Implicit motor sequence learning is represented in response locations

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Previous work (Willingham, 1999) has indicated that implicit motor sequence learning is not primarily perceptual; that is, what is learned is not a sequence of stimuli. Still other work has indicated that implicit motor sequence learning is not specific to particular muscle groups or effectors. In the present work, we tested whether implicit motor sequence learning would be represented as a sequence of response locations. In Experiment 1, learning showed very poor transfer when the response locations were changed, even though the stimulus positions were unchanged. In Experiment 2, participants switched their hand positions at transfer, so that one group of participants pushed the same sequence of keys but used a different sequence of finger movements to do so, whereas another group pushed a different sequence of keys but used the same sequence of finger movements used at training. Knowledge of the sequence was shown at transfer only if the sequence of response locations was maintained, not the sequence of finger movements.

This article concerns the representation of implicit perceptual-motor sequence learning. A number of articles in the last 10 years have shown that perceptual-motor sequences may be learned implicitly (Cohen, Ivry, & Keele, 1990; Nissen & Bullemer, 1987; Reed & Johnson, 1994; Willingham, Nissen, & Bullemer, 1989). We use *implicit* in the sense originally suggested by Graf and Schacter (1985); a task is implicit if knowledge is tested indirectly via performance and if the participant remains unaware that learning has taken place. An implicit task can be contrasted with an explicit task, in which knowledge is measured via direct query (as in a recognition or recall test) and the participant is aware of having learned.

A number of researchers have used the serial response time (SRT) task to measure implicit perceptual-motor sequencing. In this task, participants perform a choice response time task (typically with four stimuli), but unbeknownst to the participant, the stimuli appear in a repeating sequence (often 10 or 12 units long). With training, many participants show a decrease in RTs when the stimuli appear in the sequence and an increase in RTs when the stimuli appear randomly. Furthermore, many participants show this pattern of RTs when tested for implicit learning, but perform poorly on explicit measures of learning such as recognition, cued recall, or free recall

(Cohen et al., 1990; Nissen & Bullemer, 1987; Reed & Johnson, 1994; Willingham et al., 1989).

One question of interest is "What exactly do participants learn in this task?" The experimenter presents a sequence of stimuli, but in order to complete the task, on each trial the participant must select a response key to depress and program the appropriate muscles in order to press the key. Thus the participant experiences a repeating sequence of stimuli, of response selections, and of muscle movements. The participant might learn any one or more of these sequences.

Howard, Mutter, and Howard (1992) have suggested that implicit sequence learning is largely perceptual. Participants in their experiment either performed the SRT task or merely observed the stimuli. In a transfer phase, all participants responded, and the participants observing the task showed as much sequence knowledge as did those who had responded (as assessed by the RT difference between sequenced and random trial blocks). It is possible, however, that the participants observing the task relied on explicit knowledge; in a cued recall test after the transfer phase, they could produce, on the average, 95% of the sequence, and explicit knowledge of the sequence can support improved RTs (Curran & Keele, 1993). This possibility was confirmed in a recent replication of the Howard et al. design, which showed that when the participants who had significant explicit knowledge were removed from the analysis, the participants who merely observed the stimuli did not show implicit sequence knowledge (Willingham, 1999).

Mayr (1996) suggested that implicit sequence learning can be either perceptual or motor. In his experiment, the

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proper response was dictated by which of four objects appeared on the screen, but the object could appear in one of four places. Thus, the experimenter could present one sequence of locations in which the objects appeared and another sequence of objects (and therefore, of responses). Mayr reported that participants could learn both types of sequences. It may be, however, that the apparent perceptual learning (i.e., the sequence of locations) was actually supported by motor learning; the participants may have learned a sequence of eye movements. This hypothesis is supported by an experiment in which Willingham et al. (1989, Experiment 3) used a similar paradigm. In that experiment, the participants responded to the color of the stimulus, but in some conditions the stimuli appeared in a repeating sequence of locations. Willingham et al. reported no learning if the colors of the stimuli appeared at random (and therefore, responses were random), even if the stimuli appeared in a repeating sequence of locations. The stimulus locations were closer together in Willingham et al.'s experiment than in Mayr's which may have been why their participants did not learn eye movements.

