 \); task: \( P = 0.008 \); angle/type, angle/task, and type/task: \( P < 0.001 \); angle/type/task: \( P = 0.038 \)).

In striking contrast to the SP-R and all other tasks, report errors in the SP-C task were mainly negative (underestimation) at all target angles, with no initial overestimation, when subjects stopped moving their arm when the mnemonic cue appeared and reported the final static angle of their elbow with the pointer (Fig. 8). ANOVA test 3 found significant main effects and interactions for the task and angle factors between SP-C and SF tasks (angle: \( P < 0.001 \); task: \( P = 0.011 \); angle/task: \( P < 0.001 \); type: \( P = 0.579 \)). No other two-way interactions were significant (angle/type: \( P = 0.986 \); type/task: \( P = 0.622 \)), but the three-way interaction was statistically significant (angle/type/task: \( P = 0.018 \)). The mean size of the errors in the SP-C task varied from \(-3.9 \pm 5.9 \) to \(-10.0 \pm 6.4^\circ\). These errors tended to be smaller across the full range of target angles compared with the errors in all other tasks, and there was much less intertrial and intersubject variability in the report errors in the SP-C task (note the smaller SD bars for the SP-C task in Fig. 8 compared with all other tasks).

**Grouped target angles**

The errors reported after grouped presentation of target angles in the active and passive SF-G tasks (Fig. 8) were similar to those reported in the SF task (Fig. 4) where the entire range of target angles were randomly presented. Two subjects showed a possible effect of the range of experienced target angles on report errors, because their estimates were more positive for the \( 120^\circ \) target angle (1st target angle of group 2) than for \( 105^\circ \) (last target angle of group 1). However, no other subjects showed this discontinuity, and their report error patterns formed a more continuous trend across both target angle groups, similar to their responses in the SF task.

**Short range of test movement**

Report errors for the SF-S tasks, in which the range of target angles and the extent of the test movement were halved, are plotted on Fig. 8. This had very little effect on report errors (no significant main effect for the task factor between SF and SF-S tasks, angle and type: \( P < 0.001 \); task: \( P = 0.569 \); angle/type and angle/task: \( P < 0.001 \); type/task: \( P = 0.552 \); angle/type/task: \( P = 0.548 \)).

**Discussion**

Transient overestimation of hand position or joint angle before and during the early part of active arm movements has been interpreted as evidence of an efference copy-based forward prediction of limb state (Ariff et al. 2002; Dassonville 1995; Lonn et al. 2000; Sanes 1986; Wolpert et al. 1995). We also found that subjects overestimated their elbow angle early in active test movements and that they underestimated it later in the movements. The resulting error trend was a nearly linear function of target angle, with a negative slope. The subjects responded as if they associated early mnemonic cues with elbow angles that they had not yet physically attained and late cues with elbow angles that they had already passed before the cue appeared. This trend during active movement tasks is consistent with a state estimation process that relies mainly on efference copy early in the movement and mainly on delayed afferent feedback later in the movement (Vaziri et al. 2006; Wolpert et al. 1995). However, some of the underestimates, especially in the slow test movements, appear to be too large to be explained by afferent feedback delays (i.e., cue position asynchrony values more negative than about \(-0.10 \) s). Furthermore, this does not readily account for the systematic small underestimation in the SP-C task, in which subjects reported their current static elbow angle at the end of movement. For a detailed comparison of the results of this study with those of several other key studies, see the Appendix.

The main goal of this study was to test the prediction of the efference copy hypothesis that position errors will decrease or shift to underestimates when the state estimation process is deprived of an efference copy during passive movements (Wolpert et al. 1995). Contrary to the predicted result, the main finding of this study was that subjects also reported overestimates of elbow angle during passive movements that were as large as or larger than in active movements with identical kinematics, yielding a report error function with an even steeper negative slope than in active movements. The trends were very consistent across subjects and remarkably robust across several different tasks tested in different sessions, often separated by periods of weeks. A study by Cordo et al. (1994) also found some position overestimates during passive movements (see Appendix).

