Exp Brain Res (2003) 148:38–49
DOI 10.1007/s00221-002-1264-9

RESEARCH ARTICLE

Karin C. Japikse · Selam Negash · James H. Howard Jr · Darlene V. Howard

Intermanual transfer of procedural learning after extended practice of probabilistic sequences

Received: 21 September 2001 / Accepted: 26 August 2002 / Published online: 9 November 2002

Abstract Previous studies using simple, repeating patterns have suggested that the knowledge gained in early sequence learning is not effector-specific in that it transfers to muscle groups other than those used during training. The current experiments extended these findings to transfer after extensive practice with probabilistic sequences using a task on which people fail to gain declarative knowledge of the regularity. Specifically, an alternating serial reaction time (ASRT) task was used in which predictable and unpredictable trials alternated. Participants responded for the first five sessions using their right hand, then switched to the left hand for the sixth session. Stimuli were spatial in the first experiment and nonspatial in the second. Significant near-perfect transfer of pattern knowledge was seen in both experiments, suggesting that muscle-specific information for either the fingers or the eyes cannot explain the observed learning.

Keywords Sequence learning · Implicit learning · Procedural learning · Intermanual transfer

Introduction

Implicit, procedural learning involves learning "how to do" a task in the absence of knowledge about what has been learned (Reber 1993). It contrasts with explicit, declarative learning, which refers to conscious, goal-directed acquisition (Cohen and Squire 1980). The present paper focuses on the kind of procedural learning that occurs during extensive practice on perceptual/motor tasks containing subtle sequential regularities. While participants cannot describe the structure inherent in the task, the pattern can be shown to influence their behavior. The nature of the representation underlying improved performance on such procedural, sequential learning tasks is unknown (Goschke 1998). The present experiments examined the extent to which learning is effector-specific by measuring intermanual transfer in a variation of the serial reaction time (SRT) task.

In the original SRT task, developed by Nissen and Bullemer (1987), participants respond as quickly as possible to targets that occur in four locations on a computer screen. Each target maps to a unique key, which must be pressed to initiate the next trial. Speed and accuracy on blocks where the target appears in the four locations according to a repeating pattern are compared with performance on blocks containing only random trials. To the extent that people are either faster or more accurate on pattern blocks than on random ones, sequence-specific learning is said to have occurred. People who are given extensive practice at such tasks often report that their fingers seem to take over and respond on their own (Howard and Howard 1997). Thus, participants often believe that what they have learned is a series of motor responses. Research suggests, however, that the picture is more complicated.

Willingham (1999) described several types of information about SRT patterns that could be learned procedurally. Firstly, in keeping with participants' intuitions, people could learn the muscle movement sequence necessary to respond to the pattern. Secondly, they might learn the sequential order of stimuli. Thirdly, they might learn a sequence of response locations in a non-effector-specific manner.

Several studies have suggested that, contrary to the first alternative above, the knowledge gained is not effector-specific. For example, learning on the SRT task may occur without responding (Howard et al. 1992; Mayr 1996), although there is debate on this point (Kelly and Burton 2001). Transfer studies also provide evidence for effector-independent learning in that people are able to

K.C. Japikse · S. Negash · D.V. Howard (✉)
Georgetown University, Department of Psychology,
37th and 0 Streets, NW, Washington, DC 20057–1001, USA
e-mail: howardd@georgetown.edu
Tel.: +1-202-6874099
Fax: +1-202-6876050

J.H. Howard Jr
The Catholic University of America, Department of Psychology,
620 Michigan Avenue, NE, Washington, DC 20064, USA

use knowledge acquired earlier, even though they must respond using a different set of muscles during transfer. Knowledge transfer has been shown to occur, for example, from three fingers to one finger (Cohen et al. 1990), from fingers to the ipsilateral arm (Keele et al.,1995), and across modalities from manual to vocal responding (Keele et al.,1995).

Nor is there consistent support for Willingham's second alternative; learning does not appear to rely solely on stimulus sequence knowledge. For example, using a nonspatial SRT task, Gómez-Beldarrain et al. (1998) found that patients with cerebellar lesions were impaired on learning with the ipsilateral but not contralateral hand. Because the same stimulus sequence was seen regardless of which hand performed the task, this result is not consistent with purely perceptual learning. Their finding corroborates those from studies by Willingham et al. (1989) and Willingham (1999) that led to the conclusion that a motor component must contribute to learning on the SRT task. Most recently, Willingham et al. (2000) found no transfer of sequence knowledge when the stimulus sequence was held constant while other task components were changed.

Thus, although there are some inconsistencies, results to date seem to fit best with Willingham's (2000) third alternative, i.e., that people learn a sequence of response locations which is not effector specific. The studies supporting this conclusion, however, typically used deterministic sequences that had been practiced for only a few blocks.

The goal of the present experiments was to determine whether this same conclusion holds when people are highly practiced at responding to probabilistic information about sequences with a relatively complex structure. In addition, because declarative knowledge is less likely to develop when such a complex pattern is used, the current experiments focused on learning without awareness. The importance of each of these three factors (i.e., pattern structure, length of practice prior to transfer, and awareness) in the study of sequence learning will be considered in turn.

Regarding the structure to be learned, previous transfer experiments have used both hybrid and ambiguous sequences. Hybrid patterns contain at least one unique transition. Thus, in studies using hybrid patterns, knowledge about single positions or pairs of positions could support transfer (Cohen et al. 1990, experiment 2; Grafton et al. 1998; Keele et al. 1995). Ambiguous sequences contain no such unique transitions, so in studies using these, information about the previous two trials is necessary to predict the next correct position and, hence, to support transfer. (Willingham 1999; Willingham et al. 2000). In all of these aforementioned studies, individual elements followed a completely predictable sequence during patterned blocks, and participants learned deterministic rather than probabilistic information.

These similarities among earlier transfer experiments are important because different sorts of sequence structures obey different learning principles. For example, engagement in a dual task (i.e., tone-counting) disrupts learning, or at least performance, of ambiguous but not of hybrid sequences (Cohen et al. 1990, experiments 3 and 4). Similarly, older adults usually reveal sequence learning equivalent to that of college students when simple deterministic sequences are used (Howard and Howard 1989; Howard and Howard 1992; Cherry and Stadler 1995), but age-related deficits occur for more complex, probabilistic sequences (Curran 1997a; Howard and Howard 1997; Howard and Howard 2001). Instructions to try to discover and learn a pattern usually improve sequence learning of simple patterns, but not of more complex or probabilistic ones (Buchner et al. 1997; Curran 1997a; Curran and Keele 1993; Frensch and Miner 1994; Jiménez et al. 1996). Finally, probabilistic sequences lead to more anticipatory errors as learning progresses whereas deterministic ones do not (Schvaneveldt and Gomez 1998).

