RESEARCH ARTICLE

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Action observation supports effector-dependent learning of finger movement sequences

Abstract Practising a motor skill can result in effector-dependent learning (learning that does not transfer from the set of muscles used in training to a new set of muscles). Proceeding from neurophysiological evidence of motor activation during action observation, this study asked whether observational learning, learning through observation of skilled performance, can also be effector-dependent. Adult human participants observed a model's right hand as the model responded to an eight-item sequence in a serial reaction time (SRT) task. Their sequence learning was then compared in two tests with that of controls who had observed the model's right hand responding to random targets during training. All participants performed the SRT task with their right hand in the first test and with their left hand in the second. Evidence of observational learning was obtained in the right hand test but not in the left hand test. This implies that sequence learning based on observation of right hand performance did not transfer to the left hand, and therefore that observational learning can support effector-dependent learning of finger movement sequences. A second experiment used the same procedure to assess learning by a group of participants who observed a sequence of response locations only. This group did not observe the model's responses. Results suggested that action observation was necessary for the effector-dependent observational learning demonstrated in Experiment 1.

Keywords Effector-dependence · Observational learning · Motor learning · Motor activation by action observation

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Introduction

Learning is said to be effector-dependent to the extent that training of one set of muscles (such as those of the right hand) does not generalise to another (such as those of the left hand). Research investigating the effector-dependence of practice-based motor skill learning (skill developed through task performance rather than task observation) has produced mixed results. Effector-dependence has been demonstrated in both monkeys (Rand et al 1998) and humans (Bapi et al 2000; Marcovitch and Flanagan 2005; Verwey and Wright 2004), but some studies have reported effector-independent motor skill learning in these populations (Cohen et al 1990; Japikse et al 2003; Keele et al 1995). Research indicating that effector-dependence is more readily detected later in training (Nakahara et al 2001) suggests that the conflict among findings is due, at least in part, to variation between studies in the extent to which the skill was learned prior to effector transfer.

This explanation for the conflicting data is consistent with a model proposing that motor skill learning is initially effector-independent, and that it becomes effector-dependent with increasing practice (Hikosaka et al 2002). The transition from effector-independence to effector-dependence is thought to occur through the interaction of two learning processes, corresponding to two cortico-basal ganglia/cortico-cerebellum loop circuits. The first encodes the motor skill in effector-independent spatial co-ordinates and is governed by loop circuits connecting the prefrontal parietal cortex and associative areas of the basal ganglia and cerebellum. The second encodes the motor skill as a sequence of effector-dependent motor representations and is governed by loop circuits connecting the motor cortex and motor areas of the basal ganglia and cerebellum. Hikosaka et al (2002) suggested that spatial skill knowledge develops in advance of motor skill knowledge, and that learning is initially effector-independent, but later effector-dependent.

The present study investigated whether motor skill learning based on movement observation, rather than physical practice, can be effector-dependent. It is intuitively implausible that movement observation could support effector-dependent learning, but the possibility that it may occur has been raised by recent research on the human "mirror-neuron system" (Buccino et al 2001; Rizzolatti et al 2001), and electrophysiological studies of motor facilitation during action observation (Aziz-Zadeh et al 2002; Fadiga et al 1995; Heiser et al 2003; Strafella and Paus 2000). This research has revealed comparable patterns of activation in the SMA, premotor cortex, primary motor cortex, cerebellum, parietal cortex and inferior frontal gyrus during observation and execution of action. For example, using fMRI, Buccino et al (2001) reported somatotopically organised activation of the premotor cortex and posterior parietal lobe when participants observed videotapes of object-related actions (such as biting an apple) and non-object-related actions (like chewing) performed by another individual using one of three different effectors (mouth, hand and foot). Similarly, using single-pulse TMS, Aziz-Zadeh et al (2002) found that motor evoked potentials (MEPs) recorded from the right hand were greater during right hand than left hand movement observation, and vice versa for MEPs recorded from the left hand. These electrophysiological data suggest that movement observation can activate effector-dependent representations of movement stored in primary motor cortex (Aziz-Zadeh et al 2002), which is likely to be a necessary condition for effector-dependent learning by observation.