Another major finding was that subjects showed very similar error trends when they reported their elbow angles sensed...
during movement with an external pointer instead of their arm. Finally, when subjects stopped their test movements near the same target angles and reported their final static elbow angle with a pointer, report errors were smaller and less variable on average than when reporting elbow angles sensed during movement, and there was a nearly uniform underestimation of elbow angles across the entire range of tested static angles. This shows a striking difference in the perception of joint angles during movement versus static postures.

These findings show that overestimation of elbow angles during active movements is not proof on its own of forward prediction based on efference copy. This suggests either that forward prediction of limb state can still occur without an efference copy of a motor command or that some process other than forward prediction caused the perceptual errors. Nevertheless, elbow angle estimates were more accurate during active movements compared with passive movements, as has been reported for static position estimates after active arm movements (Adamovich et al. 1998; Craske and Crawshaw 1975; Lonn et al. 2000; Paillard and Brouchon 1968; Winter et al. 2005). This indicates that an efference copy improves arm state estimation during active movement.

Three main factors, afferent input, efference copy, and signal noise and uncertainty, seem to account for the main findings of this study. We will discuss each of these in turn in the following sections. A variety of other factors and confounds could have contributed to some of the results, but probably played only a minor role (for details, see Appendix).

Contribution of afferent input to the errors in elbow angle estimates

It seems reasonable to assume that kinesthetic sensations during passive movements will lag the physical motion in time because of the delays needed to relay the afferent signals to the cerebral cortex and process them. In contrast, initial position overestimates in passive movements in this study were as large as or larger than in active movements. This would suggest prima facie that the perceptual performance of the subjects during both active and passive movements resulted primarily from processing of afferent input, without having to invoke an efference copy-mediated mechanism to account for position overestimates during active movements.

Proproceptive afferent signals reach the cortex in as little as 20–30 ms in nonhuman primates (Conrad et al. 1977; Evarts and Fromm 1981; Fetz et al. 1980; Fromm and Evarts 1982; Fromm et al. 1984; Soso and Fetz 1980). As a result, the cortex is processing afferent input from the moving limb long before the subjects reached the first target angle (60°), 100–500 ms or more after movement onset (Fig. 2). Indeed, the original motivation for the fast test–movement tasks was a concern that the short latency of the afferent input might mask any forward prediction effect during slow active movements and any perceptual lag during slow passive movements. The underestimates in the late part of test movements could reflect the feedback delay, but this does not explain why negative asynchrony values are not constant and ranged from −0.02 s to values as large as −0.44 s and even longer.

Initial overestimates were velocity dependent and therefore could be caused by central processing of dynamic afferent signals generated during active and passive movement that are proportional to velocity and higher-order derivatives of joint angle or muscle length (Cordo et al. 1994; Sittig et al. 1987). Muscle spindle signals both muscle length and its rate of change during movement (Hagbarth and Vallbo 1969; Kakuda and Nagaoka 1998; Matthews and Stein 1969; Prochazka et al. 1977; Proske 2006; Scott and Loeb 1994; Vallbo and Hagbarth 1967). Furthermore, primary spindle afferents often emit a brief history-dependent initial burst in firing frequency at movement onset ("short-range stiffness": Cordo et al. 2002; Gandevia 1996; Proske 2006), which may further contribute to initial overestimates (Burke et al. 1976; Edin and Vallbo 1990; Jones et al. 2001b; Kakuda and Nagaoka 1998). Dynamic signals from tactile receptors might also contribute (Cohen et al. 1994; Collins and Prochazka 1996; Collins et al. 2005; Edin and Abbs 1991).

This suggests that the overestimation errors could result from a state estimation process that used the dynamic afferent signals generated early in active and passive movements to predict the state of the limb in the near future even in the absence of an efference copy. Alternatively, the velocity-dependent dynamic signals could simply be confounded with afferent input about current joint angle or muscle length, resulting in initial overestimation caused by a perceptual error rather than by overt forward prediction.