Ziessler (1994) used a different version of the SRT task, which also had a visual search component and in some cases mapped many stimuli onto a single response. Ziessler found that sequence learning was weak if a single response was used for most stimuli. Learning was robust only when each stimulus called for a distinct response. Ziessler concluded that learning could not be purely perceptual.

Willingham (1999) also argued that learning is not purely perceptual. In one experiment, participants who were trained with one set of stimuli (centrally presented digits) showed excellent transfer when a different set of stimuli (spatial cues) was used at transfer. In another experiment, participants were trained on the sequence, but the task used an incompatible mapping—the correct response location was one position to the right of the stimulus location. At transfer, all participants used a compatible mapping. For some participants, the stimulus sequence was the same (and hence, the response sequence was different), and for others, the stimulus sequence was changed in such a way that the response sequence matched what it had been during training. The participants seeing different stimuli but making the same responses showed excellent transfer; the participants seeing the same stimuli but making different responses showed no transfer at all.

In summary, the data seem to indicate that implicit perceptual-motor sequence learning is not purely perceptual. There are also data indicating that it is not purely motoric, meaning that it is not represented as a particular set of muscle commands. Cohen et al. (1990) had participants respond by using four fingers on the four response keys during training, and then switch to using a single finger, like a hunt-and-peck typist at response, and found excellent transfer. Keele et al. (1995) reached the same conclusion in a more complete set of experiments examining the effect of changing effectors.

If implicit perceptual-motor sequence learning is not represented as a sequence of stimuli or as a sequence of motor responses, what exactly are the participants learning? Elsewhere I have suggested that implicit sequence learning is represented as a sequence of response locations (Willingham, 1998). This proposal is based on the idea that a motor response is initially represented spatially; a target is selected as the end point of the movement, and this target is defined in egocentric space—that is, in space defined relative to part of the body. Later in processing, this spatial target is translated into a pattern of muscle movements to move the effector to the spatial target (see Willingham, 1998, for details). Motor sequences are represented as sequences of these spatial targets.

The available evidence from the SRT task appears to be consistent with this proposal, but the evidence is exclusively negative; the evidence indicates that implicit motor sequences are not purely perceptual, and that they are not specific to an effector, leaving open the possibility that they are represented in terms of spatial locations of responses. Our purpose in the two experiments reported here was to test this proposal directly, which had not been done in previous research.

EXPERIMENT 1

In this experiment, we tested the effect of changing the position of the response locations. If motor sequence learning is coded as a sequence of response locations, such a change at transfer should be devastating to learning. The participants responded on a keyboard with the response keys arranged in one of two spatial patterns. At transfer, the participants either switched keyboards or continued to use the same keyboard.

Method

Participants. Ninety-six undergraduates (37 male) at the University of Virginia participated in return for extra credit in an introductory psychology course. The participants were randomly assigned to conditions.

Stimuli and Apparatus. The participants used one of two response boards. Each board measured 34.5×23.5 cm and was mounted with four response keys (Radio Shack No. 275-1566). The response keys were configured either as a horizontal line (center-to-center key distance = 4 cm) or as a diamond (center-to-center key distance = 13 cm).

Stimuli were generated on a video monitor controlled by a Macintosh IIci computer. The four possible stimulus locations were signified by four boxes, each 2 cm square. They were arrayed in a lopsided diamond, as in Figure 1, so that the stimulus-response mapping would be compatible with either keyboard. The keyboard configurations are also shown in Figure 1. The approximate center-to-center distance of adjacent boxes was 5 cm. The stimulus on each trial was an asterisk (approximately .3 cm in diameter) appearing in the center of one of the boxes.

Procedure. There were three conditions. In the *switch* condition, the participants used one keyboard during the training phase and the other keyboard during transfer. In the *no-switch* condition, the participants used the same keyboard in both phases of the experiment. The *random* condition provided a control group; these partic-

Figure 1. Stimulus configuration and response boards used in Experiment 1.

ipants did not see a sequence during the training phase, but did see one at transfer. Thus, the random condition provided a measure of how much learning could occur within the single sequenced block at transfer. The participants in the random condition switched keyboards between training and transfer.

All participants were instructed to use the index finger of their preferred hand to make all responses. On each trial, an asterisk appeared in one of the four stimulus locations and the participant pushed the corresponding response key, whereupon there was a 250-msec pause, after which a new stimulus appeared. If the participant pushed the wrong key, a brief (120-msec) tone sounded, and the participant had to try again.

