

Effector-Dependent Learning by Observation of a Finger Movement Sequence

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Can observational learning be effector dependent? In 3 experiments, observers watched a model respond to a 6-item unique sequence in a serial reaction time task. Their sequence knowledge was then compared with that of controls who had performed an unrelated task or observed a model responding to random targets. Observational learning was indicated when the introduction of a new sequence was associated with more reaction time elevation in observers than in controls. The authors found evidence of observational learning only when observers used the finger movement sequence that they observed during training, not when they responded at the same sequence of locations using different digits. Free generation and recognition tests also detected observational learning. These results imply that observational learning can be both explicit and effector dependent.

It is well known that watching another person perform a motor skill, such as tying a shoelace or serving a tennis ball, can accelerate learning of the same skill by the observer. Watching an expert can reduce the amount of practice needed for skill acquisition and thereby save the observer some effort (Carroll & Bandura, 1990). What is not so clear is how these savings are achieved. Are practice and observation necessarily alternative routes to skill acquisition, mediated by distinct learning processes, or can observation enlist exactly the same processes of learning as direct engagement with a task? This study tests the latter hypothesis, that practice and observation can engage the same processes of learning, by investigating whether motor skill learning by observation can be effector dependent.

Learning is said to be effector dependent to the extent that training of one set of muscles (e.g., those of the right hand) does not generalize to another (e.g., those of the left hand). Effector dependence of practice-based learning has been demonstrated in both monkeys (Rand, Hikosaka, Miyachi, Lu, & Miyashita, 1998) and humans (Bapi, Doya, & Harner, 2000; Marcovitch & Flanagan, 2004; Rosenbaum & Chaiken, 2001). For example, Marcovitch and Flanagan (2004) allowed human participants to learn a sequence of movements to spatial targets with one hand and then tested performance of the other hand on the training sequence or a novel sequence. Transfer test performance of the training sequence was not superior to that of the novel sequence, which implied that

sequence learning in the training phase had been effector dependent.

Effector dependence is thought to reflect learning of movement dynamics, rather than kinematics, and to be mediated by loop circuits connecting the motor cortices with motor regions of the basal ganglia and cerebellum (Hikosaka, Nakamura, Sakai, & Nakahara, 2002). Recent work suggests that effector-dependent learning of movement dynamics is more likely when specific to the nondominant than to the dominant hand (e.g., Criscimagna-Hemminger, Donchin, Gazzaniga, & Shadmehr, 2003; Inamizu & Shimajo, 1995), but Sainberg and Wang (2002) have demonstrated interlimb transfer of learned visuomotor rotations from both the dominant and the nondominant arm. The dorsal lateral premotor cortex has also been implicated both in effector-dependent, dynamic, or anatomical representation of learned movements and in relating these to learned effector-independent, kinematic, or spatial representations (Rijntjes et al., 1999).

Most theories of observational learning or *imitation* imply that, whereas learning that arises from task practice may be effector dependent, that which occurs through task observation will always be effector independent. For example, Bandura's (1986) social learning theory suggests that the information an observer obtains by watching the body movements of a model is invariably subject to *symbolic* encoding, and Meltzoff and Moore's (1997) active intermodal mapping theory suggests that this information is represented *amodally*, that is, in a code that is neither perceptual nor motoric but which provides a medium for translation between the two. Thus, both theories postulate that information derived from model observation is always subject to flexible, higher order encoding and therefore would not predict the kind of constraint on expression of that knowledge represented by effector dependence. In contrast, Heyes and Ray's (2000; Heyes, 2001) associative sequence learning theory suggests that visual information from the model can activate motor representations directly, without intermediate symbolic or other higher order representation, and that observation-activated motor representations will be effector dependent to the extent that prior visual experience of each movement component has been paired with activation of a distinct and

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constant muscle set. The latter condition is likely to be met in the case of finger movements. When a person looks at his or her hands during manual movements, the sight of, for example, the left index finger lifting will be paired more reliably with activation of muscles in the left index finger than with activation of muscles in the left ring finger or the right index finger. Thus, associative sequence learning theory predicts that, under conditions in which practice-based learning is effector dependent, observational learning of finger movement sequences will also be effector dependent.

Until recently, the idea that task observation, rather than practice, could engage effector-dependent processes of motor learning was so implausible that observation was often used as a control for this kind of learning (Stadler, 1989; Willingham, 1999). However, recent research on the human "mirror system" (Buccino et al., 2001; Rizzolatti, Fogassi, & Gallese, 2001) and, more specifically, electrophysiological evidence of motor facilitation during action observation has made the idea of effector-dependent learning by observation more plausible (Aziz-Zadeh, Maeda, Zaidel, Mazzotta, & Jacoboni, 2002; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Strafella & Paus, 2000). In these studies, passive participants observed body movements while transcranial magnetic stimulation induced motor-evoked potentials (MEPs) were recorded from a range of effector muscles. It was found that MEPs recorded from muscles involved in execution of the observed movement were greater than those recorded at other effector sites. For example, during thumb movement observation, MEP size was greater for the abductor pollicis brevis, which is involved in executing thumb movements, than for the first dorsal interosseus, which is active during finger movements, and this relationship between abductor pollicis brevis and first dorsal interosseus activation was reversed when participants observed finger movements (Maeda et al., 2002).

These electrophysiological data suggest that movement observation can activate effector-dependent representations of movement stored in primary motor cortex (Aziz-Zadeh et al., 2002). This is likely to be a necessary condition for effector-dependent learning by observation, and therefore these data are consistent with the hypothesis that such learning occurs. However, learning involves not merely activation of existing motor representations but the formation of new connections between existing motor representations. For example, learning sign language involves the linkage of preexisting hand and finger movements into new sequences and combinations. Therefore we must look beyond these electrophysiological data to find out whether new sequences can be represented in an effector-dependent fashion when they have been learned by observation.

Studies of observational learning have confirmed that watching skilled performance influences skill acquisition, but previous researchers have not asked whether what is learned by observation is coded in an effector-dependent or effector-independent fashion (e.g., Vinter & Perruchet, 2002; Weeks & Anderson, 2000). For example, Weeks and Anderson (2000) found that observation of expert performance of the overhand volleyball serve had beneficial effects on the form and accuracy of novices' performance of the serve but did not examine whether these effects transferred to the nondominant arm or hand.

To investigate effector dependence of observational learning, we used a serial reaction time (SRT) task (Nissen & Bullemer, 1987). In a typical version of this task, a stimulus appears in one

of several locations on each trial, and the participant presses a key corresponding to that location. The stimulus follows a predictable repeating sequence and, after many cycles, participants provide evidence of sequence knowledge by responding more slowly when the sequence is changed than when stimuli are presented in the training sequence. Thus, in the SRT task, negative transfer—a tendency to respond more slowly when the sequence changes—provides a positive indication of learning.

The SRT task is an ideal tool to study effector dependence of observation learning, for several reasons. First, it can be readily adapted for the investigation of observational learning by requiring participants to watch another person, a model, perform the task during the training phase, before completing tests in which they press the keys themselves. Second, SRT tasks assess sequence learning, the kind of learning that distinguishes activation of pre-existing motor representations from acquisition of "new" motor representations. Finally, there is evidence that motor learning is involved when participants perform the task themselves (Mayr, 1996; Willingham, 1999; Willingham, Nissen, & Bullemer, 1989). For example, Willingham (1999, Experiment 3) added to the SRT task a transfer test in which the stimulus-response mapping was changed so that, relative to training, one group of participants pressed the same sequence of keys but saw new stimuli, whereas another group pressed a different sequence of keys but saw the same stimuli. Transfer to the new mapping occurred only if the motor sequence was kept constant.