Similarly, the slightly larger error amplitudes and the greater effect of speed on report errors during passive compared with active movements, despite their closely matched kinematics, could partly reflect state-dependent differences in proprioceptive feedback (Hulliger et al. 1982; Jones et al. 2001b; Kakuda and Nagaoka 1998; Prochazka 1986; Roll and Vedel 1982; Rothwell et al. 1990). This is likely because of fusimotor co-activation of muscle spindles (Vallbo 1971) and history-dependent properties of intrafusal muscle fibers, i.e., thiotropism, which may cause differences in spindle discharge rates before, during, and after active and passive movements (Ansems et al. 2006; Mel’nicchouk et al. 2006; Proske et al. 1993; Winter et al. 2005). Finally, although many neurons in the primary somatosensory cortex that receive inputs from deep (i.e., nontactile) receptors have similar discharge patterns during passive and active movements, many others have very different responses (Prud’homme and Kalaska 1994; Soso and Fetz 1980).

Efference copy, state estimation, and kinesthetic sensation

A role for efference copy in state estimation is well established in control theory and in motor control studies (Blushan and Shadmehr 1999; Miall et al. 1993; Sabes 2000; Wolpert and Kawato 1994). Evidence for a role for efference copy in kinesthetic sensation has been provided by overestimates of hand position or joint angle before and during active movements (Ariff et al. 2002; Dassonville 1995; Lonn et al. 2000; Sanes 1986; Wolpert et al. 1995), by more accurate estimates of static position after active movements than passive movements (Adamovich et al. 1998; Craske and Crawshaw 1975; Laufer et al. 2001; Lonn et al. 2000; Paillard and Brouchon 1968, 1974; Winter et al. 2005), and by perceptual deficits after cortical lesions (Wolpert et al. 1998). The reduction of position estimation errors during active compared with passive movements in this study indicates that an efference copy improves arm state estimation during active movement. This is also
supported indirectly by the activation of many proprioceptive neurons in cerebral cortex areas 2 and 5 before active movement onset (Fromm and Evarts 1982; Kalaska and Crandall 1992; Prud’homme and Kalaska 1994; Soso and Fetz 1980). The early activity could be caused by a centrally generated signal about motor output that projects onto populations of neurons that contribute to kinesthetic sensations (Christensen et al. 2007).

However, attempts to show that an efference copy on its own can generate or alter conscious kinesthetic sensations have yielded mixed results. Early studies failed to report sensations of movement or changes in limb position when clinically or experimentally paralyzed subjects or amputees tried to move a paralyzed or missing limb, provided that their attempts did not cause overt muscle contractions (Goodwin et al. 1972; Jeannerod 1988; McCloskey and Torda 1975; Prosek 2006). At best, they only elicited sensations of effort, force, and heaviness (Gandevia 1996; Jeannerod 1988; Prosek 2006). In contrast, subjects in a recent study reported sensations of movement and altered limb position that scaled with the direction and magnitude of their efforts to move during transient ischemic paralysis and deafferentation of the arm (Gandevia et al. 2006). Similarly, other recent studies reported position estimation errors after fatiguing contractions of muscles that required augmented motor commands to produce the same outputs (Allen and Prosek 2006; Walsh et al. 2004; Winter et al. 2005). Attempts to evoke sensations of movement by using transcerebral magnetic stimulation of the motor cortex to simulate an efference copy have also yielded conflicting results (Amassian et al. 1989; Brasil-Neto et al. 1993; Ellaway et al. 2004).

This study took the opposite approach to assess the role of efference copy in kinesthetic sensations by testing the prediction that psychophysical evidence for forward prediction of sensed joint angles would decrease during passive movements when no efference copy is available. The findings were opposite to the predicted results. This does not imply that there is no state estimation process in kinesthetic sensation or that efference copy is not involved. It also suggests that short-latency afferent input could make a greater contribution to future state estimation in kinesthetic sensation during arm movements than had been previously recognized.

Signal noise, uncertainty, and position estimation

A different way to regard the initial overestimates and later underestimates in this study is that the subjects perceived that their elbow dwelled near the middle of its range of motion for a greater period of time during the test movements than it actually did physically. This effect disappeared when the subjects reported their static elbow angle after movement.

The results of this study support the hypothesis that the kinesthetic system uses sensory feedback and efference copies of motor commands to estimate the current limb state. However, both signals are subject to stochastic and signal-dependent noise and so have a variable degree of uncertainty associated with them (Bays and Wolpert 2007; Geisler and Kersten 2002; Kording and Wolpert 2006a,b; Scott and Loeb 1994; Stocker and Simoncelli 2006; Tassinari et al. 2006; van Beers et al. 2002). The error trends across the different task conditions seem to parallel the likely level of uncertainty in the resulting position estimates.

