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Explicit knowledge enhances motor vigor and performance: motivation versus practice in sequence tasks

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Wong AL, Lindquist MA, Haith AM, Krakauer JW. Explicit knowledge enhances motor vigor and performance: motivation versus practice in sequence tasks. *J Neurophysiol* 114: 219–232, 2015. First published April 22, 2015; doi:10.1152/jn.00218.2015.—Motor skill learning involves a practice-induced improvement in the speed and/or accuracy of a discrete movement. It is often thought that paradigms involving repetitive practice of discrete movements performed in a fixed sequence result in a further enhancement of skill beyond practice of the individual movements in a random order. Sequence-specific performance improvements could, however, arise without practice as a result of knowledge of the sequence order; knowledge could operate by either enabling advanced motor planning of the known sequence elements or by increasing overall motivation. Here, we examined how knowledge and practice contribute to performance of a sequence of movements. We found that explicit knowledge provided through instruction produced practice-independent improvements in reaction time and execution quality. These performance improvements occurred even for random elements within a partially known sequence, indicative of a general motivational effect rather than a sequence-specific effect of advanced planning. This motivational effect suggests that knowledge influences performance in a manner analogous to reward. Additionally, practice led to similar improvements in execution quality for both known and random sequences. The lack of interaction between knowledge and practice suggests that any skill acquisition occurring during discrete sequence tasks arises solely from practice of the individual movement elements, independent of their order. We conclude that performance improvements in discrete sequence tasks arise from the combination of knowledge-based motivation and sequence-independent practice; investigating this interplay between cognition and movement may facilitate a greater understanding of the acquisition of skilled behavior.

reward; learning; skill; sequential; cognition

SEQUENCE-LEARNING TASKS are widely considered a model of motor skill acquisition. Three principal reasons underlie this assumption. First, many everyday motor tasks such as piano playing are sequential in nature and improve with practice. Second, since the seminal case of the Patient H.M., motor skill acquisition is considered largely implicit; therefore, sequence tasks are thought to serve as a model for motor skill to the extent that they have a strong implicit component (Nissen and Bullemer 1987; Reber and Squire 1994). Third, skills can be taught at least partially via instruction (i.e., coaching), and the order of elements in a sequence task can be given or acquired explicitly (Buchner et al. 1998; Ghilardi et al. 2009; Perruchet and Amorim 1992), suggesting sequence tasks may also include an additional explicit component.

To classify the learning of a sequence of discrete movements as a motor-skill task, it must exhibit a definitive property, sequence-specific execution improvements with practice. That is, performance improvements for a fixed sequence should exceed those arising from practicing the individual movement elements without regard to their order (Hikosaka et al. 1995). Execution improvements should take a form akin to a shift in the speed-accuracy trade-off function, e.g., the ability to hit targets faster without loss of accuracy (Hikosaka et al. 2013; Reis et al. 2009).

Importantly, sequence-specific motor skill must not be equated with performance gains arising from explicit knowledge of sequence order. Knowledge could improve behavior via two practice-independent mechanisms, advanced planning and motivation. During typical sequence-learning tasks, explicit knowledge of sequence fragments is acquired simultaneously with practice of the sequence (Buchner et al. 1998; Ghilardi et al. 2009; Perruchet and Amorim 1992; Perruchet and Gallego 1993); thus it is not possible to dissociate the effects of knowledge and sequence-specific practice on performance. Sequence knowledge allows earlier initiation of motor planning, which can reduce the reaction time (RT) (Churchland et al. 2006) and potentially enable subjects to plan higher-quality movements. The effects of advanced planning are necessarily restricted to known elements of a sequence.

Alternatively, sequence knowledge could modify behavior through a more general effect on motivation. Here, we define motivation broadly as that process that drives the initiation and performance of a goal-directed behavior with a particular level of intensity. Included in this definition are mechanisms that are influenced by this process, such as attention and arousal. Motivation, which is typically modulated by the promise of reward, produces behavioral changes resembling skill improvements (Hikosaka et al. 2013). When a reward is anticipated, a movement will be executed faster and with less variability, a local effect (Chen et al. 2013; Takikawa et al. 2002). Motivation can also produce a global effect; when the average available reward is high, RTs of all movements (including less rewarding ones) are improved (Wang et al. 2013). Notably, knowledge itself may be rewarding; monkeys prefer cues containing information about future reward over uninformative ones, even though such cues do not influence the forthcoming reward (Bromberg-Martin and Hikosaka 2009, 2011). Because the value of knowledge can be encoded by the same neurons that encode reward (Bromberg-Martin and Hiko-

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saka 2011; Niv and Chan 2011), knowledge may serve a similar role as reward in influencing motivation. Hence, sequence knowledge could directly invoke motivational performance improvements, which could be observed immediately without requiring motor practice. A signature of this mechanism would be the presence of both a local effect on known targets and a global effect on random targets performed in the context of a known sequence.

Here we investigated the effects of explicit sequence knowledge on motor execution with a reaching paradigm that allowed us to assess changes in RT, movement time (MT), and spatial accuracy. MT serves as a proxy for movement vigor (i.e., the rate or the speed of responding; Haith et al. 2012; Niv et al. 2007), whereas the interaction between MT and accuracy enables us to evaluate overall performance. Subjects were informed about the order of either the whole or part of an upcoming sequence to elucidate whether knowledge has planning or motivational effects on behavior and whether practice of a fixed sequence enhances skill beyond that for a random sequence.

MATERIALS AND METHODS

Sixty-three right-handed, adult (age 18–46 yr; 22 males), neurologically healthy subjects were recruited for this study (22 subjects in *experiment 1* and 41 subjects in *experiment 2*). There were no significant age differences between groups in either *experiment 1* (mean age, 23.90 yr) or *experiment 2* (mean age, 21.27 yr). All subjects provided written, informed consent, and protocols were approved by the Johns Hopkins Institutional Review Board. Subjects were seated in a stationary chair in front of a glass-surfaced table. Each subject's right forearm was placed in a wrist splint and was supported by a plastic cradle equipped with pressurized air jets to allow frictionless planar arm movements of the elbow and shoulder. Subjects' arms were obstructed from view by a mirror positioned above the table surface, through which an LCD monitor (60 Hz) displayed target cues (13 mm in diameter) and a cursor representing the position of the index finger (9 mm in diameter) in a veridical horizontal plane. Movement of the index finger was tracked at 130 Hz using a Flock-of-Birds magnetic tracker (Ascension Technology, Milton VT). Within each experiment, subjects were randomly assigned to the particular condition in which they participated.

Experimental Paradigms

Two experiments were conducted to ascertain how explicit sequence knowledge and nonspecific practice influence performance in a discrete sequence task (in which each movement is independently generated, after a random delay, in response to a target appearance). In both experiments, subjects were instructed to make out-and-back reaching movements from a central start position directly in front of the subject to one of several targets evenly spaced along a circle of radius 0.075 m around the start position. Subjects were asked to reverse direction in the target without pausing and to maintain approximately the same speed on the outward and return phases of the movement. The purpose of this reversal movement was to bring the hand back to the initial starting position and then stop completely before initiating the next movement, allowing for a direct comparison of movements to different targets regardless of the experienced sequential target order. A background image indicating the locations of all potential target locations remained visible throughout the experiment, reducing ambiguity about where targets could appear. The target disappeared once the subject reached it or after 1,200 ms following its presentation (to encourage subjects to initiate their movements as quickly as possible). If subjects initiated a reach before the target appeared, the target would not appear until subjects returned to the start circle and again waited for a random time interval; this discouraged the generation of anticipatory movements and prevented subjects from producing a continuous series of movements.

Targets were presented according to a modified version of the discrete sequence-production task, a variant of the serial RT task that relies on a short sequence of targets whose order is determined according to the identity of the first target (Verwey 1999). Here, the target sequence remained constant in a relative sense and rotated according to the position of the initial target. For example, a simple clockwise relative target sequence is one in which, given the location of the initial target, the remaining targets always appeared sequentially one target farther away in a clockwise direction.

Peak velocity of the outward phase of the reach was monitored and displayed via an onscreen graphic, which indicated whether the movement speed lay within the requested range (0.4 to 0.6 m/s). Trials were considered successful if the movement hit the target with the appropriate accuracy (the reach came within 13 mm of the target center) and exhibited a peak velocity within the requested range. A successful trial resulted in a rewarding auditory feedback tone, and subjects were awarded one point toward a cumulative score reported at the end of each block of trials. The complete experimental session (a practice block and 7 blocks of training trials) typically lasted <1 h.

Experiment 1: full sequence-knowledge task. Experiment 1 (Fig. 1*A*) examined motor performance when subjects were explicitly told the complete sequence order, compared with the performance of a separate group of subjects who experienced a random-order condition. Performance changes in the random group would arise from nonspecific practice effects, whereas any immediate performance improvements exhibited by the sequence group would be attributable to the effect of knowledge. After we accounted for both the knowledge-related shifts in performance and nonspecific practice effects, any remaining behavioral improvements in the sequence group that accumulate with practice would then provide evidence of a learned sequence-specific skill component.

