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Acquisition of Effector-Specific and Effector-Independent Components of Sequencing Skill

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ABSTRACT. In a serial reaction time task, participants practiced a repeating sequence with 1 hand. In interleaved blocks, they responded to random sequences with the other hand. Experiment 1 was composed of 5 sessions, each consisting of 30 blocks. Intermanual transfer, reflecting a hand-independent component of sequence knowledge, increased across session. A smaller but significant, nontransferable, and hand-specific component was evident in each session and did not increase with practice. Experiment 2 comprised only 1 session. Uninterrupted practice (no interleaved random blocks) improved hand-independent sequence learning in comparison with interrupted practice (as implemented in Experiment 1), whereas hand-specific sequence learning was unaffected by this between-subjects manipulation. These findings suggest separate mechanisms for effector-independent sequence learning and effector-specific acquisition of optimized response coarticulation.

Keywords: effector proficiency, effector specificity, intermanual transfer, sequence learning, skill acquisition

Most people would probably agree that a sequence of actions consistently performed with one hand (e.g., dialing a particular phone number with the right hand) cannot be executed as quickly and accurately with the other hand (e.g., the left hand). This belief implies that what has been learned with one effector cannot be transferred completely to another effector because the acquired sequence knowledge pertains, in part, to the particular muscles used during practice. Such a view has been expressed in numerous informal conversations held by us when explaining the topic of the present research.

In contrast to this common view, results from numerous experiments indicate that knowledge acquired about a sequence of actions to be performed with one hand is easily transferred to the other untrained hand (e.g., Deroost, Zeeuws, & Soetens, 2006; Grafton, Hazeltine, & Ivry, 1998, 2002; Japikse, Negash, Howard, & Howard, 2003; Keele, Jennings, Jones, Caulton, & Cohen, 1995; Panzer et al., 2007; see also Cohen, Ivry, & Keele, 1990, Experiment 2; Willingham, Wells, Farrell, & Stemwedel, 2000, Experiment 2). For example, Grafton et al. (2002) had participants respond to a sequence of spatial stimuli by pressing corresponding response keys with the fingers of their nondominant hand. When using the dominant hand in a subsequent test phase, participants' performance was no worse than it was with the practiced nondominant hand. In other words, the acquired sequence knowledge was still fully available despite the change of hand. Intermanual transfer has also been demonstrated for other types of motor skills such as adaptations to visuo-motor rotations in arm reaching movements (e.g., Sainburg & Wang, 2002; Wang & Sainburg, 2004a, 2006) and compensations to load perturbations (e.g., Bagesteiro & Sainburg, 2005; Wang & Sainburg, 2004b). However, our focus in the present article is on movement sequences.

Sequence knowledge has been shown to be represented in multiple formats (cf. Clegg, DiGirolamo, & Keele, 1998) that lend themselves to intermanual transfer. For example, sequence knowledge can pertain to sequences of response effects (e.g., Hazeltine, 2002; Hoffmann, Sebald, & Stöcker, 2001; Stöcker & Hoffmann, 2004; Stöcker, Sebald, & Hoffmann, 2003; Ziessler, 1998; Ziessler & Nattkemper, 2001) and of stimuli (e.g., Clegg, 2005; Frensch & Miner, 1995; Remillard, 2003), as well as to relational patterns between consecutive responses (e.g., Hoffmann & Koch, 1998; Hoffmann & Sebald, 1996; Koch & Hoffmann, 2000a, 2000b) or to sequences of response locations (Willingham et al., 2000; see also Willingham, 1999; Witt & Willingham, 2006). All of these different sequence representations are independent of the hand used for responding so that sequence knowledge acquired during practice with one hand can be used just as well when responding with the other hand.

However, a number of experiments have demonstrated an additional effector-specific component of sequencing skill (e.g., Berner & Hoffmann, in press; Jordan, 1995; Karni et al., 1995; Korman, Raz, Flash, & Karni, 2003; Park & Shea, 2003, 2005; see also Bapi, Doya, & Harner, 2000; Verwey & Clegg, 2005; Verwey & Wright, 2004). For example, participants in Verwey and Clegg's Experiment 1 engaged in extensive practice, completing more than 1,000 repetitions of a key press sequence with one hand in a standard serial reaction time (SRT) task (Nissen & Bullemer, 1987). In a subsequent test phase, performance with the transfer hand was clearly better for the practiced sequence than it was for a new unpracticed sequence, thus showing considerable intermanual transfer. However, responses with the transfer hand to the practiced sequence were not as fast as they were with the practiced hand, thus indicating an additional nontransferable component of sequence knowledge. The task was a standard SRT task involving simple key presses for which the left and right hand are presumably equally proficient; the performance deficit of the unpracticed hand can be presumed to be not because of differences in proficiency

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(i.e., the ability to perform the single key presses) but rather because of to differences in sequencing skill (i.e., the ability to string together the single key presses).

Evidence for a nontransferable, effector-specific component of sequence knowledge almost always emerged as a result of extensive practice. To the best of our knowledge, there is only one exception to this generalization. In a study by Japikse et al. (2003), no hand-specific, nontransferable sequence knowledge was evident even after more than 1,000 sequence repetitions. The practiced sequence was four elements long with a random element (*r*) inserted between any two sequence elements (e.g., *ArDrBrCrArDrBrCr*. . .). In accordance, the immediate succession of stimuli and responses was random. Thus, the failure to acquire hand-specific sequence knowledge may be because of the lack of consistent response transitions. Effector-specific sequence learning has been speculated to pertain to the optimization of transitions between successive responses: that is, the coarticulation of successive movements (cf. Verwey & Clegg, 2005; see also Jordan, 1995). We return to this issue in the General Discussion section of this article.

To summarize, the development of effector-specific sequence knowledge appears to depend on extensive practice of a fixed sequence of successive movements, such as entering your PIN at an ATM. The present experiments aimed at examining more closely the time course of the development of hand-specific sequence knowledge versus that of transferable, hand-independent sequence knowledge. In previous efforts to demonstrate an effector-specific component of sequence learning, researchers either only compared two levels of practice (e.g., Park & Shea, 2003, 2005) or they merely implemented one level of massive practice (e.g., Berner & Hoffmann, in press; Verwey & Clegg, 2005). In Experiment 1, the development of transferable, hand-independent sequence knowledge and of nontransferable, hand-specific sequence knowledge was assessed across five sessions of extensive practice.

EXPERIMENT 1

Participants performed an SRT task, responding in blockwise alternation to a structured, repeating sequence of stimuli with one hand (henceforth, termed *structure hand*) and to a random sequence of stimuli with the other hand (henceforth, termed *random hand*). Responding with the two hands in blockwise alternation meant that participants practiced the stimulus–response mappings equally with both hands, thus ensuring maximally equal key-pressing proficiency of both hands. We assessed sequence learning and intermanual transfer in test blocks at the end of each of the five sessions by randomizing the structured sequence for the structure hand and transferring the structured sequence to the random hand. Sequence learning would express itself in quicker responses to the structured sequence than to random sequences. To the extent that this structure-related benefit is observed not only for the structure hand but also for the random hand, the acquired sequence knowledge is available for intermanual transfer and thus is hand-independent. Nontransferable, hand-specific sequence knowledge is indicated to the extent that responses to the structured sequence are quicker with the structure hand than with the random hand. Additional test blocks were implemented in which unpracticed structured sequences appeared for the random hand. This control condition was introduced to assess the possibility of sequence learning with the random hand in a single block.

To create a maximally conservative test of hand-specific sequence knowledge, we implemented optimal conditions for intermanual transfer by vertically aligning stimulus locations and response keys. The vertical setup not only ensured comfortable operation of keys with either hand but also ensured that participants used homologous fingers for pressing the same key with either hand (e.g., the top key is pressed with the index finger of either hand). In this way, executing the structured sequence involves for each hand pressing the same sequence of identical response keys with the same sequence of movements of homologous fingers[1] in response to the same sequence of identical imperative stimuli. Therefore, the baseline and transfer conditions are equated on all levels on which sequence knowledge can be represented except for the purported level of hand-specific sequence knowledge. In accordance, imperfect intermanual transfer under these conditions could only be ascribed to the acquisition of hand-specific sequence knowledge.

Method

Participants

In all, 16 volunteers (*M* age = 20.4 years, *SD* = 1.7 years) participated for partial fulfillment of course requirements. Only right-handed participants were recruited (i.e., participants who reported that they used their right hand for each of the following tasks: painting and drawing, throwing a ball at a target, using an eraser, dealing cards).

Task and Design

Participants responded to the position of a stimulus by pressing the compatibly assigned key. Responses were to be executed in blockwise alternation with the dominant right hand and nondominant left hand. The assignment of the dominant and nondominant hand as either the structure hand or the random hand was counterbalanced across participants. Randomization, transfer, and control blocks, as previously described were repeated at the end of each of the five sessions.

Apparatus and Materials

Stimulus presentation and response registration were controlled by the E-Prime software package (Schneider, Eschman, & Zuccolotto, 2002). Four response keys were mounted vertically on a rod attached perpendicular to the tabletop, on the side of the rod facing away from participants (see Figure 1). The distance between the centers of adjacent keys was 2.5 cm. The keys were connected to the computer through the parallel port.