For instance, during static postures, afferent signals are relatively stable across time and can be sampled over hundreds or thousands of milliseconds by the subjects to reduce the effect of stochastic noise on the reliability of the position estimate drawn from the input. As a result, subjects’ estimates of static elbow angles were of nearly uniform accuracy and low intertrial variability across the entire range of tested positions during both active and passive tasks.

In contrast, input signals during movement will have substantially greater variability and uncertainty than during static postures. The motor output command and feedback signals change continually during movement and are strongly modulated by such factors as movement speed, load, and torques (Cheney 1980; Costanzo and Gardner 1980; Gardner and Costanzo 1980; Kalaska et al. 1989; Prud’homme and Kalaska 1994; Sergio et al. 2005; Soso and Fetz 1980). Furthermore, they can only be sampled for a brief period to estimate a transient position at some point during the movement. Fixed feedback delays, more rapid changes of signals with time, and greater signal-dependent noise all likely add even greater uncertainty to the signals during fast movements than during slower ones. In parallel, the slope of the position-estimate error function rotated from nearly horizontal in the static condition to negative for slow test movements and even more negative during fast movements. The negative slope was also always steeper during passive movements than active movements at any speed.

Strikingly similar trends were reported in a recent study of optimally guided pointing under different degrees of uncertainty of visual feedback (Kording and Wolpert 2004). Their results suggested that the subjects used a strategy resembling Bayesian probabilistic inference to combine information about the statistics of the task and the feedback uncertainty in an optimal fashion.

The same psychophysical trends in this study suggest that the subjects also used a Bayesian inference process to estimate elbow position. The kinesthetic system used afferent input and efference copy to continuously update the current estimate of elbow position (the sensory-motor “likelihood”). The current likelihood was combined with a kinesthetic “prior” of previously experienced sensory-motor states to produce the optimal estimate of current position (the “posterior”) under the current condition of sensorimotor uncertainty. The greater the uncertainty in the input signals generating the current likelihood, the more the optimal estimates were biased toward the mean of the prior (Bays and Wolpert 2007; Kording and Wolpert 2004, 2006a,b; Tassinari et al. 2006; van Beers et al. 2002). For instance, during passive movements, the lack of an efference copy, the afferent feedback delays, and state- or history-dependent differences in afferent input signals compared with active movements could all increase the noise and uncertainty in the current likelihood estimate. This would in turn lead to an increased reliance on the kinesthetic prior and an increase in the slope of the error function. The strong centralizing tendency in position estimates with increasing uncertainty could be explained if the kinesthetic prior, accumulated over a lifetime of arm movements, is biased toward sensorimotor states in which the elbow was near the middle of its anatomical range of motion. There have been very few studies of the statistics of arm movements during daily activity. However, one recent study of the spatial distribution of natural arm
motions suggest that this is a reasonable assumption (Graziano et al. 2004) but still requires experimental verification.

This Bayesian inference hypothesis accounts for the striking difference in position estimates during movement versus posture, explains why error patterns are overestimates early in movements and underestimates late in movements, and accounts for the effect of such factors as active versus passive movements, fast versus slow movements, and the influence of target angle location on the amplitude and pattern of estimation errors. It also leads to a number of predictions that will be tested in future studies.

APPENDIX

Comparison with previous studies

Consistent with the studies of Dassonville (1995) and Wolpert et al. (1995), our results suggest that the cortical representation of dynamic elbow position seems to lead its physical location early in movements. However, neither of these studies observed underestimates in perceived elbow angle late in the test movements or during static postures. One possible explanation is that the movements in the other studies used more than one joint and/or did not require joint angle excursions as great as the elbow rotations used in this study. Acuity of position sense varies throughout the physiological range of movement (Friden et al. 1996; Janwantanakul et al. 2001) and between joints (Hall and McCloskey 1983), which may contribute to differences in perceptual position errors. Another factor is that the subjects in this study received no visual input about arm position at any time during the experiment. In contrast, subjects in the other studies received visual feedback of the starting position of their hand in every trial. Furthermore, the late mnemonic cues in the study of Dassonville (1995) often occurred after the subjects had stopped their arm movement and therefore needed no arm movement to report their position estimate. Finally, some technical details or procedures specific to our task paradigm and task apparatus may have led to an underlying bias for static elbow angle underestimation.