Kelly and Burton (2001) failed to find evidence of observational learning of any kind (perceptual or motoric) when they compared the SRT performance of practice participants with that of observers, each of whom had watched a practice participant during training on a 12-item ambiguous sequence. In ambiguous sequences, each stimulus location is followed by more than one other stimulus location. However, Heyes and Foster (2002) reported clear evidence of observational learning when they compared participants who had observed an expert responding to a six-item unique sequence (where each stimulus location uniquely predicts the next) with controls who had performed an unrelated anagram task during training. Therefore, in the present study, to ensure that observational learning would be detected, we used the same six-item sequence and the same kind of comparison group as Heyes and Foster.

Many studies have reported implicit learning of 10- or 12-item ambiguous sequences in the SRT task, that is, that sequence knowledge reflected in chronometric measures is not accessible to conscious awareness (e.g., Seger, 1997; Willingham, 1999). A six-item unique sequence, of the kind used in the present study, is very simple compared with the sequences used in this previous work and therefore is unlikely to provide evidence of implicit learning. It would be interesting if observational learning of a six-item unique sequence could be shown to be both effector dependent and explicit, because such evidence would be incompatible with a recently formulated model of motor skill learning (Hikosaka et al., 2002). This model proposes that effector-dependent learning is typically implicit, whereas effector-independent learning is typically explicit. Therefore, in addition to asking whether participants' knowledge was effector dependent, we investigated whether it was implicit or explicit using free generation (Experiment 1) and recognition (Experiment 2) tests (Shanks & Johnstone, 1999).

In a standard SRT task, practice-based learning is indexed by comparing reaction times (RTs) to stimuli presented in the training sequence and in an alternative sequence, that is, by a main effect of sequence type. This comparison is not sufficient to demonstrate observational learning in the SRT task because the test phase, in which participants respond to sequential stimuli, provides a significant opportunity for sequence learning. Therefore, if participants who observe a model performing the training sequence subsequently respond faster to that sequence than to an alternative, this main effect of sequence may be due solely to learning during the test phase. To overcome this problem, we compared sequence observers with controls who did not observe a model responding to a sequence during training. In this case, observational learning is indexed by an interaction between group and sequence type. Thus, the control group provides a baseline, and if the introduction of a new sequence delays responding more in the observers than in the controls, there is evidence that the former group learned the sequence by observation. This logic applies to both of the control groups used in the present study. In Experiment 1, control participants were untrained (Dienes & Altmann, 2003; Perruchet & Reber, 2003), they performed an unrelated anagram task during the training phase, and in Experiments 2 and 3, controls observed a model performing the SRT task when order of target presentation was randomly determined.

All three experiments reported in this study began with a block of trials in which all participants pressed the keys themselves and stimuli were presented in random order. This allowed participants to familiarize themselves with general task demands but did not permit sequence learning. On each trial, a stimulus appeared in one of six boxes in a horizontal line on a computer screen, and the participant was required to locate this target by pressing the spatially corresponding key in a horizontal line of six response keys. Each key was operated by a different finger. In the subsequent training phase of the experiment, observer participants watched the male experimenter's fingers as he performed the task with which they had been familiarized in the first block, but the experimenter was responding to targets presented in a six-item unique sequence. Immediately after training, all participants were given an initial test in which they completed three blocks of trials themselves. In the first and third of these blocks, stimulus presentation was determined by the same sequence as during training, and in the second block it was determined by a new six-item unique sequence. Introduction of the new sequence was expected to produce a greater elevation in RTs in the observers than in controls who had not seen the model responding to the training sequence. This result would provide evidence that the observers had learned the sequence during training, that is, of observational sequence learning.

To find out whether observational learning had been effector dependent, we gave participants in all experiments two transfer tests following the initial test. In Experiments 1 and 2, each transfer test consisted of a block of trials in which stimulus presentation was determined by the training sequence followed by a block in which it was determined by the new sequence. In one of these tests, the *stimulus transfer test*, the stimuli appeared in a vertical rather than a horizontal array of boxes on the screen and responses were made, as during training, with the fingers. In the other, the *response transfer test*, the stimuli appeared in a horizontal array, as they had during training, but participants were

required to respond using their thumbs rather than their fingers (Stadler, 1989).

In Experiment 3, we used an alternative transfer test procedure in which participants crossed their hands on the keyboard. The purpose of this alternative procedure was to obtain convergent evidence of effector dependence and to investigate whether, in addition to learning a sequence of finger movements, observers of SRT performance learn a sequence of response locations.

In summary, associative sequence learning theory (Heyes, 2001) predicts that, like practice-based learning, learning by observation of skilled performance can be effector dependent. Electrophysiological evidence of motor facilitation during action observation provides indirect support for this hypothesis. To test the hypothesis directly, the present study examines learning of a sequence of finger movements in an SRT task.

Experiment 1

The first experiment involved two groups of participants who received different treatment in the training phase: the observe sequence group watched the experimenter's fingers as he performed the SRT task, whereas the control group completed an unrelated anagram task. After initial testing for observational learning, both groups were given transfer tests in which all participants responded first to the training sequence and then to a new sequence under two conditions: when the stimulus array was unchanged but participants were required to use their thumbs rather than their fingers to respond (response transfer test) and when responses were made with the fingers but the stimuli appeared in a vertical rather than a horizontal array (stimulus transfer test).

If observational sequence learning in the SRT task is effector independent, we would expect to find in both transfer tests that introduction of the new sequence is associated with a greater increase in RT in the observe sequence group than in the control group. This result would imply that sequence knowledge learned by observation can withstand alterations of both stimulus array and response effector. Alternatively, if the knowledge learned through observation is encoded as a sequence of stimulus locations, or of eye movements to those locations, one would expect evidence of transfer to be confined to the response transfer test. In this case, the performance of observers would not differ from that of controls when both groups are responding to a vertical rather than a horizontal stimulus array, but introduction of the new sequence would produce more RT elevation in observers than in controls when both groups are responding with their thumbs rather than their fingers. Finally, if observational sequence learning in the SRT task can be effector dependent, one would expect evidence of transfer to be confined to the stimulus transfer test. In this case, introduction of the new sequence would be associated with more RT elevation in observers than in controls when participants are responding to a vertical rather than a horizontal stimulus array but would have equivalent effects on the two groups when they are responding with their thumbs rather than their fingers. This outcome would implicate effector-dependent learning by observation by showing that, relative to that of controls, the observers' sequence knowledge transfers across alterations in the stimulus array but not to a situation where different effectors are used to perform the task.

Method

Participants. Twenty-four students (8 men and 16 women) at University College London participated in the experiment, 12 in each of groups observe sequence and control. Their mean age was 23.6 years, and each was paid a small honorarium (£5 or \$8) for their participation. Five participants who made more than 10% errors during the random and initial test blocks were replaced.

Stimuli and apparatus. Stimulus presentation, RT measurement, and response recording were all implemented on IBM-compatible PCs with 43-cm color monitors and standard QWERTY keyboards. Six boxes were presented in a horizontal row in the center of the screen, drawn with black lines against a gray background. The boxes were 2.2 cm wide \times 1.2 cm high, spaced 1 cm apart, and viewed at a distance of approximately 60 cm. A white asterisk (Arial font, Size 36, subtending approximately 0.5° of visual angle) appeared in the center of one of these boxes on each target location trial. Target locations are referred to as 1–6 from left to right. Participants were instructed to indicate Locations 1–6 as quickly as possible by using the *X*, *C*, *V*, *B*, *N*, and *M* keys located across the bottom of the keyboard, respectively. They operated the *X*, *C*, and *V* keys with the ring, middle, and index fingers of their left hand, and the *B*, *N*, and *M* keys with the index, middle, and ring fingers of their right hand, respectively.