The basic task employed eight targets spaced 45° apart. A target set began with a cue in which a small triangular arrow near the start circle pointed at the location of the upcoming first target. The cue could point to any one of the four targets on the diagonals. Following a randomized intertrial interval (ITI; uniformly distributed between 2,900 and 3,500 ms), this first target appeared at the cued location along with an auditory tone, and the subject was allowed to initiate a reach. Four additional trials followed the cued trial and were spaced at random ITIs (uniformly distributed between 400 and 1,000 ms). These four targets appeared sequentially in a clockwise order (SEQ condition) or randomly at any of the eight possible targets (RND condition). Together, these five targets (the cue and 4 uncued trials) comprised a "set" of trials; a block included five sets of trials for each of the four possible cue locations (20 sets total). Subjects were given a brief rest break between blocks. The number of target appearances in the RND condition was controlled so that subjects reached to any given target the same number of times as they did in the SEQ condition.

Subjects were evenly divided into two groups (11 subjects per group; 1 subject in each group was later excluded because of inability to comply with the directions of the experiment, e.g., to accurately reverse the hand direction at the target without stopping). All subjects, regardless of group designation, received one practice block consisting of trials in the random condition during which they became familiar with the speed and accuracy requirements of the task and the novelty of moving their arm in a frictionless environment (all subjects were naïve to the experimental setup). Subjects then performed seven training blocks with targets appearing according to the assigned condition. In the SEQ condition, subjects were explicitly told about the presence and nature of the target sequence immediately following the initial practice block although they were reminded that they still

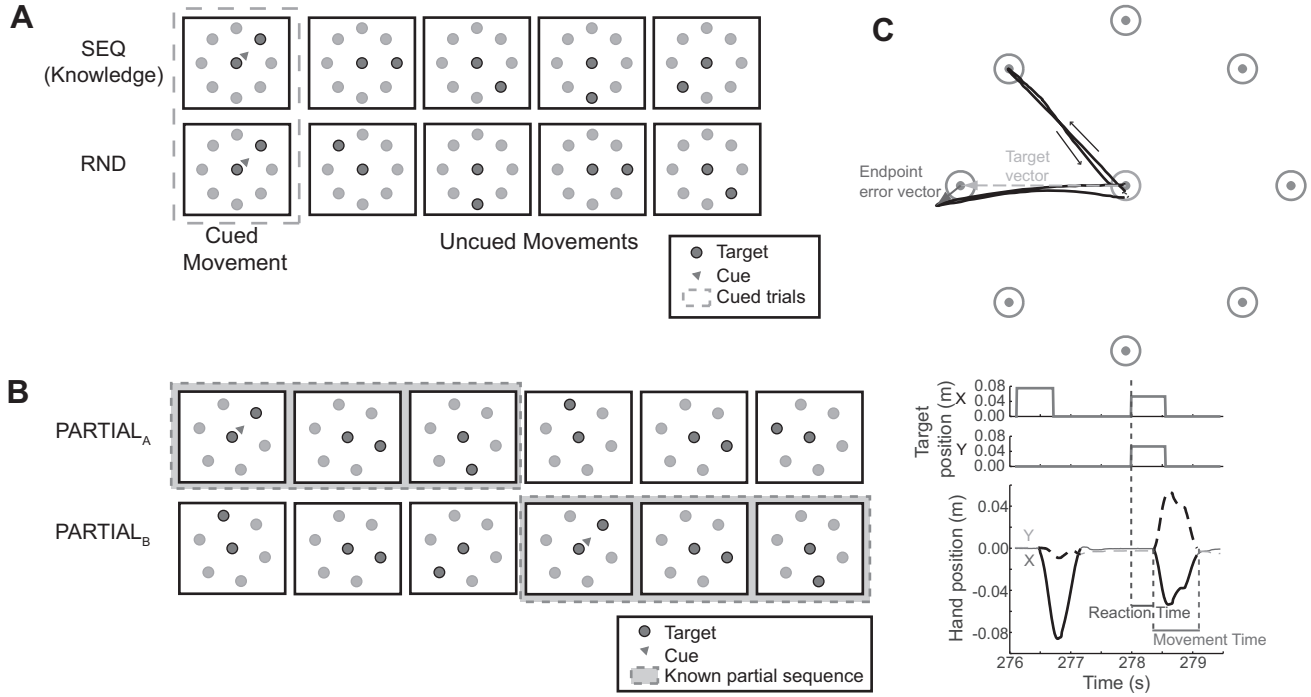

Fig. 1. Sequence-learning tasks. *A*: in *experiment 1*, the performance of a group that was given explicit sequence knowledge (SEQ) was contrasted with that of a group generating reaches to a random series of targets (RND). The initial cued movement of the set was followed by 4 additional uncued movements. *B*: *experiment 2* introduced 2 PARTIAL-knowledge conditions. The A and B versions of the PARTIAL-knowledge condition differed in the order of known and unknown trials; in condition A, the cue occurred at the start of the set, and the first 3 targets obeyed the sequence; in condition B, the cue occurred halfway through the set of trials, and only the last 3 trials were sequence trials. The remaining 3 trials consisted of targets at random locations. Analogous random conditions were also introduced (not shown), in which the cued trial occurred either on the 1st trial ($RAND_A$) or 4th trial ($RAND_B$) of the set. *C*: hand movement trajectories were recorded for analysis of the reaction time (RT) (time between target onset and movement initiation) and movement time (MT) (time between movement initiation and return of the arm to the starting position). Accuracy (endpoint error) was measured as the difference between the turn-around point of the hand and the midpoint of the target; the sign of the error was assigned by projecting the endpoint-error vector onto the vector connecting the starting position and the target.

had to wait for the appearance of the target before they could begin their movement.

Experiment 2: partial sequence-knowledge task. Experiment 2 was designed to directly investigate whether knowledge-based performance improvements arose from advanced planning or from motivation. One important distinction between these two mechanisms is how subjects behave on trials to unknown targets that are performed in the context of a partially known sequence; i.e., whether there are any global effects of knowledge. Presence of a global effect would argue for a motivational rather than a planning mechanism.

Such a situation evolves naturally during typical sequence-learning tasks, in which sequence knowledge is gradually accumulated; subjects initially only have awareness of fragments of the sequence (Buchner et al. 1998; Ghilardi et al. 2009; Perruchet and Amorim 1992; Perruchet and Gallego 1993). This state of incomplete sequence knowledge was mimicked in *experiment 2*, where only a subset of all trials contained a known sequence and targets appeared at random locations on the remaining unknown trials. This allowed for a study of the local effects of knowledge, i.e., performance changes that were specific to trials to known targets in the partial sequence, as well as an investigation of the global effects of knowledge, i.e., whether performance to random targets changes when they are embedded in the context of a known partial sequence. Global knowledge effects can be examined by comparing the performance of movements made to unknown targets in the partial-knowledge condition to that of movements in the wholly random condition. Because knowledge of the target location was absent in both cases, any differences in behavior would be attributable to a motivational effect of partial sequence knowledge.

To evenly divide the trial set into known and unknown movements, the number of trials in a sequence was increased to six. To keep the total number of training trials similar to that of *experiment 1*, a block was reduced to consist of only eight sets of trials to each of two cued locations (16 sets per block). Additionally, the number of potential targets was reduced to six (spaced every 60°) such that, within a set, subjects made as many reaches as there were potential targets (i.e., a subject could potentially make 1 reach to each of the 6 targets within a set of trials). Between sets, all visual information on the screen was blanked for 1,500 ms to demarcate a clear boundary between the end of one set and the beginning of the next. After this blanking time, the background display (which showed the 6 potential target locations and, in some conditions, the cue) appeared; the wait time between the onset of this background display and the appearance of the first target in the set was shortened (uniformly distributed between 1,000 and 1,600 ms) to approximate the ITI between the remaining trials in the set (ITI uniformly distributed between 400 and 1,000 ms, including the cued trials in some conditions).

Subjects were divided evenly across four experimental conditions (41 subjects were recruited: 10 subjects per group; 1 subject was excluded for failing to maintain similar speeds on the outward and return phases of the movement). There were two partial-knowledge groups and two random groups (Fig. 1*B*). All groups made the same number of reaches to each target; only the order of target appearance varied. Group $PARTIAL_A$ received a cued trial on the first trial of the set, followed by two additional sequence trials in which the target appeared at a location clockwise to that of the prior trial; this was followed without delineation by three trials in which the target could appear randomly at any of the six possible locations (including ones in which targets had previously appeared during the known

sequence trials). The corresponding group $RAND_A$ was similar to the RND condition from *experiment 1*; the set started with a cued trial, which was then followed by five trials to random targets. In contrast, the $PARTIAL_B$ group started with three trials to random targets; the cue appeared immediately following the conclusion of the third trial to mark the presence of the cued movement on the fourth trial, and this trial was subsequently followed by two clockwise sequence trials. Note, the time between the cue presentation and the target appearance in the B conditions was the same as the ITI of all other trials. The corresponding $RAND_B$ group similarly had a cued trial on the fourth trial of the set rather than the first trial, but all other trials consisted of targets appearing at random locations.

All subjects initially received a practice block of trials to random targets, with the timing of the cue within the set consistent with their group designation (A or B). This was followed by explicit instructions about the nature of the partial sequence for the PARTIAL-knowledge groups, and then subjects completed seven training blocks in their respective condition.