Dissociations of this sort suggest that different sequence structures involve learning systems that are at least partially distinct and that rely on different underlying representations. This argument is strengthened by Curran's (1997b) finding that people with anterograde amnesia are impaired at learning higher-order, but not lower-order, aspects of a sequence. Thus, the fact that procedural learning of simple deterministic regularities transfers from one set of effectors to another does not necessarily imply that the same will be true for higher-order probabilistic regularities. The present experiments tested whether the lack of effector specificity seen with deterministic patterns would generalize to more complex sequences.

Previous studies of intermanual transfer of sequence learning have measured transfer after relatively brief practice. Different brain systems are likely involved, however, in early versus late learning (Honda et al. 1998). For example, Karni et al. (1995) found that primary motor cortex activation increased over the course of learning.

It is unknown whether the effector independence seen after brief practice is also a feature of late learning (Hazeltine and Ivry 2002). Several studies have investigated this issue using a 2×5 sequence task in which participants learn to press buttons in a specific order via trial and error (Hikosaka et al. 1995). Nakahara et al. (2001) proposed a model that assumes that two separate brain circuits underlie sequence learning. Specifically, a visual pathway and a motor pathway operate in parallel, with their sequence knowledge then combined by the presupplementary motor area. In this model, the visual loop learns a spatial sequence rapidly, thus contributing most to early learning. The motor loop learns more gradually, becoming more involved later in learning.

According to this two-system framework, while early visual learning is not effector specific, later learning is because of its significant motor component. In monkeys, transfer between hands has been shown to be complete early in sequence learning and incomplete following extended practice (Rand et al. 1998; Rand et al. 2000). Consistent with this pattern of results, Bapi, Doya, and

Harner (1998) demonstrated that people's knowledge transferred better after extended learning when the finger-keypad mapping was held constant than when it changed. This differential transfer was not seen in early learning. Performance in this latter study, however, may well have been based on both procedural and declarative knowledge. It is unknown if the late-phase effector specificity would hold for a sequence learning task that involves only procedural knowledge.

Studies have shown different patterns of brain activation depending on whether or not learning is accompanied by conscious sequence knowledge. For example, Honda et al. (1998) found that explicit learning activated right dorsolateral prefrontal cortex, supplementary motor area, and premotor cortex, among other areas. In contrast, learning-associated changes occurred in the contralateral primary sensorimotor cortex under implicit conditions. Both implicit and explicit pattern learning may occur simultaneously (Willingham and Goedert-Eschmann 1999) and it is unclear how much explicit knowledge contributed to the transfer seen in studies using simple, deterministic patterns. This is particularly important because research using event-related potentials has suggested that people who develop explicit knowledge in an SRT task learn both perceptual and motor dependencies, but people with implicit but not explicit knowledge only learn motor dependencies (Russeler and Rosler 2000). One advantage of the pattern structure used in the current study is that it allowed investigation of transfer between effectors when explicit knowledge was unlikely to develop (Howard and Howard 1997).

In general, then, with respect to the three factors of type of structure, level of practice, and awareness, earlier studies have usually examined transfer after brief practice of simple repeating patterns which are likely to result in at least some explicit, declarative knowledge. The research reviewed above indicates that these are the conditions under which effector specificity is least likely to be found. The present experiments provided a more stringent test of the extent to which implicit sequence learning really is effector-independent, because they examine conditions under which effector specificity might be more likely.

The two experiments reported here addressed the question of whether transfer from one set of motor effectors to another occurs after extended practice of probabilistic sequential information where declarative knowledge is unlikely to occur. In both experiments, people were highly practiced, having performed the task for at least 1,000 pattern repetitions before transfer. In addition, the patterns were structured so that the information available to participants was no lower than second order (i.e., they required knowledge of what target appeared two trials back in order to anticipate correctly the current stimulus and response). The sequences were eight positions long, with four pattern elements alternating with random ones. For example, in the repeating pattern 1r2r3r4r, each of the four stimulus positions occurred equally often, and these predictable stimuli alternated with random trials (r) on which the stimulus appeared in any of the four positions with equal probability. Previous studies have shown that, without being aware of doing so, people learn the relative probability of three successive trials, or triplets. They respond more quickly to those triplets (three-position-long runs of trials) that have occurred more often over the course of the experiment (Howard and Howard 1997).

The presence of both pattern and random trials in each block of this task allows immediate measurement of knowledge after transfer. With simple repeating sequences of the sort used in most previous transfer studies, by contrast, pattern knowledge could not be assessed until after at least two blocks (one pattern and one random) had been completed in the transfer condition. Further, this task produced relatively pure procedural learning; in previous studies using this version of the alternating serial reaction time (ASRT) task, no participants were able to describe accurately anything about the pattern (Howard and Howard 1997).

In the first experiment described below, the stimuli followed a spatial pattern whereas, in the second experiment, the stimulus pattern was nonspatial. If transfer occurs from one effector set to another in both experiments, this will suggest that learning of an effector-specific set of finger movements, or of eye movements to stimuli, cannot account for procedural learning of higher-order probabilistic patterns.

Experiment 1

Materials and methods

Participants

Eighteen right-handed Georgetown University students (five women and 13 men; mean age 20.33, range 18–22 years) were paid to participate. This study was approved by Georgetown University's Institutional Review Board, and participants gave informed consent to participate.

Apparatus and behavioral paradigm

Participants performed the ASRT task (Howard and Howard 1997) in which four circles were displayed horizontally 1.2 in., apart across an 8×6 in. window on a computer screen. On a given trial, one of the circles filled in and people were told to respond to the stimulus by pressing one of four keys on a keyboard. One key corresponded to each circle on the screen, and participants were required to hit the correct key in order to initiate a new trial. Once the correct key had been pressed, the circle was cleared, and, after a 120 ms delay, the next circle filled in to begin a new trial.

The order in which the circles filled followed a repeating pattern that occurred on every other trial. The pattern itself was four positions long, with each position occurring once, but the presence of the alternating random trials meant that eight trials were required to cycle once through the pattern. Thus, a sample pattern would be ArDrBrCr, where A represents the position on the far left on the computer screen and D denotes the circle on the far right. For this sample pattern, a participant would see the following: A r D r B r C r A r D r B r C r..., where 'r' denotes a random trial on which any one of the four positions might occur with equal probability. The measure of learning is the difference between the pattern and random trials on accuracy and response time, with either faster or more accurate responding on pattern than on random trials being taken as evidence of learning.

Procedure

Participants first gave informed consent. They then performed the ASRT task for six sessions over the course of several days. Only one session could be completed per day, and no more than 2 days could elapse between sessions. For the first five sessions, people responded using the right, dominant hand to press the *j*, *k*, *l*, and *;* keys. On the sixth session, they switched to the left hand, pressing the *a*, *s*, *d*, and *f* keys. The mapping between the four circles on the screen and the fingers used to respond was parallel for the right and left hands. Thus, the circle on the far left corresponded to the *j* and *a* keys, the circle second from the left corresponded to the *k* and *s* keys, and so forth.

