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# Divided Attention Impairs Human Motor Adaptation But Not Feedback Control

# Jordan A. Taylor and Kurt A. Thoroughman

Department of Biomedical Engineering, Washington University in St. Louis, St. Louis, Missouri

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Taylor JA, Thoroughman KA. Divided attention impairs human motor adaptation but not feedback control. J Neurophysiol 98: 317-326, 2007. First published April 25, 2007; doi:10.1152/jn.01070.2006. When humans experience externally induced errors in a movement, the motor system's feedback control compensates for those errors within the movement. The motor system's predictive control then uses information about those errors to inform future movements. The role of attention in these two distinct motor processes is unclear. Previous experiments have revealed a role for attention in motor learning over the course of many movements; however, these experimental paradigms do not determine how attention influences within-movement feedback control versus across-movement adaptation. Here we develop a dual-task paradigm, consisting of movement and audio tasks, which can differentiate and expose attention's role in these two processes of motor control. Over the course of several days, subjects performed horizontal reaching movements, with and without the audio task; movements were occasionally subjected to transient force perturbations. On movements with a force perturbation, subjects compensated for the force-induced movement errors, and on movements immediately after the force perturbation subjects exhibited adaptation. On every movement trial, subjects performed a two-tone frequencydiscrimination task. The temporal specificity of the frequency-discrimination task allowed us to divide attention within and across movements. We find that divided attention did not impair the withinmovement feedback control of the arm, but did reduce subsequent movement adaptation. We suggest that the secondary task interfered with the encoding and transformation of errors into changes in predictive control.

## INTRODUCTION

Attention is seemingly required to learn a novel motor skill, such as learning a new racquetball serve, but how attention assists in the control of movement and learning is unclear. Motor learning requires the detection and evaluation of movement errors and the subsequent transformation of those errors into changes in predictive control of future movements. Recent studies of motor adaptation revealed that the learning process occurs on a trial-by-trial basis; an error in a single movement informs the immediately subsequent movement (Fine and Thoroughman 2006; Scheidt et al. 2001; Thoroughman and Shadmehr 2000; Thoroughman and Taylor 2005). The role of attention in the monitoring of movement errors, initiation of feedback control, and trial-by-trial adaptation is currently unknown.

The role of attention in motor control and learning can be investigated using a dual-task paradigm. Interference effects between a primary motor task and the secondary task occur if one or both of the tasks require sufficient attention and the two tasks share limited resources (Frensch 1998; Schmidt 1988). Most dual-task implicit learning research has focused on the learning of an underlying sequence of key presses in a serial reaction time task. In a serial reaction time (SRT) task (Nissen and Bullemer 1987), subjects are presented with a series of cued key presses and subjects are required to press a key when cued. If the series of key presses has an underlying sequence, then over training subjects learn to make the key presses faster than if the series was random. However, when subjects are distracted by a secondary task, they do not learn (Nissen and Bullemer 1987) or become aware of the underlying sequence (Curran and Keele 1993). Further SRT task studies have suggested that the learning process was not impaired by the imposition of the secondary task, but rather the expression of what was learned was impaired (Frensch et al. 1998). Although these studies have established a role of attention in implicit learning, the results are difficult to interpret because of the structure of the sequences in the task (Stadler 1995) and may not be applicable to sensorimotor transformation/recalibration experiments.

The experimental paradigm used in these studies limits the temporal separation of how divided attention affects the within-movement feedback control of the arm and across-movement adaptation. In general, these experiments use the secondary task in between key presses; therefore we cannot determine how divided attention affects within-movement control. To determine learning, the sequences are presented repeatedly in blocks and the learning from one block of multiple key presses is compared with the previous block of multiple key presses. This makes it difficult to determine how the dual task affects the learning from a single trial to the immediately subsequent trial. In addition, the implicit learning of sequence may involve different learning processes (Hikosaka et al. 1999; Seidler 2006) and neural systems than sensorimotor transformation learning (Ghilardi et al. 2000).

A few studies have provided evidence that attention is necessary to learn sensorimotor transformations. In a pointing prism adaptation task, imposition of a cognitive load (mental arithmetic) interfered with adaptive eye/hand coordination (Redding et al. 1992). Specifically, the cognitive task led to less reliable pointing and reduced ability to correct for terminal errors (Redding et al. 1992). Imposing a visuomotor gain change during a reaching movement combined with a cognitive load (counting backward) significantly affected adaptation in a deafferented patient (Ingram et al. 2000). To account for the

Address for reprint requests and other correspondence: K. A. Thoroughman, Department of Biomedical Engineering, Washington University in St. Louis, Campus Box 1097, One Brookings Drive, St. Louis, MO 63130 (E-mail: thoroughman@wustl.edu).

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loss of proprioceptive sense, the deafferented patient required attention to monitor position errors in movement (Ingram et al. 2000). When patients with lesions of the cerebellum performed a figural-drawing task under a cognitive load (letter detection), the number of figures drawn was reduced (Lang and Bastian 2002). In the same study, they found decreased learning rates for the figural drawing task in neurologically normal subjects (Lang and Bastian 2002). These studies suggest that when subjects initially perform a motor task or have a motor deficit, attention is necessary to monitor movements and evaluate errors to facilitate learning and successful performance of the task.

However, these studies examined only the learning of kinematic parameters, such as visuomotor transformations, and did not focus on the learning of dynamic parameters such as force production. Translating the results from visuomotor transformation studies to dynamic force learning may not be prudent. While engaging overlapping neural systems, the learning of kinematic variables as opposed to dynamic variables has shown differences in memory consolidation (Tong and Flanagan 2003) and neural activation (Clower et al. 1996; Ghilardi et al. 2000; Imamizu et al. 2000; Seidler et al. 2004, 2006). In addition, similar to the SRT experiments, these studies required subjects to perform the dual-task experiment over the course of many movements. The secondary tasks were not closely coupled with the motor tasks; therefore the temporal specificity of attention during a single movement cannot be elicited nor how divided attention in previous movements influence future movements. To examine the moment-to-moment role of attention within a movement and how it translates into trial-by-trial changes in motor control, the secondary task needs to vary temporally within a movement and repeat across movements.