Each block consisted of 100 target location trials. Incorrect responses were signaled by a tone. A trial ended when a participant pressed the correct key, at which time the target was erased. The next trial began 200 ms later. Response latencies were measured from the onset of the target to the completion of a correct response.

Procedure. Participants were told that they were taking part in a choice RT task designed to measure their speed of response. For all participants, the experiment had five phases: familiarization, training, initial testing, transfer, and free generation. The two groups received identical treatment in all phases except the training phase. During training, the observe sequence group watched the experimenter's fingers as he performed the SRT task, and the control group completed anagram problems for a comparable period of time.

Familiarization. In the familiarization phase, participants were given one block of target location trials in which the order of target presentation was randomly determined.

Training. Before the first block of training trials, participants in the observe sequence group were asked to "Pay close attention to the experimenter's hands as he completes the task" and told "It has been shown that the more closely you attend to the hands, the better you will perform in later stages of the experiment." As participants in this group watched the experimenter, he completed six blocks of target location trials, in which the sequence of targets was 2–5–1–4–6–3. Each block of 100 trials included 16 repetitions of the whole training sequence and began at a random point in that sequence. Observers were seated to the right and just behind the experimenter, on a chair that had been raised to give them a slightly elevated view of his fingers on the keyboard. The screen was turned away from the observers so that they could not see the target stimuli to which the experimenter was responding. The experimenter provided a model of expert performance, with a mean RT ranging from 273 ms ($SE = 7$) to 299 ms ($SE = 9$) across the 6 blocks. Error rate varied from 0% to 2%. For the duration of the training period (8 min), participants in the control group solved anagram problems.

Initial testing. The initial test of sequence learning consisted of three blocks of target location trials completed by all participants. In the first and last of these blocks, targets were presented in the training sequence, that is, 2–5–1–4–6–3. In the second block, they were presented in a new, six-item unique sequence: 4–2–6–3–1–5.

Transfer. The order of the stimulus transfer and the response transfer tests was counterbalanced, with half of the participants in each group completing the stimulus transfer test first. Each transfer test consisted of two blocks of trials. In the first, targets were presented in the training sequence, and in the second they were presented in the new sequence. In

the stimulus transfer test, the stimulus boxes were arranged in a vertical, rather than a horizontal, line in the center of the computer screen. As during training, participants were required to respond to Targets 1–6 (running from the top to the bottom of the screen) using the ring, middle, and index fingers of each hand applied to Keys *X*, *C*, *V*, *B*, *N*, and *M*. In the response transfer test, the stimulus boxes were arranged in a horizontal line as they were during training, but participants were required to respond with their thumbs rather than their fingers. The left thumb was used to operate the *X*, *C*, and *V* keys, and the right thumb was used to operate the *B*, *N*, and *M* keys.

Free generation. For the first time during testing, participants were informed that the asterisks had followed a repeating sequence during earlier phases of the experiment and that they would be performing a slightly different task in the next phase. We asked them to press the keys 100 times, in an attempt to generate freely the sequence that they had experienced during the training phase and at the beginning of each subsequent test. They were told that they could proceed at their own pace and that their key presses would have no effect on the stimulus array, that is, a static image of the horizontal line of boxes representing stimulus locations.

Results

A mean RT for each participant in each block was calculated after exclusion of RTs greater than 1,000 ms. Each analysis of RT data was accompanied by a parallel analysis of error data. The error data from all three experiments are shown in Table 1. The results of error analyses are reported only if they yielded significant effects or interactions. For all analyses, all significant effects are reported.

A one-way analysis of variance (ANOVA), with group as a between-subjects factor, indicated that in the familiarization phase, when participants were responding to random targets, the RTs of observers ($M = 597$, $SEM = 14$) and controls ($M = 598$, $SEM = 22$) did not differ ($F < 1$).

Figure 1 presents mean RTs to the training sequence and the new sequence during initial and transfer testing for each of the two groups of participants. In the initial test, RTs in the first and third blocks, when participants were responding to the training sequence, were compared with RTs in the second block, when they were responding to a new sequence. A two-way ANOVA, with group (observe sequence and control) as a between-subjects factor and sequence (training and new) as a within-subjects factor, indicated a significant effect of sequence, $F(1, 22) = 4.31$, $p = .05$, and a significant Group \times Sequence interaction, $F(1, 22) = 5.88$, $p = .02$. Thus, introduction of the new sequence was associated with a greater increase in RTs in the observers than the controls, which suggests that the former group learned the sequence by observing the experimenter's fingers while he was performing the task.

RT data from the stimulus transfer test were analyzed using a three-way ANOVA, with group (observe sequence and control) and test order (before and after the response transfer test) as between-subjects factors and sequence (training and new) as a within-subjects factor. This revealed a significant effect of sequence, $F(1, 20) = 6.40$, $p = .02$, and a significant Group \times Sequence interaction, $F(1, 20) = 6.15$, $p = .02$. Parallel analysis of error data from the stimulus transfer test indicated that participants also made more errors when responding to the new sequence ($M = 6.0$, $SEM = 0.6$) than when responding to the training sequence ($M = 4.3$, $SEM = 0.6$), $F(1, 20) = 9.19$, $p = .007$. When the same three-way ANOVA was applied to RT data from the response

Table 1
Mean (\pm SE in Parentheses) Percentages of Error for Training and New Sequences in Initial and Transfer Tests for Each Group in Experiments 1–3

Experiment	Initial test		Stimulus ^a and anatomical ^b transfer tests		Response transfer ^a and location ^b tests	
	Training sequence	New sequence	Training sequence	New sequence	Training sequence	New sequence
Experiment 1						
Observe sequence	2.8 (0.4)	3.0 (0.7)	4.4 (0.8)	6.6 (0.8)	5.2 (1.4)	4.9 (1.1)
Control	3.0 (0.7)	3.9 (0.8)	4.2 (0.9)	5.5 (0.9)	6.5 (1.6)	8.7 (2.7)
Experiment 2						
Observe sequence	1.9 (0.6)	3.2 (0.6)	7.3 (1.5)	7.2 (2.3)	4.6 (1.2)	6.4 (2.5)
Control	2.3 (0.5)	2.4 (0.7)	4.7 (0.8)	5.3 (1.0)	7.9 (1.8)	6.1 (1.3)
Experiment 3						
Observe sequence	3.9 (0.5)	5.1 (0.8)	17.4 (1.4)	16.0 (1.8)	14.9 (1.4)	17.7 (1.8)
Control	2.6 (0.4)	2.7 (0.5)	12.3 (2.4)	11.8 (2.1)	9.6 (1.5)	9.4 (1.4)

^a Experiments 1 and 2. ^b Experiment 3.

transfer test, there was a significant effect of group, $F(1, 20) = 4.54, p = .05$, and the effect of sequence approached significance, $F(1, 20) = 3.47, p = .08$, but the Group \times Sequence interaction was not reliable ($F < 1$). The main effect of group implies that the observers' experience during the training phase provided them with confidence or information about general task demands, which allowed them to respond faster with their thumbs than the controls. The fact that both groups tended to respond more slowly to the new sequence suggests that all participants had acquired some knowledge of the training sequence in the course of the 2–3, 16-cycle test blocks in which they had responded to this sequence.