As far as we are aware, only one published study has reported effector-dependent learning by observation (Heyes and Foster 2002). This study used a variant of the serial reaction time (SRT) task (Nissen and Bullemer 1987) in which participants first observed a model performing a six-item sequence of finger movements in response to spatial targets, and were then required to perform the task themselves under a variety of conditions. When, like the model, the observers responded to targets using the first three fingers on each hand, they provided more evidence of sequence knowledge than controls who had watched the model responding to a random sequence of spatial targets. That is, the observers showed a greater elevation in RT when stimulus presentation ceased to be governed by the sequence observed during training and began to be determined by a new six-item sequence. However, when the observers were required to use their thumbs rather than their fingers to depress the response keys, their performance was no better than that of the controls.

The pattern of results obtained by Heyes and Foster (2002) is consistent with effector-dependence of observational learning, but it is not decisive. The order of blocks completed using the thumbs was fixed: participants always responded to a block governed by the training sequence before a block governed by the new sequence. It is likely that participants have little prior experience of using their thumbs to depress keys on a standard QWERTY keyboard, and therefore RTs would be expected to decrease significantly with practice. Consequently it is possible that Heyes and Foster failed to detect observational learning in their thumbs test because RT elevation upon introduction of the new sequence was masked by a general decrease in RT across test blocks due to task practice.

The present study also used an SRT task but, to overcome the problem encountered by Heyes and Foster (2002), we counterbalanced the order of training-sequenced and new-sequenced blocks after effector-transfer. In addition, we examined transfer from the dominant to the nondominant hand, rather than from fingers to thumbs. Marcovitch and Flanagan (2005) have argued that within-hand transfer of effectors (such as from fingers to thumbs) is open to interference from the use of shared muscles required to move digits of the same hand. Using a variant of the SRT task in which participants responded to spatial stimuli with whole arm movements, Marcovitch and Flanagan found that practice-based sequence learning did not transfer from the dominant to the nondominant arm/hand.

In the first phase of the present experiment, all participants performed one block of trials using the four fingers on their right hand to respond to four spatial targets. This phase was designed to familiarise participants with general task demands but, because the targets were presented in random order, it did not provide an opportunity for sequence learning.

In the second (training) phase, one group of participants (Observe Sequence) watched a video presentation of the finger movements of a model's right hand recorded as the model completed eight blocks of SRT trials in an eight-item sequence. In the video presented to the other, control group (Observe Random), the model was responding to a random sequence of targets.

Immediately after observation training, all participants were required to perform two blocks of the SRT task using their right hand. In the first of these blocks, target stimuli were presented in the eight-item sequence modelled for Group Observe Sequence, and in the second block targets were presented in a new eight-item sequence. In a standard SRT task, practice-based sequence learning is indexed by comparing RTs to stimuli presented in the training sequence and in a new sequence (in other words, by a main effect of sequence type). However, when, as in the present study, sequence observers are compared with controls who did not observe responding to a structured sequence during training, observational learning is indexed by an interaction between group and sequence type. In this case, the control group provides a baseline, and if the introduction of a new sequence slows responding more in the observers than in the controls, there is evidence that the former group learned the sequence by observation.

The new sequence presented in the second block of the right hand test was the reverse of the training sequence. Thus, when stimuli were presented to the model during training (and to the participant in the first block

of the right hand test) in the sequence 42312413, they were presented in the sequence 31421324 in the second block of the right hand test. Reversal of the stimulus sequence required participants to press the response keys, and to use their fingers, in reverse order relative to training (Table 1a,b). Therefore, if introduction of the new sequence has a more detrimental effect on RT in Group Observe Sequence than in Group Observe Random, it would indicate that the former group had learned by observation a sequence of response locations, a sequence of finger movements, or both.