Participants were read instructions prior to beginning the ASRT task on the first session. They were not informed of the presence of any regularities, but, instead, were told that this was a study about how practice affects motor performance. They were told to respond as quickly as possible while maintaining 92% accuracy over each block of trials. At the end of each block, the computer provided feedback to help guide them to an accuracy level close to 92%. If the percent correct for the last completed block was less than 90%, the computer instructed the participant to "focus more on accuracy." If the accuracy was greater than 92%, the computer instruction was to "focus more on speed."

After each of the first five sessions, participants filled out an end-of-session questionnaire in which they were asked three questions probing for declarative knowledge of the presence of regularities while not giving any hint of their existence. Specifically, people were asked if they had used any strategy to try to improve their performance, and, if so, they were asked to describe the strategy and to evaluate how well that strategy worked. They were also encouraged to write down any comments they had about the task.

At the end of the sixth session, participants were given a postexperimental interview in which the experimenter read aloud five questions about the presence and nature of the pattern. These questions were read one at a time and the experimenter recorded the participant's responses. The following questions were asked: (1) Do you have anything to report regarding the task? (2) Did you notice anything special about the task or the material? (3) Did you notice any regularity in the way the stimulus was moving on the screen? (4) Did you attempt to take advantage of the regularities you noticed in order to anticipate subsequent targets? If so, did this help? (5) In fact, there was some regularity to the sequences you observed. What do you think it was? That is, try to describe any regularity you think might have been there. People who answered "yes" to the second or third questions were encouraged to describe what they had noticed before the experimenter moved on to the next question. The fourth question was posed only if the participant answered "yes" to question 3.

The participants were divided into three groups for the purpose of addressing a separate question that will not be discussed here. The groups were similar in that all performed the ASRT task for 21 pattern blocks per session. Each block consisted of 90 trials – ten random trials followed by 80 trials during which the pattern cycled through ten times. The ten initial random trials from each block were not included in the data analysis.

For each participant, the pattern remained the same for these 21 blocks of each session. Thus, of the eighteen participants, three saw each of the six possible patterns (ArBrCrDr, ArBrDrCr, ArCrBrDr, ArCrDrBr, ArDrBrCr, and ArDrCrBr). In analyses of variance performed on these data, none of the interactions involving the group variable were significant, so participants are collapsed across groups for the data shown below.

Results

Response time and accuracy measures were obtained for both pattern and random trials on a block-by-block basis for each participant. The median response time for each type of trial (pattern and random) was obtained for each person for each block. Then, the mean of these medians was calculated for both pattern and random trials by collapsing across the 21 blocks per session for each participant. A similar data reduction was used for the accuracy measure. Fig. 1 shows these data averaged across participants.

Learning prior to transfer

Analyses of variance were performed to evaluate learning on the sessions during which the right hand was used (sessions 1–5). A 2 (trial type) × 5 (session) repeated-measures ANOVA of the response time data revealed both a significant main effect of trial type[1] ($F_{(1,17)}$= 105.47, MS_e=85.08), and a significant trial type × session interaction ($F_{(4,68)}$=16.94, MS_e=18.04). Similarly, a 2×5 repeated measures ANOVA of the accuracy data revealed a significant main effect of trial type ($F_{(1,17)}$=132.07,

---

[1] For all statistical tests discussed in this paper, an alpha level of.05 was used.

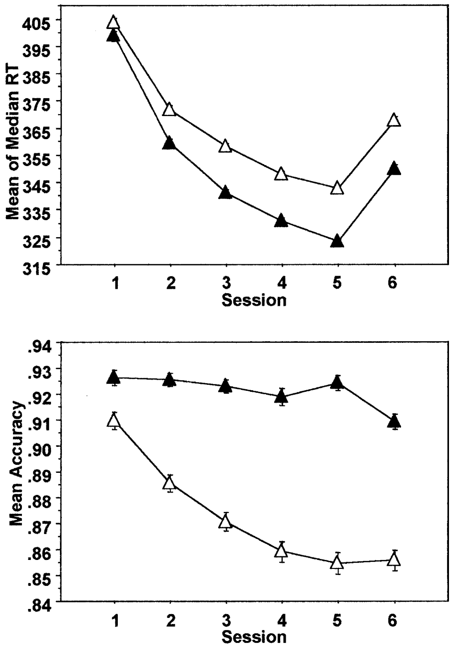


Fig. 1 Performance on pattern (*filled-in triangles*) and random (*open triangles*) trials over the course of the six sessions of experiment 1. The first five sessions were performed using the right hand while on the sixth session participants used their left hand. *Top graph*: Average response times (in milliseconds). *Bottom graph*: Mean accuracy (proportion correct). The *error bars* are ±1 standard error for both graphs, and are only visible when greater in magnitude than the size of the symbol

MS_e=0.001), and a significant trial type × session interaction ($F_{(4,68)}$=22.13, MS_e=1.7×10^{-4}). Thus, by both performance measures, participants demonstrated learning of the sequence regularities before transfer.

Performance after transfer

People demonstrated significant pattern-specific knowledge after transfer (session 6) in that performance was better on pattern trials for both measures (see Fig. 1). Consistent with this observation, there was a significant difference on paired *t*-tests comparing pattern and random trial data from session 6. This was true for both the response time and accuracy measures, $t_{(17)}$=6.65 and 6.86, respectively.

Next, it was important to determine whether the significant trial type effects on session 6 resulted from transfer of the knowledge acquired during right-hand training over the first five sessions rather than from rapid relearning over the course of the transfer session. To do this, the data from the first and sixth sessions were examined by block. For this block-by-block analysis, difference scores were calculated for each participant, reflecting the extent to which, on any given block, performance on pattern trials was superior to that on random trials. Thus, for the response time measure, the difference score for each block was calculated by subtracting the median response time for pattern trials from the median response time for random trials. For the accuracy measure, the proportion correct on random trials was subtracted from that on pattern trials. For both measures, therefore, difference scores significantly above zero demonstrated pattern knowledge.

Fig. 2 shows the difference scores averaged across participants for sessions 1 and 6, broken down by block.