Here we developed a dual-task paradigm that has the temporal resolution to interrogate within- and across-movement interaction of attention with motor control and adaptation. Infrequent transient force perturbations were randomly introduced into movements to investigate the feedback control of arm movements while subjects performed a frequency-discrimination task that varied in time of presentation and performance level. In addition, the force perturbations induced changes in predictive control of arm movements (Fine and Thoroughman 2006), which allowed the single-trial adaptive properties of the motor system to be examined under divided attention. We report three significant findings: 1) the within-movement feedback control of arm movements was unaffected by the secondary task; 2) perturbing the arm delayed the secondary task

Movement Feedback Target Appearance **First Tone** Tone @ 9cm Non-pulsed Movements (prepulse and postpulse) **Pulse Movement** orc 0 3 9 5 10 cm

response time; and 3) the temporal coincidence of movement error and the secondary task presentation differentially affected subsequent motor adaptation.

#### METHODS

## Experiment design

Twelve healthy human subjects (five female, seven male), aged 18-22 yr, participated in the experiment over the course of four consecutive days. All subjects were screened for handedness by using the Edinburgh handedness inventory (Oldfield 1971); all subjects were right-hand dominant. All subjects gave their informed consent and the experimental protocol was approved by the Washington University Hilltop Human Studies Committee. The dual-task experiment consisted of a movement task and an audio task (Fig. 1). Components of the dual-task were designed such that each component of the task could be performed separately. On the first day of the experiment, subjects performed audio task screening, followed by the audio single task. The audio task required subjects to perform frequency discriminations (FDs) between two sequentially presented tones. On days 2, 3, and 4 of the experiment, all subjects performed reaching movements. On the second day, subjects practiced reaching movements while holding a robotic manipulandum; no forces were presented on this day so that subjects could become accustomed to the passive dynamics of the manipulandum. On the third and fourth days, subjects made additional movements, but 20% of the movements experienced a transient viscous rightward or leftward force perturbation (movement single task; Fig. 1, bottom). The FD task was combined with the movement task on either day 3 or day 4 (dual task; Fig. 1).

# Audio task screening

All subjects were screened for their ability to perform the FD task. This allowed us to determine FD task performance levels for each subject. Subjects performed 250 two-interval, two-alternative forcedchoice frequency discriminations. Subjects made their discrimination decisions by pressing one of two buttons on a two-button box that corresponded to higher or lower frequency. Subjects held the twobutton box in their nondominant hand (left hand) and made all FD task responses with their left-hand thumb throughout the entire experiment. The first tone was centered at 2,000  $\pm$  100 Hz and the second tone frequency changed from the first tone at random from  $\pm 1$  to  $\pm 150$  Hz. Both tones were presented for 100 ms at identical volumes. Subjects were instructed to quickly and accurately determine whether the second tone was of higher or lower pitch than the first tone. Each frequency change was repeated 10 times. The interval between the tones varied from 150 to 450 ms. After each discrimination, subjects were provided with feedback of the correctness of their response.

Audio Task Feedback

FIG. 1. Experimental setup. On all movements, the first tone is played at target appearance (black arrow). Top: subjects move toward the target (10 cm distance): a single second tone is played at 3 (green), 5 (turquoise), 7 (magenta), or 9 (yellow) cm into movement. After subjects complete the movement, feedback is provided for both the movement and audio task. Bottom: transient viscous force pulse (gray) is centered at 5 cm (Eq. 1). Tone position is held constant over the prepulse (top), pulse (bottom), and postpulse (top) movement triplet.

White noise was presented at 10% of the tone volume during the entire experiment, including all movement task trials.

After FD screening, we generated a performance curve for each subject to determine the magnitude of tone frequency change ( $\Delta f$ ) between the first and second tone that resulted in 90, 75, and 60% correct (Table 1). Only one subject was removed from the study because of an inability to discern two tones within the range of the screening frequencies.

All tones were encoded to 16 bits at 16 kHz in Matlab (The MathWorks, Natick, MA), transformed into audio signals by a soundcard (Creative SoundBlaster, Milpitas, CA), and played through headphones (model UR29, Koss, Milwaukee, WI). Subjects were allowed to adjust the volume of the headphones to a comfortable volume. Response times were recorded with a custom-built, twobutton box. Response times or reaction times were quantified as the time interval between the start of the second tone and the button press.

### Audio single task

Immediately after the FD screening, subjects performed the FD task without the movement task. The audio single task was designed to be integrated with the movement task to create the dual-task condition. Subjects made three sets of 200 discriminations. The interval between the first and second tone varied within a set (150–450 ms), but  $\Delta f$  was varied only across sets. The specific  $\Delta f$  for each set was determined from the subject's performance on the FD screening task that resulted in 90, 75, and 60% correct discriminations. The ordering of the  $\Delta f$  was counterbalanced across subjects. Subjects were required to respond within 1 s after the second tone for a correct trial.

#### Movement training task

On the second day of the experiment, subjects made three sets of 200 movements while holding a five-link, two-bar robotic manipulandum with their dominant hand (right hand) (Interactive Motion Technologies, Cambridge, MA). This day of experimentation was designed to let the subjects become accustomed to the task and the passive dynamics of the manipulandum. The manipulandum confined movement to the horizontal plane. The goal of the movement task was for subjects to move their hand from an initial starting position to a single visually displayed target and come to a complete stop within the target. The target cued a 10-cm reaching task oriented directly away from the body. For a correct movement, the subject needed to move from the initial starting position to the target and make a complete stop within 0.45–0.55 s. If the subject reached the target within the allotted time, the target turned green and burst; otherwise, the target turned blue if the subject was too slow or red if too fast.