Data Analysis

All data were analyzed offline using programs written in MATLAB (The MathWorks, Natick, MA). Reaches were selected using a semiautomated program that identified movement start and end according to a velocity criterion (tangential velocity greater than 0.06 m/s; velocity changes when the hand reversed direction at the target were excluded from the determination of movement end). All movements were verified by visual inspection. RT was computed as the time between the onset of the target appearance and the initiation of the movement; MT was the duration between initiation of the outward movement and conclusion of the return movement. MT is the parameter we used to investigate vigor, as it has identical units to RT and is related to the rate at which movements are executed. Furthermore, MT is frequently measured alongside RT in sequence tasks (e.g., response time in keypress tasks is the sum of RT and MT; Pascual-Leone et al. 1993). Peak velocity was used solely as a criterion to determine compliance with task requirements and was determined by differentiating the smoothed position trace (using a second-order Savitzky-Golay filter with a half width of 73 ms) then selecting the maximum velocity achieved during the outward phase of the movement. Finally, movement accuracy (i.e., endpoint error) was computed as the magnitude of the vector distance between the reversal point of the reach (denoted as the point at which the tangential velocity first returned to 0 in the vicinity of the target array) and the center of the target. To distinguish between overshoots and undershoots, endpoint errors were assigned a sign according to the projection of that error vector onto the vector from the central start position to the target such that positive errors were overshoots and negative errors were undershoots (see Fig. 1*C*). In all data figures, error bars report SE.

Trials were excluded if subjects failed to perform a movement according to the task instructions, which meant satisfying the following parameters: an RT between 100 and 1,000 ms (i.e., no anticipatory movements), an MT less than the trial duration of 1,200 ms, a peak velocity of the outward reach between 0.20 and 0.80 m/s (i.e., no excessively slow or fast movements), reasonably similar peak velocities on the outward and return phases of the reach (a return peak velocity less than twice that of the outward peak velocity), and an accuracy greater than half the distance between two neighboring targets (0.031 m for *experiment 1*, and 0.043 m for *experiment 2*). This resulted in the exclusion of on average 9.5% of all trials across subjects, with nonsignificant differences in the number of excluded trials for each condition in each experiment according to a one-way ANOVA (*experiment 1*, $P = 0.45$; *experiment 2*, $P = 0.99$). The majority of these trials were excluded because subjects failed to maintain similar movement velocities on the outward and return phases of the movement despite our reasonably lax criterion; applying a less stringent criterion merely served to increase the variability of measured MTs both within and across subjects. Restricting RT with a more stringent definition of anticipation (RT $<$ 200 ms) had little effect on the significance of the results and increased the average percentage of excluded trials by $<1\%$.

Analysis of performance differences between sequence and random groups across the course of training. To examine time courses of training, comparisons were conducted by fitting generalized linear models in R with factors of group and block (R Core Team 2015), using the *nlme* package (Pinheiro et al. 2015) to account for the autocorrelated covariance structure across time within subjects. These models do not contain a random-effects term to represent variability across individual subjects; rather, they first remove any autocorrelation structure across trials for individual subjects before examining main effects for group and block. The form of the autocorrelation structure was selected by fitting Autoregressive-Moving Average models and selecting the model fit that yielded the lowest Aikake Information Criterion on average across subjects; in almost all cases, this led to a choice of an AR(1) process.

In *experiment 1*, a generalized linear model was used to compare the SEQ and RND groups. Planned *t*-test comparisons (where noted in RESULTS) were used to compare changes in movement parameters (RT, MT, and accuracy) between *block 1* and *block 7* within the SEQ group and the RND group separately. Additional *t*-tests were used to assess whether significant differences between the SEQ and RND groups were already present within the first block of trials. All tests were performed separately for the cued and the uncued trials. All *t*-tests were two-tailed, and *P* values were adjusted using the step-down Bonferroni method for multiple comparisons.

In *experiment 2*, generalized linear models were used to compare the time courses of the four experimental groups. As no significant differences across training were evident between groups experiencing the same amount of sequence knowledge (i.e., between $PARTIAL_A$ and $PARTIAL_B$ or $RAND_A$ and $RAND_B$), data for the two random groups were collapsed together, as were data from the two PARTIAL-knowledge groups. To address the question of whether there was evidence specifically for local effects (on trials to known targets only) and global effects (on trials to unknown targets performed in the context of known targets) of sequence knowledge on performance, behavior in the RAND conditions was individually compared with the two types of trials in the PARTIAL conditions: *1*) trials to known targets that were part of the partially known sequence, and *2*) trials to unknown targets that comprised the remainder of trials in the PARTIAL-sequence conditions. Trials to known and unknown targets in the PARTIAL-sequence conditions were also compared with each other. Because this latter analysis is a repeated-subjects comparison, the time-course analyses were conducted as a set of three pairwise tests: RAND vs. PARTIAL-known, RAND vs. PARTIAL-unknown, and PARTIAL-known vs. PARTIAL-unknown. For this analysis, both the cued trials as well as the first trial of the set (i.e., the first uncued trial for the $PARTIAL_B$ and $RAND_B$ conditions) were excluded, as this enabled the fairest comparison of the effects of sequence knowledge (by excluding any effect of the cue or the first trial of the set) on behavior.

Analysis of the effects of individual trial features on performance. Experiment 2 additionally provided the opportunity to investigate the manner in which movement parameters were modulated with respect to three critical trial features in the set: the cued trial, the first trial of the set, and trials to known targets. To analyze these data, the response to each trial of the set was individually averaged across the seven training blocks (e.g., all cued trials were averaged together), for each of the four groups of subjects. The behavior of all four groups was then compared using a separate generalized linear mixed-effects model for each of the three movement parameters of interest (RT, MT, and accuracy) with intersubject differences treated as a random effect

and the three trial features as fixed effects. These mixed-effects models were conducted using R (R Core Team 2015) and the *lme4* package (Bates et al. 2015). As the *lme4* package does not return a *t* statistic for the coefficients of the effect terms, *P* values were obtained using likelihood ratio tests of the full model including the effect of interest against the model without that effect (*P* values are reported along with the corresponding χ^2 value). Use of a likelihood ratio test evaluates whether the feature of interest has a significant effect on the model; in contrast, the *t* statistic describes whether that effect has a nonzero coefficient.

The effects of individual trial features on RT and MT were explored further by fitting the data using a simple model with six parameters. The effect of the start of the set was described with a two-parameter exponential equation (i.e., $a \times e^{-bt}$) where *t* refers to the trial number in the set. Similarly, the effect of the cue was modeled as a two-parameter exponential. Note, in the case of MT, the model did not converge unless the cued trial was treated as the last trial of the set instead of the first trial, such that it resided at the lowest point of a concave-down exponential. The shape of the resulting effect of the cue then resembled the observed effect of reward noted by Takikawa et al. (2002). The model also contained two additional parameters, one to describe the effect of knowledge and the other as a constant. The parameters of the model were estimated using a least-squares fit to the group data from all four conditions in MATLAB. These parameters provided a rough description of the individual contributions to the observed RT and MT of the cued trial, the first trial of the set, and trials to known targets.

RESULTS

Experiment 1: The Effects of Full Sequence Knowledge on Motor Performance

By providing complete knowledge of the target sequence before the onset of training, we could distinguish between knowledge-related effects (which would occur immediately within the first block only for the SEQ group), sequence-independent practice effects (which would occur similarly for all subjects in the SEQ and RND groups), and sequence-specific practice effects (any remaining practice-related improvements not accounted for in the SEQ group). We examined RT and MT separately to see whether there were any differential effects of either sequence knowledge or practice on these movement variables (Fig. 2). We also separately analyzed data for the cued (first trial of the set) and uncued trials to examine how cuing affected performance; as the amount of local knowledge about the current trial was similar between the cued trials in the two conditions, we were primarily interested