Stimuli were presented on a 17-in. computer monitor. A black asterisk appeared on a white background in any one of four vertically aligned locations on the screen, each of which was marked by a black square (side length = 22 mm). There was an equal distance of 6 mm between any two adjacent squares. The keys were assigned compatibly to the squares (locations) on the screen. The keys, in turn, were assigned from top to bottom to the index, middle, ring, and little finger of either hand.

A 12-element second-order conditional sequence (*ABA-CDBCADCBD*) was used as the primary structured sequence in regular structure-hand block as well as in the transfer blocks in which the sequence was to be performed with the random hand. Four additional second-order conditional sequences that did not share a single triple with the primary structured sequence served as structured sequences in the control condition blocks for the random hand (*ABCBADBDCDAC*, *ABCDACBADBDC*, *ABDBA-DACBCDC*, *ABDCACBCDADB*).

The random sequences presented in random-hand blocks were constructed as follows: (a) each location appeared equally often in each block, (b) each block contained a maximum of four triples that were also included in the primary structured sequence, and (c) each block contained from three to six occurrences of the remaining triples. The random sequences presented in randomization test blocks for the structure hand adhered to the same constraints. Randomization test blocks began with 24 structured trials followed by 96 randomized trials and a final set of 24 structured trials.

The elements (i.e., *A*, *B*, *C*, *D*) in the stimulus sequences were assigned to the four stimulus locations on the screen (i.e., 1, 2, 3, 4; from top to bottom) according to a Latin square scheme. This did not alter the statistical properties (e.g., location frequencies, transition probabilities) of any of the sequences. The four implemented assignments were counterbalanced across participants.

Procedure

The experiment was conducted in five sessions scheduled for consecutive days. Each session contained 30 blocks: 15 blocks with the sequence hand alternating with 15 blocks with the random hand. We randomly determined whether a session started with a sequence-hand block or a random-hand block. As an exception, the first block of Session 1 in which participants performed with the sequence hand served as a warm-up block during which stimuli were presented in a random sequence.

Also, 3 of the 30 blocks in each session were test blocks (randomization [R], transfer [T], control [C]). R test blocks always occurred either before or after the other two types of test blocks (R first vs. R last). For each participant, this ordering of test blocks alternated between sessions, with one half of participants beginning with the one ordering and the other half of the sample beginning with the other ordering. Independently of this counterbalancing of the position of randomization blocks relative to the other test blocks, the ordering of the transfer and control condition blocks alternated between sessions (TC vs. CT), with one half of participants beginning with the one ordering and the other half of the sample beginning with the other ordering. Together, these counterbalancing measures resulted in four possible test block schedules (RTC, RCT, TCR, and CTR), which were counterbalanced across participants.

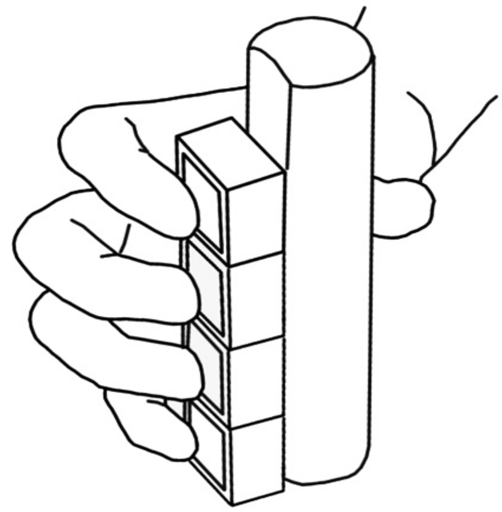

FIGURE 1. Illustration of the key rod response device. Response keys were vertically aligned on a wooden stick that was attached perpendicular to the tabletop. Participants assumed a grip-like hand position during operation of the keys.

Specifically, the randomization test block was either the 10th or the 14th sequence-hand block (i.e., the 19th or 27th overall block in the session if the session began with a sequence-hand block or the 20th or 28th overall block in the session if the session began with a random-hand block). In accordance, the transfer and control condition blocks were either the 12th and 14th or the 10th and 12th random-hand block, respectively (i.e., the 20th, 24th, or 28th overall block or the 19th, 23rd, or 27th overall block; for an example illustration, see Figure 2A). Thus, on average, participants completed 120, 288, 456, 624, and 792 sequence repetitions prior to the randomization block in Sessions 1, 2, 3, 4, and 5, respectively (not counting sequence repetitions in transfer blocks and at the start and end of randomization blocks). Control condition structured sequences were randomly assigned to the five sessions, with one of them appearing in two sessions.

Each block was composed of 144 trials. Each sequence-hand block began at a randomly determined position in the 12-element sequence. Each trial began with the presentation of the imperative stimulus. Following the participant's response, 120 ms elapsed before the next trial was initiated. In case of an error, the German word for error (*Fehler*) appeared in red, centered below the vertical row of squares; it was accompanied by a short beep tone for the duration of that response–stimulus interval.

Written instructions were presented on the screen at the beginning of Session 1, informing participants about the assignment of locations on the screen to keys and fingers, as previously described. Participants were told that in every trial an asterisk would appear in one of the locations, indicating which key to press. Participants were also told that they would be responding in blockwise alternation with the left and right hand, and they were asked to rest the fingers of the respective hand lightly on the keys. Speed and accuracy were stressed in the instructions. Specifically, participants were asked to try and keep the number of errors per block below 10. No mention was made of regularities in the order of stimuli. These instructions were repeated before each of the following sessions. Prior to each block, additional written instructions informed participants which hand to use in the upcoming block. Participants initiated each block by pressing the space bar on the keyboard with the other hand. After completion of each block, a text on the screen provided participants with feedback about their mean reaction time (RT) and number of errors in the previous block and reminded them of the requirements regarding speed and accuracy. This feedback text was presented for 20 s. The experimenter was present in the laboratory throughout the experiment to verify that participants switched hands as instructed.

After completing Session 5, participants were debriefed about the presence of a sequence for one of the hands and its exact length, and they were then asked to recall that sequence. Specifically, participants were asked to write down the sequence of stimuli or the sequence of key presses and were encouraged to guess if they could not recall parts of the sequence. Participants were also told that they could use their hand during recall and start at any position in the sequence.

Results

To ensure a maximally sensitive test for completeness of intermanual transfer, we restricted statistical analyses to data from the second half of each block. In this way, analyses were biased in favor of complete intermanual transfer for the following reasons: (a) By the second half of transfer blocks, participants had ample time to notice the presence of the structured sequence instead of a random sequence and (b) some within-block learning of the structured sequence may have already occurred for the random hand.

RTs from error trials (3.9%) were excluded from analyses, as were RTs more than 3 *SD*s above or below the *z*-transformed mean RT, as determined separately for each participant and each block in each session (1.7%). Because error data analyses confirmed the pattern of results observed in RT data and did not yield any additional information, they are not reported here. Median RTs were computed for each type of test block and the corresponding baseline blocks separately for each session (see Table 1). The baseline for randomization blocks consisted of adjacent structure-hand blocks. Randomization blocks consisted of 96 random trials embedded in 48 structured trials (24 before and 24 after the random trials); we computed median RTs for randomization blocks on the basis of data from the random trials only. The baselines for transfer and control blocks consisted of adjacent random-hand blocks. Random-hand performance in transfer blocks was also compared with structure-hand performance in adjacent structure-hand blocks to assess completeness of intermanual transfer (see Figure 2A).

Unless otherwise noted, RT data were analyzed in Session (1, 2, 3, 4, 5) × Blocktype (test vs. baseline) repeated measures of analyses of variance (ANOVAs). Depending on the test block to be analyzed, median RTs from that test block and from the corresponding baseline blocks were assigned to the two levels of the blocktype factor. Direction of transfer (from the dominant to the nondominant hand vs. from the nondominant to the dominant hand) did not yield a significant main effect and was not involved in any significant interactions when included as a factor in any of the ANOVAs subsequently reported. Therefore, this factor was dropped from all analyses to focus presentation of results. Whenever necessary, the degrees of freedom in repeated measures of ANOVAs were adjusted with the Greenhouse-Geisser epsilon (ε_{GG}) to correct for any significant violations (Mauchly test) of the sphericity assumption. If a correction has been carried out, the unadjusted degrees of freedom are reported together with the respective ε_{GG}, and the corresponding reported *p* values reflect the adjusted degrees of freedom. All pairwise comparisons are two-tailed.

All analyses subsequently reported showed a significant main effect of session, all Fs$(4, 60) > 90.76$, all ps $\leq .001$, all η_p^2s $> .857$, $.505 < \varepsilon_{GG} > 858$, reflecting a general decrease in response latencies across sessions. However, in the following section, we focus not on the absolute level of RTs but on the RT differences between test blocks and baseline blocks. These RT differences are summarized in Figure 2B.

Randomization Blocks

Structure-hand responses were significantly slower in randomization blocks than in structured baseline blocks, thus indicating overall sequence learning in each session, all ts$(15) > 7.31$, all ps $< .001$, as well as across sessions, $F(1, 15) = 290.71$, $p < .001$, $\eta_p^2 = .951$. Overall, sequence learning increased across sessions as indicated by the significant Session × Blocktype interaction, $F(4, 60) = 44.45$, $p < .001$, $\eta_p^2 = .748$, $\varepsilon_{GG} = .644$.