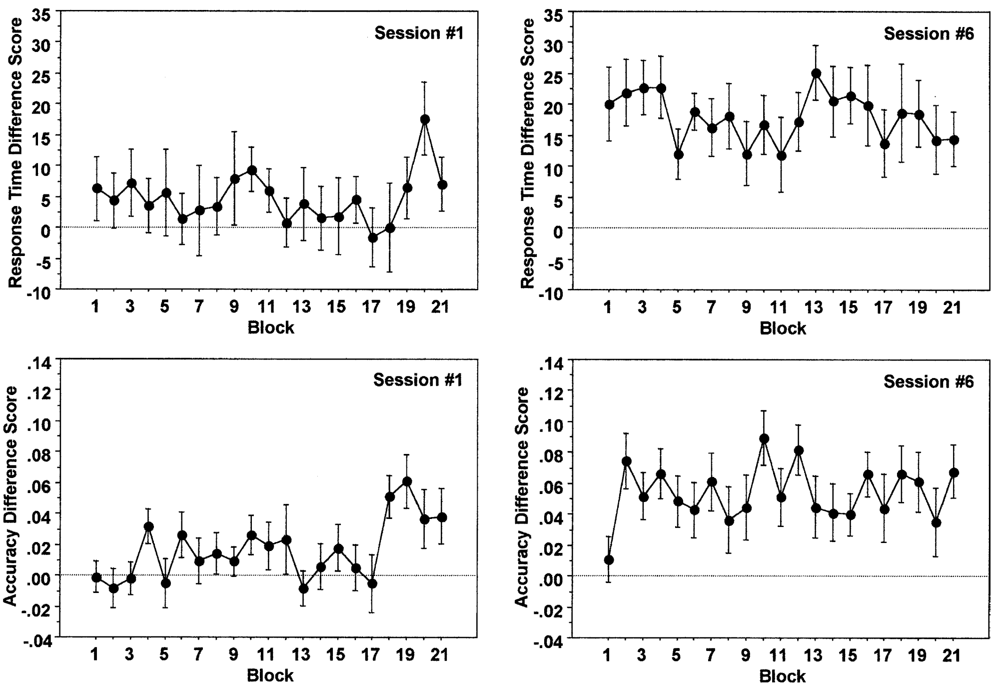


Fig. 2 Trial type effect (the difference between performance on pattern and random trials) split by block for session 1 (*left side*) and session 6 (*right side*) of experiment 1. Difference scores significantly greater than zero indicate that performance on the pattern trials was superior to that on the random trials. The *top two graphs* show difference scores for the response time measure (in milliseconds). The *bottom two graphs* show difference scores for the accuracy measure (in terms of differences in proportion correct between the two trial types). The *error bars* are ±1 standard error for all graphs

As these graphs show, the amount of pattern knowledge displayed on session 6 was markedly greater than that on session 1. This was confirmed by 2 (session 1 versus 6) × 21 (block) repeated measures ANOVAs on the difference scores. Both accuracy and response time ANOVAs yielded main effects of session ($F_{(1,17)}$=16.1, MS_e=2.04×10$^{3)}$ for response time and ($F_{(1,17)}$=20.3, MS_e=0.013) for accuracy. Furthermore, Fig. 2 shows that participants demonstrated this larger amount of knowledge from the beginning of session 6 on the response time measure, and from the second block on for the accuracy measure. The presence of significant amounts of pattern knowledge during early blocks of the sixth session suggests transfer from the right hand rather than rapid relearning by the left hand. This observation was confirmed by one-way ANOVAs on the session 6 difference scores, which revealed no significant effect of block for either the response time ($F_{(20,340)}$=0.70, MS_e=382.6, P=0.82), or the accuracy measure ($F_{(20,340)}$=1.16, MS_e=0.005, P=0.29).

Performance after transfer was further evaluated by comparing the amount of learning shown during session 6 with that displayed during session 5. For the accuracy data, a 2 (trial type) × 2 (session) repeated measures ANOVA showed a significant session × trial type interaction ($F_{(1,17)}$=8.79, MS_e=1.33×10^{-4}). The session × trial type interaction was not significant, however, for the response time measure ($F_{(1,17)}$0.72, MS_e=13.61). As may be seen in Fig. 1, these results suggest that, at least in the case of the accuracy measure, transfer from the right to the left hand was incomplete, though substantial.

Declarative knowledge

When asked in the end-of-session questionnaire given after each of the first five sessions, four out of 18 participants indicated that, as a strategy, they were either searching for a pattern or trying to anticipate which screen position would fill in on the next trial. A fifth person indicated in the postexperimental interview that he had looked for a pattern while performing the ASRT task. No one believed that this pattern-searching strategy helped, however.

After being told in the postexperimental interview that there was in fact a pattern, nine participants gave guesses as to what regularity had been present. None of these guesses was accurate. For example, four people commented that the target was more likely to repeat in the same position than to move to another (i.e., if position A lit up, the next target was more likely to occur in position A again than to occur in any of the other three positions). Two other participants believed that when they made a mistake the next trial would occur in the position that corresponded to the key they incorrectly hit. The most specific guess made was by one participant who commented that position A was followed by position C, but she failed to mention anything about the alternating nature of the pattern.

Thus, participants' responses on the end-of-session questionnaires and the postexperimental interviews showed no evidence of declarative knowledge about the nature of the pattern. On this basis, one may infer that the intermanual transfer that occurred relied on procedural, and not declarative, knowledge.

Discussion

This first experiment implies that the procedural knowledge acquired after extensive practice with probabilistic sequences shows significant transfer from one hand to another, and so is not effector-specific. Learned patterns of eye movements could contribute to the transfer observed, however, because the spatial configuration of stimulus presentation remained the same for transfer.

Most studies demonstrating effector-independent procedural learning have held eye movement patterns constant across training and transfer (Cohen et al. 1990; Howard et al. 1992; Keele et al. 1995), so this same limitation applies to them. There are exceptions, however. For example, using a simple repeating pattern in a spatial SRT task, Willingham et al. (2000) held eye movements constant while changing motor movements and response locations after six blocks (40 pattern repetitions) and found no transfer. In addition, transfer of learning without eye movements has been demonstrated after sixteen blocks (approximately 98 pattern repetitions) of a simple repeating pattern in an SRT task with nonspatial stimuli (Grafton et al. 1998). These previous results suggest that early learning of simple repeating patterns on the SRT task can occur without eye movements, and that transfer of this type of pattern knowledge to another set of effectors can occur without eye movements to guide it.

The second experiment, therefore, was designed to examine whether this same conclusion holds after extended practice of probabilistic sequential information and to evaluate better the claim that learning on this task is implicit in nature.

Experiment 2

This experiment used the same task as the first, except that the stimulus display was a nonspatial one adapted from Gómez-Beldarrain et al. (1998) so as to rule out eye movements as a possible source of transfer. Also, three additional tests of pattern knowledge, i.e., production, recognition, and preference, were included. While participants' verbal reports are commonly used to infer the absence of declarative knowledge (Gómez-Beldarrain et al. 1998; Honda et al. 1998; Willingham et al. 1989), these tasks were added to probe the ways in which pattern knowledge can be expressed.