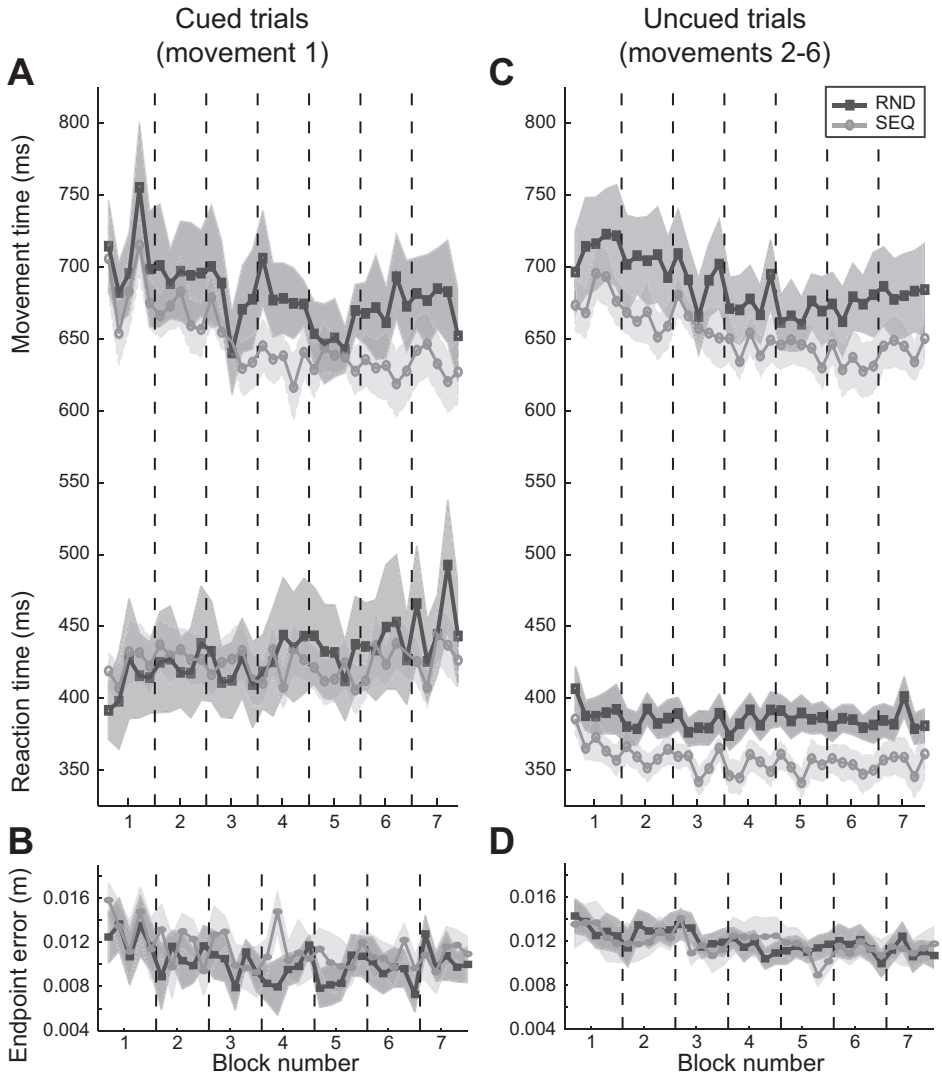

Fig. 2. *Experiment 1*. Data show the time courses of RT, MT, and movement accuracy (endpoint error) across 7 training blocks for both the RND group ($n = 10$, dark gray) and the SEQ group ($n = 10$, light gray). Data are presented separately for cued trials (*A* and *B*) and uncued trials (*C* and *D*). Differences between conditions were observed predominantly for the uncued trials, with both an immediate, sustained shift in RT and MT in the SEQ group (*t*-test in *block 1*; RT: $P < 0.01$; MT: $P = 0.05$), as well as similar reductions in MT with practice for both groups (*t*-test between *blocks 1* and *7*; SEQ: $P < 0.01$; RND: $P = 0.05$). There were no changes in accuracy.

in behavioral differences on the uncued trials. Together, these results enabled us to assess how the introduction of advanced knowledge affected movement execution, independent of any motor practice effects.

Sequence knowledge decreased RT and MT for uncued trials. The RTs for uncued trials were significantly shorter in the SEQ group compared with the RND group, and this difference could be observed as early as the first block of trials (Fig. 2*C*; RT in *block 1*, SEQ: 368.74 ± 11.48 ms, RND: 392.91 ± 14.64 ms; *t*-test, $P < 0.01$). This lower RT for the SEQ group occurred despite randomized ITIs that made the target onset time unpredictable, reducing the likelihood of anticipatory movement initiations. Thus explicit sequence knowledge led to an immediate reduction in the RT.

The MTs for uncued trials were also significantly shorter for the SEQ group within the first block (Fig. 2*C*; SEQ: 681.36 ± 18.24 ms, RND: 714.39 ± 32.71 ms; *t*-test, $P = 0.05$). Therefore, explicit sequence knowledge also produced an immediate reduction of the MT. Together, these data suggest that sequence knowledge led to a practice-independent behavioral improvement that affected both RT and MT for uncued trials.

Cued trials exhibited no statistically significant difference within the first block between the SEQ and RND conditions for either RT (SEQ: 422.55 ± 17.82 ms, RND: 409.41 ± 29.61 ms, $P = 0.80$) or MT (SEQ: 686.60 ± 22.21 ms, RND: 709.27 ± 34.27 ms, $P = 0.21$). Interestingly, however, MTs were noted to be faster in general for cued trials in the SEQ group across all training blocks (effect of group, $P = 0.03$) with no notable interaction between group and block ($P = 0.65$). This difference is surprising because the amount of advanced knowledge directly pertaining to the location of the cued trial was identical in both groups and suggests a contextual effect of whether the remaining trials to be executed were known or random.

Practice had only sequence-independent effects on MT. The RTs of uncued trials did not modulate across training; there were no significant differences between the first and last training blocks within either the SEQ group (first: 368.73 ± 11.48 ms, last: 356.46 ± 14.62; *t*-test, $P = 0.14$) or the RND group (first: 392.91 ± 14.64 ms, last: 385.54 ± 12.30 ms; *t*-test, $P = 0.20$). Interestingly, there was also no significant interaction between group and block ($P = 0.55$), suggesting that the immediate knowledge-related differences in RT were sustained throughout the course of the experiment. Together, these results suggest that RT was not influenced by practice.

In contrast, the MTs of uncued trials showed a consistent decline with practice (Fig. 2*C*); subjects generated movements of shorter duration in the last block compared with the first block (*t*-tests; SEQ: first, 681.36 ± 18.24 ms, last, 644.67 ± 16.23 ms, $P < 0.01$; RND: first, 714.39 ± 32.71 ms, last, 682.35 ± 29.26, $P = 0.05$). However, the magnitudes of these changes between *blocks 1* and *7* were similar for the two groups (a decline of 36.68 ms in the SEQ group and 32.04 ms for the RND group; no significant difference was found, *t*-test, $P = 0.75$). There was no evidence of a significant interaction between group and block according to the mixed-effects model ($P = 0.15$). In fact, knowledge reduced MT immediately in the first block by 31.82 ms in the SEQ group according to a regression fit to the data; nonspecific practice led to a 42.70-ms improvement in MT across training in the RND group. To the extent that there was a sequence-specific improvement in behavior with practice, it was negligible; subjects in the SEQ group exhibited only an additional 3.89-ms improvement in the MT by the end of training compared with the RND group. This suggests that the rate of acquisition of practice-related MT improvements was unaffected by the presence of a sequence; i.e., practice led only to sequence-independent behavioral improvements.

A similar sequence-independent practice effect was observed on cued trials. No difference in RT was observed for either the SEQ group (first: 422.55 ± 17.82 ms, last: 428.18 ± 17.33 ms; *t*-test, $P = 0.80$) or RND group (first: 409.41 ± 29.61 ms, last: 455.00 ± 34.92 ms; *t*-test, $P = 0.09$) throughout training (Fig. 2*A*); this is consistent with no change in RT for uncued trials with practice. In contrast, the MT of cued trials differed between *blocks 1* and *7* for the cued SEQ trials (first: 686.60 ± 22.21 ms, last: 633.69 ± 21.20 ms; *t*-test, $P < 0.01$). Although no significant difference was noted for the RND group (first: 709.27 ± 34.21 ms, last: 675.65 ± 29.95 ms; $P = 0.21$), the magnitude of the change in MT between *blocks 1* and *7* was similar between the two groups (not significantly different according to a *t*-test, $P = 0.31$), and there was no interaction between group and block ($P = 0.65$). Together, these results suggest that both cued and uncued trials exhibited only practice-related (sequence-independent) modulations of MT across the training session.

No sequence-dependent effects on practice, accuracy, and rate of reward. The lack of a difference in the rate of improvement with practice across the two groups suggests that there is no sequence-specific effect of practice; practicing movements in a specific sequence offered no obvious improvement in training compared with practicing movements in a random order. That is, after we accounted for the immediate and sustained effect of sequence knowledge, the rate of improvement in MT was identical in the two groups.

Critically, all observed differences in RT and MT occurred without a compensatory trade-off in accuracy; no significant difference in endpoint error was observed between the SEQ and RND groups for either cued or uncued trials (Fig. 2, *B* and *D*; cued trials, difference of 0.9 mm, $P = 0.52$; uncued trials, difference of 0.2 mm, $P = 0.81$). That movement accuracy does not improve further may be attributed to the fact that errors are already quite small; subjects on average are able to reverse direction within the diameter of the target as early as the first block of trials. These changes in RT and movement vigor with no loss of accuracy could not be attributed to a difference in overt reward experienced by subjects in the SEQ and RND groups. No significant difference was found between the number of "correct" trials that resulted in positive feedback to the subject for any given training block (no effect of group, $P = 0.43$; uncorrected *t*-tests for each individual block, $P > 0.08$). That is, subjects in both the SEQ and RND groups received an equal amount of explicit rewards (in the form of points and rewarding tones) during training.

Experiment 2: The Effects of Partial Sequence Knowledge on Trials to Known (Local) and Unknown (Global) Targets

The results of *experiment 1* established a gradual sequence-independent change in motor performance related to practice, which occurred alongside but did not interact with the immediate effect of explicit knowledge, i.e., reductions in RT and

MT without requiring any practice. This result could be attributable either to improved planning enabled by advance knowledge of the upcoming movement in the sequence or to a motivational effect. A critical distinction between these two hypotheses is that only the motivational argument can account for global effects on movement vigor (Niv et al. 2007; Wang et al. 2013), i.e., effects on the unknown trials when only partial knowledge of the sequence is available. Indeed, during typical sequence-learning tasks, subjects accumulate fragmentary explicit knowledge as they repeatedly practice the sequence (Buchner et al. 1998; Ghilardi et al. 2009; Perruchet and Amorim 1992; Perruchet and Gallego 1993). Thus, to distinguish whether knowledge enhances performance via advanced planning or motivation, it is necessary to examine the case in which only a fragment of the sequence is known.