TABLE 1. Average subject performance on the frequency discrimination (FD) screening task, the audio single task, and the dual task

Task	Discrimination Performance		
	90%	75%	60%
FD screening task $\Delta f$ , Hz Audio single task, % Dual task, %	$60.4 \pm 12.0$ $93.0 \pm 3.7$ $83.0 \pm 7.4$	$\begin{array}{c} 25.6 \pm 7.1 \\ 72.9 \pm 5.9 \\ 66.9 \pm 5.7 \end{array}$	$8.75 \pm 2.1$ $59.1 \pm 5.0$ $55.8 \pm 3.3$

During the audio screening, the  $\Delta f$  between the first and second tones was varied to determine the  $\Delta f$  that resulted in 90, 75, and 60% correct discrimination (first row). Frequency changes that resulted in 90, 75, and 60% correct were chosen for the experiment and were used on the audio single task (second row) and dual task (third row). Subjects had performance levels in the audio single task similar to those in the FD screening task (second row). The dual task resulted in lower performance levels for frequencies that resulted in 90, 75, and 60% correct in the FD screening task (third row).

After the subject reached the target, the target was removed and the robotic manipulandum returned the hand to the start position.

An LCD monitor displayed the visual target and cursor positions. A yellow cursor represented the current position of the robotic handle. At the onset of a trial, a 0.8-cm-diameter target appeared in the periphery of the screen.

The manipulandum moved in the horizontal plane by revolution at two joints. Hand position and velocity were recorded by encoders on the robotic manipulandum. The manipulandum estimated states and generated forces at 200 Hz. The manipulandum was capable of generating dynamic forces through two brushless DC motors, but during the movement training task, no forces were generated during the movement.

## Movement single task

On either day 3 or day 4 of the experiment, subjects made three sets of 200 movements while holding the manipulandum. The ordering of the movement single-task and dual-task days was counterbalanced across subjects such that six subjects experienced the single task first and the other six subjects experienced the dual task first. The movement task was identical to the movement training task except on 20% of the movements subjects experienced a leftward or rightward transient viscous force perturbation. The perturbing forces (Fig. 1, *bottom*) were generated by the following expression

$$F_{x} = \pm B \left( 1 - \left\langle \frac{1}{1 + \exp\{-a[y - b - (c^{2})]\}} + \frac{1}{1 + \exp\{a[y - b + (c^{2})]\}} \right\rangle \right) v_{y}$$
(1)

where  $F_x$  represents the forces perpendicular-to-target direction; B (=36 N  $\cdot$  s  $\cdot$  m<sup>-1</sup> for experiment) is the viscous gain of the force perturbation; a (=3.33 cm<sup>-1</sup>) controls the shape of the force perturbation, which was chosen to generate a Gaussian profile; b (=5 cm) is the center of the pulse window; c (=2 cm) sets the width of the pulse window; y is the parallel-to-target position; and v<sub>y</sub> is the velocity parallel-to-target direction.

#### Dual task

On either day 3 or day 4 of the experiment, subjects performed the FD task while conducting the movement task. The FD task was performed on each movement trial. The first tone coincided with target appearance (Fig. 1). A single second tone was presented when the hand position in the direction parallel to the target reached 3 (early), 5 (middle), 7 (late), or 9 (end) cm into the movement (Fig. 1, *top*). The second tone position was varied pseudorandomly within a set (Fig. 1, *top*). The  $\Delta f$  was changed across sets identical to the audio single task. The tone position and  $\Delta f$  were held constant on the movement before a force perturbation (prepulse; Fig. 1, *top*), during a pulse (pulse; Fig. 1, *bottom*), and after a pulse (postpulse Fig. 1, *top*). However, whether the second tone frequency was higher or lower than the first tone was randomly varied across the prepulse, pulse, and postpulse triplet of movements. Subjects were given feedback for both the movement task and the FD task (Fig. 1).

Subjects were instructed to make FD responses quickly and accurately. If the movement task was completed before the FD task, then the visual display was frozen until the subject made a response. After the subject responded, the robot returned the subject's hand to the starting position.

### Data analysis

Hand kinematics and audio task responses were analyzed in Matlab. All position data were shifted such that all movements started at the same position (x = 0 and y = 0). We used a fourth-order Savitsky–Golay filter with a cutoff frequency of 6.36 Hz to determine acceleration from 25-ms windows of velocity data. The Savitsky-Golay filter introduces less noise than difference differentiation (Savitsky and Marcel 1964; Smith et al. 2000). The x- and y-positions represent the perpendicular- and parallel-to-target direction components of the movement, respectively. Data for individual subjects were averaged and the means within a subject were compared across subjects. Because the leftward pulses induce negative x-direction errors and rightward pulses induce positive x-direction errors, simple averaging would cancel any metric. In addition, on postpulse movements, adaptation is in the opposite direction of the force pulse in the pulsed movement; leftward pulses cause adaptation in the positive x-direction and rightward pulses cause adaptation in the negative x-direction. Therefore we combined across-pulse direction by subtracting leftward from rightward metrics for pulsed movements and by subtracting rightward from leftward metrics for postpulse movements, then dividing by two. Because the movement target is always in the ydirection, any movement state (position, velocity, etc.) in the x-direction different from the prepulse movement can be considered an error signal.