Transfer Blocks

Random-hand responses were faster in transfer blocks than in random baseline blocks, thus indicating intermanual transfer in each session, all ts$(15) > 9.08$, all ps $< .001$, and across sessions, $F(1, 15) = 178.88$, $p < .001$, $\eta_p^2 = .923$. The significant Blocktype × Session interaction, $F(4, 60)$

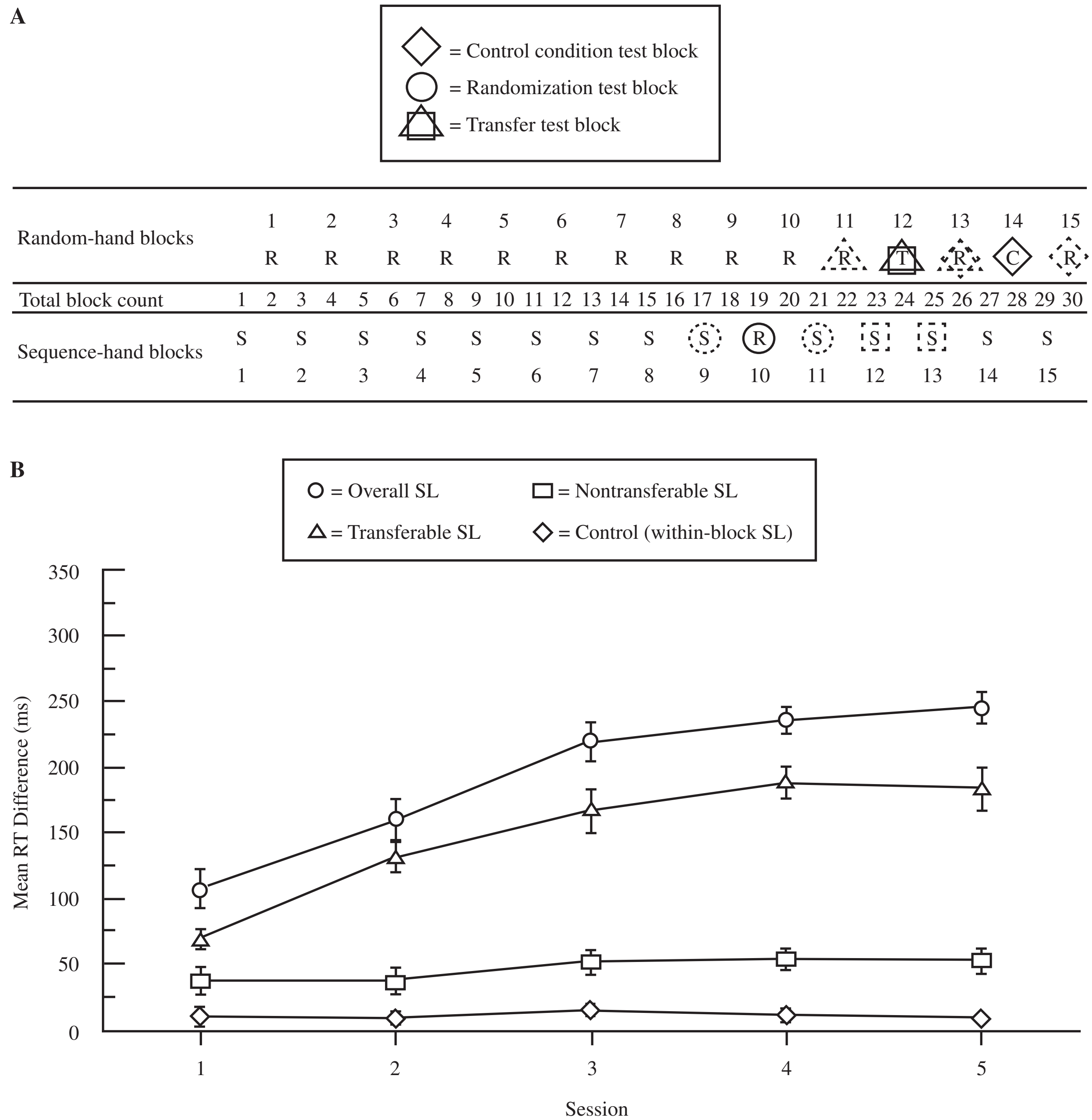

FIGURE 2. (**A**) Example of a possible test block schedule in Experiment 1. Each type of test block is represented by a different shape drawn with a solid line. Baseline blocks for these test blocks are indicated by corresponding shapes drawn with a dashed line. S, T = practiced structured sequence block; R = random sequence block; C = unpracticed structured sequence. (**B**) Mean reaction time (RT) difference (in ms) between the various types of test and baseline blocks (implemented for assessing the different forms of sequence knowledge) in each of the five sessions in Experiment 1. Only data from the second half of blocks were included. Error bars represent *SE* of the *M*. SL = sequence learning.

= 34.52, $p < .001$, $\eta_p^2 = .697$, indicated that intermanual transfer increased across sessions. The observed benefit for responding with the random hand to the practiced structured sequence versus random sequences was not because of within-block learning. Although random-hand responses were significantly faster in control blocks in which an unpracticed structured sequence was presented (M = 366.9 ms, SE = 10.2 ms) than in random baseline blocks (M = 377.3 ms, SE = 8.9 ms), $F(1, 15) = 14.90$, $p < .001$, $\eta_p^2 = .498$, this small, within-block learning effect cannot completely account for the observed intermanual transfer. The Blocktype × Session interaction was not significant, $F(4, 60) = 0.21$, $\eta_p^2 = .014$, $\varepsilon_{GG} = .710$, indicating that there was no change in the amount of within-block learning across sessions.

TABLE 1. Means and Standard Errors of Reaction Times (ms) in Each Session in Experiment 1 for Different Types of Blocks

	Sequence hand						Random hand							
	Practiced sequence		Random sequence		Transfer baseline		Practiced sequence		Random sequence		Control sequence		Random sequence	
Session	*M*	*SE*	*M*	*SE*	*M*	*SE*	*M*	*SE*	*M*	*SE*	*M*	*SE*	*M*	*SE*
1	319.1	20.3	426.7	13.0	326.4	18.4	363.9	13.8	433.2	11.5	427.3	13.0	436.8	12.5
2	224.4	21.7	383.9	11.1	224.4	20.9	261.7	16.6	393.7	9.9	385.5	11.5	394.3	10.3
3	144.0	19.5	363.5	7.6	144.9	18.6	195.4	20.9	362.2	8.3	350.4	10.9	364.1	9.2
4	103.6	14.7	339.5	8.6	107.8	14.4	161.8	17.1	350.6	8.1	339.0	10.4	350.3	7.7
5	95.2	12.0	340.9	8.3	97.3	12.7	150.3	16.9	334.0	9.7	332.2	9.8	341.1	8.0

Completeness of Intermanual Transfer

Despite considerable intermanual transfer, responses to the practiced structured sequence were still significantly slower with the random hand than with the sequence hand in each session, all ts(15) > 3.54, all ps < .005. In a Session × Hand (sequence hand vs. random hand) repeated measures of ANOVA, this expressed itself as a significant main effect of hand, $F(1, 15) = 66.58$, $p < .001$, $\eta_p^2 = .816$. The Session × Hand interaction was not significant, $F(4, 60) = 0.89$, $\eta_p^2 = .056$, $\varepsilon_{GG} = .595$. This pattern of results indicates that the nontransferable component of sequence knowledge already evident in Session 1 did not increase significantly across the remaining sessions (i.e., with increasing practice; see Figure 2B).

Analyses Not Restricted to Second Half of Blocks

The same set of analyses performed on mean RTs computed from data from all trials of each block confirmed all the major findings previously reported, all relevant ps < .05. An additional Session × Hand (sequence hand vs. random hand) × Block Half (first half vs. second half) ANOVA resulted in a significant Hand × Block Half interaction, $F(1, 15) = 30.98$, $p < .001$, $\eta_p{}^2 = .674$, which shows that the comparison between the sequence hand and the random hand in terms of RTs for responses to the practiced structured sequence yielded a significantly more pronounced assessment of the hand-specific component of sequence knowledge in the first block half ($M_{sequence\_hand}$ = 174.6 ms vs. M_{random_hand} = 249.3 ms) than in the second block half ($M_{sequence\_hand}$ = 180.1 ms vs. M_{random_hand} = 226.6 ms). This confirms that restricting analyses to data from the second half of each block constituted the more conservative test for incompleteness of intermanual transfer.

Sequence Recall Task and Possible Role of Explicit Sequence Knowledge

In all, 9 participants recalled the practiced sequence completely. The remaining 7 participants exhibited considerable fragmentary explicit knowledge of the practiced sequence by recalling a mean number of 7.14 (SD = 1.86) corresponding triples (out of 12).

We wanted to assess the possibility that participants with full explicit knowledge may differ from participants with fragmentary explicit knowledge in terms of the nature of sequence representations acquired by them. Therefore, the analyses on data from the second half of blocks were repeated with the degree of explicit sequence knowledge (complete vs. fragmentary sequence recall) as an additional between-subjects factor. The results are summarized in Figure 3. The degree of explicit sequence knowledge had no significant effect on overall sequence learning, all Fs < 1.10, all $\eta_p^2 < .073$, or on within-block learning, all Fs < 2.06, all ps > .098, all $\eta_p^2 < .128$.