However, the absence of a Group \times Sequence interaction means that the results of the response transfer test did not provide any evidence of sequence learning by observation.

Thus, when the stimulus array, which was horizontal during training and initial testing, was presented vertically, introduction of the new sequence had a more detrimental effect on the performance of observers than on that of controls. This indicates that, in spite of the change in the stimulus array, the observers were still able to use their sequence knowledge. However, when participants were required to use their thumbs rather than their fingers to press the response keys, the transition from the training to the new

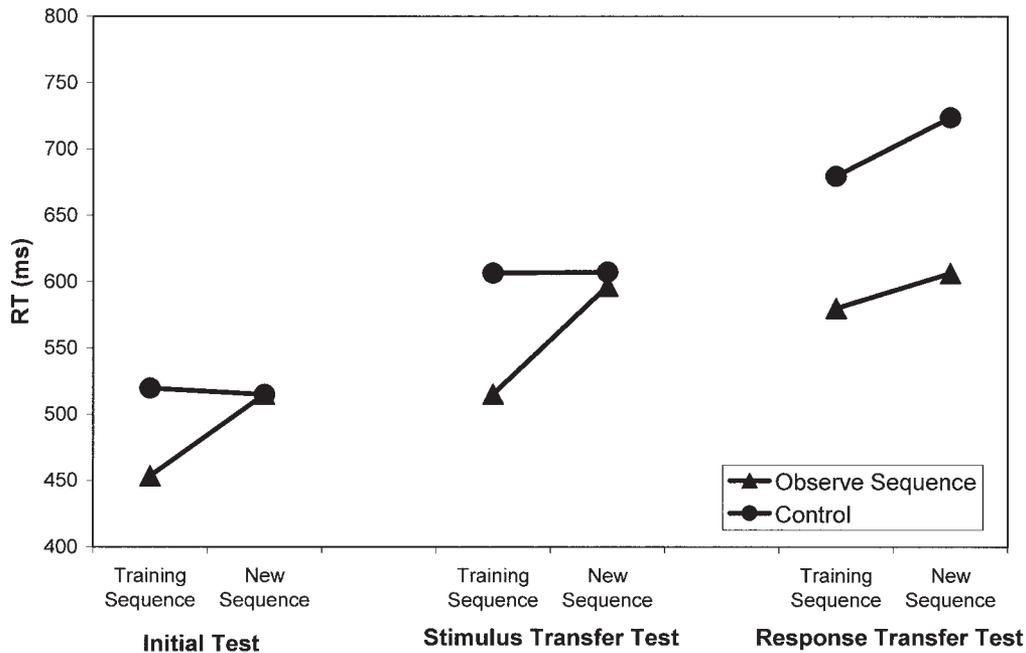


Figure 1. Mean reaction times (RTs) in initial and transfer test blocks for groups that had observed a model's fingers as he responded to the training sequence (observe sequence group) or solved unrelated anagram problems (control group) during training in Experiment 1.

sequence had the same impact on the performance of observers and controls. This implies that, when responding with their thumbs, the observers were unable to use the sequence knowledge they had gained during training and is therefore consistent with the hypothesis that the sequence knowledge they acquired by observation was effector dependent.

In the free generation test, participants created sequences of 100 key presses based on what they had learned about the training sequence. We coded the data from each participant as 98 consecutive response triplets and computed the number of triplets that was consistent with the training sequence (2-5-1-4-6-3) and the number that was consistent with the new sequence (4-2-6-3-1-5). Thus, if a participant generated the sequence 2-5-1-5-4-2 at some point during the free generation test, this would be coded as Triplets 2-5-1, 5-1-5, 1-5-4, and 5-4-2. The first of these triplets is consistent with the training sequence, whereas the third and fourth are consistent with the new sequence. Given that the participants had already completed three blocks of trials with the new sequence, this was a conservative test of explicit knowledge, but it was passed by the observers. Figure 2 shows the mean number of training and new triplets generated by participants in the two groups. A two-way ANOVA, with group (observe sequence and control) and triplet type (training and new) as factors, indicated significant effects of group, $F(1, 22) = 5.88, p = .02$, and triplet type, $F(1, 22) = 11.65, p = .002$, and a significant Group \times Type interaction, $F(1, 22) = 7.00, p = .02$. The control group generated more training triplets than new triplets, $F(1, 11) = 6.03, p = .03$, reflecting the fact that they had completed more test

blocks with the training sequence than with the new sequence. However, the difference between triplet types was significantly greater for the observers, $F(1, 11) = 9.41, p = .01$, than for the controls, indicating that the former group had acquired explicit knowledge of the training sequence during observation.

To summarize the results of Experiment 1, we found evidence that participants could learn a six-item sequence by observing a person's fingers as he or she performs an SRT task and that the sequence knowledge gained through observation was not used when the participants were required to respond with their thumbs rather than their fingers. We also found that observers could use their knowledge to generate the sequence in a test of explicit learning.

Experiment 2

Experiment 1 provided evidence of effector-dependent, explicit sequence learning by observation using an untrained control group. While the observers were watching the experimenter perform the SRT task, control participants in Experiment 1 completed an unrelated anagram task. This kind of control is of limited value because it means that, in addition to being unable to acquire sequence information by observation, controls have less opportunity than observers to familiarize themselves with general task demands. As a consequence of being less familiar with, for example, response locations, untrained control participants may acquire sequence information more slowly than observers during subsequent test blocks in which all participants respond to the training

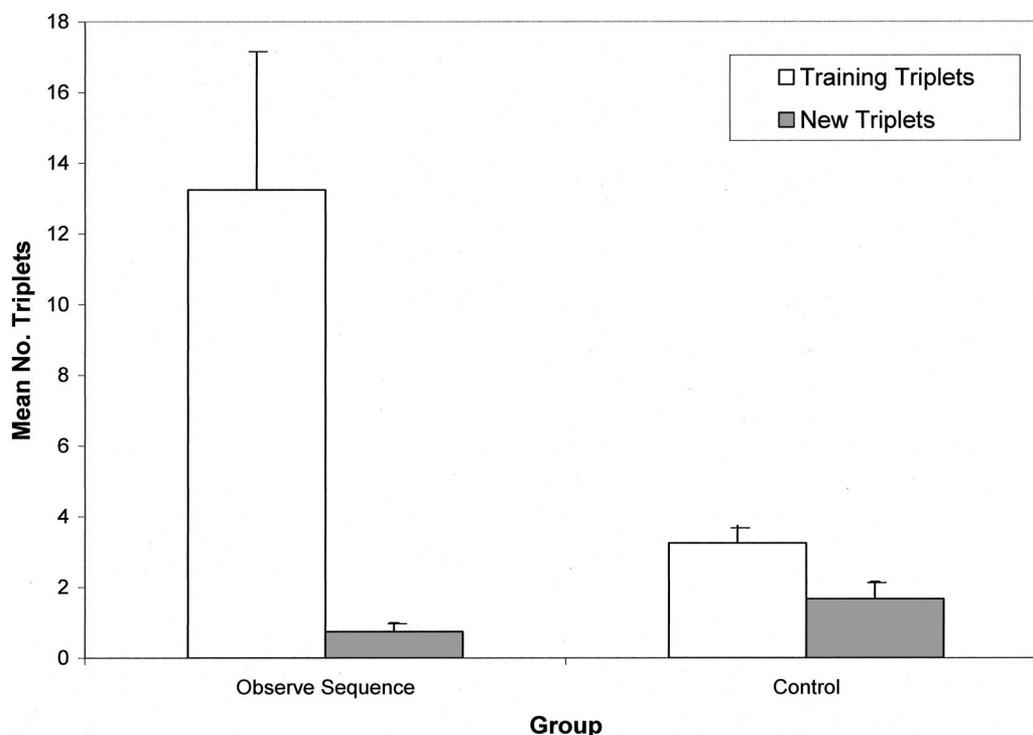


Figure 2. Mean number of training and new triplets generated in the free generation test by groups that had observed a model's fingers as he responded to the training sequence (observe sequence group) or solved unrelated anagram problems (control group) during training in Experiment 1. Error bar represents standard errors.

sequence. If this is the case, observers may provide evidence of more sequence knowledge in initial and transfer tests, not because they acquired this information by observation but because they learned more than controls on test. To overcome this interpretive problem, we used a more subtle control procedure in Experiment 2. During the training phase, both groups watched a model's fingers. As in Experiment 1, the model observed by the observe sequence group responded to stimuli presented in the training sequence. However, the model observed by control participants, the observe random group, responded to stimuli presented in random order.