For pulsed movement analysis, we aligned all movements by the time of maximum force before averaging across movements. This temporal alignment will better preserve temporal differences in the feedback response by providing a common temporal reference for the feedback metrics after the force perturbation. During pulse movements, we were interested in the extent of error induced by the force perturbation and subjects' ability to correct the movement on-line. Therefore we chose metrics for the pulsed movements to reveal differences in disturbance rejection properties and the speed of feedback response. To this avail, we focused on the last half of the movement after the maximum of the force perturbation (>5 cm into movement). Although there may be feedback control before the force perturbation (<5 cm into movement), this feedback response would not be specific to our external force; therefore we define the feedback response as the state trajectory after the maximum of the force perturbation. To determine the contributions of the short- and longloop feedback responses, we included metrics that separate and quantify both the early and late portions of the feedback response. All metrics are reported as mean  $\pm$  the 95% confidence interval of the mean.

Two metrics were used to measure the speed of the feedback response: the time at which corrective control was initiated and the time at which the position of the arm reached a steady-state position (settling time). The initiation of the corrective response was measured as the interval between the time of the maximum force and the time at which the *x*-acceleration changed sign (Saunders and Knill 2005). This metric provides an estimate of feedback speed that is more dominated by segmental reflexes. The settling time was measured as the time interval between the time of maximum force and the time at which the *x*-component of hand position was within 10% of its final value when the trial was completed. This metric provides a better estimate of the speed of the transcortical feedback response because it occurs near the end of movement.

The amount of error induced by the force perturbation was measured by two metrics: maximum perpendicular displacement (PD) and the integral squared error (ISE) (Kording and Wolpert 2004; Smith and Corripio 1985). Maximum PD was measured to provide an estimate of the stiffness or the segmental reflex properties of the arm after the force perturbation. The ISE metric is the squared *x*-position area from the time of corrective control initiation to the time of steady state. It provides a better estimate of the transcortical feedback response because it measures the total amount of error after the time of corrective control initiation until steady state.

For postpulse movement analysis, we aligned all movements by the start of movement before averaging across movements. This temporal alignment will better preserve changes in predictive control early into movement. To quantify the changes in predictive control in postpulse movements, three analyses were used to define the early kinematic features of adaptation: PD at 5 cm, take-off angle, and movement area. We chose to consider metrics early into movement to capture the feedforward aspects of subjects' trajectories rather than metrics that are defined later in movement in which feedback control dominates. Metrics of adaptation were quantified by subtracting the subjects' average prepulse metrics from the subjects' postpulse movement metrics. PD was used to determine the magnitude of adaptation after a force perturbation. Each subject's mean PD at 5 cm into movement was computed for postpulse movements after leftward and rightward perturbations. Take-off angle was used to capture the initial direction of the postpulse movement. We calculated PD when the hand was 1 and 2 cm displaced from the start in the parallel-to-target direction. A line was drawn between these two points: the angle between this line and the parallel direction determined the takeoff angle. Movement area was used to account for the entire feedforward portion of the adaptation. The area was defined as the sum of the positive and negative area of the perpendicular-to-target direction component of the postpulse for the first 5 cm of movement. The area metric was also used to quantify prepulse movements.

To quantify the relationship between second tone presentation and force-induced movement error in pulsed movements, we defined a positional overlap metric as the difference between the position into movement (*y*-component) when the second tone was present and the position into movement when the *x*-component of hand velocity was a maximum.

#### RESULTS

#### Audio single task

The subjects' ability to discern two tones of varying frequencies was evaluated in the auditory screening and the  $\Delta f$ values that resulted in 90, 75, and 60% correct discrimination were chosen for the experiment (Table 1). The  $\Delta f$  chosen in the FD screening task resulted in similar performance in the audio single task (Table 1). In the audio single task, subjects repeatedly heard the same  $\Delta f$  (higher or lower) over a set (200 discriminations), but performance early in the set, over the first 10 trials, did not differ significantly from that of the last 10 trials (ANOVA, P = 0.16). In addition, there were no differences in performance between times of tone presentation (ANOVA, P = 0.45).

#### Movement single task

Single-task prepulse movements followed a relatively straight line from the start of movement to the target (Fig. 2A). Averaged PD at 5 cm was  $-0.047 \pm 0.054$  cm and the area swept out during the movement from the start to 5 cm was  $-0.184 \pm 0.178$  cm<sup>2</sup>. The hand velocity profile exhibited a single-peaked bell-shaped velocity profile with a peak movement velocity of 29.7  $\pm$  2.59 cm/s.

On pulse trials, subjects' movement trajectories were perturbed in the direction of the force (Fig. 2*B*, leftward solid and rightward dashed) and subjects were able to correct the movement and arrive at the target. In the pulsed movement, subjects' peak movement velocity in the direction of the target was  $30.67 \pm 2.40$  cm/s. The initiation time of the corrective response and maximum PD were used to quantify the shortloop feedback response. The peak of the force perturbation during a pulsed movement was  $10.16 \pm 0.80$  (Fig. 3, *A* and *C*, *inset*), which induced a maximum PD of  $2.96 \pm 0.24$  cm (Fig. 3, *B* and *C*, *inset*). During the pulsed movement, *x*-velocity followed a smooth trajectory characterized by a velocity error



FIG. 2. Average movement trajectories for prepulse, pulse, postpulse movements. A: average prepulse movement trajectories (x- and y-positions) for single-task (black), dual-task (gray), and dual-task late (7 cm) tone (purple). B: average leftward (solid) and rightward (dashed) force pulsed movements. *Inset*: average force perturbation magnitude (N) as a function of distance into movement (cm) for single-, dual-, and dual-task late tones. C: average postpulse movements after leftward (solid) and rightward (dashed) pulses. D: average postpulse movement minus the average prepulse movement.

in the direction of the force pulse followed by negative velocity to return the hand to the desired trajectory (Fig. 3*C*). The initial speed of the feedback response, as measured by the time at which the *x*-acceleration of the hand changed direction, occurred at 0.058  $\pm$  0.003 s from the time of maximum force (Fig. 3*C*, *inset*). The time to reach steady-state error and integral squared error (ISE) were used to quantify the speed and ability of the long-loop feedback response to correct the movement. The settling time, which was the time from corrective control initiation until the time at which the position of the hand reached 10% of its final value, was 1.16  $\pm$  0.13 s (Fig. 3*C*, *inset*). During the time from corrective control initiation until steady state, the ISE was 18.43  $\pm$  2.70 cm<sup>3</sup> (Fig. 3*C*, *inset*).