To create a state of partial knowledge in a more controllable manner, we provided two groups of subjects with a sequence that was only partially predictable. Subjects were informed that only the first half ($PARTIAL_A$) or the second half ($PARTIAL_B$) of the targets in a set followed a predictable and consistent sequence (i.e., that the targets would appear in a clockwise order); targets in the remaining trials occurred at different random locations each time and thus could never be learned. Two additional control groups received random targets throughout the entire set of trials; the only difference between these two random groups was whether the cued trial occurred at the beginning of the set ($RAND_A$) or halfway through ($RAND_B$), consistent with the timing of occurrence of the cued trials in the two PARTIAL-knowledge groups. Subjects were given full knowledge of the circumstances of their group (e.g., that only half the targets would occur in a sequence) so that the effects of explicit knowledge and practice could be distinguished.

Partial sequence knowledge produced local effects on RT. First, the time course of learning was examined to see how task knowledge and practice broadly affected behavior across training under PARTIAL-knowledge conditions (Fig. 3). Only uncued trials were examined in this analysis because, during the cued trial, the target location was presented explicitly to subjects in both the partial and random groups, and hence performance could be modulated by anticipation in a manner independent of sequence knowledge. Indeed, no differences were noted between PARTIAL and RAND cued trials for either RT or MT ($P > 0.45$), consistent with what was found for *experiment 1*. For these analyses, data from the two PARTIAL groups were combined together, as were data from the two RAND groups because behavior was comparable regardless of whether the partial sequence was present in the first half or the second half of the set of trials. Trials in the PARTIAL conditions were classified as being made to either known or unknown targets; local effects were explored by examining pairwise comparisons between trials to known and unknown targets in the PARTIAL conditions.

The RT differed significantly depending on the type of trial (Fig. 3*A*); RTs were significantly shorter for trials to known targets than to unknown targets in the PARTIAL conditions ($P < 0.01$). Hence, sequence knowledge had an immediate local effect on the RT of trials to known targets.

In contrast, trials to known targets were unexpectedly found to have longer MTs compared with trials to unknown targets in the PARTIAL conditions ($P < 0.01$). That is, although complete sequence knowledge served to lower MT (as shown in *experiment 1*), partial sequence knowledge seemed to reverse this effect (trials to known targets were performed more slowly in *experiment 2*). Although these data appear contradictory, further analyses reconcile this discrepancy (see the trial-features analysis below). Nonetheless, there was a local effect on MT that was specific for trials to known targets.

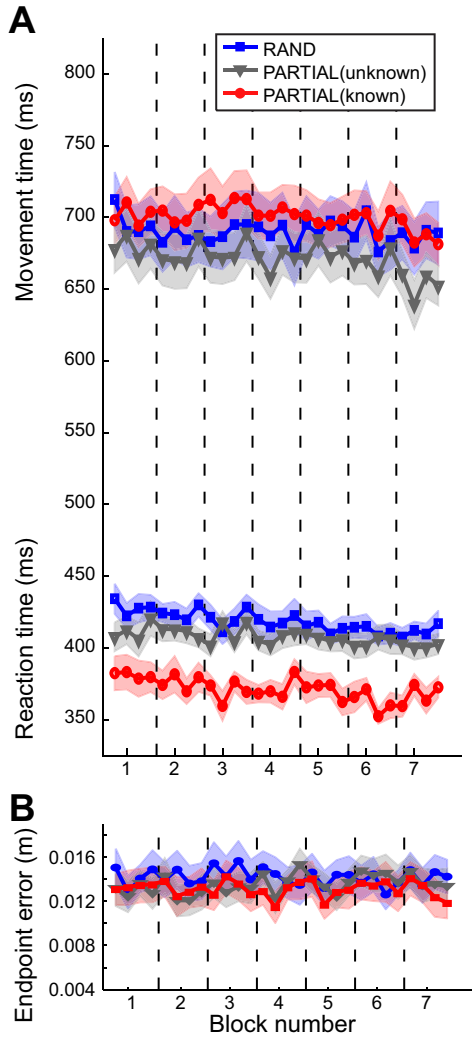

Fig. 3. *Experiment 2*, time courses. Data were collapsed across the 2 versions of each condition (e.g., $PARTIAL_A$, $n = 10$, and $PARTIAL_B$, $n = 10$). The RT and MT (*A*) and accuracy (endpoint error, *B*) were compared in 3 cases: random conditions (blue squares), known (sequence) trials in the PARTIAL-knowledge conditions (red circles), and unknown (random) trials in the PARTIAL-knowledge conditions (gray triangles). Significant differences were observed between all pairs of trial types for RT (mixed-effects models, effect of type, $P < 0.02$) and between trials to known and unknown targets in the PARTIAL conditions for MT (mixed-effects model, effect of type, $P < 0.01$). There were no differences in accuracy

Thus knowledge had local effects on both RT and MT; in particular, sequence knowledge served to lower RT. Interestingly, these data suggest that RT and MT do not necessarily covary. That is, although RT was lower for trials to known targets in the PARTIAL-knowledge condition, subjects made faster movements (without loss of accuracy) on trials to unknown targets (note, data from *experiment 1* showed the opposite relationship). Thus the RT does not predict how a movement will be executed; longer planning time (RT) does

not necessarily translate into more "skilled" performance (i.e., an improvement in movement vigor without loss of accuracy).

Partial sequence knowledge produced global effects on the RT. Comparison of performance on trials to unknown targets in the PARTIAL-knowledge conditions to that of trials in the RAND conditions provided a way to identify the global influence of sequence knowledge on behavior. A global influence of knowledge was apparent upon examination of the RT. Trials to unknown targets in the PARTIAL conditions had significantly lower RTs than did trials in the RAND conditions ($P = 0.02$) despite these trials being identical with respect to ambiguity in target location. No such global effect could be detected in the MT although we suspect that is attributable to limited statistical power, as the MT data are more noisy than the RT data. Hence, there appeared to be a global effect on performing trials to unknown targets in the context of partial sequence knowledge. This global influence of knowledge can be explained by a motivational but not a planning effect.

Practice led to sequence-independent improvements in MT. As with *experiment 1*, practice facilitated MT improvements across training that were independent of sequence knowledge. MT exhibited a significant effect of block for both the RAND vs. PARTIAL-unknown and the PARTIAL-known vs. PARTIAL-unknown pairwise comparisons ($P = 0.03$ and $P < 0.01$, respectively). Furthermore, a lack of significant interaction between group and block for any of the pairwise tests (RAND vs. PARTIAL-unknown, $P = 0.08$; RAND vs. PARTIAL-known, $P = 0.80$; PARTIAL-known vs. PARTIAL unknown, $P = 0.14$) suggests that subjects exhibited similar practice-related performance improvements in all conditions. This supports the argument made in *experiment 1* that practice-related improvements across the training block were knowledge independent, as such effects were similar regardless of whether trials were made to known or unknown targets.

Experiment 2: Trial Features (Cue, Start of Set, and Trials to Known Targets) Differentially Affected RT and MT

Interestingly, we observed that fluctuations in RT and MT across individual trials within a set (e.g., the consecutive series of 3 sequence and 3 random trials) showed a clear structure that was highly conserved across subjects. That is, the majority of observed performance variability arose from intersubject differences (i.e., subjects tended to be characteristically faster or slower on all of their movements; Fig. 4). This stereotypical behavior across subjects suggests that features of the different trial types had very specific and reproducible effects on performance. We identified three distinguishing features of interest: whether the trial occurred at the start of the set or not, whether the trial contained a known or unknown target location, and whether the trial was cued or uncued. For this analysis, data within each knowledge condition were collapsed across the seven training blocks. Here, we show the pronounced and highly predictable influence that each of these three trial features had on behavior.

The first trial of a set was marked by a prolonged RT. The first trial of the set exhibited a significantly increased RT, being about 110 ms longer than that of the remaining trials [Fig. 5*A*; $\chi^2(1) = 340.19$, $P < 0.01$]. This prolonged RT occurred regardless of whether the first trial was a cued trial or not or whether all the remaining trials in the set were random or not. Therefore, this prolonged RT cannot be attributed to planning the partial movement sequence in advance. Although MT also was found to be significantly affected by the first trial of the set [$\chi^2(1) = 5.38$, $P = 0.02$], this effect was driven by the two groups in which the start of the set coincided with the cued trial (i.e., PARTIAL_A and RAND_A); thus, MT did not appear to be uniquely modulated on the first trial of the set (Fig. 5*B*). No effect of the start of the set on accuracy was observed [Fig. 5*C*; $\chi^2(1) = 0.77$, $P = 0.38$]. Together, this suggests that the first trial of the set only influenced the RT.

Trials to known targets had a decreased RT. The effect of trial type (known or cued trials) was best explored when the data were aligned to the cued trial (note in the PARTIAL_B and RAND_B conditions this meant the pause between sets occurred between the second and third post-cue trials, as denoted by the dashed lines in Fig. 5, *D–F*). Consistent with the time-course analyses from *experiment 2*, subjects initiated their movements at lower RTs [$\chi^2(1) = 72.18$, $P < 0.01$] on trials in which the target was known according to the partial sequence (post-cue trials 1 and 2 in Fig. 5*D*). Thus the RT was modulated on trials to known targets in the context of a partial sequence.