However, the amount of intermanually transferable sequence knowledge was higher in participants with perfect sequence recall than in participants with fragmentary sequence recall from Session 2 onward. This difference was significant only in Session 4, $t(14) = 2.21$, $p < .05$, but not in the remaining sessions, all $|t(14)| < 1.98$, all $p > .067$, as reflected in the significant three-way interaction Degree of Explicit Sequence Knowledge × Blocktype × Session, $F(4, 56) = 3.32$, $p < .05$, $\eta_p^2 = .192$. No other effects involving degree of explicit sequence knowledge were significant, all $F < 2.41$, all $p > .143$, all η_p^2s < .147.

In contrast, the amount of nontransferable sequence knowledge was lower in participants with perfect sequence recall than it was in participants with fragmentary sequence recall in all sessions except Session 1. This difference was significant in Sessions 3 and 4, both ts(14) > 2.21, both ps < .05, but not in the remaining sessions, all $|ts(14)|$ < 1.55, all ps > .144, as expressed in a significant three-way interaction among degree of explicit sequence knowledge, hand, and session, $F(4, 56) = 3.81$, $p < .01$, $\eta_p{}^2 = .214$. The two-way Degree of Explicit Sequence Knowledge × Hand interaction approached significance, $F(1, 14) = 3.97$, $p < .066$, $\eta_p{}^2 = .221$. No other effects involving degree of explicit sequence knowledge were significant, both Fs(4, 56) < 0.68, both $\eta_p{}^2$s < .046.

Discussion

Participants responded in blockwise alternation to a repeating sequence of stimuli with one hand (sequence hand) and

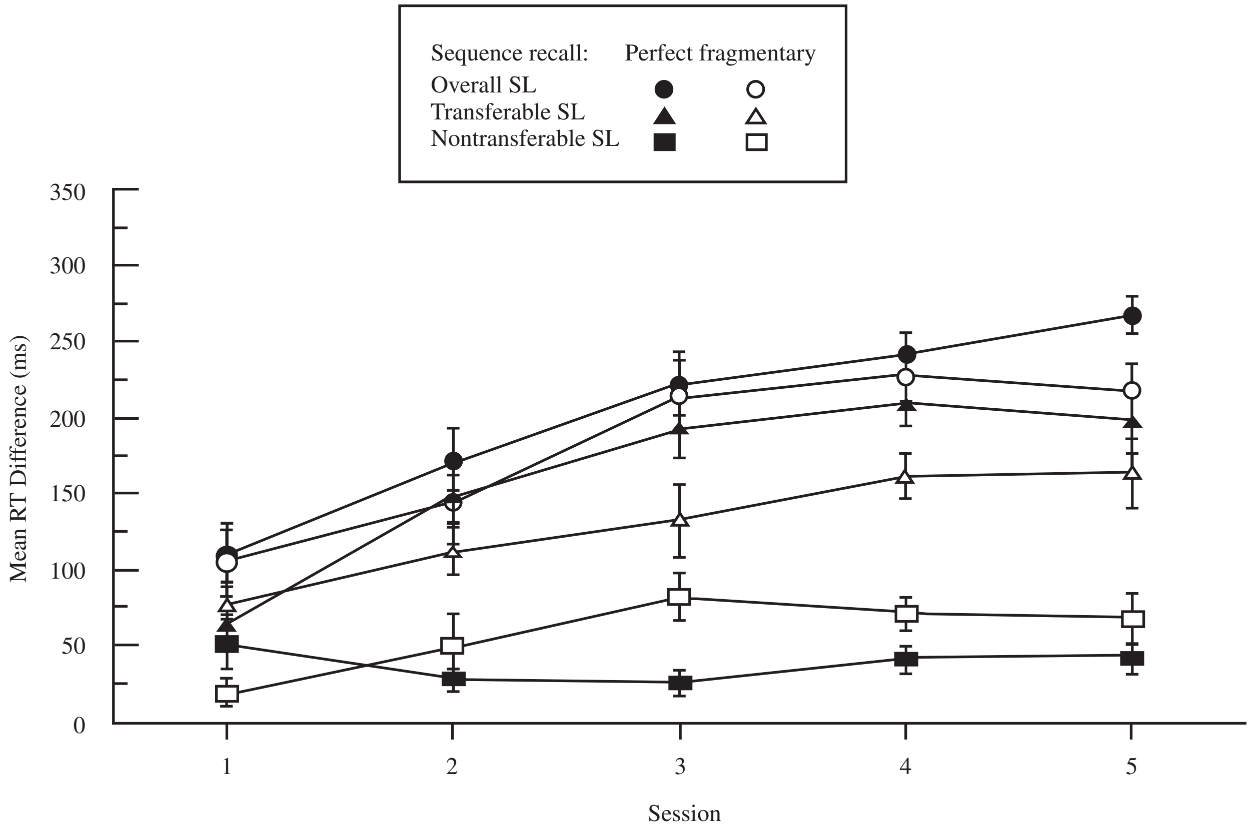

FIGURE 3. Mean reaction time (RT) difference (ms) between various types of test and baseline blocks (implemented for assessing the different forms of sequence knowledge) in each of the five sessions in Experiment 1 shown separately for the subsamples of participants with perfect and fragmentary sequence recall. Only data from the second half of blocks were included. Error bars represent *SE* of the *M*. SL = sequence learning.

to a random sequence of stimuli with the other hand (random hand). Sequence learning and intermanual transfer were assessed in test blocks at the end of each of five sessions. Replacing the repeating sequence with a random sequence disrupted performance with the sequence hand substantially, indicating sequence learning. A considerable portion of the acquired sequence knowledge was available for intermanual transfer, as the random hand responded faster to the repeating sequence than it did to a random sequence. However, the random hand never reached the same level of performance as the sequence hand. This evidence for a hand-specific component of sequence knowledge was obtained although participants responded with both hands to the same stimuli by pressing the same keys with the same (homologous) fingers; thus, any sequence knowledge in terms of stimuli, keys, or even fingers should have been available for intermanual transfer. Furthermore, the incompleteness of intermanual transfer can hardly be because of different levels of practice of the stimulus–response assignment as participants practiced the stimulus–response mapping to the same extent with both hands. The data suggest that part of the acquired sequence knowledge has been represented in a hand-specific format to which the other hand has no access.

After completing the final session, 9 participants recalled the repeating sequence in its entirety, whereas the remaining 7 exhibited only fragmentary sequence recall. Additional analyses suggested that participants with perfect sequence recall acquired more transferable sequence knowledge—but less nontransferable sequence knowledge—than did participants with fragmentary sequence recall. This pattern of results is consistent with the notion that nontransferable, effector-specific sequence knowledge is predominantly implicit, whereas transferable, effector-independent sequence knowledge is usually explicit (Hikosaka, Nakamura, Sakai, & Nakahara, 2002; see also Rüsseler & Rösler, 2000).

Last, it must be noted that the hand-specific component of sequence knowledge emerged after relatively little practice and was already evident at the end of the first session (i.e., after an average of only 120 sequence repetitions). Moreover, the hand-specific component of sequence learning did not increase across sessions, whereas the transferable component of sequence knowledge continued to increase until Session 4. This early development of hand-specific sequence knowledge is at odds with the finding that hand-specific sequence knowledge typically is acquired only after extensive practice (e.g., Park & Shea, 2005; see also Verwey & Clegg, 2005). Thus, the following question arises: Which features of the present experimental setting may have caused the early acquisition of hand-specific sequence knowledge?

One atypical aspect of our setting is the alternation between structured and random blocks that may have led to partial reduction of learning, in particular, of stimulus and key sequences because these were regularly interrupted by random sequences pertaining to the same stimuli and keys. In contrast, the finger sequences of the structure hand were not interrupted in this manner because the random sequences in alternating blocks were performed with the other hand. Thus, whereas learning of the hand-independent stimulus and key sequences may have been hampered, this cannot have been the case for learning of the hand-specific finger sequence.

Another atypical aspect of the setting concerns the fact that the view of the keys was blocked by the key rod. This setup may have induced participants to conceptualize the task more in terms of which finger to move than in terms of which key to press in response to a stimulus. This, in turn, may have promoted learning of the hand-specific finger sequence instead of the hand-independent stimulus and key sequences. A similar argument can be made with regard to recent studies by Heyes and colleagues, who reported the acquisition of hand-specific sequence knowledge from watching, for example, a video of someone's right hand continuously repeating a simple eight-element key press sequence (Osman, Bird, & Heyes, 2005; see also Bird & Heyes, 2005; Heyes & Foster, 2002). In a subsequent test phase, participants exhibited knowledge of the watched sequence only when pressing the corresponding keys with their right hand, but not when using their left hand. This suggests that watching the model person's fingers may have induced participants to form a sequence representation pertaining to finger movements rather than key presses, thus promoting hand-specific sequence learning relative to hand-independent sequence learning.[2]

Both of the proposed accounts (partial reduction of transferable sequence learning because of interrupted practice schedule and focus on the learning of finger movement sequence because of hidden keys) for the early development of hand-specific sequence knowledge in Experiment 1 lend themselves to experimental testing, and both were tested in Experiment 2.