Each trial block was composed of 96 stimuli. During training, the participants in the switch and no-switch groups performed five trial blocks in which the stimuli appeared in a repeating sequence, with a final random block. The random group saw only random stimuli during training. Trial blocks were separated by 45-sec rest breaks. For the switch and the no-switch groups, the repeating sequence was selected from a corpus of 563 twelve-unit sequences, each of which met the following constraints: The same stimulus could not appear on successive trials; each stimulus appeared an equal number of times; the sequence could not contain runs (e.g., 1234) or trills (e.g., 1313) of four units.

The transfer phase was composed of four trial blocks. For the participants in all three conditions, the first two blocks were random, the third was sequenced, and the final was random. The participants in the switch condition used a different keyboard at transfer, and the participants in the no-switch and the random conditions used the same keyboard that they had used during training. The assignment of keyboard (line or diamond) was counterbalanced across conditions.

At the end of the transfer phase, the participants' explicit knowledge of the sequence was measured. The participants were told that the stimuli had appeared in a repeating sequence and were asked to reproduce the sequence on the keyboard in a free recall task. Participants could use either keyboard they chose. Their responses were echoed on the screen. They were told to push the "Q" button when they had produced as much of the sequence as they could remember. A maximum of 13 responses was allowed.

Results and Discussion

Four of the participants did not follow instructions to maintain high accuracy. The criterion was that accuracy should not fall below 80% correct on any trial block. These 4 participants were removed from all other data analyses (2 from the switch condition, and 2 from the random condition).

Two keyboards were employed in this experiment (line and diamond), and the type of keyboard was counterbalanced with condition (switch, no-switch, random). The type of keyboard had no influence on RTs or accuracy in any analysis, and so all analyses were conducted a second time, excluding this factor. These analyses are reported here, and type of keyboard is not mentioned again.

Response times. RTs were summarized by finding the median RT of each set of 12 responses, yielding 8 medians for each trial block for each participant. The mean of these 8 medians was calculated, which served as the summary RT measure for each trial block for each participant. The mean RTs across training and transfer are shown in Figure 2, separated by condition. As expected, the two groups seeing a sequence during training (switch, no-switch) showed greater improvement in RTs than did the group that did not see a sequence (random). Furthermore, these two groups showed an increase in RTs on the final block of training when they too saw random stimuli. These impressions from the figure were confirmed in an analysis of variance (ANOVA) showing a reliable effect of trial block [$F(5,445) = 79.0$, $MS_e = 2,327.6$, $p < .001$] and showing that this effect of trial block varied across training groups [$F(10, 445) = 2.0$, $MS_e = 2,327.6$, $p < .05$]. The main effect of condition was not reliable ($p > .20$).

To better assess the effect of sequence learning, a learning measure was derived by subtracting Block 5 RTs from Block 6 RTs—in other words, by examining the extent to which RTs changed when the participants who had seen a sequence began to see random stimuli. This measure was likely to be the purest measure of sequence knowledge. The simple reduction in RTs with practice on Blocks 1–5 could reflect learning the sequence but could also be due to learning the stimulus–response mapping, the response–stimulus interval, and so on. An ANOVA of this learning measure showed that, as expected, the participants seeing the sequence (switch, no-switch) showed a greater decrement than did the participants seeing random stimuli [$F(2,89) = 7.8$, $MS_e = 3,945.7$, $p < .001$].

For this experiment, the crucial data were those at transfer. There was a main effect of trial block [$F(3,267) = 57.3$, $MS_e = 1,019.1$, $p < .001$], which is not surprising, given that the third block was sequenced as in training, whereas the others were random. The key question was whether performance would differ across blocks, depending on whether the participants were using the same or different keyboard; and the answer was that it did [$F(6,267) = 7.2$, $MS_e = 1,019.1$, $p < .001$].