Experiment 2 differed from Experiment 1 in two further respects. First, to achieve better stimulus control, we arranged to have the model's finger movements presented on video, rather than live. Second, a recognition test, rather than a free generation test, was used at the end of the experiment to assess whether sequence knowledge was implicit or explicit. This substitution was made because, as a measure of explicit knowledge, the free generation test may be contaminated by sensitivity to implicit motor learning. In other words, the observers in Experiment 1 may have passed the free generation test, not because their knowledge of the sequence was consciously accessible but because their skill in performing the finger movement sequence was sufficient to allow them to execute it without differential stimulus input. Motor learning of this kind could not explain success on a recognition test in which participants respond to, and then rate their familiarity with, se-

quences derived from the training sequence and from an alternative, new sequence. If participants are able to learn effector-dependent, explicit sequence information by observation, the pattern of results obtained in Experiment 2 should be the same as that obtained in Experiment 1.

Method

Participants. A further 24 volunteers (12 women and 12 men) participated in the experiment, 12 in the observe sequence group and 12 in the observe random group. Their mean age was 30.08 years. Two participants who made more than 10% errors during the random and initial test blocks were replaced.

Procedure. The procedure was exactly the same as for Experiment 1 except as noted. During the training phase, the control participants in the observe random group observed a model's fingers as he responded to target stimuli presented in random order. Participants in both groups, observe sequence and observe random, viewed video recordings of the model's finger movements, presented at full frame on a 38-cm TFT Active Matrix Display (Dell; Andover, United Kingdom) computer screen. Each of the model's hands subtended approximately 26.5° of visual angle. The images were recorded using a Sony digital camcorder, encoded as AVI (720×576 pixels) files, and displayed on an IBM-compatible laptop computer using Microsoft Windows Media Player. The video frame included all eight of the model's fingers, the response keys, and four rows of keys above the response keys. The viewing angle was similar to that of a person's own hands while typing (see Figure 3). When filmed for the observe sequence group, the model's mean RT ranged from 347 ms to 398 ms across blocks,



Figure 3. A frame from the training video presented to the observe sequence group in Experiments 2 and 3 showing the model making a response with the index finger of his left hand.

and he made no errors. When filmed for the observe random group, his mean RT ranged from 501 ms to 543 ms across blocks, and he made no errors.

In the final phase of the experiment, participants were given a recognition test. They were told that they would be presented with sequences of six asterisk locations, presented in the standard, horizontal array of boxes. They were to respond to these stimuli as they had during training and initial testing, using Keys X–M, which were operated by three fingers on each hand, and then give a rating of how confident they were that the test sequence was the same as the sequence used during training and initial testing. Ratings were made on a scale from 1 to 6, where 1 = *certain I have not seen the sequence before*, 2 = *fairly certain I have not seen the sequence before*, 3 = *guess I have not seen the sequence before*, 4 = *guess I have seen the sequence before*, 5 = *fairly certain I have seen the sequence before*, and 6 = *certain I have seen this sequence before*. We recorded both ratings and trial-by-trial RTs for the test sequences. There were 12 test sequences in total, presented in random order. Six old sequences were derived from the training sequence, and six new sequences were derived from the sequence: 1–3–5–4–2–6. One sequence in each of these groups started at each serial location.

Results

The results were analyzed in the same way as those of Experiment 1. A one-way ANOVA indicated that in the familiarization phase, when participants were responding to random targets, the RTs of the observe sequence group ($M = 611$, $SEM = 20$) and of the observe random group ($M = 610$, $SEM = 22$) did not differ ($F < 1$).

Figure 4 presents mean RTs to the training sequence and the

new sequence during initial and transfer testing for each of the two groups. A two-way ANOVA of the initial test data indicated a significant effect of sequence, $F(1, 22) = 11.22$, $p = .003$, and a significant Group \times Sequence interaction, $F(1, 22) = 5.92$, $p = .02$. Thus, introduction of the new sequence was associated with a greater increase in RTs in the observe sequence group than in the observe random group, indicating observational learning of the sequence by participants in the former group.

As in Experiment 1, a three-way ANOVA of the RT data from the stimulus transfer test yielded a significant effect of sequence, $F(1, 20) = 5.47$, $p = .03$, and a significant Group \times Sequence interaction, $F(1, 20) = 4.13$, $p = .05$, but the same analysis of the response transfer test indicated no significant effects or interactions.

In the recognition test, we recorded trial-by-trial RTs for each test sequence as well as the participants' rating of how confident they were that they had seen the sequence before. Table 2 shows, for both groups, the mean RT and mean rating for test sequences derived from the training sequence and from the new sequence. A two-way ANOVA of the RT data, with group (observe sequence and observe random) and sequence type (training and new) as factors, indicated significant effects of sequence type, $F(1, 22) = 9.61$, $p = .005$, and a marginally significant Group \times Sequence Type interaction, $F(1, 22) = 4.00$, $p = .06$. Parallel analysis of the recognition rating data yielded the same pattern of results, a main effect of sequence type, $F(1, 22) = 4.19$, $p = .05$, and a significant interaction, $F(1, 22) = 5.80$, $p = .03$.

In each of the three tests, the main effect of group was numerically smaller in Experiment 2 than in Experiment 1 (cf. Figures 1