The left hand test was designed to distinguish these possibilities. After completing the right hand test, participants performed one more block with the training sequence using their right hand, and were then required to complete two blocks of trials with their left hand. For half of each group, stimuli were presented in the training sequence during the first left hand block and in a new, reversed sequence during the second left hand block, whereas the other half of each group had the opposite assignment. These features of the procedure allowed us to test for transfer of sequence learning to the left hand using both between-subjects and within-subjects comparisons.

In the between-subjects case we compared elevation in RT between the last right hand block and the first left hand block between participants given the training sequence in the first left hand block, and those given the reverse sequence in the first left hand block. The training sequence of stimuli required participants to press response keys in the same order as in the previous right hand block (and as the model during training), but to use the reverse sequence of finger movements. In contrast, the reverse sequence of stimuli required participants to press the response keys in reverse order, but to use the same sequence of finger movements as in the previous right hand block (Table 1b,c). Therefore, if Group Observe Sequence had learned an effector-independent sequence of response locations during model observation, those given the training sequence in the first left hand block would be expected to show better transfer, relative to controls, than those given the reverse sequence in the first left hand block. Alternatively, if Group Observe Sequence had learned a sequence of finger movements by observation, and if this learning transferred from the right to the left hand, participants given the reverse sequence in the first left hand block should perform better than those given the training sequence in the first left hand block. Superior transfer by both sub-groups of observers, relative to controls, would imply that they had learned by observation a sequence of response locations *and* a sequence of finger movements, both in an effector-independent manner. Finally, if observers and controls show the same RT elevation when transferring from the right to the left hand, it would suggest that the observers had learned an effector-dependent sequence of finger movements.

Transfer from the dominant to the nondominant hand would be expected to slow responding in all participants, regardless of group assignment, and this non-specific effect could conceal evidence of effector-independent sequence knowledge in those who observed the model. To guard against this possibility, the within-subjects contrast compared left hand responses to the training sequence with left hand responses to the reverse sequence. The logic of this contrast was similar to that of the between-subjects comparison. Compared with model performance, the training sequence of stimuli required participants to respond using the same sequence of response locations, but the reverse sequence of finger movements, whereas the reverse sequence of stimuli required responses to the reverse sequence of response locations, and with the same sequence of finger movements (Table 1a,c). Therefore, when compared with controls, Observe Sequence participants should respond faster to the training sequence than to the reverse sequence if they had learned a sequence of response locations from the model, and faster to the reverse sequence than the training sequence if they had learned an effector-independent sequence of finger movements. Faster responding by observers than by controls to both sequences would indicate effector-independent learning of both response location and finger movement sequences, whereas comparable RTs to both sequences by observers and controls would indicate that the former group had learned an effector-dependent sequence of finger movements by model observation.

A second, follow-up experiment used the same procedure to assess the performance of a group of participants who observed the required sequence of response locations, but not the model's responses, during training. By comparing the performance of this group to that

Table 1 Sequences of stimulus locations (screen boxes 1–4), response locations (Qwerty keys V, B, N, M) and finger movements (i = index, r = ring, m = middle, l = little) during (A) observation training, (B) the right hand test, and (C) the left hand test. Bold letters indicate sequences that were novel with respect to observation training

	A. Model (right hand)	B. Right hand test		C. Left hand test	
		Training sequence	New (reverse) sequence	Training sequence	New (reverse) sequence
Stimuli	4 2 3 1 2 4 1 3	4 2 3 1 2 4 1 3	3 1 4 2 1 3 2 4	4 2 3 1 2 4 1 3	3 1 4 2 1 3 2 4
Responses	M B N V B M V N	M B N V B M V N	**N V M B V N B M**	M B N V B M V N	**N V M B V N B M**
Fingers	l m r i m l i r	l m r i m l i r	**r i l m i r m l**	i r m l r i l m	m l i r l m r i

of the Observe Sequence group in Experiment 1, who observe both the required sequence of responses and response locations, we can identify learning effects specific to action observation.