Adaptation was evident in movements immediately after the force perturbation (Fig. 2C). On the postpulse movement immediately after a leftward perturbation the subjects' angled the movement to the right (Fig. 2D, solid), whereas on the movement immediately after a rightward perturbation subjects'

angled the movement to the left (Fig. 2*D*, dashed). Take-off angle, PD measured at 5 cm, and movement area of the postpulse movement were measured to quantify the postpulse adaptation early into movement, midway into movement (5 cm), and during the entire first half of movement (<5 cm). The force perturbation induced a take-off angle of  $1.50 \pm 0.20^{\circ}$ . The average PD at 5 cm into movement was  $0.143 \pm 0.017$  cm and the movement area from the start to 5 cm was  $0.32 \pm 0.04$ cm<sup>2</sup>.

# Dual-task movements: across all dual-task conditions

Prepulse movements were similar to single-task prepulse movements. The movements followed a relatively straight line from the start to the end of movement (Fig. 2A, gray line). The average PD perpendicular to movement direction at 5 cm was  $-0.039 \pm 0.045$  cm and the movement area from start to 5 cm was  $-0.17 \pm 0.18$  cm<sup>2</sup>, both of which were not significantly different from that of the single task (P = 0.82 and P = 0.91,



FIG. 3. Average force perturbation, position, and velocity trace for pulsed movements as a function of time. *x*-axis: 0 represents the time of maximum force, negative values represent time before the maximum force, and positive time values represent time after the maximum force. Leftward forces were subtracted from rightward forces and divided by 2 to average across perturbation directions. Lines were layered on the figure to best visualize the differences between single-and dual-task conditions. A: average force perturbation strength for single task (black) and dual task (gray). B: average *x*-component of position for single task (black) and dual task (gray). C: average *x*-component of velocity for single task (black) and dual task (gray). Inset: percentage change from single task to dual task (or maximum force (Fx) and the 4 feedback metrics used: maximum perpendicular displacement (PD), corrective control initiation time (Tc), settling time (Ts), and integral squared error (ISE). Error bars represent the 95% confidence interval of the mean.

respectively). Subjects had a tendency to speed up their movements in the dual task; average single-task prepulse movement speed was 29.67  $\pm$  2.59 cm/s, whereas in the dual task velocity was increased to 31.53  $\pm$  2.56 cm/s (P = 0.04). The increase in speed was independent of the tone position (ANOVA, P =0.81) or  $\Delta f$  (ANOVA, P = 0.70).

Because force perturbation magnitude was dependent on movement speed and subjects' had a tendency to increase movement speed in the dual task, the subjects subsequently experienced larger force perturbations in the dual task (Fig. 3A). In pulsed movement the peak velocity in the direction of the target was  $33.05 \pm 2.76$  cm/s and the averaged force magnitude in the dual task was  $10.94 \pm 0.92$  N, which is larger than the averaged force magnitude in the single task (P =0.011). Although the force was slightly larger in the dual task, the maximum PD in the dual task was the same as that in the single task (Fig. 3B). The average maximum PD values were  $2.96 \pm 0.24$  and  $2.95 \pm 0.24$  cm for single task and dual task, respectively (P = 0.98). The similar displacement in the dual task given the larger force perturbation suggests that subjects were stiffer in the dual task than in the single-task. Stiffness, measured as the maximum force divided by the maximum displacement, was larger (P = 0.011) in the dual task (3.81 ± 0.43 N/cm) than in the single task (3.51  $\pm$  0.36 N/cm).

Was either the short-loop or long-loop response of the feedback controller compromised by the dual task? The corrective control initiation time was  $0.057 \pm 0.003$  s, which is nearly identical to that of the single task (P = 0.39). The time to reach steady state was  $1.01 \pm 0.09$  s, which is nearly faster than the single-task settling time (P < 0.07). This reduction in settling time may be dependent on movement speed because subjects tended to move faster in the dual task. However, the ISE between corrective control initiation and end of movement was not significantly different (P = 0.10); the ISE was 17.54  $\pm$  2.62 cm<sup>3</sup>. Therefore the ability of both the short-loop and long-loop feedback responses was not slowed nor was it unable to reduce the error in movement.

In the dual task, the postpulse adaptation was conserved; however, the magnitude of postpulse adaptation was significantly reduced for the dual-task condition (Fig. 2D, gray). Early movement adaptation was reduced in the dual task (P =0.01); take-off angle was reduced by nearly 30% (1.07 ± 0.11°). There was a 17% reduction in PD from the single task to the dual task (0.118 ± 0.012 cm; P = 0.03). The total area of movement from the start of movement to 5 cm was also significantly reduced by 25% (0.24  $\pm$  0.03 cm<sup>2</sup>; *P* = 0.02). This result is surprising given the fact that the dual-task force perturbation was greater than the single-task force perturbation.