Trials to known targets also had slightly but significantly prolonged MTs relative to those of unknown targets [Fig. 5*E*; $\chi^2(1) = 63.25$, $P < 0.01$], consistent with the findings in the previous section that MT was shorter for trials to unknown than known targets. However, this effect arose predominantly from the effect of the cued trial, as noted in the next section.

The cued trial strongly modulated MT across the set of trials. The cued trial had a very strong and lingering effect on MT across the set [$\chi^2(1) = 277.93$, $P < 0.01$] but no consistent effect on RT [$\chi^2(1) = 0.08$, $P = 0.77$]. Subjects moved much faster on the cued trial compared with all other trials. This MT effect was a true shift of the speed-accuracy trade-off; movement accuracy actually improved slightly on the cued trial [$\chi^2(1) = 30.67$, $P < 0.01$]. Following the very fast cued trial, MT sharply slowed on the next trial (paired *t*-test between the cued trial and second trial, $P < 0.01$; note this second trial was a known trial in the partial-sequence conditions), and then the MT appeared to gradually speed back up across the set, particularly for subjects in the PARTIAL conditions [slope = -9.81 ms/trial, $\chi^2(1) = 72.825$, $P < 0.01$; Fig. 5*E*].

These strong modulations of MT following the cued trial imply that fluctuations in the availability of information (particularly the sudden injection of a large amount of information on the cued trial) had a particularly dramatic impact on the MT. The strength of this effect could explain the apparent discrepancy in the local effect of knowledge on MT between *experiments 1* and *2*; i.e., the increased vigor from information acquired on the cued trial and the corresponding decrease in vigor on the trials immediately following it may have outweighed all other motivational effects of sequence knowledge on performance. Interestingly, a similar pattern of fluctuations in movement vigor has been previously observed for saccades made in response to rewarding trials (Takikawa et al. 2002), in which movement vigor was strongly suppressed on trials following a reward.

On the other hand, because the cue had no effect on RT, movement preparation was not apparently different for the first movement of a known sequence of trials relative to the other trials to known targets. That is, there is no indication that subjects expend additional planning time during the RT

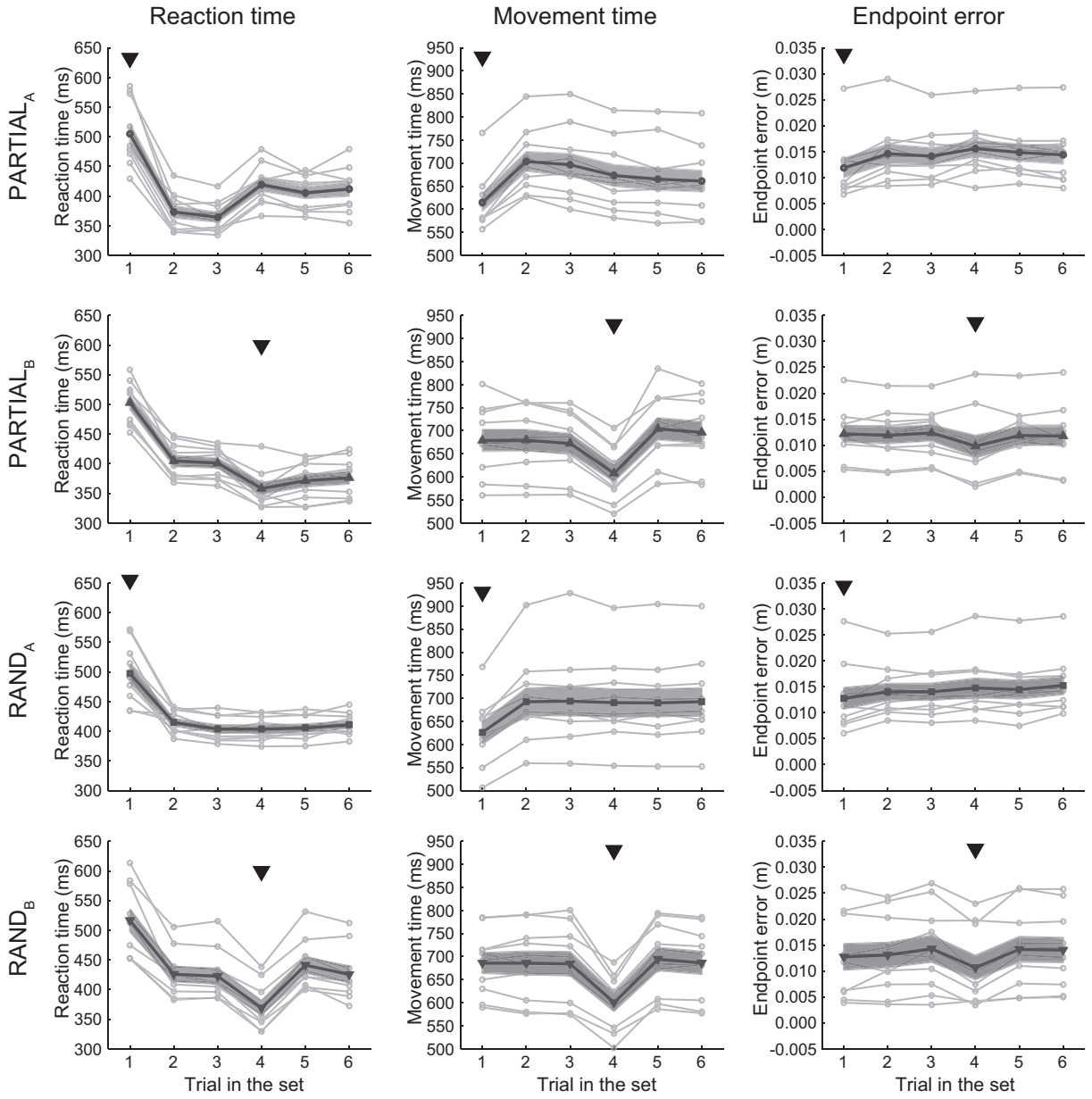

Fig. 4. *Experiment 2*, contributions of individual trial features; data from all subjects. Black triangles indicate the timing of the cued trial, light gray lines represent data from individual subjects ($n = 10$ in each group), and dark gray lines represent the mean across subjects. Note the consistency with which each subject in a particular condition exhibited stereotypical behavior across the set of trials.

to prepare the entire sequence fragment in advance, contrary to what has been hypothesized to occur during the preparation of chunks of movement sequences (Nissen and Bullemer 1987; Perruchet and Amorim 1992). Thus changes in RT on trials to known targets are unlikely to arise because those movements have been planned several trials in advance. Instead, these findings are most consistent with the hypothesis that sequence knowledge drives performance changes via motivation.

Effects on RT and MT were dissociable. To summarize, RT was modulated by the first trial in a set (denoting initiation of a group of movements) and by trials to known targets (in which the upcoming target location is already known, and the only uncertainty relates to the onset of the target appearance). The MT, in contrast, was modulated primarily by the cued trial in a manner suggestive of motivational vigor. Therefore, there is a clear dissociation of the influence of particular trial features on the RT and MT of a movement, suggesting that the RT and MT should be viewed as independent movement parameters.

The individual contributions of the three trial features to RT and MT can be quantified by fitting a model to the data that approximates the impact of the start and the cued trial across the trials in the set as exponential functions and the discrete effect of trials to known targets as a constant effect specific to only those trials that are part of the sequence (Fig. 6). These fits illustrate the critical trial features that contribute to the average RT and MT exhibited by subjects on any given trial in the set. The model fits (i.e., the sum of the influence of the individual trial features) closely resembled the behavioral data (model fits compared with the average group data, $r^2 > 0.90$). In partic-