Experiment 1

Method

Participants

Twenty-four students at University College London (UCL) were paid a small honorarium for their participation. All were right-handed and had normal or corrected-to-normal vision. They were randomly assigned to two groups (Observe Sequence, Observe Random). Their mean age was 23 years, and thirteen were male. Three participants who made more than 10% errors were replaced.

Procedure

Stimulus and video presentation, RT measurement, and response recording were all implemented on IBM-compatible PCs with 43 cm colour monitors and standard QWERTY keyboards. All participants completed three phases of the experiment: (1) familiarization, (2) training, (3) testing. The two groups received identical treatment in all phases except during the training phase.

Familiarisation Four boxes were presented in a horizontal row in the centre of the screen, drawn with black lines against a grey background. The boxes were 2.2 cm wide, 1.2 cm high, and spaced 1-cm apart. A white asterisk (Arial font size 36, subtending approximately 0.5° of visual angle) appeared in the centre of one of these boxes on each target location trial. Target locations are referred to as 1–4 from left to right. Participants were instructed to indicate locations 1–4 as quickly as possible using the V, B, N, and M keys, respectively. The V, B, N, and M keys were operated by the index, middle, ring, and little fingers of the right hand, respectively.

In the familiarisation phase, participants were presented with one block of 128 target location trials with the order of target presentation randomly determined. A trial ended when a participant pressed the correct key, at which time the target was erased and the next trial was initiated. The next target appeared 200 ms later. The RTs were measured from the onset of the target stimulus to completion of the correct key press response. Incorrect responses were followed by a tone.

Training Each group observed a video recording of a model's right hand as the model performed eight, 128-trial blocks of the target location task described above.

In the video presented to Group Observe Random, the model was responding to target stimuli presented in random order, and in the video shown to Group Observe Sequence, she was responding to stimuli presented in an eight-item "training sequence". For half of the participants in this group the training sequence was 42312413 (sequence 1), and for the other half it was 31421324 (sequence 2). Each block began at a randomly-selected point in the training sequence, and included 16 sequence repetitions.

The video images were recorded using a Sony digital camcorder, and encoded as AVI (720×576 pixels) files. They were displayed at full frame and in colour using Microsoft Windows Media Player. The model's right hand subtended approximately 26.5° of visual angle. The video frame included all four of the model's fingers, one key on either side of the four response keys, and two rows of keys above the four response keys. The viewing angle was similar to that of ones own hands while typing. The model was skilled: when filmed for Group Observe Sequence, her mean RT was 346 ms (SEM = 2.8), and when filmed for Group Observe Random her mean RT was 354 ms (SEM = 3.6). Across blocks, the model's error rate ranged between 0 and 3%.

Testing Immediately after observing the model's performance, participants were required to perform the target location task themselves, first using their right hand and then using their left hand.

The right hand test consisted of two 128-trial blocks of the target location task. In the first of these blocks, target presentation was determined by the training sequence, and in the second it was determined by the "new" sequence, which was the reverse of the training sequence. Half of the participants in each group had sequence 1 as the training sequence and sequence 2 as the new sequence, and the other half had the reverse assignment. Test blocks in both the right and left hand tests started at a random point in the sequence.

After the right hand test, all participants completed a further block of trials with the right hand in which targets were presented in the training sequence. This was to establish a baseline for assessment of performance with the left hand.

The left hand test consisted of one block of 128 trials in which targets appeared in the training sequence and one block of 128 trials in which they appeared in the new sequence. The order of these two blocks was counterbalanced so that half of the participants in each group responded to the new sequence first, and half responded to the training sequence first. The identities of the training and new sequences (sequence 1 or 2) were the same as in the right hand test, and this variable was counterbalanced with group and order. In the left hand test, participants pressed the V, B, N and M keys with their little, ring, middle, and index fingers, respectively.

Results and discussion

A mean RT was calculated for each participant in each block after exclusion of RTs greater than 1000 ms (less than 3% of trials for any subject on any block). Each analysis of RT data was accompanied by a parallel analysis of error data. The results of these error analyses are reported only if they yielded significant effects. Figures show data from both Experiment 1 (dashed lines) and Experiment 2 (solid line).