EXPERIMENT 2

The purpose of Experiment 2 was to confirm the early acquisition of hand-specific sequence knowledge observed in Experiment 1 and to explore the conditions that may be responsible for this. Practice was restricted to one session only; thus, Experiment 2 was, for the most part, a replication of Session 1 from Experiment 1. Two additional manipulations concerned the blockwise alternation between the sequence and random hand (interrupted vs. uninterrupted practice) and whether participants could see the keys (hidden vs. reflected keys). Uninterrupted practice was introduced to improve the conditions for the acquisition of transferable sequence knowledge. If, as previously speculated, the early acquisition of hand-specific sequence knowledge in Experiment 1 was the result of hampered learning on hand-independent levels of sequence learning, the hand-specific component of sequence knowledge should be reduced under uninterrupted practice conditions in comparison with interrupted practice conditions. Furthermore, if the setup with hidden keys enhances early learning of hand-specific finger movement sequences, as also previously speculated, the hand-specific component of sequence knowledge should be reduced in the visible keys condition.

Method

As Experiment 2 was highly similar to Experiment 1 in several respects, only the differences between the two experiments are subsequently described.

Participants

In all, 48 volunteers (*M* age = 22.2 years, *SD* = 2.6 years) participated for partial fulfillment of course requirements. Again, only participants who reported to be right-handed were recruited.

Task and Design

Unlike Experiment 1, only randomization and transfer test blocks were implemented. Two additional between-subjects manipulations were implemented: (a) One half of participants responded with the sequence hand and the random hand in blockwise alternation throughout the session as in Experiment 1 (interrupted practice condition), whereas the remaining participants switched to responding with the random hand only for the transfer block and corresponding baseline blocks (uninterrupted practice condition). Orthogonally to this factor, (b) one half of participants had no view of the keys mounted on the far side of the rod, as in Experiment 1 (hidden keys condition), whereas the remaining participants were provided with the opportunity for a peripheral view of these keys (reflected keys condition). Twelve participants were assigned to each of the four cells in the design, resulting from crossing these two between-subjects factors. In each cell, direction of transfer was counterbalanced across participants, except in the reflected keys condition with uninterrupted practice in which—because of experimenter error—transfer was from the dominant to the nondominant hand for 7 participants and from the nondominant to the dominant hand for 5 participants.

Apparatus and Materials

We provided participants with a view of the keys in the reflected keys condition by placing a mirror (11 cm wide, 15 cm high) approximately 8 cm behind the key rod (from the participants' point of view) so that participants were able to see the keys on the far side of the key rod (as well as their fingers on these keys) in the mirror.

Procedure

In contrast to Experiment 1, Experiment 2 encompassed only a single session. Participants in the interrupted practice condition completed 30 blocks: 15 with the sequence hand and 15 with the random hand. Participants in the uninterrupted practice condition completed only 18 blocks: 15 with the sequence hand and 3 with the random hand. The ordering of randomization and transfer blocks was counterbalanced across participants. The randomization test block was the 12th or 14th sequence-hand block. In accordance, the transfer block was inserted prior to the 14th or 12th sequence-hand block, respectively. In the uninterrupted practice condition, two additional random-hand blocks, which served as baselines for the transfer, were inserted before and after the structure-hand blocks immediately preceding and succeeding the transfer block. See Figure 4 for an example illustration. On average, participants completed 144 sequence repetitions prior to the randomization block (not counting sequence repetitions in transfer blocks).

After completing the SRT task, participants were debriefed about the presence of a sequence and its exact length. Then, they completed a set of tasks designed to assess the extent of their explicit sequence knowledge that was modeled closely after Destrebecqz and Cleeremans's study (2001; cf. Goschke, 1998). Participants were instructed to generate a sequence that resembled the sequence present in the experiment as much as possible (inclusion instructions). Following that, participants were instructed to generate a sequence that resembled the practiced sequence as little as possible (exclusion instructions). Participants had to generate a sequence consisting of 96 key presses in the inclusion and exclusion tasks; for both tasks, they were instructed to use the hand with which they had practiced the sequence and to avoid immediate repetitions, as no such repetitions occurred in the practiced sequence. Generating chunks from the practiced sequence under inclusion instructions would likely reflect not only explicit sequence knowledge but also some implicit sequence knowledge. In contrast, generating chunks from the practiced sequence under exclusion conditions would only reflect an influence of implicit sequence knowledge on performance; because if participants had intentional control over all sequence knowledge, they would be able to completely avoid producing any chunks from the practiced sequence. Thus, the extent of the participants' explicit sequence knowledge can be estimated by subtracting that participants' score under exclusion conditions from their score under inclusion conditions.

Results

Data were treated in the same way as in Experiment 1. RTs from error trials (4.6%) and outlier RTs (1.9%) were excluded. Unless otherwise noted, RT data were analyzed in Practice Schedule (interrupted vs. uninterrupted) × Keyview (hidden vs. reflected) × Structure Hand Assignment (left hand = structure hand vs. right hand = structure hand) × Blocktype (test vs. baseline) ANOVAs with repeated measures on the last factor. Depending on the test block to be analyzed, median RTs from that test block and the corresponding baseline blocks were assigned to the two levels of the blocktype factor. Relevant means are given in Table 2. The critical RT differences are summarized in Figure 5.

Randomization Blocks

Structure-hand RTs were significantly slower on random blocks than on structured baseline blocks, $F(1, 40) = 198.60$, $p < .001$, $\eta_p^2 = .832$. This main effect of blocktype was involved in a significant interaction with practice schedule, $F(1, 40) = 7.32$, $p < .01$, $\eta_p^2 = .155$, indicating that these randomization costs were significantly more pronounced in the uninterrupted practice condition, $t(23) = 14.43$, $p < .001$, than in the interrupted practice condition, $t(23) = 7.13$, $p < .001$. There was no comparable effect of the keyview manipulation on the size of randomization costs, $F(1, 40) = 0.26$, $\eta_p^2 = .003$. Sequence learning tended to be more pronounced with the nondominant left hand than with the dominant right hand, but the appropriate Sequence Hand Assignment × Blocktype interaction was not significant, $F(1, 40) = 3.36$, $p < .074$, $\eta_p^2 = .077$. No other main effects or interactions were significant, all Fs(1, 40) < 1.69, all η_p^2s < .041.

Transfer Blocks

Intermanual transfer was evident as random-hand RTs were faster on transfer blocks than on random baseline blocks, $F(1, 40) = 124.84$, $p < .001$, $\eta_p^2 = .757$. This blocktype main effect was involved in a significant interaction with practice schedule, $F(1, 40) = 6.56$, $p < .05$, $\eta_p^2 = .141$, such that this transfer benefit was significantly larger in the uninterrupted practice condition, $t(23) = 8.79$, $p < .001$, than in the interrupted practice condition, $t(23) = 7.17$, $p < .001$. Again, there was no comparable Keyview × Blocktype interaction, $F(1, 40) = 0.05$, $\eta_p^2 = .001$. The four-way interaction came closest to significance but did not reach it, $F(1, 40) = 3.04$, $p < .089$, $\eta_p^2 = .071$. The other main effects and interactions were not significant, all Fs(1, 40) < 2.77, all ps > .104, all η_p^2s < .065.

Completeness of Intermanual Transfer

A Practice Schedule × Keyview × Structure Hand Assignment × Hand (structure hand vs. random hand) ANOVA revealed that, despite considerable intermanual transfer, responses to the practiced structured sequence were still significantly slower with the random hand than with the sequence hand, $F(1, 40) = 24.66$, $p < .001$, $\eta_p^2 = .381$. Unlike the amount of sequence learning and of intermanual transfer, the size of this nontransferable, hand-specific component of sequence knowledge was not influenced by practice schedule, $F(1, 40) = 0.51$, $\eta_p^2 < .013$.

Participants in the group practicing the structured sequence with the nondominant left hand tended to be faster than participants in the other group, but this main effect was not significant, $F(1, 40) = 3.34$, $p < .075$, $\eta_p^2 = .377$.