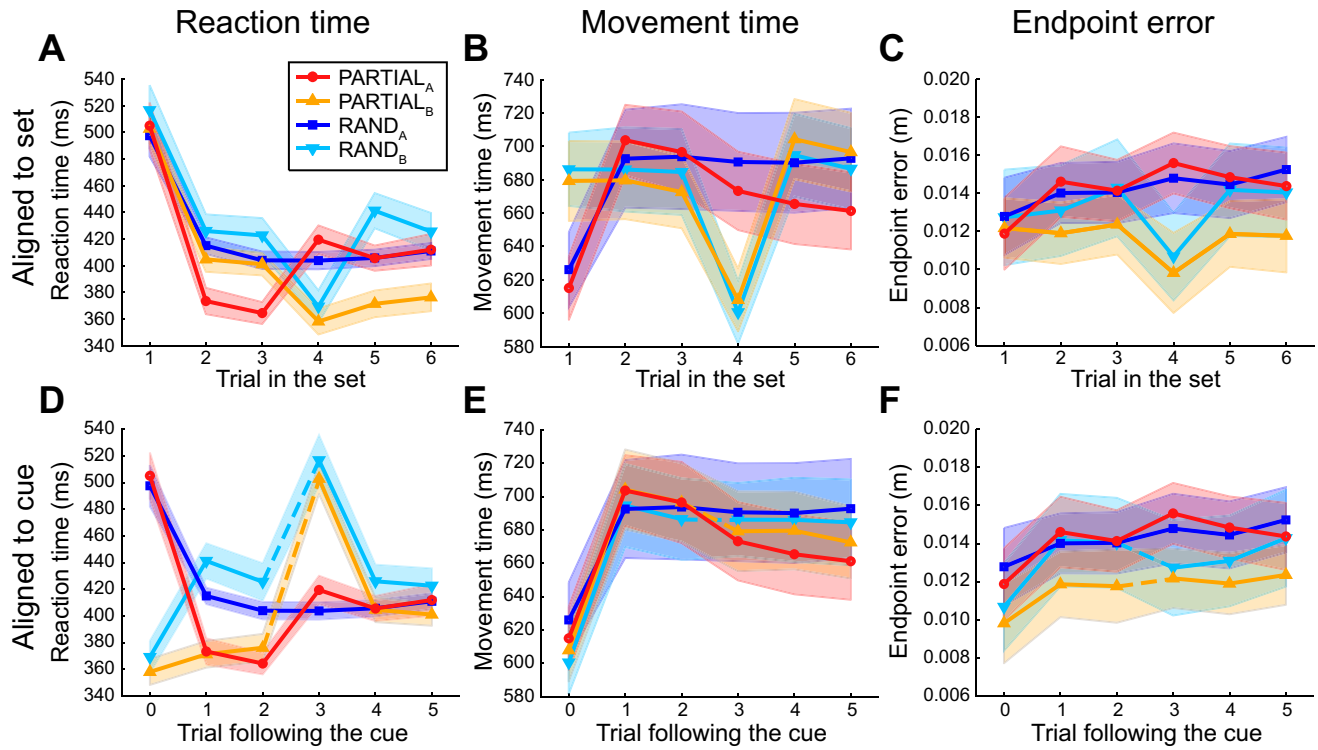

Fig. 5. *Experiment 2*, group summary of the contributions of individual trial features within a set. Data for the 4 conditions are aligned in 2 ways. *A–C*: data were aligned according to the trial number in the set. The RTs of the first trial in the set were consistently higher than the RTs of other trials across all 4 knowledge conditions, regardless of when the cued trial (and the partial sequence) occurred (mixed-effects model, effect of 1st trial in the set, $P < 0.01$). *D–F*: data were aligned according to the occurrence of the cued trial. Note, the brief pause between sets falls between the 2nd and 3rd trials for the $PARTIAL_B$ and $RAND_B$ conditions. The MT was quite low on the cued trial; following this, there was an abrupt rise in MT on the 1st trial following the cue (e.g., on known trials; paired *t*-test, $P < 0.01$), and, particularly in the case of the PARTIAL-knowledge conditions, this was followed by a gradual recovery of MT [mixed-effects model, slope $= -9.81$ ms/trial, $\chi^2(1) = 72.825$, $P < 0.01$]. Accuracy was found to slightly increase for the cued trial (mixed-effects model, effect of the cued trial, $P < 0.01$) but remained consistent across the remaining trials. In contrast, RT was lower for known trials than for unknown trials. These data suggest that RT and MT may be modulated independently.

ular, RT was found to be largely affected by two main trial features: first, the start of the set, which primarily served to prolong RT on only the first trial, and second, trials to known targets, which reduced RT compared with trials to unknown targets. The cue was found to have a minimal effect on RT. In contrast, MT was driven only by the cue, which appeared to dictate, not only a short MT on the cued trial, but also the sharp increase in MT on the trial following the cue and the subsequent gradual decay of MT across the remaining trials in the set. Both model fits were consistent with the statistical analyses (mixed-effects models) performed above and supported the finding of a dissociation between RT and MT with respect to different trial features.

DISCUSSION

Discrete sequence tasks are thought to exhibit three features characteristic of many everyday motor skills, a sequential nature, a sequence-specific, possibly implicit component that improves with practice, and the ability to improve performance with explicit instruction (coaching). Here, we sought to determine how explicit sequence knowledge affects motor performance. Explicit knowledge, which allowed for the prediction of upcoming target locations, did not facilitate motor practice effects beyond those attainable from rehearsing a random sequence; there was no interaction between knowledge and practice. That is, there was no evidence for sequence-specific motor skill. Instead, the effect of sequence knowledge was immediate, increasing vigor (without loss of accuracy) globally to unknown targets performed in the context of a known partial sequence as well as locally to known targets. This suggests that, in typical sequence tasks, all sequence-specific learning is attributable to the gradual acquisition of explicit knowledge of sequence fragments and that this knowledge modulates behavior through a motivational effect similar to what has been previously described for reward (Takikawa et al. 2002; Wang et al. 2013).

The Absence of Sequence-Specific Motor Skill Learning

The term motor skill is often used to refer to a practice-induced shift of the speed-accuracy trade-off function (Reis et al. 2009; Shmuelof et al. 2012). Here, movement vigor increased with no loss of accuracy in response to sequence knowledge, but subsequent reductions in MT with practice were identical for both the known and random sequence conditions. Thus practice-related performance improvements depended only on repetition of the individual movement elements, regardless of their order. The fact that explicit knowledge led to immediate changes in the same performance variables used to evaluate skill (RT, MT, and accuracy) highlights the dangers of attributing sequence-specific improvements to motor learning. That is, upon careful dissection, the gradual sequence-specific improvements in performance that

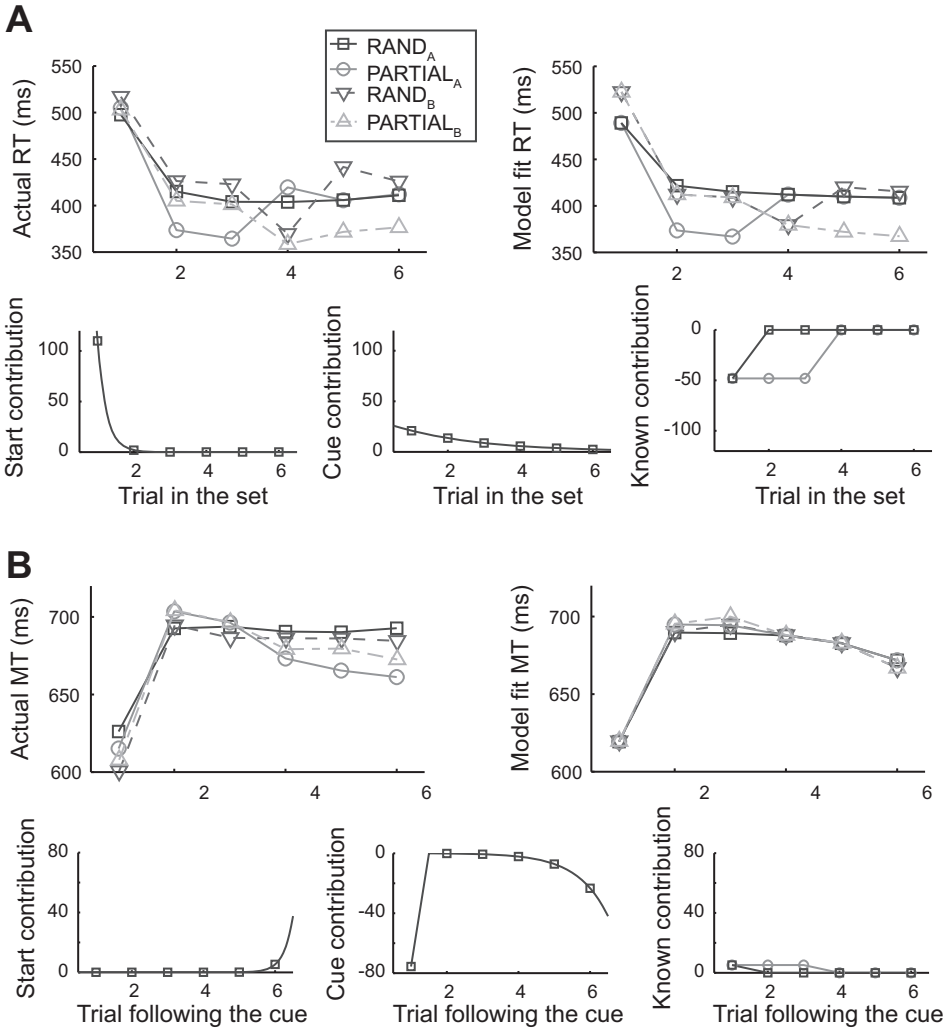

Fig. 6. Model summary showing the individual contributions of the cued trial, the start of the set, and trials to known targets on RT (*A*) and MT (*B*). *A* and *B*, *top*, *left*: actual data (replicated from Fig. 5); *right*: results of the model fits. *A* and *B*, *bottom*: individual contributions of the 3 types of trial features: the start of the set (*left*), the cue (*middle*), and trials to known targets (*right*).

can be observed during typical sequence-learning tasks (and which are generally attributed to implicit sequence learning; for review see Robertson 2007) may actually arise from a combination of the accumulation of sequence knowledge and nonspecific motor skill. This linear summation of nonspecific practice and fragmentary sequence knowledge is suggested by the results of Willingham and colleagues (1989), who stratified performance on a sequence-learning task according to the amount of explicit knowledge acquired at the conclusion of the experiment; subjects who reported having the most explicit sequence knowledge also exhibited the greatest performance improvements in every block within the training session. Furthermore, in a task similar to ours that used arm-reaching movements to explore the serial RT task, Ghilardi and colleagues (2009) showed that gradual improvements in sequence-specific performance were correlated with the amount of explicit sequence knowledge acquired. Thus the extent of acquired explicit knowledge of sequence fragments relates directly to motor-performance improvements (Buchner et al. 1998; Ghilardi et al. 2009; Perruchet and Amorim 1992; Shanks and Johnstone 1999). As it is challenging to be confident in assessing a subject's state of knowledge at all times during training, we opted to impose a fixed amount of explicit sequence knowledge (i.e., full or partial knowledge of the sequence order) to mimic how accumulated knowledge affects performance. Finally, we demonstrated in *experiment 2* that the behavioral improvements arising from explicit sequence knowledge can spill over to trials in which the target location can never be known (i.e., trials in which the target appeared at random locations). This global influence of partial explicit knowledge leads to behavioral improvements in the absence of explicit sequence knowledge, an observation that could be misattributed to implicit sequence learning. Hence, our data caution against assuming that performance improvements not directly attributable to explicit knowledge must therefore be caused by implicit knowledge; knowledge produced performance improvements even on random trials, for which sequence order could not be learned either explicitly or implicitly.