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 Group Observe Sequence ($M = 419$, SEM $= 34$) did not differ from those of Group Observe Random ($M = 413$, SEM $= 40$) ($F < 1$).

Figure 1 presents mean RTs to the training sequence and the new sequence in the right hand test. Three-way ANOVA with group (Observe Sequence and Observe Random), and training sequence identity (sequences 1 and 2) as between-subjects factors, and sequence type (training and new) as the within-subjects factors, indicated a significant effect of sequence type, $F_{(1,20)} = 10.34$, $p = 0.004$, and a significant group×sequence type interaction, $F_{(1,20)} = 22.14$, $p < 0.001$. Thus, in the right hand test, switching from the training to the new sequence caused an elevation in RT in the Observe Sequence group, but not the Observe Random group. This indicates that the former group had learned the training sequence through observation of its performance by the model.

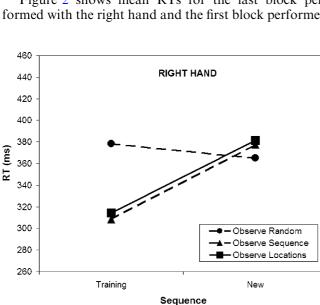Figure 2 shows mean RTs for the last block performed with the right hand and the first block performed with the left hand. These data were analysed using four-way ANOVA in which group (Observe Sequence and Observe Random), sequence identity (sequences 1 and 2) and sequence type in the left hand block (training and new) were between-subjects factors, and hand (right and left) was the within-subjects factor. (In the last right hand block, targets were presented in the training sequence to all participants.) There was a main effect of hand on RT, $F_{(1,16)} = 8.23$, $p = 0.01$, but no other effects or interactions were significant. Similarly, parallel analysis of error data indicated only that more errors were made in the first left hand block ($M = 8.46$, SEM $= 1.09$) than in the last right hand block ($M = 5.67$, SEM $= 0.82$). Thus, switching from the right to the left hand was associated with a modest overall elevation in RT and error rate, but this elevation was no greater in the Group Observe Sequence than in the Group Observe Random group, and it was no greater when the responses in the first left hand block were to the new sequence than when they were to the training sequence. Therefore, comparison of performance in the last right hand block with performance in the first left hand block failed to detect any evidence of transfer of observational learning from the right to the left hand.

Figure 3 presents mean RTs to the training sequence and the new sequence when all responses were being made with the left hand. These data were analysed using four-way ANOVA in which group (Observe Sequence and Observe Random), sequence identity (sequences 1 and 2), and order of left hand blocks (training sequence
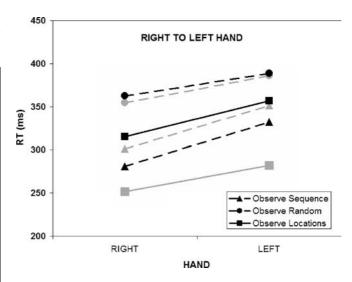

Fig. 1 Right hand test—Experiments 1 (*dashed lines*) and 2 (*solid line*). Mean reaction times (RTs) to the training sequence and the new sequence for groups that had observed a sequence of response locations (Observe Locations), observed the fingers of model's right hand responding to the training sequence (Observe Sequence), or observed the fingers of a model's right hand responding to random targets (Observe Random)