Unlike the subjects in Wolpert et al. (1995), our subjects did not overestimate their elbow angle when they stopped their test movement shortly after its onset in the SP-C test. However, the earliest cue to stop movement in our task did not occur until after the period of peak overestimates in the study of Wolpert et al. (1995) had occurred. Had we given mnemonic cues earlier in the movement and therefore needed no arm movement to report their position estimate. Finally, some technical details or procedures specific to our task paradigm and task apparatus may have led to an underlying bias for static elbow angle underestimation.

Speed of movement cannot account for the error patterns

Test movement speed had a strong effect on perceived joint angles. However, movement speed per se was not the main causal factor for the error trends. First, the effect of speed on report errors depended strongly on when a given speed occurred in the test movement. Higher speeds resulted in greater overestimates for a given target angle early in the movement but underestimates late in the movement. Second, the greatest speeds during fast-movement tasks occurred at the middle target angles, but report errors were the smallest at those angles.

Psychophysical “range effect” cannot account for the error patterns

One possible origin for the error biases is a “range effect” whereby the responses of subjects to stimuli or events at the extremes of the range of experienced conditions tend to migrate toward the mean value of the conditions (Poulton 1979, 1981). This centralizing tendency would cause the reports associated with early and late target angles to drift toward the mid-range of target angles, resulting in early overestimates and late underestimates.

The SF-G and SF-S tasks tested this possibility by reducing the range of target angles or the test movement in a block of trials. If the error biases were primarily caused by a range effect, over- and underestimates should redistribute symmetrically around the mean value of the smaller range. In contrast, errors in the SF-S and SF-G tasks were very similar to those in the standard tasks. This indicated that the location of the target angle relative to the start of the test movement had a much bigger effect on report errors than the range of target angles experienced in a given block of trials. Furthermore, the report errors in the SP-C task were always underestimates and were nearly uniform across all target angles. They did not show any evidence of a range effect even though the range of static target angles was very similar to those experienced in the other tasks.

One criticism of our tests for a range effect is that the subjects did not have all the other tasks, and so they had considerable prior experience with the full range of target angles. This may have made them less likely to change their report errors to match the range of target angles in a given block of trials. However, it is once again noteworthy that the same experienced subjects showed no evidence of a range effect in the SP-C task. It is also not apparent how a range effect could account for other robust trends, such as the large difference in the effect of movement speed on error estimates for early and late target angles.
Report movements are not the cause of errors in elbow angle estimation

In the basic task design, subjects used the same arm for the test and report movements rather than, for instance, reporting elbow angles with the other arm. This could have introduced confounds that affected the reports. For instance, the duration of the memorized delay interval between the mnemonic cue and the end of the report movement was longer for early than late target angles in the SF and FF tasks. The perceived elbow angle could arise from different combinations of dynamic and static afferent signals during the test movement and at the end of the report movement. Finally, kinesthetic sensations during the report movement could have interfered with the memory of the target angle sensed during the test movement. However, several findings showed that the means by which the subjects reported their elbow angle estimates was not responsible for the pattern of report errors.

Reversing the direction of the report movement from flexion (SF and FF tasks) to extension (SE and FE tasks) caused a small but nearly uniform shift of report errors toward increased overestimation, but otherwise had little effect on the overall error trend.

More importantly, subjects showed the same basic error trends when they held their sensing arm fully extended at the end of the test movement and reported with a pointer (SP-R task). This deprived the subjects of all proprioceptive input that they could use to match their report angle to the memory trace of the target angle and required a spatial transformation to align the pointer visually with the kinesthetically sensed elbow angle. It also eliminated many confounding factors related to different sources of position signals during movement versus static postures and to the mechanics of report movements on the observed estimation errors of elbow angles.