A learning measure was derived for the transfer phase; the RT of the sequenced block (Block 9) was subtracted from the mean of the two neighboring random blocks (Blocks 8 and 10). An ANOVA of these learning scores showed that the three groups differed [$F(2,89) = 12.8$, $MS_e = 1,843.2$, $p < .001$], and follow-up tests showed that the participants using the same keyboard that they had used at training showed better sequence knowledge than did the participants who had switched keyboards and then

Figure 2. Response times across training and transfer, separated by condition, for Experiment 1. Error bars are standard errors. R, random stimuli; S, sequenced stimuli.

the control participants who had never seen a sequence ($F_s > 12$). The participants who had switched keyboards showed no more sequence knowledge than did the participants who had never seen a sequence at all ($p > .20$).

Accuracy. ANOVAs of the accuracy data showed a reliable effect of trial block [$F(5,445) = 2.7$, $MS_e = 2.3$, $p < .05$], which reflected a general tendency among all conditions to become gradually less accurate from the first block (mean = 98.0% correct) to the last block (mean = 97.6% correct). Other effects did not approach reliability ($p_s > .10$). Although the mean decrease was quite small, the effect was reliable because the variability was extremely low.

The same pattern was observed at transfer. There was a main effect of trial block [$F(3,267) = 2.7$, $MS_e = 1.7$, $p < .05$], which was due to the final trial block accuracy's being slightly lower than that for the first three (97.7 vs. 98.1 or 98.2).

These accuracy effects were not of a pattern that would raise concerns about a speed-accuracy tradeoff.

Explicit knowledge. The data of 1 participant from the switch condition was lost because of computer failure. The free recall test was scored by summing the total number of positions correctly recalled, whether they were consecutive or not. To be considered correctly recalled, a position had to be part of a segment of at least length

3. For example, if a participant simply recalled "14," the score would be 0 even if "14" appeared in the sequence the participant saw because "14" appears in so many 12-unit sequences that it could easily be a chance occurrence. Suppose that the participant saw the sequence 314324123142. If the participant produced "123432" on the free recall test, the score would be 6 because both "123" and "432" occur in the sequence. If the participant produced "2413412," the score would be 4. Both "241" and "412" appear in the sequence, but they overlap, and the participant would get credit for recalling the overlapping "41" only once.

The free recall scores are shown in Table 1. An ANOVA showed that there was no reliable difference among the means of the three conditions [$F(2,88) = 2.8$, $MS_e = 9.1$, $p = .07$]. In other words, the participants who had seen the pattern during training showed no more explicit knowledge than did the participants who had seen the pattern for just one block of trials at transfer. The high free recall scores of the random participants may have been due to the rather liberal scoring method for the free recall task or due to some explicit knowledge's having been acquired by the participants during the single sequenced block in the random condition.

Although there was not good evidence for reliable explicit knowledge, it should be noted that the effect was

Table 1
Free Recall, Experiment 1

Positions Recalled	Condition		
	No-switch	Switch	Random
0-2	2	4	9
3-5	12	16	9
6-8	12	6	12
9-12	6	3	0
<i>M</i>	5.8	4.5	4.1
<i>SE</i>	0.5	0.6	0.6

marginal ($p = .07$), that the participants in the no-switch group showed the greatest explicit knowledge in absolute terms, and that this group showed the greatest implicit knowledge at transfer. As can be seen from the breakdown in Table 1, the greatest difference occurred among the participants who remembered the nine or more positions. Several participants who had seen the sequence reached this level of explicit knowledge. A second analysis of the RT data was therefore undertaken in which all participants with scores of 9 or greater on the free recall measure were removed. This procedure resulted in the removal of 6 participants from the no-switch group, 3 participants from the switch group, and none from the random group. Not surprisingly, an ANOVA showed no reliable difference among groups on the free recall measure [$F(2,79) = 1.2$, $MS_e = 6.4$, $p = .30$]. The RT effects on the transfer task remained robust, however, with the no-switch group still showing excellent transfer relative to the random and the switch groups ($F > 7$), which did not differ from one another ($F < 1.5$). Another analysis showed that explicit knowledge scores (free recall) were indeed correlated with implicit knowledge at transfer ($r = .31$, $p < .01$); this correlation was mediated almost entirely by outliers, however. When the participants with free recall scores of 11 or 12 ($N = 5$) were removed from the analysis, the correlation was no longer reliable ($r = .07$, n.s.). In summary, it appears that the excellent transfer observed by the no-switch group and the lack of transfer observed in the switch group was not due to differences in explicit knowledge for two reasons: There was little difference in the amount of explicit knowledge in the first place, and when participants with significant explicit knowledge were removed from the analysis, the pattern of transfer effects was unchanged.