Fig. 2 Right to left hand test—Experiment 1 (*dashed lines*) and Experiment 2 (*Solid lines*). Mean reaction times (RTs) during the last block completed with the right hand and the first block completed with the left hand, for groups that had observed the training sequence of response locations (Observe Locations), the fingers of a model's right hand responding to the training sequence (Observe Sequence) or to random targets (Observe Random). In the last right hand block, all participants were responding to the training sequence. In the first left hand block, the subgroups shown in grey were responding to the training sequence, and the subgroups shown in black were responding to the new sequence
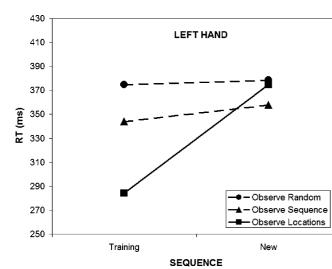
Fig. 3 Left hand test—Experiment 1 (*dashed lines*) and Experiments 2 (*solid lines*). Mean reaction times (RTs) to the training sequence and the new sequence for groups that had observed the training sequence of response locations (Observe Locations) or the fingers of a model's right hand responding to the training sequence (Observe Sequence) or to random targets (Observe Random)

first and new sequence first) were the between-subjects factors, and sequence type (training and new) was the within-subjects factor. This analysis did not reveal any significant effects or interactions

The training sequence required participants to respond using the same sequence of response locations as the model, but the reverse sequence of finger movements, whereas the new sequence required them to respond using the same sequence of finger movements as the model, but the reverse sequence of response locations (Table 1a,c). Therefore, equivalent RTs to the training sequence and the new sequence in Group Observe Sequence could mean that they had learned by observation *both* a sequence of response locations and an effector-independent sequence of finger movements. In this case, one would expect Group Observe Sequence to respond faster to both sequences than Group Observe Random. Disconfirming this prediction, the main effect of group did not even approach significance ($F < 1$, $p = 0.6$). Thus, like the between-subjects analysis, the within-subject analysis of left hand performance failed to detect any evidence of transfer of observational learning from the right to the left hand. This implies that what was learned by model observation, and reflected in right hand performance, was a sequence of finger movements encoded in an effector-dependent fashion.

Thus, participants who had observed a model demonstrating the required finger movement sequence with her right hand provided more evidence of sequence knowledge than controls when both groups were tested with their right hand. This indicates that sequence information was learned by observation. However, when participants were required to use their left hand to perform the task, those who had had the opportunity to learn by sequence observation did not provide any more

evidence of sequence knowledge than controls. This was the case both when performance on the last right hand block was compared with performance on the first left hand block, and when left hand responses to the training sequence were compared with left hand responses to the new sequence. Thus, consistent with the hypothesis that observational learning can be effector-dependent, the present study failed to detect any evidence of transfer of observational learning from the right to the left hand.

Experiment 2

Experiment 1 suggested that observation of a model's response to a sequence can produce effector-dependent learning of the observed sequence. Experiment 2 attempted to determine whether observation of the model's responses are necessary in order for this type of learning to occur in the SRT paradigm. This question is pertinent as during observational training in Experiment 1, the Observe Sequence group were able to observe both the model's responses (her action) and the sequence of key movements (more accurately the sequence of response locations, as the keys were largely obscured by the fingers). It is possible that observation of the sequence of response locations, rather than the model's responses, resulted in the effector-dependent learning shown by the Observe Sequence group. Therefore, it could be argued that Experiment 1 provided good evidence of effector-dependent learning through observation, but did not show that *action* observation was necessary for effector-dependent observational learning to occur. If participants in Experiment 1 learned in an effector-dependent fashion through observation of the response location sequence rather than through observation of the action sequence, then observation of the sequence of response locations alone may also result in effector-dependent learning.

In order to test this possibility, Experiment 2 used the same procedure as Experiment 1 in order to assess learning obtained through the observation of a sequence of response locations (Group Observe Location). During training, participants observed video clips of a keyboard in which response keys (and thus response locations) were highlighted in sequential order. Performance on both the right and left hand tests used in Experiment 1 was used to determine how any sequence information gained through this type of training was encoded.

Methods

Participants

Twelve students at UCL were paid a small honorarium for their participation. All were right-handed and had normal or corrected-to-normal vision. Their mean age was 23.4 years, and eight were male.