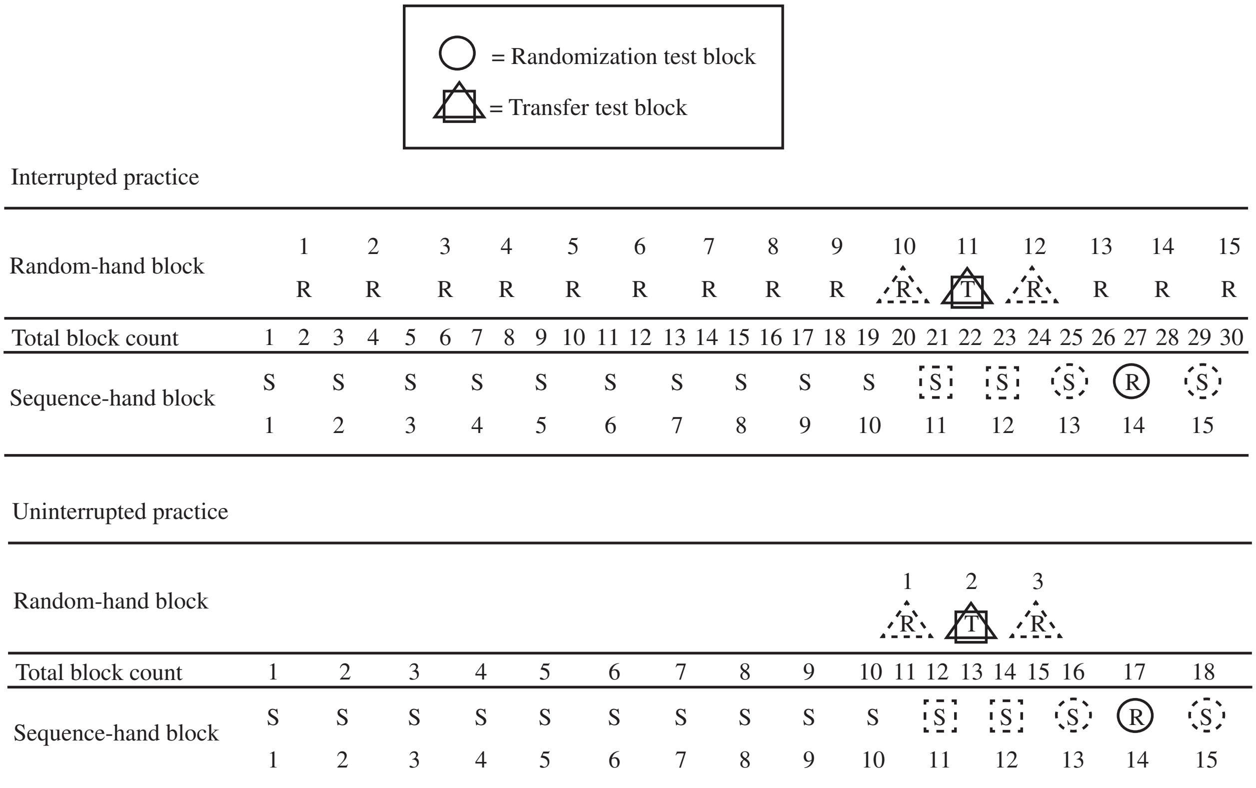

FIGURE 4. Example of possible test block schedules in the two-practice schedule conditions (interrupted vs. uninterrupted) in Experiment 2. Each type of test block is represented by a different shape drawn with a solid line. Baseline blocks for these test blocks are indicated by corresponding shapes drawn with a dashed line. S, T = practiced structured sequence block; R = random sequence block.

TABLE 2. Means and Standard Errors of Reaction Times (ms) in Experiment 2 Computed Separately for and Across the Levels of the Practice Schedule and Keyview Manipulations for Different Types of Blocks

	Sequence hand						Random hand			
	Practiced sequence		Random sequence		Transfer baseline		Practiced sequence		Random sequence	
Keyview manipulation	*M*	*SE*	*M*	*SE*	*M*	*SE*	*M*	*SE*	*M*	*SE*
Interrupted practice										
Hidden keys	311.1	26.6	430.6	15.1	285.0	27.0	347.0	27.4	424.7	15.9
Reflected keys	302.8	26.6	397.4	15.1	314.0	27.0	313.4	27.4	399.5	15.9
Across keyviews	307.0	18.8	414.0	10.7	299.5	19.1	330.2	19.4	412.1	11.2
Uninterrupted practice										
Hidden keys	295.7	26.6	450.8	15.1	295.8	27.0	318.5	27.4	449.1	15.9
Reflected keys	290.6	26.9	451.3	15.3	279.5	27.3	302.8	27.8	433.5	16.1
Across keyviews	293.1	18.9	451.0	10.7	287.7	19.2	310.6	19.5	441.3	11.3
Across practice schedules										
Hidden keys	303.4	18.8	440.7	10.7	304.9	19.1	332.7	19.4	436.9	11.2
Reflected keys	296.7	18.9	424.3	10.7	282.3	19.2	308.1	19.5	416.5	11.3
Across keyviews	300.1	13.3	432.5	7.6	293.6	13.5	320.4	13.8	426.7	8.0

The other main effects and interactions were not significant either, all Fs(1, 40) < 1.40, all η_p^2s < .034.

Generation Task and Possible Role of Explicit Sequence Knowledge

Participants' performance in the generation task was scored separately for the inclusion and exclusion conditions by determining whether each of the 94 triples contained in the 96-trial sequence generated by participants was a triple that also occurred in the (to-be-recalled or to-be-avoided) practiced sequence or not. The acquisition of explicit sequence knowledge would be indicated by better recall performance under inclusion conditions than under exclusion instructions (cf. Destrebecqz & Cleeremans, 2001). Because of experimenter error, generation task data were not recorded for 1 participant in the reflected-keys condition with uninterrupted practice.

The number of corresponding triples was analyzed in a Task (inclusion vs. exclusion) × Practice Schedule (interrupted vs. uninterrupted) × Keyview (hidden vs. reflected) mixed-factors ANOVA with repeated measures on the first factor. Relevant means are given in Table 3. Participants produced more corresponding triples under inclusion conditions than they did under exclusion conditions, $F(1, 43) = 54.29$, $p < .001$, $\eta_p^2 = .558$. Also, participants in the uninterrupted practice group produced more corresponding triples than did participants in the interrupted practice group, $F(1, 43) = 5.99$, $p < .05$, $\eta_p^2 = .122$. The interaction between these two factors was not significant, $F(1, 43) = 2.51$, $p < .121$, $\eta_p^2 = .055$. The other main effects and interactions were not significant either, all Fs(1, 44) = 0.39, all η_p^2s < .009.

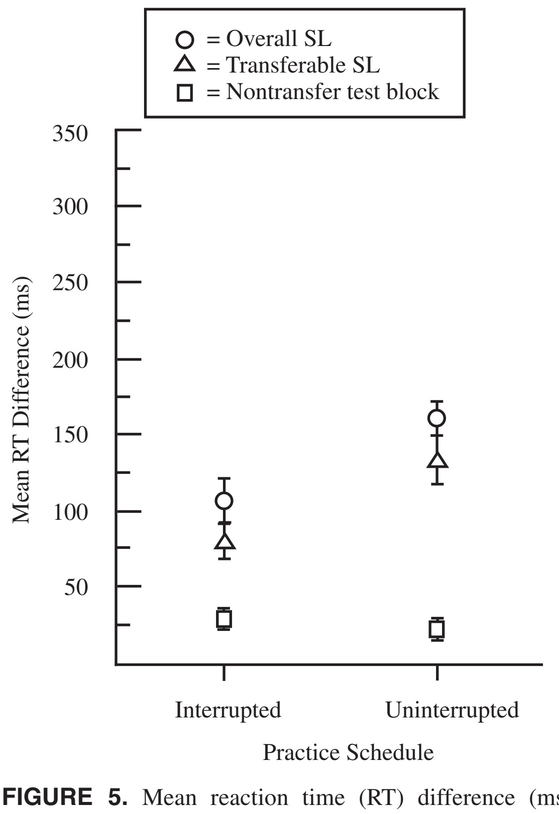

FIGURE 5. Mean reaction time (RT) difference (ms) between the various types of test and baseline blocks (implemented for assessing the different forms of sequence knowledge) in Experiment 2. Only data from the second half of blocks were included. Error bars represent *SE* of the *M*. SL = sequence learning.

The sample was split along the median of participants' individual difference scores between recall performance under inclusion and exclusion instructions. Repeating the analyses on data from the second half of blocks with the degree of explicit sequence knowledge (substantial vs. fragmentary sequence recall) as an additional between-subjects factor yielded no significant effects of degree of explicit sequence knowledge or any that involved it, all Fs(1, 43) < 1.89, all η_p^2s < .043.

Discussion

The development of hand-specific sequence knowledge after relatively little practice as observed in Experiment 1 was replicated in Experiment 2. Moreover, the use of an interrupted practice schedule can be ruled out as a possible cause for this finding because the amount of acquired nontransferable hand-specific sequence knowledge did not differ between the interrupted and uninterrupted practice schedules. In contrast, the amount of acquired overall sequence knowledge as well as transferable sequence knowledge was significantly higher in the uninterrupted practice condition than it was in the interrupted practice condition. In other words, the uninterrupted practice schedule interfered with the acquisition of hand-independent sequence knowledge, but this was not the case for the acquisition of hand-specific sequence knowledge. This dissociation is consistent with the notion that these two components of sequence knowledge may rely on different learning mechanisms.

An effect of the practice schedule was also apparent in the sequence-generation task, as participants in the uninterrupted practice condition produced significantly more corresponding triples than did participants in the interrupted practice condition. Furthermore, participants exhibited considerable explicit sequence knowledge. However, the amount of explicit sequence knowledge did not differ significantly between participants in the two practice conditions. Moreover, participants with substantial explicit sequence knowledge did not differ significantly from those with fragmentary explicit sequence knowledge with regard to the amount of acquired overall, transferable, and nontransferable sequence knowledge. This is consistent with results from Experiment 1 in which no such differences were evident for the first session either.