What, then, is the role of implicit knowledge in sequence generation? After we accounted for the effects of practice and explicit knowledge, any acquired implicit knowledge of the sequence order did not appear to affect performance. Therefore, although implicit sequence knowledge may be acquired, there is no clear evidence thus far that it contributes to performance. Implicit sequence-specific learning may only become relevant under conditions in which coordination matters; during continuous sequence tasks when subjects are not required to stop between individual movements, subjects can learn the dynamic interactions when linking two particular

movements into one continuous action. The dynamics of continuous sequential movements depends on the order of movement elements and might improve with practice, as when learning transitions between sequential finger presses (Wiestler and Diedrichsen 2013). Indeed, whereas knowledge of the ordinal position of elements in the sequence can be explicitly recalled, knowledge of transitions between sequence elements cannot (Song and Cohen 2014). Discrete tasks, such as ours and the majority of sequence tasks, do not assay this aspect of sequence learning; thus implicit motor skill perhaps lies in this ability to execute movement transitions in nondiscrete sequence tasks.

Explicit Knowledge Does Not Improve Behavior Through Planning

Here we demonstrated that explicit sequence knowledge produced practice-independent RT and MT improvements, consistent with previously reported effects of explicit knowledge on the response time (Pascual-Leone et al. 1993). These results stand in contrast to recent findings suggesting that subjects who are given explicit knowledge at the start of the experiment do not exhibit a performance benefit over subjects who learn a sequence gradually (Sanchez and Reber 2013). Unfortunately, the results these authors present are problematic because the sequence employed in this task was difficult to learn explicitly (i.e., subjects had to be reminded of the sequence halfway through the task). Furthermore, performance scores were based on a composite measure involving both knowledge of the target order and the ability to initiate movements at the appropriate time, and it is unclear whether it was target order or timing that primarily influenced performance scores. Although the authors assert that they found no evidence of explicit knowledge when training with this task under implicit conditions (Sanchez et al. 2010), their assessment was not sufficiently sensitive to fragmentary knowledge because they compared recognition and recall of the trained sequence to foils that may have contained identical sequence fragments. To the extent that learning was truly implicit in this task, it may have been reflected in the ability of subjects to link individual actions together when responding at the very short ITIs used in this task; as we assert earlier, this linking of discrete actions into a continuous motion may be where true implicit sequence learning resides.

Nevertheless, we show clear evidence in favor of the hypothesis that explicit sequence knowledge does provide a benefit to motor performance. Although such performance improvements could be attributable to motor planning, we argue against this possibility for two reasons. First, RT and MT were modulated independently; the length of time spent preparing a movement (RT) had no bearing on its execution quality. Despite ~30-ms reductions in RT with sequence knowledge, subjects in *experiment 1* but not those in *experiment 2* performed higher-quality movements than the random group. Similarly for monkeys, a 30-ms RT reduction arising during a delay-period task did not affect motor performance (Ames et al. 2014; Churchland et al. 2006). Thus anticipation affects only the RT, not movement quality. Second, partial sequence knowledge had global effects; planning can only produce local effects on trials in which anticipation is possible.

Sequence Knowledge Acts Like Reward: Motivational Effects on Vigor and Accuracy

We found striking parallels between the effects of sequence knowledge and those previously noted for reward. Global reductions in RT from partial sequence knowledge resemble the global effect of large rewards on the response times of less rewarding trials; for a given amount of reward, mice initiated movements sooner if the average possible reward across all trials was larger (Wang et al. 2013). Also, global effects on MT are suggested by *experiment 1* because cued trials were performed faster when subjects knew the remaining sequence despite the RND group being equally knowledgeable about the target location on cued trials. Locally, RTs and MTs were shortest for trials to known targets; similarly, monkeys generated faster and more accurate saccades at lower latencies to rewarded targets (Chen et al. 2013; Takikawa et al. 2002). In humans, saccades were faster to view a face than to view meaningless visual noise (Xu-Wilson et al. 2009); additionally, speed and accuracy were improved for saccades to varied vs. repetitive faces (Reppert 2012). These similarities between the effects of knowledge and reward suggest that both may have analogous influences on motivation.

The systematic decrease of movement vigor following the highly informative cued trial (providing information about both the current target location and the upcoming sequence fragment) also resembles a phenomenon observed for reward, rewarded trials, which were vigorously completed, strongly suppressed movement vigor on future unrewarded trials (Takikawa et al. 2002). These trial-to-trial effects of knowledge availability appear strong enough to override the global effects of knowledge on the MT, resulting in the seemingly contradictory findings of Experiments 1 and 2. Alternatively, the modulation of trial-to-trial movement vigor with knowledge is consistent with a desire to maximize the rate of information in the same manner that individuals seek to maximize the rate of reward (Haith et al. 2012; Niv et al. 2007; Shadmehr et al. 2010). The motivation to perform trials to known targets could explain why trials to unknown targets were completed faster (which cannot be attributed to planning); subjects rapidly completed trials to unknown targets to reach the next grouping of trials to known targets, where less target uncertainty may have produced a perception of greater likelihood of success.

Similarities between the effects seen here for knowledge and those reported by others for reward (Takikawa et al. 2002; Wang et al. 2013), alongside lack of evidence for a benefit of advanced planning, argue that knowledge improves behavior by affecting motivation.

Prolonged RTs Indicate Task Onset

An interesting finding in our study was the elevated RT at the beginning of each set of trials, regardless of whether the location of that or any upcoming target was known in advance. This RT increase was unlikely to be caused by the longer ITI resulting from the set break (in contrast to the correlation between RT and go-cue delay; Karlin 1959) because the background target array (notifying subjects of the impending target onset) appeared with a timing comparable to that of all other ITIs. Furthermore, the longer delay when the cue was presented on the first trial of the set did not produce a corre-

spondingly longer RT compared with conditions where the first trial was uncued.

Thus the prolonged RT appears to simply reflect the fact that subjects are beginning a set of movements (i.e., a task boundary). Interestingly, RT was also longer on the first trial of the block during visuomotor adaptation (Benson et al. 2011). This may be a behavioral analog to neurons in the basal ganglia that respond to sequence onset (Jin and Costa 2010; Jin et al. 2014), which are important for learning sequences of actions. The prolonged RT on the first trial of a set might therefore reflect a cognitive process that recognizes task boundaries.

Summary

In this study, we demonstrated that sequence knowledge produced immediate decreases in RT and increases in movement vigor with no loss of accuracy but did not facilitate practice-related performance improvements of the individual motor elements. These improvements, which operate on the same performance variables used to measure skill, were attributable to a motivational effect of explicit sequence knowledge, comparable to what has been previously reported for reward (Takikawa et al. 2002; Wang et al. 2013). Thus performance enhancements in sequence-learning tasks may arise primarily from nonspecific practice supplemented by a motivational effect attributable to acquisition of fragmentary explicit sequence knowledge. Confounding learning and motivation may be exacerbated by use of keypress tasks, which rely on a composite response-time measure (RT plus MT; Pascual-Leone et al. 1993) and measure error as choice of the incorrect key rather than as motor accuracy. Hence, discrete sequence tasks may not be a good model for motor-skill acquisition. Nevertheless, these motivational influences are intriguing and may provide an alternative explanation for the sequence-learning abnormalities reported in patients with Parkinson's disease (Jackson et al. 1995; Pascual-Leone et al. 1993) because Parkinson's disease is associated with impairments in the selection of vigorous movements (Mazzoni et al. 2007). Appreciation of the fact that knowledge and practice both enhance motor performance could lead to the design of better laboratory-based tasks that capture the interplay between cognition and movement that is often an essential component of skilled action (Stanley and Krakauer 2013).

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Author contributions: A.L.W., A.M.H., and J.W.K. conception and design of research; A.L.W. performed experiments; A.L.W. and M.A.L. analyzed data; A.L.W., A.M.H., and J.W.K. interpreted results of experiments; A.L.W. prepared figures; A.L.W. drafted manuscript; A.L.W., A.M.H., and J.W.K. edited and revised manuscript; A.L.W., A.M.H., and J.W.K. approved final version of manuscript.

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