Procedure

The procedure of Experiment 2 was as that of Experiment 1 except during the training phase. During training Group Observe Location watched a video recording of a static keyboard on which keys were highlighted according to eight, 128-trial blocks of the training sequence. One training sequence (42312413) was used as there were no significant differences in performance between participants trained on the different sequences in Experiment 1. Each block began at a randomly selected point in the training sequence, and included 16 sequence repetitions.

The video images were constructed so that the rate of stimulus presentation ($M = 560$ ms, SEM = 1.7) approximated that of the Observe Sequence group in Experiment 1 ($M = 546$ ms, SEM = 2.8). The viewing angle of the keyboard matched that of the Observe Sequence training videos so that, as far as possible, Observe Sequence and Observe Location videos differed only in terms of the presence or absence of the model's response.

Results and discussion

As in Experiment 1, a mean RT for each participant in each block was calculated after exclusion of RTs greater than 1000 ms (less than 3% of trials for any subject on any block). Each analysis of RT data was accompanied by a parallel analysis of error data. The results of these error analyses are reported only if they yielded significant effects.

Figure 1 presents mean RTs to the training sequence and the new sequence in the right hand test for both Experiments 1 and 2. Analysis of the performance of the Observe Locations group by ANOVA with sequence type (training and new) as a repeated measures factor revealed a significant increase in RT upon transfer from the training sequence ($M = 314$, SEM = 22.6) to the new sequence ($M = 381$, SEM = 24.7), indicating knowledge of the training sequence.

Figure 2 shows mean RTs for the last block performed with the right hand and the first block performed with the left hand for Experiments 1 and 2. Data from the Observe Locations group were analysed using two-way ANOVA in which sequence type in the left hand block (training and new) was a between-subjects factor, and hand (right and left) was the within-subjects factor. Analysis of the RT data revealed no significant main effects or interactions. Similarly, parallel analysis of error data indicated only that more errors were made in the first left hand block ($M = 5.92$, SEM = 1.86) than in the last right hand block ($M = 3.5$, SEM = 1.25). Thus, switching from the right to the left hand was associated with an increase in error rate, but this increase was no greater when the responses in the first left hand block were to the new sequence than when they were to the training sequence. Therefore, comparison of performance in the last right hand block with performance in the first left hand block failed to detect any evidence of transfer of observational learning from the right to the left hand.

Figure 3 presents mean RTs to the training sequence and the new sequence when all responses were being made with the left hand for Experiments 1 and 2. Data from the Observe Locations group were analysed using two-way ANOVA in which order of left hand blocks (training sequence first and new sequence first) was the between-subjects factor, and sequence type (training and new) was the within-subjects factor. This analysis revealed a significant effect of sequence type ($F_{(1,10)} = 20.3$, $p = 0.001$), reflecting the fact that responses to the training sequence ($M = 284$ ms, SEM = 33.3) were faster than those to the new sequence ($M = 375$ ms, SEM = 37.1). No other effects or interactions were significant.

The training sequence required participants to respond using the same sequence of response locations as the model, but the reverse sequence of finger movements, whereas the new sequence required them to respond using the same sequence of finger movements as the model, but the reverse sequence of response locations (Table 1a,c). Group Observe Locations responded significantly faster to the training sequence block than the new sequence block, suggesting that their knowledge was encoded as a sequence of effector-independent response locations.

General discussion

Neurophysiological research has provided evidence of central and peripheral motor activation during action observation (Aziz-Zadeh et al 2002; Buccino et al 2001). This evidence raises the question of whether, like task practice, observation of task performance can result in effector-dependent learning. The present study addressed this question using a SRT task and an experimental design which provided the opportunity for right hand to left hand transfer to be detected via both between-subjects and within-subjects comparisons. However, no evidence of transfer was obtained.

Participants who had observed a model demonstrating the required finger movement sequence with her right hand provided more evidence of sequence knowledge than controls when both groups were tested with their right hand. This indicates that sequence information was learned by observation. However, when participants were required to use their left hand to perform the task, those who had had the opportunity to learn by observation did not provide any more evidence of sequence learning than controls. This was the case both when performance on the last right hand block was compared with performance on the first left hand block, and when left hand responses to the training sequence were compared with left hand responses to the new sequence. Thus, consistent with the hypothesis that observation learning can be effector-dependent, the

present study failed to detect any evidence of transfer of observational learning from the right to the left hand.