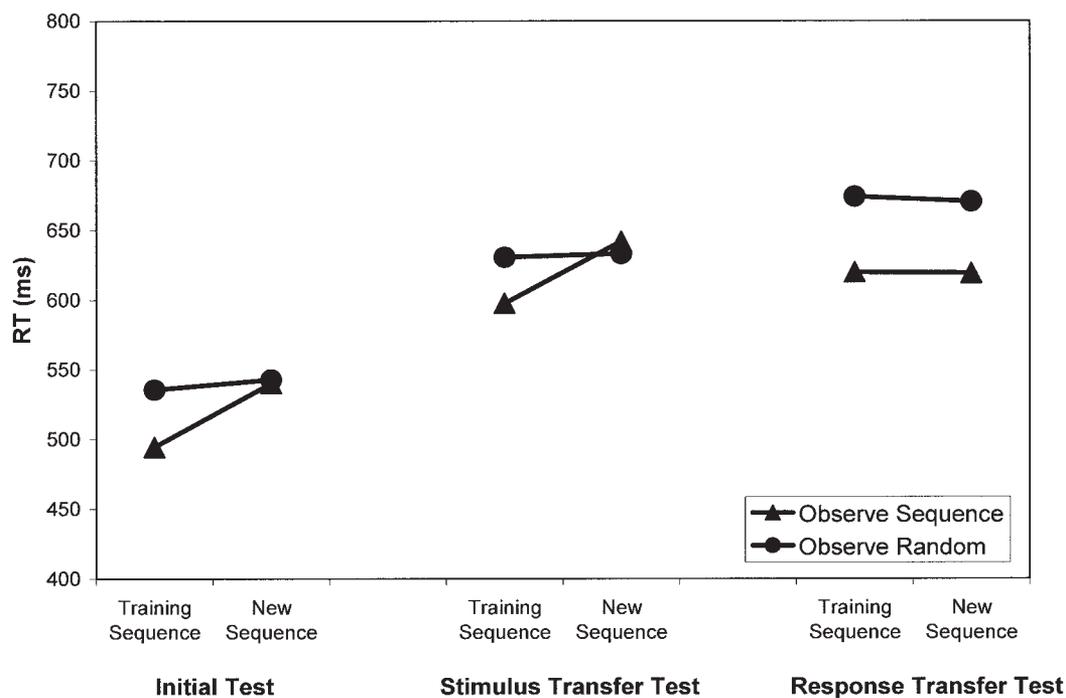


Figure 4. Mean reaction times (RTs) in initial and transfer test blocks for groups that had observed a model's fingers as he responded to the training sequence (observe sequence group) or to a random sequence (observe random group) during training in Experiment 2.

Table 2
Mean (\pm SE in Parentheses) Reaction Times (RTs) and Recognition Ratings Given to Training and New Sequences by Groups That Had Observed a Model's Fingers as the Model Responded to the Training Sequence (Observe Sequence) or to a Random Sequence (Observe Random) During Training in Experiment 2

Group	Mean rating training	Mean rating new	Mean RT training	Mean RT new
Observe sequence	4.13 (0.24)	3.26 (0.16)	538 (26.9)	592 (22.2)
Observe random	3.79 (0.16)	3.86 (0.13)	563 (28.8)	575 (26.9)

& 4). It is likely that this reflects the use of a more subtle control procedure in Experiment 2, which allowed control observers to acquire as much information as sequence observers about general task demands during the observation phase. However, despite the use of a different control procedure, video presentation finger movement stimuli, and a recognition test of explicit knowledge, the pattern of results in Experiment 2 was substantially the same as that of Experiment 1.

Experiment 3

In combination, Experiments 1 and 2 provide compelling evidence that participants can learn a six-item sequence by observing a model's finger movements and that this sequence knowledge is accessible to conscious awareness. It could be argued, however, that the foregoing experiments do not provide equally strong evidence that observational sequence learning can be effector dependent. This hypothesis rests on the finding that, in Experiments 1 and 2, the transition from the training sequence to a new sequence was associated with greater RT elevation in observers than in controls when they were responding to targets in a transformed stimulus array but not when they were responding with their thumbs rather than their fingers. This finding is consistent with effector dependence of observational sequence learning, but it is also susceptible to an alternative explanation. It is possible that what was learned by observation was a sequence of response locations encoded in an effector-independent fashion, either symbolically or as locations in egocentric space (Willingham, 1999). If the stimulus transfer test, in which the stimulus array was vertical, and the response transfer test, in which participants responded with their thumbs, were of equal sensitivity, effector-independent knowledge of a sequence of response locations should be evident in both. However, it could be that, in Experiments 1 and 2, no evidence of sequence knowledge was detected in the response transfer test because that test was less sensitive than the stimulus transfer test. For example, the participants may have found it very difficult to use their thumbs to press the keys, and accommodating to this difficult task may have interfered with expression of effector-independent sequence knowledge about response locations.

Consistent with this hypothesis there is evidence that both extension of the response-stimulus interval (RSI) (Willingham,

Greenberg, & Thomas, 1997) and presentation of a concurrent tone-counting task (Frensch, Lin, & Buchner, 1998) during testing in an SRT procedure increases RT and retards expression of prior sequence learning. In Experiment 2, RTs were not significantly longer when participants were responding with their thumbs than when they were responding with their fingers to a vertical array. It is therefore unlikely that requiring participants to use their thumbs instead of their fingers is comparable in its effects to extending RSI or to giving a concurrent task. However, to guard against the possibility that the awkwardness of the response transfer test somehow reduced its sensitivity relative to that of the stimulus transfer test, Experiment 3 compared performance in two transfer tests that were equally challenging at the motor level; they both required participants to press keys with their hands crossed on the keyboard.

After training and initial testing, all participants in Experiment 3 crossed their hands on the keyboard for two transfer tests. The anatomical transfer test compared RTs to a sequence of screen targets that preserved the finger movement sequence used during training with RTs to a sequence of screen targets that produced a new sequence of finger movements. The response location transfer test compared RTs to the training sequence of screen targets with RTs to a new sequence of screen targets. The training sequence of screen targets in the response location test preserved the sequence of response locations used during training, but neither of the target sequences in the anatomical test preserved the training sequence of response locations. Therefore, if the observe sequence group learned a sequence of response locations during training but not an effector-dependent sequence of finger movements, then, relative to the observe random group, they should be slower to respond to the new sequence than to the training sequence in the response location test but not in the anatomical test. In contrast, if the observe sequence group learned an effector-dependent sequence of finger movements during training and did not learn a sequence of response locations, then, relative to the observe random group, they should be slower to respond to the new than to the training sequence in the anatomical test but not in the response location test. If the observe sequence group learned both an effector-dependent sequence of finger movements and a sequence of response locations during training, a Group \times Sequence interaction effect should occur in both tests.

Method

Participants. A further 48 volunteers (33 women and 15 men) participated in the experiment, 24 in each of groups observe sequence and observe random. Their mean age was 22.17 years. Eight participants who made more than 10% errors during the random and initial test blocks were replaced.

Procedure. The procedure was exactly the same as for Experiment 2 except as noted. The experiment had four phases: familiarization, training, initial testing, and transfer.

Transfer. After initial testing, all participants were asked to cross their hands so that Keys *X*, *C*, and *V* were operated by the index, middle, and ring finger of the right hand, respectively, whereas Keys *B*, *N*, and *M* were operated by the ring, middle, and index fingers of the left hand, respectively. With their hands crossed, participants completed, in counterbalanced order, two transfer tests each consisting of three blocks of 100 target location trials.

In the first and third blocks of the anatomical test, screen targets were

presented in the sequence 5–2–4–1–3–6. This sequence has no transitions in common with the training sequence of screen stimuli (2–5–1–4–6–3), that is, each target is immediately followed by a different target than it was during training. Given that the target locations and the response locations were spatially compatible, this also means that the sequence of response locations associated with this sequence had no transitions in common with the training sequence of response locations. However, in the context of the anatomical test, the target sequence 5–2–4–1–3–6 constitutes the training sequence because correct responses occur in the finger movement sequence observed during training. Where R = right, L = left, i = index, m = middle, and r = ring, this sequence was Lm–Rm–Lr–Ri–Rr–Li. In the second new block of the anatomical test, screen targets were presented in the sequence 2–1–5–3–6–4. This sequence has no transitions in common with the training sequence of targets and response locations, and just one transition (Rr–Li) in common with the training sequence of finger movements.

In the first and third blocks of the response location transfer test, target stimuli were presented in the training sequence, that is, the sequence of screen stimuli and response locations had all six transitions in common with those used during training. In the second block, targets were presented in the sequence 4–2–6–3–1–5, which has only one transition in common with the training sequence. Given that the hands were crossed, both of the sequences presented in the response location transfer test produced finger movement sequences that did not have any transitions in common with the finger movement sequence used during training.