#### Dual-task movements: specific dual-task effect

The dual-task conditions changed both within a movement set (tone positions) and across movement sets (tone  $\Delta f$ ). The first tone was presented on target appearance, whereas the presentation of the second tone varied pseudorandomly when the hand passed 3, 5, 7, or 9 cm into movement (Fig. 4A). Changing the tone position allowed us to examine the effect of positional overlap of the second tone location relative to the force-induced movement error in pulsed movements. The position of the tone varied with respect to the force onset and subsequent force-induced error (Fig. 4A). Tones at 3 cm were presented before the force perturbation (Fig. 4A, green line), whereas tones at 9 cm were after the force perturbation (Fig. 4A, vellow line). This difference in positional overlap of the tone presentation and movement error did not lead to a difference in PD in the pulse movement (Fig. 4B). Although the displacement perpendicular to movement did differ depending on the distance into movement (3, 5, and 7 cm into movement; Fig. 4B), there was no dependency on tone presentation position. There was no significant linear trend between the pulse PD at 3, 5, and 7 cm and the x-component of velocity in the pulse movement (P = 0.616, P = 0.48, and P = 0.76 for 3, 5, and 7 cm, respectively). The average subjects' movement trajectory for a pulsed movement with a 7-cm tone is presented in Fig. 2B (purple).

The metrics used to quantify the feedback response did not show significant differences either for changing  $\Delta f$  or for changing tone positions. Time of corrective control initiation was not significantly different for  $\Delta f$  (ANOVA, P = 0.23) or for tone position (ANOVA, P = 0.95). Settling time and ISE did not show differences for  $\Delta f$  (settling time ANOVA, P =0.97; ISE ANOVA, P = 0.94) or for tone position (settling time ANOVA, P = 0.21; ISE ANOVA, P = 0.75). In addition, we did not find any specific effects for 7-cm tones. Maximum PD was 2.95  $\pm$  2.58 and time of corrective control initiation after 7-cm tones was 0.056  $\pm$  0.003 s, neither of which was significantly different from the single-task response (P = 0.98



FIG. 4. Positional overlap between tone presentation and movement error. Positional overlap is the difference between the position into movement (y-component) when the second tone was presented and the position into movement when x-component of hand velocity was a maximum in the pulsed movement. A: x-component of hand velocity (black) as a function of position into movement. Vertical lines represent the second tone presentation position for early (3 cm; green), middle (5 cm; turquoise), late (7 cm; magenta), and end (9 cm; yellow) tones. B: pulse PD at 3 (dash-dotted), 5 (dashed), and 7 (solid) cm into movement error. C: postpulse perpendicular displacements at 3 (dash-dotted), 5 (dashed), and 7 (solid) cm into movement as a function of the positional overlap of the tone and movement error after early, middle, late, and end tones of the pulse movement. Average maximum x-component of velocity occurred 7.04 cm into movement.

and P = 0.34, respectively). The settling time was  $1.01 \pm 0.09$ and ISE was  $17.54 \pm 2.61$  cm<sup>3</sup> after 7-cm tones, which were nearly decreased from the single task (P = 0.07 and P = 0.10, respectively), but did not show any differences from other dual-task conditions (ANOVA, P = 0.44 and P = 0.91).

Although pulsed movements were not specifically affected by the varied position of the second tone, the postpulse movement adaptation was dependent on when the tone was presented in the previous movement. Subjects adapted the most when the second tone did not overlap with force-induced movement error on the pulsed movement. The subjects exhibited the most adaptation on postpulse movements after tones that occurred before the force perturbation (3 cm); the adaptation in these postpulse movements was not distinguishable from single-task adaptation (PD, P = 0.64; Fig. 4C). The largest velocity error occurred at 7 cm into pulsed movement and when the tone was presented at 7 cm into movement on the pulsed trial, subjects adapted the least (Fig. 2, C and D). Take-off angle, PD, and movement area for tones presented at 7 cm were reduced by 50% (0.728  $\pm$  0.23°), 37% (0.090  $\pm$ 0.018 cm), and 50% (0.16  $\pm$  0.04 cm<sup>2</sup>). Tones occurring at 5 and 9 cm into the pulsed movement resulted in less postpulse adaptation than tones at 3 cm, but more adaptation than 7-cm tones (Fig. 4C). The adaptation for 7-cm tones is significantly less than the adaptation at 3 cm (PD, P = 0.0139) and adaptation at 9 cm (PD, P = 0.0322) and, although less than adaptation at 5 cm, it is not significantly different (PD, P =0.1877). However, the trend of the positional overlap of the second tone and the force-induced error resulting in differential adaptation is significant (Fig. 4C). There was a significant linear trend between the postpulse PD slices at 3, 5, and 7 cm and velocity error in the pulse movement (P = 0.01, P = 0.01, and P = 0.02 for 3, 5, and 7 cm, respectively).

Changes in frequency between the first and second tones that resulted in 90, 75, and 60% correct did not affect subject reaction time for the FD task or scale postpulse adaptation. Prepulse and postpulse FD task reaction times (RTs) were not significantly different from each other (ANOVA, P = 0.909) and were not different across  $\Delta f$  (ANOVA, P = 0.989); RT values for prepulse and postpulse movements were 481.5  $\pm$  $33.7, 478.5 \pm 24.6, 478.7 \pm 31.0$  ms for  $\Delta f$ , resulting in 90, 75 and 60% correct, respectively. Pulse FD task RT was also not significantly different across  $\Delta f$  (ANOVA, P = 0.84), but pulse RT was significantly increased from prepulse and postpulse RTs (ANOVA, P < 0.001). Pulse FD task RTs were  $569.8 \pm 59.8, 561.31 \pm 35.5, \text{ and } 558.1 \pm 34.7$  for frequencies that resulted in 90, 75, and 60% correct, respectively. In addition, the postpulse PD was not significantly different across  $\Delta f$  (ANOVA, P = 0.17). Postpulse PD values were  $0.13 \pm 0.020, 0.10 \pm 0.023, \text{ and } 0.13 \pm 0.016 \text{ cm for } \Delta f \text{ that}$ resulted in 90, 75, and 60%, respectively.