It is possible that the effector-dependent learning demonstrated by the Observe Sequence group in Experiment 1 may not have resulted from observation of the sequence of actions, but instead from observation of the sequence of response locations, during training. We know of no theory nor empirical work which would predict effector-dependent learning by observation of response locations, in contrast to effector-dependent learning by action observation which can be predicted from neurophysiological work into the human "mirror system" (Aziz-Zadeh et al 2002; Buccino et al 2001). Nevertheless, in order to guard against the possibility that observation of the sequence of response locations produced effector-dependent learning in Experiments 1 and 2 we used the same procedure as Experiment 1 to assess the sequence knowledge of a group of participants who observed a sequence of response locations alone (Group Observe Locations). Results from Experiment 2 suggest that Group Observe Locations encoded their sequence knowledge as effector-independent response locations.

Group Observe Locations (in Experiment 2) and Group Observe Sequence (in Experiment 1) differed in their experience during training; actions were not observed by Group Observe Locations, but were observed by Group Observe Sequence. Although cross-experimental comparison makes inference difficult, the effector-dependent learning shown by Group Observe Sequence, and the effector-independent learning shown by Group Observe Locations, suggests that it was action observation that produced the effector-dependent learning in Group Observe Sequence.

The results of the present study are consistent with research reporting effector-dependence of practice-based learning in sequential tasks (Marcovitch and Flanagan 2005; Rand et al 2000), but not with studies, which have found learning of this kind to be effector-independent. For example, using an SRT task, Japikse et al (2003) reported transfer of practice-based sequence learning from the dominant to the nondominant hand. The hypothesis that learning becomes effector-dependent in the later stages of training (Nakamura et al 2001) suggests that the contrast between our results and those of Japikse et al is due to our use of a simpler training sequence. We used hybrid training sequences in which each item was followed equally often by two of the three other items. In contrast, Japikse et al used an exceptionally cryptic sequence in which each item was followed equally often by each of the other three items, and random targets alternated with sequence items. Therefore, although Japikse et al gave extended training, it is likely that in our study learning was more advanced at the time of transfer testing.

A recent study by Sakai et al (2003, Experiment 3) reported that practice-based learning of information about the temporal structure of a learned sequence of finger movements transferred from the nondominant to the dominant hand, but not vice versa. In the light of these findings, and given the growing body of behavioural and neurophysiological evidence indicating equivalence of action observation and execution, it cannot be assumed on the basis of the present results that observational learning of a finger movement sequence would not transfer from the nondominant to the dominant hand. The symmetry of effector-dependence of observational learning would, therefore, be an appropriate focus for future study.

Studies recording TMS-induced MEPs suggest that motor activation during action observation is specific to the observed action (Aziz-Zadeh et al 2002; Strafella and Paus 2000). Functional imaging studies, however, show either a general activation of motor cortical areas during action observation (Iacoboni et al 1999), or observation-related activation in accordance with a gross motor somatopy (Buccino et al 2001). The results of the present study support the tight coupling between observation and execution of specific actions suggested by the former group of experiments, and by that of Heyes and Foster (2002) who reported effector-dependent learning by observation. Furthermore, these results suggest that future-imaging studies may be able to demonstrate motor cortical activation, which is specific to an observed action.

Neuroimaging and electrophysiological research have demonstrated that observation and execution of body movements give rise to remarkably similar patterns of central and peripheral neural activation (Grezes and Decety 2001; Fadiga et al 1995). In combination with evidence of effector-dependence of practice-based learning, the results of the present study suggest that the equivalence between movement observation and execution extends beyond the perceptual level to their effects on learning. They imply that, rather than representing alternative routes to skill acquisition, practice and observation mediate skill development through the very same processes of motor learning.

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