Materials and methods

Participants

Twelve right-handed Georgetown University students (six women and six men; mean age 20.67, range 19–24 years) were included, none of whom had been in any previous SRT experiments. Two additional students took part; however, because they skipped more than 2 days between consecutive sessions, their data were not included. As was the case with experiment 1, this study was approved by Georgetown University's Institutional Review Board. Participants gave informed consent and were paid to participate.

Apparatus and behavioral paradigm

For the ASRT task with nonspatial stimuli, the computer displayed a 2 cm × 2 cm square box in the center of the screen. On each trial, one of four letters (A, B, C, or D) appeared in the box in black, upper case 16-point font.

For the first five sessions, participants placed the four fingers of their right hand on the *j*, *k*, *l*, and *;* keys to respond to the targets A, B, C, and D, respectively. These keys were covered with circular stickers so that their usual labeling could not be seen. If the letter A appeared in the box, participants' task was to press the *j* key with their right index finger. Similarly, B mapped to the *k* key, etc. On the sixth session, participants placed the four fingers of their left hand on the *a*, *s*, *d*, and *f* keys (also marked with stickers) to respond to the targets A, B, C, and D, respectively. All other details of the task were identical to experiment 1.

Procedure

The procedure was the same as experiment 1, with the following exceptions. Participants completed 20 blocks per session. At the end of each block, they were asked to read aloud their most recent speed and accuracy scores. If their accuracy scores on the preceding three blocks were all less than 87% or all greater than 97%, the experimenter told them to focus more on accuracy or on speed, respectively.

Participants completed up to two sessions in a given day. If two sessions were done in a single day, a break of at least 45 min was required between the two. Each session consisted of the ASRT task followed by a production task used to probe for sequence knowledge.

For the production test, a 2 cm × 2 cm square was displayed on the computer screen, as in the ASRT task. In this test, however, participants did not respond to letters appearing in the square. Instead, they were asked to use their right (sessions 1–5) or left hand (session 6) to press the four keys "to create a sequence like the ones to which you have been responding." Pressing one of the four valid keys (*j*, *k*, *l*, and *;* for sessions 1–5 and *a*, *s*, *d*, and *f* for session 6) caused the corresponding letter to appear inside the square on the computer screen. Participants completed two 80-trial production blocks per session. This task was self-paced.

After completion of the production test, participants filled out the same end-of-session questionnaire given during experiment 1, with one additional question about whether they had found the production task easy or difficult. Following this in session 6, participants completed two additional sequence knowledge tests – namely, a recognition task followed by a preference task.

For the recognition test, each participant was shown 20, 16-trial sequences. Ten of these contained the pattern to which that participant had responded during the ASRT portion of the experiment. The other ten sequences were random. After the participants had viewed each sequence, they were asked to rate on a 4-point scale how certain they were that the preceding sequence had occurred before. A rating of 4 corresponded to "certain it did occur," whereas 1 corresponded to "certain it did not occur."

The preference test was identical to the recognition test, except that, rather than rating recognition, participants were asked to rate how much they liked each sequence. A rating of 4 corresponded to "strongly liked the sequence," while 1 corresponded to "strongly disliked the sequence."

The postexperimental interview from experiment 1 was given at the end of session 6. In addition, an expanded battery of supplementary tasks was used in this experiment to facilitate comparison with older adults; these will not be reported here.

Results

Learning prior to transfer

Fig. 3 shows the mean response time and accuracy data across sessions for the pattern and random trials. As in experiment 1, there was significant learning during the first five sessions. The response time ANOVA showed a significant main effect of trial type ($F_{(1,11)}$=57.18, MS_e=244.81), and a significant trial type × session interaction ($F_{(4,44)}$=6.55, MS_e=39.31). Similarly, the accuracy ANOVA showed both a significant main effect of trial type ($F_{(1,11)}$=193.77, MS_e=3.13×10^{-4}), and a significant trial type × session interaction ($F_{(4,44)}$=9.51, MS_e=1.41×10^{-4}).

Performance after transfer

As in experiment 1, the knowledge acquired using the right hand transferred to the left hand (see Fig. 3). Paired *t*-tests on the session 6 data revealed differences between the two trial types on both response time and accuracy measures, $t_{(11)}$=5.49 and 7.29, respectively.

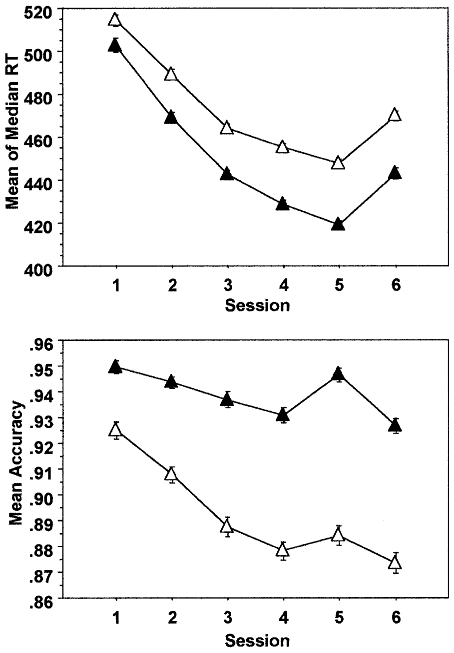


Fig. 3 Performance on pattern (*filled-in triangles*) and random (*open triangles*) trials over the course of the six sessions of experiment 2. The first five sessions were performed using the right hand while on the sixth session participants used their left hand. *Top graph*: Average response times (in milliseconds). *Bottom graph*: Mean accuracy (proportion correct). The *error bars* are ±1 standard error for both graphs, and are only visible when greater in magnitude than the size of the symbol