#### Dual-task audio

Subjects' correct discrimination performance was dramatically reduced from the single task to dual task (Table 1; P < 0.01 between single task and dual task). Subjects' ability to correctly identify the pitch difference between the first and second tones was reduced in all  $\Delta f$  sets. The presence of a force perturbation did not affect subject performance across the  $\Delta f$ sets. Percentages of correct discriminations made on prepulse, pulse, and postpulse trials were not significantly different from each other (P = 0.83).

Subjects' RTs to the tones varied with tone presentation position for prepulse, pulse, and postpulse movements (Fig. 5). Subjects' RT to the tones decreased with increasing tone position regardless of whether the movement was a prepulse, pulse, or postpulse movement. Subjects responded to 3-cm tones at approximately the same time as the movement was completed. Subjects' average RT to the 3-cm tone was 511 ms and the average movement time after the tone was 509 ms. For later tones (5, 7, and 9 cm), subjects responded after the movement was completed. The decreasing RT trend with tone position had a slope that was significantly different from zero slope for prepulse (P = 0.03), pulse (P = 0.03), and postpulse (P = 0.01) movements. In addition, subject RT on pulse movements was increased on average by 84.5 ms from prepulse movements (Fig. 5). The decreasing RT with increasing tone position and the increase in RT on pulsed trials indicate that the movement task significantly interfered with FD task processing.

# DISCUSSION

Our experimental paradigm allowed us to examine the functional contribution of attention on within-movement motor control and trial-by-trial adaptation. Previous experiments (Ingram et al. 2000; Lang and Bastian 2002; Nissen and Bullemer 1987; Redding et al. 1992; Stadler 1995) observed attentional effects on motor learning over hundreds of trials, rather than within and across individual trials. The processes underlying even the initial learning of a task may be multifaceted (Smith et al. 2006); our paradigm allowed us to precisely identify the direct effect of divided attention on the transformation of single-trial experiences on within-movement feedback and across-movement adaptation. The spatial and temporal specificities of both the tones and the transient force perturbation allowed us to examine the role of attention on within-movement feedback control and across-movement adaptive control of the motor system. We found that the corrective feedback control was unaffected by the FD task, but delayed subjects'



FIG. 5. Average subject reaction time as a function of position of tone presentation for prepulse (light gray), pulse (dark gray), and postpulse (black) movements. Reaction time (RT) model based on Welford's psychological refractory period (PRP) effect (dashed-black line).

response times to the FD task. However, the FD task caused significant interference on motor adaptation if the force perturbation and tone presentation occurred at the same time.

## Dual-task interference affecting FD task

Although the within-movement feedback control on pulsed movements remained intact in the dual-task condition, subjects' RTs to the FD task on pulsed movements were longer than on prepulse and postpulse movements (Fig. 5). The linear trend in the FD task RT with tone positions and the additional delay in FD task RT on pulsed movements indicate that the movement task interfered with the FD task. The manifestation of the interference is similar to a psychological refractory period (PRP) effect and suggests that the interference arises from a single channel or bottleneck in processing (Pashler et al. 2001; Welford 1952). Although subjects did not respond until after the movement was completed for tones at 5, 7, and 9 cm, subjects did respond at approximately the same time as movement completion for 3-cm tones. This suggests that processing of the FD task was not completely delayed until the movement was completed. In addition, force perturbation in a pulsed movement increased movement time from an average of 637 to 926 ms, but the RT was increased by only 84.5 ms. A simple model, based on the Welford PRP model, can partially explain the increase in RT during pulsed movements

# $RT_{pulsed} = RT_{prepulse} + m(MT_{pulsed})$

where RT<sub>prepulse</sub> is the reaction time of the prepulse, RT<sub>pulsed</sub> is the reaction time of the pulsed movement, MT<sub>pulsed</sub> is the remaining movement time after the force perturbation, and m scales the remaining movement time. The model fits the pulsed movement data quite well; root mean square error was only 0.012 and the correlation coefficient was 0.95 (Fig. 5, dotted black line). This fit predicts only a 29% (m = 0.29) delay in RT from prepulse to pulse trials. This suggests that the dual-task interference in the pulsed movement may be attributable to a bottleneck in the processing pathway; however, some components of the task must be processed in parallel because the FD task is not completely delayed until after the movement task. Further, generation of the feedback control to correct the movement after a force perturbation must have higher processing priority than generation of the FD task response because the feedback control remains intact on pulsed movements. The bottleneck in processing may occur when the motor system needs to generate two separate motor commands in close temporal proximity (Schmidt 1988).

# Dual-task interference affecting adaptation but not feedback

The subject data suggest that the within-movement feedback control is unaffected by the secondary task. Subjects initiated both speedy and efficient corrective responses after force perturbations (Figs. 2*B* and 3), even though the force perturbations tended to be greater in magnitude in the dual task than in the single task (Fig. 3*A*). In the dual task, the feedback response was robust to both the force perturbation and the changing tone positions and  $\Delta f$  (Fig. 4*B*).

From pulse to postpulse movements, adaptation is reduced by the secondary task (Fig. 2, C and D). This suggests that either I) the estimation of the error in movement, or 2) the transformation of errors into changes in predictive control were impaired by the second tone interference on the pulsed trial, or 3) execution of the changes in predictive control is impaired from the second tone on the postpulse trial. We do not believe that the interference occurs with error estimation or predictive control execution. Movement state information is collected by vision (Ghez et al. 1995) and proprioception (Gordon et al. 1995) and the FD task uses the auditory system. In addition, within-movement feedback control is unaffected by the dual task. Therefore it is unlikely that error estimation is compromised by the dual task. Interference with the implementation of predictive control would be apparent early into the postpulse movement. Although there are tones on the postpulse movement that could potentially interfere with predictive control, the second tone cannot appear until after 3 cm into movement. Our postpulse adaptation metrics, such as take-off angle and movement area, take into account kinematic features of movement before the second tone in the postpulse movement is presented. In addition, the correlation between tone presentation and force perturbation suggests that the interference is occurring during the pulsed movement. Therefore we posit that interference with adaptation on postpulse movements arises from the encoding and transformation of errors into changes in predictive control.