The observed detrimental effect of interrupted practice on transferable sequence learning is reminiscent of the contextual-interference effect (CIE; Shea & Morgan, 1979; for reviews, see Brady, 1998; Magill & Hall, 1990). When to-be-learned tasks are arranged in a way that is

TABLE 3. Means and Standard Errors for Corresponding Triples Produced in Postexperimental Sequence Generation Task in Experiment 2

	Instructions					
	Inclusion		Exclusion		Inclusion and exclusion	
Practice schedule	*M*	*SE*	*M*	*SE*	*M*	*SE*
Uninterrupted	58.38	4.18	33.56	2.70	45.97	2.90
Interrupted	44.04	4.09	28.00	2.64	36.02	2.84
Uninterrupted and interrupted	51.21	2.92	30.78	1.89	—	—

likely to promote interference between them (e.g., practicing tasks in a randomly determined order), acquisition is typically impeded and retention is enhanced in comparison with practice arrangements that minimize interference during acquisition (e.g., blocked practice). The present results are pertinent only to the acquisition aspect of the CIE. Future researchers will investigate whether nontransferable sequence knowledge is exempt not only from acquisition interference but also from the retention aspect of the CIE.

In contrast to the practice schedule manipulation, the keyview manipulation influenced neither sequence learning nor intermanual transfer significantly. In implementing this manipulation, we supposed that enabling participants to view the keys in a mirror (reflected keys condition) may counteract their supposed inclination to conceptualize the task in the regular setup (hidden keys condition) in terms of which finger to move rather than which key to press, which, in turn, may promote hand-specific sequence learning. One cannot decide from the lack of an effect of the mirror manipulation whether the way in which participants conceptualize the task (as key pressing or as finger moving) is irrelevant for what is learned about a sequence or whether this manipulation simply did not affect participants' conceptualization of the task.

GENERAL DISCUSSION

Evidence has accumulated in recent years indicating that a nontransferable, effector-specific component of sequencing skill can develop under conditions of extensive practice of the same deterministic sequence of movements (Bapi et al., 2000; Berner & Hoffmann, 2008; Jordan, 1995; Karni et al., 1995; Korman et al., 2003; Park & Shea, 2003, 2005; Verwey & Clegg, 2005; Verwey & Wright, 2004). The aim of Experiment 1 was to address two shortcomings of previous demonstrations of hand-specific sequence learning. To this end, we obtained a fine-grained record of the time course of the acquisition of nontransferable hand-specific sequence knowledge and compared it with the time course of the acquisition of transferable hand-independent sequence knowledge. Furthermore, we actively dealt with the issue of possible differences between the practice hand and the transfer hand in terms of proficiency in executing the single component movements, which were to be strung together in a sequence. Specifically, sequence practice with one hand in regular blocks was interrupted by random blocks in which participants responded with their other hand to a random sequence of stimuli. In this way, participants practiced the stimulus–response mapping equally with both hands so that the possible difference between the two hands in terms of proficiency, thus the possibility of a confound between sequence practice and proficiency, is minimized.

Stimulus positions were vertically aligned, and so were response keys, which were mounted on a rod attached perpendicularly to the tabletop. In this way, the baseline and transfer conditions were equated on all levels on which sequence knowledge can be represented (e.g., sequence of stimuli, response keys and locations, response effects, movements of homologous fingers), except for the purported level of hand-specific sequence knowledge.

Results of Experiment 1 showed sequence learning with the sequence hand and considerable transfer of acquired sequence knowledge to the other hand. However, intermanual transfer was not complete, indicating a hand-specific component of sequence knowledge. This hand-specific component of sequence knowledge was already evident after only 120 sequence repetitions, and—unlike the hand-independent transferable component of sequence knowledge—it did not increase with additional practice.

Experiment 2 replicated the early development of hand-specific sequence knowledge and showed that the interrupted practice schedule was not responsible for this finding. Although the amount of acquired hand-independent sequence knowledge was higher in the uninterrupted practice condition than it was in the interrupted practice condition, the amount of acquired hand-specific sequence knowledge was unaffected by this manipulation. Also, the fact that response keys were effectively hidden from participants' view—because of their being mounted on the far side of a rod—did not appear to have affected sequence learning. Thus, it remains unclear why hand-specific sequence knowledge developed so relatively quickly under the conditions implemented in the present study.

It is possible that hand-specific sequence knowledge developed so relatively quickly under the conditions implemented because operation of the vertically aligned keys on the key rod involved a grip-like hand posture (see Figure 1) that may have also involved the exertion of counterforce on the rod with the thumb so that a greater number of different muscles are involved than when pressing horizontally aligned keys; therefore, the task probably entails more pronounced requirements for coarticulation between the muscles involved in consecutive finger movements. Verwey and Clegg (2005; see also Jordan, 1995) argued that effector-specific sequence learning pertains to the fine-tuning of sequence production given the biomechanical properties of the effector used. In essence, this is the equivalent of the development of coarticulation (cf. for the domain of speech production, see Daniloff & Moll, 1968; Kent & Minifie, 1977)—that is—the optimization of transitions between single movements in a sequence of movements. Pressing keys vertically aligned on a rod may—because of the possibly greater number of muscles involved—provide more basis for hand-specific sequence learning in the form of coarticulatory optimization (e.g., Jordan; Verwey & Clegg) than does pressing horizontally aligned keys. This speculation awaits empirical testing. The possible role of coarticulatory optimization for hand-specific sequencing skill could also be investigated by manipulating the response–stimulus interval (RSI). Single movements do not overlap as much when RSIs are long as opposed to short (such as the 120-ms RSI used in the present study), thus providing less opportunity for coarticulation. Furthermore, if the nontransferable component of sequencing skill pertains to coarticulatory optimization, it is conceivable that such optimizations that emerge during performance cannot be retained but instead develop anew during each session. This would explain why the amount of nontransferable sequencing skill did not increase across successive practice sessions. Assessing this possibility in future research would require implementing several sets of test blocks in the course of a session.

In conclusion, the experiments reported in this article add to the growing number of demonstrations of an effector-specific contribution to sequence learning (Bapi et al., 2000; Berner & Hoffmann, 2008; Jordan, 1995; Karni et al., 1995; Korman et al., 2003; Park & Shea, 2003, 2005; Verwey & Clegg, 2005; Verwey & Wright, 2004). Our findings are in line with the notion that a separate sequence-learning module may exist for each hand (Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003; see also Berner & Hoffmann, in press). It appears that the representation of sequence knowledge is not restricted to higher abstract levels in a hierarchy of movement control and it can also extend to lower levels responsible for the specification and coordination of specific muscle movements. Presumably, the acquisition of effector-specific sequence knowledge serves the purpose of optimizing coarticulation of consecutive movements as an ultimate contribution to refining the execution of sequential actions and attaining high levels of performance.

NOTES

1. It has been suggested that sequence learning may occur in terms of a schema of homologous fingers equally applicable to either hand (e.g., Deroost et al., 2006) on the basis of findings of better performance at transfer for the mirrored version of a practiced sequence than for a random or an unpracticed sequence (e.g., Deroost et al.; Grafton et al., 2002; see also Wachs, Pascual-Leone, Grafman, & Hallet, 1994). However, there are reasons to question whether such a mirror-sequence benefit truly reflects transfer to homologous fingers of the unpracticed (contralateral) hand: Mirror transfer is not always complete (Grafton et al.; see also Karni et al., 1995), and a mirror-sequence benefit has also been observed for the practiced (ipsilateral) hand (Verwey & Clegg, 2005). This suggests that the mirror-sequence benefit relies on a more abstract level of sequence representation that requires additional transformations to be used for execution with either hand (e.g., Grafton et al.).

2. Heyes and colleagues interpreted their findings in reference to research showing that execution and observation of actions engender comparable patterns of neural activation (e.g., Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Rizzolatti, Fogassi, & Gallese, 2001). Given this human "mirror system," it is conceivable that "movement observation may substitute for movement execution" (Heyes & Foster, 2002, p. 594). However, this does not explain the acquisition of hand-specific sequence knowledge. Regarding this issue, Bird and Heyes (2005; see also Osman et al., 2005) point out that they used very simple sequences, and they argue that sequence learning may have been more advanced in their experiments than in the other experiments using more complex sequences after a comparable amount of trials. In that sense, their finding of hand-specific sequence learning would still be reconcilable with the notion that effector-specific sequence knowledge develops with increasing practice. This argument does not apply to the present experiments as the sequences used in the present study were more complex.

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REFERENCES

Aziz-Zadeh, L., Maeda, F., Zaidel, E., Mazziotta, J., & Iacoboni, M. (2002). Lateralization in motor facilitation during action observation: A TMS study. *Experimental Brain Research, 144,* 127–131.

Bagesteiro, L. B., & Sainburg, R. L. (2005). Interlimb transfer of load compensation during rapid elbow joint movements. *Experimental Brain Research, 161,* 155–165.

Bapi, R. S., Doya, K., & Harner, A. M. (2000). Evidence for effector independent and dependent representations and their differential time course of acquisition during motor sequence learning. *Experimental Brain Research, 132,* 149–162.

Berner, M. P., & Hoffmann, J. (2008). Effector-related sequence learning in a bimanual-bisequential serial reaction time task. *Psychological Research, 72,* 138–154.