Results

Owing to the difficulty of performing the task with crossed hands, we did not remove RTs greater than 1,000 ms from the data prior to analysis. A one-way ANOVA indicated that in the famil-

iarization phase, when participants were responding to random targets, the RTs of the observe sequence group ($M = 526$, $SEM = 12$) and of the observe random group ($M = 552$, $SEM = 13$) did not differ, $F(1, 46) = 2.04$, $p = .16$.

Figure 5 presents mean RTs to the training sequence and the new sequence during initial and transfer testing for each of the two groups. A two-way ANOVA of the initial test data indicated a significant effect of sequence, $F(1, 46) = 23.90$, $p < .0001$, a significant effect of group, $F(1, 46) = 5.52$, $p = .02$, and a significant Group \times Sequence interaction, $F(1, 46) = 6.78$, $p = .01$. Thus, as in the previous experiments, introduction of the new sequence was associated with a greater increase in RTs in the observe sequence group than in the observe random group, indicating observational learning of the sequence by participants in the former group.

Parallel analysis of error data from the initial test indicated an effect of group, $F(1, 46) = 7.35$, $p = .009$, with the observe sequence group making more errors ($M = 4.31$, $SEM = 0.53$) than the observe random group ($M = 2.63$, $SEM = 0.35$). This implies that the main effect of group on RT was due to the observe sequence group assigning a higher priority to speed over accuracy. This, in turn, may have been due to the fact that, during training, the observe sequence group saw faster responding than did the observe random group. However, the Group \times Sequence interaction effect on errors was not significant, indicating that variation in speed–accuracy trade-off was not responsible for the RT evidence of observational learning of the sequence.

The anatomical and response location tests were each analyzed in the same way as initial test data. A three-way ANOVA of the

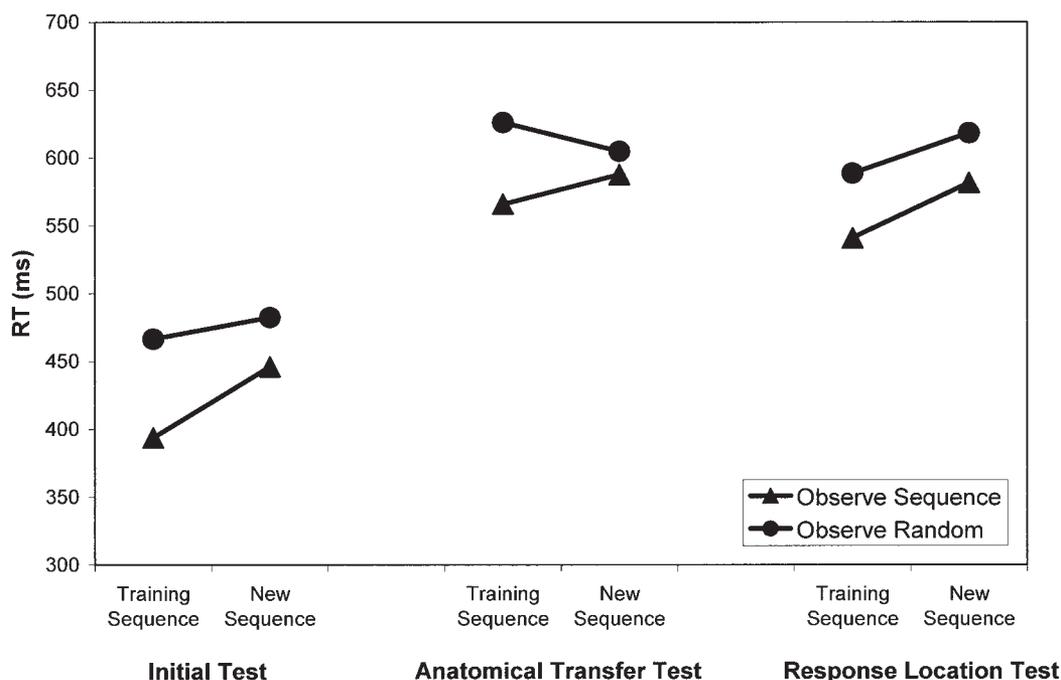


Figure 5. Mean reaction times (RTs) in initial and transfer test blocks for groups that had observed a male model's fingers as he responded to the training sequence (observe sequence group) or to a random sequence (observe random group) during training in Experiment 3.

RT data from the anatomical test, in which group and test order (anatomical first and anatomical second) were between-subjects factors and sequence (training and new) was the within-subjects factor, yielded a significant effect of group, $F(1, 44) = 4.08, p = .05$, and a significant Group \times Sequence interaction, $F(1, 44) = 5.10, p = .03$. Parallel analysis of error data from the anatomical test showed that more errors were made when it was the first test completed with crossed hands ($M = 17.9, SE = 1.8$) than when it was the second ($M = 11.1, SE = 9.6$), $F(1, 44) = 4.08, p = .05$, and that more errors were made by the observe sequence group ($M = 16.9, SE = 1.4$) than by the observe random group ($M = 12.1, SE = 2.2$), $F(1, 44) = 8.35, p = .006$, but did not indicate a significant Group \times Sequence interaction effect on error. Thus, whereas a speed-accuracy trade-off may explain why the observe sequence group responded faster overall than the observe random group, it cannot explain the fact that this difference was greater when participants were responding to the new sequence in the anatomical test than when they were responding to targets that preserved the finger movement sequence used during training. This interaction therefore implies that the observe sequence group had learned an effector-dependent sequence of finger movements by observation.

The results of the response location test did not provide any evidence of effector-independent learning by observation of a sequence of response locations. A three-way ANOVA of the RT data from this test indicated significant main effects of group, $F(1, 44) = 4.78, p = .03$, and sequence, $F(1, 44) = 15.5, p < .0001$, but not a significant Group \times Sequence interaction. Parallel analysis of error data showed that more errors were made when the response location test was the second test completed with crossed hands ($M = 16.5, SE = 1.4$) than when it was the first ($M = 8.9, SE = 1.2$), $F(1, 44) = 20.4, p < .0001$, and that the observe sequence group ($M = 15.8, SE = 1.3$) made more errors than the observe random group ($M = 9.6, SE = 1.4$), $F(1, 44) = 16.6, p < .0001$. Thus, it appears that the observe sequence group responded faster than the observe random group as part of a speed-accuracy trade-off. However, the impact on RTs and error rate of the transition from the training to the new sequence was the same for the two groups, and therefore the response location test provided no evidence that participants in the observe sequence group acquired knowledge about the sequence of response locations by observation rather than during testing.

The main effect of sequence on RT in the response location test suggests that both groups had acquired some knowledge of the sequence of response locations in the course of testing. This is not surprising given that 32 cycles of the six-item training sequence of response locations were experienced in the initial test, and performance in the response location test itself was assessed on the basis of 32 more sequence cycles. However, it is notable that, whereas the controls had experienced the response location sequence and the finger movement sequence equally often, they provided evidence of having learned the former but not the latter during testing. This is consistent with Willingham's (1999) suggestion that performance (rather than observation) of an SRT task typically promotes learning about response locations, and with evidence from a variety of practice-based tasks that effector-dependent sequence learning occurs more slowly than effector-independent sequence learning (Nakahara, Doya, & Hikosaka, 2001).

In combination, the results of the anatomical and response location tests are consistent with the hypothesis that the observe sequence group learned by observation an effector-dependent sequence of finger movements and not a sequence of response locations.