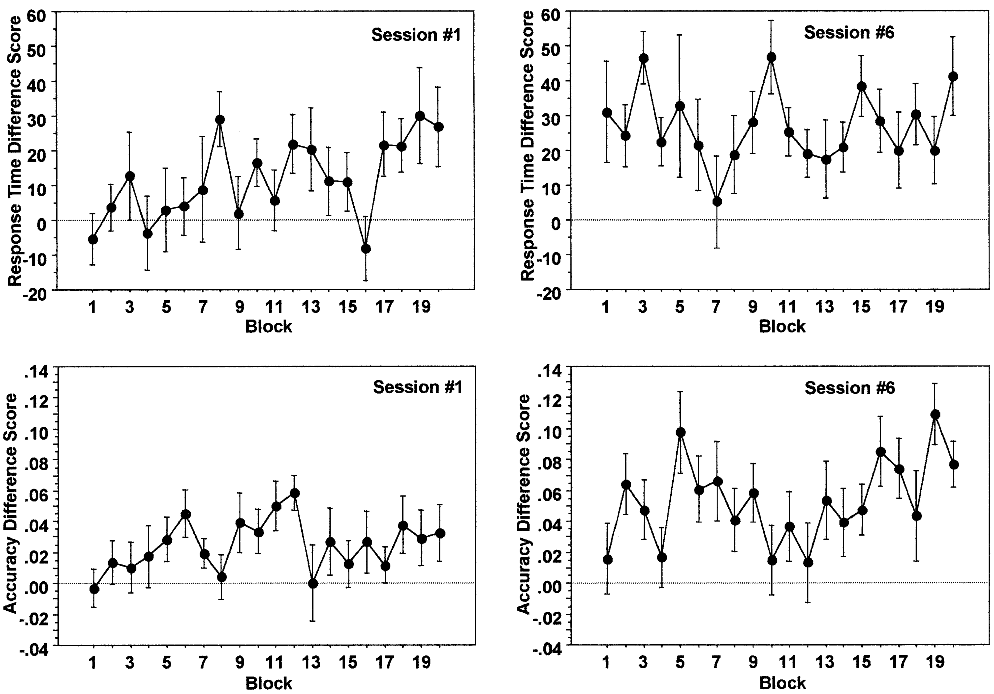
A block-by-block comparison of the amounts of learning on sessions 1 and 6 is shown in Fig. 4. As was the case in experiment 1, more sequence knowledge was present in the sixth session than in the first for both response time and accuracy. This was confirmed by significant main effects of session on 2 (session) × 20 (block) repeated-measures ANOVAs on the response time difference scores ($F_{(1,11)}=9.47$, $MS_{\mathrm{e}}=2983.15$), and the accuracy difference scores ($F_{(1,11)}=11.04$, $MS_{\mathrm{e}}=0.009$). The figure also suggests that the superiority on session 6 was not due to rapid relearning of the pattern; the response time difference score on the first block of session 6 was as high as that on the last block of session 1. A one-way ANOVA on the session 6 response time data confirmed this observation in that there was no significant main effect of block ($F_{(19,209)}=1.11$, $MS_{\mathrm{e}}=1.17\times10^{3}$, $P=0.34$). The main effect of block was marginally significant for the accuracy data, however ($F_{(19,209)}=1.63$, $MS_{\mathrm{e}}=0.005$, $P=0.052$), suggesting that there was some additional pattern learning during session 6.

A comparison of sessions 5 and 6 suggests that, as in experiment 1, transfer was nearly perfect. Repeated-measures 2 (session) × 2 (trial type) ANOVAs revealed no significant session × trial type interaction for the response time data ($F_{(1,11)}=0.218$, $MS_{\mathrm{e}}=22.64$, $P=0.65$), and a marginally significant session × trial type interaction for accuracy ($F_{(1,11)}=3.994$, $MS_{\mathrm{e}}=6.38\times10^{-5}$, $P=0.07$).

Declarative knowledge

As in experiment 1, participants' responses on the end-of-session questionnaires and the postexperimental inter-

Fig. 4 Trial type effect (the difference between performance on pattern and random trials) split by block for session 1 (*left side*) and session 6 (*right side*) of experiment 2. The *top two graphs* show difference scores for the response time measure (in milliseconds). The *bottom two graphs* show difference scores for the accuracy measure (in terms of differences in proportion correct between the two trial types). The *error bars* are ±1 standard error for all graphs



views did not reveal any declarative knowledge about the nature of the pattern. In addition, there were three other tests given that could reveal pattern knowledge. These will be considered in turn.

The production test, completed at the end of each of the six sessions, required participants to create sequences that mirrored those to which they had been responding. The data produced from this task were analyzed to determine what proportion of responses was consistent with the pattern present during the ASRT task. The analysis focused on three-position-long runs of trials (triplets). With the alternating patterns used in this experiment, triplets represent the lowest order of information that could be learned. For example, the triplet A-A-B is consistent with the pattern ArBrCrDr, whereas A-A-C is not. In the production task, if the average number of times a typical pattern-consistent triplet was produced was significantly higher than the average number of times a typical pattern-inconsistent triplet was produced, this indicated the influence of pattern knowledge on performance.

To analyze these data for each participant, the triplets were first divided into two categories (pattern-consistent and pattern-inconsistent). Triplets in which the first and third elements were identical were discarded from this analysis because they were pattern-inconsistent for all participants and thus were not counterbalanced across patterns. The expected ratio of pattern-consistent to pattern-inconsistent triplets produced by chance was therefore 1:2 for each participant. For example, the triplets A-A-*x* broke down as follows for the pattern ArBrCrDr: A-A-B was pattern-consistent, A-A-C and A-A-D were pattern-inconsistent, and A-A-A was excluded from the production data analysis.

A repeated-measures ANOVA on the pattern-consistent triplets revealed no main effect of session, indicating that the number of pattern-consistent triplets produced did not increase across the experiment ($F_{(5,55)}$=1.55, MS_e=31.5, P=0.19). In addition, the pattern-consistent production rate on session 6 was compared with chance (0.33) and found not to differ, $t_{(11)}$=0.63, P=0.54. Thus, there was no evidence that participants were able to apply the knowledge they had gained during the ASRT task in order to generate similar sequences during the production task.

For the recognition test, participants rated 20 sequences on a 4-point scale to reflect their confidence that each had occurred earlier. The average ratings for pattern-consistent and random sequences were calculated for each person. The mean across participants was 2.64 (SD=0.34) for the pattern-consistent and 2.42 (SD=0.45) for the random. A paired *t*-test showed no difference between the ratings for the two types of sequences, $t_{(11)}$=1.51, P=0.16. Thus, participants did not reveal significant pattern knowledge on this recognition test.

The instructions for the preference test were to rate sequences on a 4-point scale to reflect how much they liked each one. The mean across participants was 2.66 (SD=0.29) for the pattern-consistent sequences and 2.48 (SD=0.36) for the random sequences. A paired *t*-test was marginally significant, $t_{(11)}$=1.82, P=0.096, suggesting that, although people did not reveal declarative knowledge of the pattern, they tended to prefer pattern-consistent sequences to random ones. This test relies upon the mere exposure effect (Bornstein 1989), i.e., the fact that people tend to prefer stimuli they have encountered earlier, and is usually viewed as a test of implicit memory.

General discussion

In the present experiments, probabilistic pattern knowledge was evaluated using a perceptual/motor sequence learning task in which pattern and random trials alternated, allowing for the immediate evaluation of transfer across effectors. The first experiment demonstrated knowledge transfer between hands when a spatial stimulus sequence was used. The second experiment showed transfer of learning of a nonspatially presented sequence. Transfer occurred in these experiments after 9,000 or more trials (i.e., at least 1,000 pattern repetitions) on the ASRT task. Furthermore, this learning was procedural in nature, as participants showed no evidence of declarative pattern knowledge. Thus, the procedural knowledge acquired after extensive practice of a probabilistic sequence is not effector-specific, nor is it dependent on eye movements to a stimulus array.