Berner, M. P., & Hoffmann, J. (in press). Integrated and independent learning of hand-related constituent sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition.*

Bird, G., & Heyes, C. (2005). Effector-dependent learning by observation of a finger movement sequence. *Journal of Experimental Psychology: Human Perception and Performance, 31,* 262–275.

Brady, F. (1998). A theoretical and empirical review of the contextual interference effect and learning of motor skills. *Quest, 50,* 266–293.

Clegg, B. A. (2005). Stimulus-specific sequence representation in serial reaction time tasks. *Quarterly Journal of Experimental Psychology, 58,* 1087–1101.

Clegg, B. A., DiGirolamo, G. J., & Keele, S. W. (1998). Sequence learning. *Trends in Cognitive Science, 2,* 275–281.

Cohen, A., Ivry, R. I., & Keele, S. W. (1990). Attention and structure in sequence learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 16,* 17–30.

Daniloff, R., & Moll, K. (1968). Coarticulation of lip rounding. *Journal of Speech and Hearing Research, 11,* 707–721.

Deroost, N., Zeeuws, I. & Soetens, E. (2006). Effector-dependent and response location learning of probabilistic sequences in serial reaction time tasks. *Experimental Brain Research, 171,* 469–480.

Destrebecqz, A., & Cleeremans, A. (2001). Can sequence learning be implicit? New evidence with the process dissociation procedure. *Psychonomic Bulletin & Review, 8,* 343–350.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology, 73,* 2608–2611.

Frensch, P. A., & Miner C. S. (1995). Zur Rolle des Arbeitsgedächtnisses beim impliziten Sequenzlernen [On the role of working memory for implicit sequence learning]. *Zeitschrift für Experimentelle Psychologie, 42,* 545–575.

Goschke, T. (1998). Implicit learning of perceptual and motor sequences. In M. A. Stadler & P. A. Frensch (Eds.), *Handbook of implicit learning* (pp. 401–444). Thousand Oaks, CA: Sage.

Grafton, S. T., Hazeltine, E., & Ivry, R. B. (1998). Abstract and effector-specific representations of motor sequences identified with PET. *Journal of Neuroscience, 18,* 9420–9428.

Grafton, S. T., Hazeltine, E., & Ivry, R. B. (2002). Motor sequence learning with the nondominant left hand. *Experimental Brain Research, 146,* 369–378.

Hazeltine, E. (2002). The representational nature of sequence learning: Evidence for goal-based codes. In W. Prinz & B. Hommel (Eds.), *Common mechanism in perception and action* (pp. 675–689). New York: Oxford University Press.

Heyes, C. M., & Foster, C. L. (2002). Motor learning by observation: Evidence from a serial reaction time task. *Quarterly Journal of Experimental Psychology, 55,* 593–607.

Hikosaka, O., Nakamura, K., Sakai, K., & Nakahara, H. (2002). Central mechanisms of motor skill learning. *Current Opinion in Neurobiology*, *12,* 217–222.

Hoffmann, J., & Koch, I. (1998). Implicit learning of loosely defined structures. In M. A. Stadler & P. Frensch (Eds.), *Handbook of implicit learning* (pp. 161–199). Thousand Oaks, CA: Sage.

Hoffmann, J., & Sebald, A. (1996). Reiz- und Reaktionsmuster in seriellen Wahlreaktionen [Stimulus and response patterns in serial choice reactions]. *Zeitschrift für experimentelle Psychologie, 63,* 40–68.

Hoffmann, J., Sebald, A., & Stöcker, C. (2001). Irrelevant response effects improve serial learning in serial reaction time tasks. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 27,* 470–482.

Japikse, K. C., Negash, S., Howard Jr., J. H., & Howard, D. V. (2003). Intermanual transfer of procedural learning after extended practice of probabilistic sequences. *Experimental Brain Research, 148,* 38–49.

Jordan, M. I. (1995). The organization of action sequences: Evidence from a relearning task. *Journal of Motor Behavior, 27,* 179–192.

Karni, A., Meyer, G., Jezzard, P., Adams, M. M., Turner, R., & Ungerleider, L. G. (1995, September 14). Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature, 377,* 155–158.

Keele, S. W., Ivry, R., Mayr, U., Hazeltine, E., & Heuer, H. (2003). The cognitive and neural architecture of sequence representation. *Psychological Review, 110,* 316–339.

Keele, S. W., Jennings, P., Jones, S., Caulton, D., & Cohen, A. (1995). On the modularity of sequence representation. *Journal of Motor Behavior, 27,* 17–30.

Kent, R. D., & Minifie, F. D. (1977). Coarticulation in recent speech production models. *Journal of Phonetics, 5,* 115–133.

Koch, I., & Hoffmann, J. (2000a). Patterns, chunks, and hierarchies in serial reaction-time tasks. *Psychological Research, 63,* 22–35.

Koch, I., & Hoffmann, J. (2000b). The role of stimulus-based and response-based spatial information in sequence learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26,* 863–882.

Korman, M., Raz, N., Flash, T., & Karni, A. (2003). Multiple shifts in the representation of a motor sequence during the acquisition of skilled performance. *Proceedings of the National Academy of Sciences, USA, 100,* 12492–12497.

Magill, R. A., & Hall, K. G. (1990). A review of the contextual interference effect in motor skill acquisition. *Human Movement Science, 9,* 241–289.

Nissen, M. J., & Bullemer, P. (1987). Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology, 19,* 1–32.

Osman, M., Bird, G., & Heyes, C. (2005). Action observation supports effector-dependent learning of finger movement sequences. *Experimental Brain Research, 165,* 19–27.

Panzer, S., Büsch, D., Shea, C. H., Mühlbauer, T., Naundorf, F., & Krüger, M. (2007). Dominanz visuell-räumlicher Codierung beim Lernen von Bewegungssequenzen [Movement sequence learning and the dominance of visual-spatial coding]. *Zeitschrift für Sportpsychologie, 14,* 123–129.

Park, J.-H., & Shea, C. H. (2003). Effect of practice on effector independence. *Journal of Motor Behavior, 35,* 33–40.

Park, J.-H., & Shea, C. H. (2005). Sequence learning: Response structure and effector transfer. *Quarterly Journal of Experimental Psychology, 58,* 387–419.

Remillard, G. (2003). Pure perceptual-based sequence learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 29,* 581–597.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action: Nature reviews. *Neuroscience, 2,* 661–670.

Rüsseler, J., & Rösler, F. (2000). Implicit and explicit learning of event sequences: Evidence for distinct coding of perceptual and motor representations. *Acta Psychologica, 104,* 45–67.

Sainburg, R. L., & Wang, J. (2002). Interlimb transfer of visuomotor rotations: Independence of direction and final position information. *Experimental Brain Research, 145,* 437–447.

Schneider, W., Eschman, A., & Zuccolotto, A. (2002). *E-Prime user's guide.* Pittsburgh, PA: Psychology Software Tools.

Shea, J. B., & Morgan, R. L. (1979). Contextual interference effects on the acquisition, retention, and transfer of a motor skill. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 5,* 179–187.

Stöcker, C., & Hoffmann, J. (2004). The ideomotor principle and motor sequence acquisition: Tone effects facilitate movement chunking. *Psychological Research, 68,* 126–137.

Stöcker, C., Sebald, A., & Hoffmann, J. (2003). The influence of response-effect compatibility in a serial reaction time task. *Quarterly Journal of Experimental Psychology, 56,* 586–703.

Verwey, W. B., & Clegg, B. A. (2005). Effector dependent sequence learning in the serial RT task. *Psychological Research, 69,* 242–251.

Verwey, W. B., & Wright, D. L. (2004). Effector-independent and effector-dependent learning in the discrete sequence production task. *Psychological Research, 68,* 64–70.

Wachs, K., Pascual-Leone, A., Grafman, J., & Hallet, M. (1994). Intermanual transfer of implicit knowledge of sequential finger movements [Abstract]. *Neurology, 44*(Suppl. 2)*,* A329.

Wang, J., & Sainburg, R. L. (2004a). Limitations in interlimb transfer of visuomotor rotations. *Experimental Brain Research, 155,* 1–8.

Wang, J., & Sainburg, R. L. (2004b). Interlimb transfer of novel inertial dynamics is asymmetrical. *Journal of Neurophysiology, 92,* 349–360.

Wang, J., & Sainburg, R. L. (2006). The symmetry of interlimb transfer depends on workspace locations. *Experimental Brain Research, 170,* 464–471.

Willingham, D. B. (1999). Implicit motor sequence learning is not purely perceptual. *Memory & Cognition, 27,* 561–572.

Willingham, D. B., Wells, L. A., Farrell, J. M., & Stemwedel, M. E. (2000). Implicit motor sequence learning is represented in response locations. *Memory & Cognition, 28,* 366–375.

Witt, J. K., & Willingham, D. T. (2006). Evidence for separate representations for action and location in implicit motor sequencing. *Psychonomic Bulletin & Review, 13,* 902–907.

Ziessler, M. (1998). Response-effect learning as a major component of implicit serial learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 24,* 962–978.

Ziessler, M., & Nattkemper, D. (2001). Learning of event sequences is based on response-effect learning: Further evidence from a serial reaction task. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 27,* 595–613.

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