Why is the within-movement feedback control unaffected by the FD task, whereas the across-movement predictive control is affected by the FD task? The force perturbations induced significant displacements of the arm in the second half of movement. When the arm is displaced, stretch receptors induce a short-loop reflex (40–80 ms), long-loop reflex (80–200 ms), and voluntary response ( $\geq 200$  ms) after the displacement (Allum 1975; Marsden et al. 1972). In our study, subjects initiated feedback control approximately 9 ms after the maximum of the force, which is within the temporal boundary of these reflexive responses. In addition, the settling time in the dual task was about 1 s, which was less than the settling time in the single task (1.16 s). The dual task did not compromise the speed or efficiency of the subjects' feedback response. Therefore the on-line feedback control of the arm may depend on a reflexive response or be dominated by an unattentional process (Frensch 1998). Unattentional processes may, however, include supraspinal structures. When patients with Huntington's disease (HD) make reaching movements that are subjected to force perturbations, similar to the force perturbations we used in this task, HD patients are unable to execute efficient feedback control to correct the movement (Smith et al. 2000). The basal ganglia are the primary motor structures affected by HD. Because our task uses similar force perturbations, the basal ganglia are likely contributing to subjects' within-movement feedback control in our task. However, subjects' within-movement feedback control is intact under divided attention; therefore we suggest that although spinal reflexes and the basal ganglia are contributing to withinmovement correction, they are not affected by divided attention.

Although we attributed the decrement of adaptation after a force pulse to divided attention, an alternate consideration would be whether the left thumb press generates motor signals that provide the neurophysiological basis for our observed behavioral interference. One part of that consideration is whether the left-thumb modality would likely cause interfer-

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ence with controlling the right arm. The simultaneous control of a left digit or hand and the right arm (or vice versa) is commonplace in video games, driving, cooking, ironing, and computer use. Sometimes these bimanual tasks require coupled movements but often the two movements are uncoupled. We saw no evidence for a decrement in mid-movement control arising from the secondary task and therefore do not conclude that the neuronal signals coordinating left-thumb movement interfere with coincident motor processing of the right arm.

It is possible that a component of the left-thumb motor processing kept mid-movement processing intact but interfered with coincident yet covert capture of right-arm movement sensation. To consider this possibility we turn to the temporal details of thumb movement and across-trial decrement of adaptation. The thumb press after 3-cm tones occurred coincident with arm movement conclusion; the thumb press after 5, 7, and 9 cm tones occurred after completion of the movement. The timing of the motor signals driving the thumb press would therefore maximally overlap right-arm movement sensation in the case of the 3-cm tone. This tone, however, generated the minimum interference, leaving trial-by-trial adaptation as intact as in the single-task experiment. We infer that the maximal interference after the 7-cm tone indicates that the division of attention is more likely to drive interference of adaptation than coincident motor signals underlying left-thumb control.

# Possible neurophysiological loci of intact feedback but impaired adaptation

Our observed dichotomy between within-movement feedback control and across-movement control systems has also been suggested by recent motor learning experiments with HD patients and cerebellar degeneration patients (Smith and Shadmehr 2005). Although HD patients cannot execute efficient corrections within a movement, they can learn novel force dynamics over the course of many movements. Contrastingly, cerebellar degeneration patients can correct movement errors on-line, but they cannot learn to counteract force dynamics across movements. These results suggest that separate motor areas are involved in within-movement feedback control versus across-movement adaptive control. Our results complement this dissociation because the feedback control is unaffected by the dual task, whereas the across-movement error correction is compromised. Adaptation across movements may occur between movements and engage different motor systems to maintain memory of the error and translate it into updated force production for the next movement. In addition, recent studies have provided additional evidence of dissociations between neural systems involved in the on-line correcting of movements (Della-Maggiore et al. 2004; Desmurget et al. 1999, 2001; Grea et al. 2002; Seidler et al. 2004) and error learning (Diedrichsen et al. 2005; Kitazawa et al. 1998).

Recent functional magnetic resonance imaging (fMRI) data have shown specific changes in neural activation of both classical motor areas and attentional areas during motor learning. During the initial stages of learning a motor task, fMRI and positron emission tomographical studies have observed increased activation in frontal regions of cortex, specifically dorsolateral prefrontal cortex and anterior cingulate (Floyer-Lea and Matthews 2004, 2005; Jueptner et al. 1997; Shadmehr and Holcomb 1997). As the task becomes learned, the activation shifts from attentionally associated frontal areas to more classical motor structures such as premotor and motor cortex, basal ganglia, and the cerebellum (Floyer-Lea and Matthews 2004; Shadmehr and Holcomb 1997), suggesting a functional change in neural representation over the course of learning. Our study provides functional behavioral evidence to complement the neuroanatomical evidence of the interaction between attention and motor control.

Our findings suggest a substantial role for attention in motor adaptation. Although dual-task interference does not disrupt the feedback control of arm movements, it does interfere with adaptation. The correlation between the positional overlap between tone presentation and movement error shows that the dual-task paradigm induces a specific dual-task effect on learning. Postpulse movements after pulsed movements with 3-cm tones resulted in the same adaptation as the single task. Only tones at 5, 7, or 9 cm caused reduced adaptation. These results show that the impaired adaptation is not the result of a nonspecific effect of the dual task, but is a temporally specific interference effect. This interference most likely disrupts proper encoding and transformation of previously experienced errors into changes in predictive control. We conclude that neural processes-and therefore putative neural regions, encoding decision making and incremental motor adaptationoverlap with great temporal precision.

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