This showed that the subjects did not make report errors because they used different combinations of dynamic and static afferent inputs to sense and report elbow angles with their arm. The striking difference in errors between the SP-R and SP-C tasks, when subjects stopped near the same target angles and reported their final static elbow angle, further reinforced this conclusion. This also showed that a given elbow angle can be perceived differently during and after movement and that subjects can reliably report those differences by various means.

Fixed central processing delay or afferent feedback delay cannot account for the error patterns

Larger overestimates with higher movement speeds could result from a constant central processing delay, during which time perceptual and cognitive processes detect and interpret the mnemonic cue before retrieving and memorizing the current perceived limb position. During this delay before registering the perceived limb position, the arm would continue to move and would move a greater distance at higher speeds. This would produce cue position time asynchrony values that are positive and constant throughout the test movement. However, this predicts that the pattern of report error amplitudes should parallel the speed profiles in each task, and they clearly did not. Furthermore, the cue position time asynchrony measures were not constant. Instead, they were positive early in the movements, but decreased progressively and became negative late in the movements. In contrast, if position estimate errors had been caused by a fixed feedback delay, the asynchrony values would have been uniformly negative throughout the movements. This is consistent with the negative asynchrony values late in the movements but not with the initial positive values. It also does not explain why negative asynchrony values ranged from as low as $-0.02$ s to as large as $0.44$ s. Finally, there is no obvious reason why the range of asynchrony values should be much larger and more variable during slow movements than fast movements. Fixed central or peripheral delays cannot provide an explanation for the overall error patterns.

Finally, the SP-C task was the only one in which subjects did not memorize a transiently sensed position and then recall it later. It is not obvious, however, how memorization per se could account for the target angle- and speed-dependent features of the report error trends seen in all the other tasks.

Cognitive factors

A number of other factors could have contributed to the amplitude or pattern of position errors in this task.

ATTENTION. The paradigms were demanding. The subjects had to divide or switch their attention between a sequence of sensory instructions, kinesthetic sensations, and motor events in each trial. This attentional load could have contributed to the amplitude of perceptual errors. However, several subjects noted that the passive tasks were easier to perform because they did not have to attend to as many different factors as in the active tasks, yet their errors were slightly greater than in the more demanding active tasks.

EXPECTATION. The distribution of mnemonic cues was uniform across the range of test movements in all tasks. As a result, a cue presented very early in the movement may have been relatively unexpected, whereas cues presented late in the movement would be increasingly anticipated as the subjects performed the test movement. The surprise value of early cues could have delayed the response of the subjects to their appearance, whereas increasing expectation of late cues could have facilitated their response. This could explain why cue position asynchrony values for early targets were more positive in slow movements than fast movements (i.e., longer central processing delay), because the greater temporal dispersion of cue appearance during slow movements would make early targets more “surprising.” However, this does not explain the negative asynchrony values for later cues, which would imply that the subjects were responding to the cues before they actually appeared.

DISTORTIONS IN THE RELATIVE TIMING OF EVENTS. Subjects often show distortions in the perceived timing of sensory and motor events around the time of movement onset (Eagleman et al. 2005; Haggard and Cole 2006; Haggard and Magnon 1999; Haggard et al. 2002; Spence et al. 2001; van de Grind 2002). Similarly, Dassonville (1995) suggested that arm position overestimates resulted from a transient temporal asynchrony in the cortical representation of tactile inputs and limb movements. Similar processes could have altered the subjects’ experience of the relative timing of movement onset, mnemonic cue presentation, and current elbow angle in both active and passive conditions in this study. However, this mechanism also does not explain the underestimation of elbow angles in the late part of the movements.

MENTAL REHEARSAL. The passive tasks should have eliminated any efference copy of an overt motor command. However, covert mental processes may have caused the overestimates seen in the passive tasks. For instance, the subjects knew at the start of every trial that they would experience a passive elbow extension. As a result, the onset of the passive movement may have evoked a covert mental rehearsal of the expected motion. Mental rehearsal activates cortical motor circuits (Buccino et al. 2001; Cisek and Kalaska 2004; Crammond 1997; Jeannerod 2001) and may have the same effect on limb state estimation as an efference copy of an overt motor command.

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