General Discussion

The critical question addressed by the present experiments is whether observational learning of a finger movement sequence can be effector dependent. Experiments 1 and 2 provided evidence of effector dependence in the form of a dissociation between two transfer tests: Relative to controls who had not been exposed to the sequence during the training phase, participants who had observed the model performing the finger movement sequence responded faster to the training sequence than to a novel sequence when they used their fingers to press the keys (stimulus transfer test) but not when they used their thumbs (response transfer test). Experiment 3 provided further evidence of effector dependence by controlling for the possibility that the dissociation reported in Experiments 1 and 2 was due to a difference between the stimulus and response transfer tests in their sensitivity to effector-independent knowledge of a sequence of response locations. For both transfer tests in Experiment 3, participants' hands were crossed on the keyboard. In the anatomical crossed-hands test, stimuli were presented in two sequences, both of which generated a sequence of response locations distinct from that observed during training. In spite of this, relative to controls, participants who had observed the model performing the finger movement sequence during training responded faster to stimuli that generated the observed finger movement sequence than to stimuli that generated a different finger movement sequence. Thus, the skill learned by observation did not transfer across fingers.

Effector-dependent learning by observation of a finger movement sequence is consistent with the associative sequence learning model of observational learning (Heyes, 2001) because it proposes that movement observation can activate motor representations directly, that is, without intermediate representation in a symbolic or amodal code. The results of the present experiments are harder to reconcile with theories that assume that observational learning is invariably mediated by symbolic (Bandura, 1986) or amodal (Meltzoff & Moore, 1997) representation. Neither social learning theory nor active intermodal matching theory specify the nature of symbolic or amodal codes, but they both imply that these codes are of a kind that supports a broad range of inferences. Therefore, to accommodate the transfer effects found in the present experiments, these theories would have to (a) assume that participants initially represented the observed sequence of finger movements in a symbolic or amodal code with anatomical content (e.g., in linguistic form: left middle-right middle-left ring-right index-right ring-left index) rather than abstract content (e.g., Response Location 2-5-1-4-6-3) and (b) explain why, given background knowledge of canonical finger locations, the former could not be translated into the latter such that participants' observation-based sequence knowledge was apparent in response transfer (Experiments 1 and 2) and response location transfer (Experiment 3) tests.

In connection with the first of these requirements, it is important to note that the results of the free generation and recognition tests

do not show that the participants in our experimental groups had sequence knowledge represented in a symbolic or amodal code with anatomical content. Successful performance in the free generation test may reflect implicit, or consciously inaccessible, effector-dependent learning, and whereas the recognition test provides a better measure of explicit knowledge, successful performance in this kind of test may be based on a consciously accessible experience of perceptual-motor fluency (Shanks & Johnstone, 1999).

A recent study of intermanual transfer of observational learning in the SRT task provides more direct evidence that participants do not code observed finger movements verbally using labels such as *ring*, *middle*, and *index* (Osman, Bird, & Heyes, 2004). After watching a female model perform an eight-item sequence with her right hand, observers performed no better than controls when responding with their left hands to the training sequence, which preserved the observed sequence of response locations, or to the reverse of the training sequence, which preserved the observed sequence of verbally coded finger movements.

The present study found evidence that observational sequence learning can be both explicit and effector dependent. This is consistent with a previous study of observational learning in the SRT task, which reported chronometric evidence that observers had acquired sequence knowledge only when posttest interviews indicated that they had explicit knowledge of the sequence (Kelly & Burton, 2001). However, our findings are not consistent with a model of motor skill learning that proposes that effector-dependent knowledge is implicit, whereas effector-independent knowledge is explicit (Hikosaka et al., 2002). In combination with recently reported evidence of implicit, effector-independent, practice-based learning (Japikse, Negash, Howard, & Howard, 2003), our results therefore imply that these relationships are not invariant either for practice-based or for observational sequence learning.

The results of other previous SRT studies are apparently inconsistent with our findings because they indicate effector independence of practice-based learning. For example, when participants perform the task themselves during training, sequence knowledge has been shown to transfer from three fingers to one finger (Cohen, Ivry, & Keele, 1990), from the fingers to the arm (Grafton, Hazeltine, & Ivry, 1998), from the dominant to the nondominant hand (Japikse et al., 2003), and across modalities from manual to vocal responding (Keele, Jennings, Jones, Caulton, & Cohen, 1995). The contrast between these results and those of the present study may be related to our use of a simple, unique sequence under single task conditions. Cohen et al. (1990), Grafton et al. (1998), and Keele et al. (1995) used hybrid unique, ambiguous sequences and required participants to complete an auxiliary tone-counting task during training. Therefore, it is likely that in our study sequence learning was more advanced at the time of transfer testing, and there is evidence from both human and animal studies that effector-dependent motor learning is more readily detected later in training (Nakahara et al., 2001). Japikse et al. (2003) reported effector independence after training involving approximately 1,000 sequence repetitions, but their sequence was exceptionally cryptic (an ambiguous sequence, in which items alternated with random targets), and therefore learning is likely to have been exceptionally slow.

In the observation phase of the present experiments, participants were asked to attend to the model's finger movements, and those

finger movements largely obscured movement of the response keys. It could be argued that, under these circumstances, it is inevitable that observers will learn about finger movements and therefore that the present experiments do not provide an adequate test of the hypothesis that observational learning can be effector dependent. We agree with the first component of this challenge but not with the second. The procedure was such that, if anything was learned by observation, it would be about effectors, that is, the model's finger movements would provide the input for learning. However, it was not inevitable that this input would be encoded in an effector-dependent fashion, that is, using intrinsic (body-centered) coordinates and a nonsymbolic code. Instead, the observers could have coded the finger movements symbolically relative to intrinsic coordinates (e.g., ring, middle, index), or, in a symbolic or nonsymbolic code, relative to extrinsic, spatial coordinates.

Research using two perceptual-motor paradigms that do not involve learning, spatial precuing and stimulus-response compatibility (SRC), has been interpreted as evidence of effector-independent coding. In four-choice precuing experiments, where a cue presented prior to the imperative stimulus indicates that it will occur at one of two locations, the advantage is greater when the precue indicates two responses by the same hand than when it indicates two responses by different hands (e.g., Miller, 1982). However, this effect disappears when participants' hands are overlapping, with the fingers of both hands alternating on the response keys, implying that it is effector independent (Reeve & Proctor, 1984). Similarly, when one uses an SRC paradigm, choice responses to lateral stimuli are faster when the relative positions of the stimulus and the response correspond than when they do not (Fitts & Seeger, 1953). However, using a crossed-effector response condition indicates that the SRC effect arises from the relative correspondence between the response location and the stimulus location rather than the specific limb and the stimulus location (e.g., Riggio, Gawryszewski, & Umiltà, 1986). These findings indicate effector-independent control of performance when the effectors are in atypical positions (e.g., when the hands are crossed or overlapping), but it would be premature to infer that effector dependence is rare outside the learning domain. Recent work that compared the time course of standard and crossed-hand SRC effects suggests that they are mediated by different sets of processes and that the standard effect depends on effector-dependent activation, which is inhibited when the effectors are in atypical positions (Wascher, Schatz, Kuder, & Verleger, 2001). If inhibition of this kind also occurs in learning tasks, it is possible that learning in the SRT task would be effector independent if, for example, the hands of the participant or the model are crossed on the keyboard during training.

In conclusion, building on electrophysiological evidence of motor facilitation during action observation and guided by associative sequence learning theory, the present study found evidence of effector-dependent motor learning by observation. It has long been known that skill observation can accelerate skill learning. Our findings imply that skill observation and direct engagement with a task can enlist exactly the same processes of learning—that we can learn the movements of another person's body as if they were our own.

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