These results are consistent with earlier studies in demonstrating that the knowledge acquired while responding to sequential patterns is at least partially effector-independent. For example, in a PET study by Grafton et al. (1998), participants learned a six-position-long, simple, repeating pattern by responding with four fingers of their right hand. A concurrent tone-counting task was performed to help prevent declarative knowledge. At transfer, participants switched and performed the SRT task via movements of the entire right arm. Brain areas such as the inferior parietal cortex and the cingulate motor area, both of which are thought to be involved in processing abstract motor information, remained active after transfer, suggesting that learning occurred at a higher level of processing than that of effector-specific information.

Consistent with these imaging data, Willingham et al. (2000) presented evidence from a series of transfer studies suggesting that knowledge of simple repeating sequences is not based on learning a specific sequence – either of effector movements, of eye movements, or of stimuli – but rather on learning a sequence of response locations. For example, Willingham et al. (2000) showed that transfer was good when muscle movements were changed, but that learning did not transfer when the sequence of response locations was altered.

The present results add to the literature in three ways. First, they show that intermanual transfer of learning occurs not only for the completely predictable patterns used in previous studies, but also for higher-order sequences in which the lowest level of knowledge available to be learned is probabilistic and second order. This similarity between predictable and probabilistic sequential learning is notable in light of the variety of findings summarized in the introduction indicating that these different kinds of sequences often obey different principles.

A second way in which the current experiments extend earlier findings is in showing that effector independence of learning holds not only early in learning– the situation examined in most earlier transfer studies – but also after more extensive practice with the pattern. One earlier series of experiments by Zeissler (1994) did address the question of whether a series of stimuli was learned during extended practice on a reaction time task. In his experiments, participants were asked to search matrices to find letters amidst distracter items. One target item occurred in each matrix, and its identity (whether it was W, S, F, X, or V) predicted where the target item would occur in the next matrix. Those who responded to each of the five target items by pressing a unique key showed learning over the course of the experiment, but those for whom the five targets did not map to unique keys showed little learning. This result suggests that distinct motor responses need to be associated with the stimuli in order for learning to occur, even after 12,000 trials. Whether this necessary motor component is effector-specific or independent was previously unknown. The current study suggests that, as with early learning, the motor component of late learning is largely independent of the effectors used.

Finally, the effector independence observed here occurred despite the absence of conscious pattern knowledge, as measured by several tests. Participants revealed no evidence of declarative knowledge by verbal reports or by performance on production and recognition tests. Thus, the ability to transfer knowledge from one hand is not dependent on conscious control of sequential knowledge.

One striking feature of the current data is the near-completeness of sequence knowledge transfer. On the response time measure, the amount of learning shown during session 6 (after transfer) was not significantly different from the amount shown during session 5 (before transfer) for either experiment. While the advantage for pattern trials over random ones decreased from session 5 to session 6 on the accuracy measure in experiment 1, this change was not significant for experiment 2. Thus, for three out of four measurements, there was no significant change in the amount of sequence knowledge demonstrated before and after transfer.

It is possible, of course, that the amount of learning demonstrated on the sixth session was less than what would have been seen had participants continued to respond with their right hands, thus indicating incomplete transfer. A comparison with other data using the ASRT task over six sessions suggests, however, that if there was a cost associated with transfer to the left hand it was quite small. For example, comparison of fifth and sixth session data from a later experiment (n=12) with a procedure comparable to that of experiment 1 (except that the task was performed with the right hand on all six sessions) showed an advantage of pattern trials over random ones of 22.611 ms on session 6, compared to 21.192 ms on session 5 – a small but marginally significant increase in learning scores of only 1.419 ms. Similarly, the pattern-trial advantage increased for accuracy (proportion correct) by 0.007, from 0.076 on session 5 to 0.083 on session 6 – also a nonsignificant increase (Japikse et al. 2000).

While comparisons made across experiments must be interpreted with caution, these data suggest that the amount of learning demonstrated does not typically increase significantly from session 5 to session 6 in the ASRT task used here, thus implying that the response time data in the current study indicates near-perfect transfer of learning. Even with the small (but significant) decrease in learning scores on the accuracy measure after transfer, the present data indicate that muscle-specific learning is not responsible for the majority of learning of probabilistic sequences.

Transfer across effectors was studied in the current experiments by having each participant switch from the right, dominant hand to the left, nondominant hand. Thus, one question that may be asked is whether the savings seen from session 5 to session 6 in this study are restricted by direction of transfer or, by contrast, whether transfer also occurs from the nondominant left hand to the dominant right hand. This question is interesting in light of previous studies that imply that direction of transfer matters. For example, learning of an inverted-reversed writing task by the right, dominant hand transfers to the left, nondominant hand to a greater extent than learning by the left, nondominant hand transfers to the right dominant hand (Parlow and Kinsbourne 1989). There is evidence, however, to suggest that transfer of ASRT learning can occur from the left, nondominant hand to the right, dominant hand (Feeney et al. 1999).

One issue unresolved by the current study concerns exactly what is learned that enables transfer across effectors. Previously presented evidence based on trial-by-trial analyses of error types and response times (Howard and Howard 1997) has suggested that what people learn when responding to the alternating regularity used in the present experiments is knowledge of the relative frequency with which triplets occur. This knowledge is procedural rather than declarative, in that people cannot describe what they have learned. In fact, when pattern knowledge was probed further via additional tests in the present experiment 2, people were unable to reveal their knowledge either in the sequences they generated in a production task or in being able to differentiate between pattern-consistent and random sequences in a subsequent recognition test. The present results indicate that procedural knowledge of relative triplet frequencies is not effector-specific, in that it transfers nearly perfectly from the dominant to the nondominant hand.

The present results are consistent with the proposal of Willingham et al. (2000) that the non-effector-specific knowledge being acquired encodes information about response locations. The present data provide no direct evidence for such learning of response locations, however, because both experiments involved transfer using parallel mapping. The left-most position on the screen was paired with the index finger of the right hand and the pinky finger of the left hand; the second position from the left was paired with the right middle finger and the left ring finger, and so forth. Thus, because they were held constant across transfer, learning of response locations could not be assessed in these experiments.

The question of whether transfer would occur after extended practice with a complex pattern if response locations were changed could be studied by using a mirror image mapping between the two hands. Thus, the left-most position on the screen would map to the index fingers of both hands, meaning that transfer from the right hand to the left hand would switch the response location of that stimulus position from the left-most response key to the right-most one.

In conclusion, earlier research has indicated that different principles govern the learning of probabilistic sequences as opposed to completely predictable ones. Similarly, there is evidence that partially distinct brain mechanisms are involved early in learning as opposed to later. Nonetheless, the current results indicate that in all of these cases the type of sensorimotor information underlying performance is similar in that it is not muscle-specific. While there may be some learning of effector-specific information, this type of knowledge is not critical for successful performance on the SRT task.

References

Bapi RS, Doya K, Harner A (1998) Evidence for effector independent and dependent representations and their differential time course of acquisition during motor sequence learning. Exp Brain Res 132:149–162

Bornstein RF (1989) Exposure and affect: overview and meta-analysis of research, 1968–1987. Psychol Bull 106:265–289

Buchner A, Steffens MC, Erdfelder E, Rothkegel R (1997) A multinomial model to assess fluency and recollection in a sequence learning task. Q J Exp Psychol A 50A:631–663

Cherry KE, Stadler MA (1995) Implicit learning of a nonverbal sequence in younger and older adults. Psychol Aging 10:379–394

Cohen A, Ivry RI, Keele SW (1990) Attention and structure in sequence learning. J Exp Psychol Learn Mem Cogn 16:17–30

Cohen NJ, Squire LR (1980) Preserved learning and pattern-analyzing skill in amnesia: dissociation of knowing how and knowing that. Science 210:201–210

Curran, T (1997a) Effects of aging on implicit sequence learning: accounting for sequence structure and explicit knowledge. Psychol Res 60:24–41

Curran, T (1997b) Higher-order associative learning in amnesia: Evidence from the serial reaction time task. J Cogn Neurosci 9:522–533

Curran T, Keele SW (1993) Attentional and nonattentional forms of sequence learning. J Exp Psychol Learn Mem Cogn 19:189–202

Feeney JJ, Howard, JH Jr (1999) Motor transfer effects in learning third order serial patterns. J Cogn Neurosci [Suppl] 11:45

Frensch PA, Miner CS (1994) Effects of presentation rate and individual differences in short-term memory capacity on an indirect measure of serial learning. Mem Cognit 22:95–110

Gómez-Beldarrain M, García-Moncó JC, Rubio B, Pascual-Leone A (1998) Effect of focal cerebellar lesions on procedural learning in the serial reaction time task. Exp Brain Res 120:25–30

Goschke T (1998) Implicit learning of perceptual and motor sequences: evidence for independent learning systems. In: Stadler, MA, Frensch, PA (eds) Handbook of implicit learning. Sage, Thousand Oaks, pp 401–444

Grafton ST, Hazeltine E, Ivry RB (1998) Abstract and effector-specific representations of motor sequences identified with PET. J Neurosci 18:9420–9428

Hazeltine E, Ivry, RB (2002) Can we teach the cerebellum new tricks? Science 296:1979–1980

Hikosaka O, Rand MK, Miyachi S, Miyashita K (1995) Learning of sequential movements in the monkey: process of learning and retention of memory. J Neurophysiol 76:617–621

Honda M, Deiber M-P, Ibáñez V, Pascual-Leone A, Zhuang P, Hallett M (1998) Dynamic cortical involvement in implicit and explicit motor sequence learning: a PET study. Brain 121:2159–2173

Howard DV, Howard JH Jr (1989) Age differences in learning serial patterns: direct versus indirect measures. Psychol Aging 4:357–364

Howard DV, Howard JH Jr (1992) Adult age differences in the rate of learning serial patterns: evidence from direct and indirect tests. Psychol Aging 7: 232–241

Howard DV, Howard JH Jr (2001) When it does hurt to try: adult age differences in the effects of instructions on implicit pattern learning. Psychon Bull Rev 8:798–805

Howard JH Jr, Mutter SA, Howard DV (1992) Serial pattern learning by event observation. J Exp Psychol Learn Mem Cogn 18:1029–1039

Howard JH Jr, Howard DV (1997) Age differences in implicit learning of higher order dependencies in serial patterns. Psychol Aging 12:634–656

Japikse KC, Howard DV, Howard, JH Jr (2000) Interference from intermittent patterns on a procedural sequence learning task. Abstracts of the Psychonomic Society, 5:69

Jiménez L, Mendez C, Cleeremans A (1996) Comparing direct and indirect measures of sequence learning. J Exp Psychol Learn Mem Cogn 22:948–969

Karni, A, Meyer, G, Jezzard, P, Adams, MM, Turner, R, Ungerleider, LG (1995) Functional MRI evidence for adult motor cortex plasticity during motor skill learning. Nature 377:155–158

Kelly SW, Burton AM (2001) Learning complex sequences: no role for observation? Psychol Res 65:15–23

Keele SW, Jennings P, Jones S, Caulton D, Cohen A (1995) On the modularity of sequence representation. J Mot Behav 27:17–30

Mayr U (1996) Spatial attention and implicit sequence learning: evidence for independent learning of spatial and nonspatial sequences. J Exp Psychol Learn Mem Cogn 22:350–364

Nakahara H, Doya K, Hikosaka O (2001) Parallel cortico-basal ganglia mechanisms for acquisition and execution of visuomotor sequences – a computational approach. J Cogn Neurosci 13:626–647

Nissen MJ, Bullemer P (1987) Attentional requirements of learning: evidence from performance measures. Cognit Psychol 19:1–32

Parlow SE, Kinsbourne M (1989) Asymmetrical transfer of training between hands: implications for interhemispheric communication in normal brain. Brain Cogn 11: 98–113

Rand MK, Hikosaka O, Miyachi S, Lu X, Miyashita K (1998) Characteristics of a long-term procedural skill in the monkey. Exp Brain Res 118:293–297

Rand MK, Hikosaka O, Miyachi S, Lu X, Nakamura K, Kitaguchi K, Shimo Y (2000) Characteristics of sequential movements during early learning period in monkeys. Exp Brain Res 131:293–304

Reber, AS (1993) Implicit learning and tacit knowledge: an essay on the cognitive unconscious. Oxford University Press, New York

Russeler J, Rosler, F (2000) Implicit and explicit learning of event sequences: evidence for distinct coding of perceptual and motor representations. Acta Psychol (Amst) 104:45–67

Schvaneveldt RW, Gomez RL (1998) Attention and probabilistic sequence learning. Psychol Res 61:175–190

Willingham DB (1999) Implicit motor sequence learning is not purely perceptual. Mem Cognit 27:561–572

Willingham DB, Goedert-Eschmann, K (1999) The relation between implicit and explicit learning: Evidence for parallel development. Psychol Sci 10:531–534

Willingham DB, Nissen MJ, Bullemer P (1989) On the development of procedural knowledge. J Exp Psychol Learn Mem Cogn 15:1047–1060

Willingham DB, Wells LA, Farrell JM, Stemwedel ME (2000) Implicit motor sequence learning is represented in response locations. Mem Cognit 28:366–375

Zeissler M (1994) The impact of motor responses on serial-pattern learning. Psychol Res 57:30–41