The switch group may show some residual knowledge. It is possible that this knowledge would be observable, given greater statistical power. This may be true, and it may be due either to a small learning effect of the consistency of the motor requirements for eye movements at transfer in the switch condition, or to a parallel attentional learning system apparently much less important to performance. We, of course, cannot conclude on the basis of these data that such a system does not exist.

Experiment 1 showed that changing the response locations eliminated implicit sequencing knowledge, even if the sequence of stimulus positions was identical. Naturally,

the sequence of motor movements must change if the sequence of response locations changed. In Experiment 2, we examined the effect of changing the sequence of motor movements when the sequence of response locations was unchanged.

EXPERIMENT 2

Method

Participants. Eighty undergraduates (36 male) at the University of Virginia participated in return for extra credit in an introductory psychology course. The participants were randomly assigned to condition.

Stimuli and Apparatus. The stimuli and types of responses were the same as those in Experiment 1, with two exceptions: First, only the line keyboard was used. Second, the stimulus positions were arrayed in a horizontal line with a center-to-center distance of 5 cm, and centered vertically.

Procedure. The procedure in this experiment was identical to that of Experiment 1, with the exception of the conditions. In Experiment 2, the participants in three of the conditions were asked to position the index and middle finger of each hand on the response keys, but with their hands crossed, as in Figure 3. At transfer, the participants in all conditions responded with their hands uncrossed.

The participants in the *random* condition did not see a sequence during training, and so they saw a sequence for the first time at transfer. As in Experiment 1, this control condition allowed the assessment of sequence learning possible within a single block of trials. In the *fingers* condition, the stimuli were changed at transfer so that responding required the same sequence of finger movements used during training, but because the hands had been uncrossed, the response locations were necessarily different. In the *locations* condition, the stimuli were the same at transfer as they had been during training; thus, the same sequence of response locations was required, but with a different sequence of finger movements. In the *both* condition, the participants did not cross their hands during training; thus, at transfer, both the finger sequence and the response location sequence matched the training condition.

Results and Discussion

Three participants did not follow the instructions to maintain high accuracy. The criterion was that accuracy should not fall below 80% correct on any trial block. These 3 participants were removed from all other data analyses

Figure 3. Stimulus configuration, response board, and position of participants' hands at training (left) and transfer (right) for Experiment 2.

Figure 4. Response times across training and transfer, separated by condition, for Experiment 2. Error bars are standard errors. R, random stimuli; S, sequenced stimuli.

(2 from the fingers condition, and 1 from the random condition).

Response times. RTs were summarized as in Experiment 1. The RTs for the training phase are presented by condition across trial blocks in Figure 4. The results of an ANOVA show that there was an effect of condition [$F(3,72) = 5.7$, $MS_e = 41,630$, $p < .01$], which was due to the participants in the both condition responding quickly because their hands were not crossed. There was also a reliable effect of trial block [$F(5,360) = 73.4$, $MS_e = 1,071$, $p < .001$], because the participants improved across trial blocks, and a reliable interaction [$F(15,360) = 2.6$, $MS_e = 1,071$, $p < .01$], because RTs of the participants who had seen a sequence slowed on the sixth trial block when the stimuli began to appear randomly. As in Experiment 1, a learning measure for training was derived by subtracting RTs for the fifth trial block from RTs for the sixth trial block. An ANOVA showed a difference in learning among the four conditions, reflecting the fact that the participants observing the sequence responded more slowly on the sixth trial block, whereas the participants observing only random stimuli did not [$F(3,73) = 7.0$, $MS_e = 2,042$, $p < .001$].

At transfer, there was a reliable effect of trial block [$F(3,216) = 35.2$, $MS_e = 672$, $p < .001$], but neither a main effect of condition nor an interaction ($ps > .10$). This analysis did not, however, focus on the crucial difference of interest—the effect of the single sequenced trial block—and so a second analysis was conducted, employing a difference score of RTs to this sequenced block and the mean of the neighboring random blocks, just as in Experiment 1. These data are shown in Figure 5. This analysis showed a reliable effect of condition [$F(3,72) = 4.8$, $MS_e = 796$, $p < .01$]. Follow-up analyses showed that learning was greater in the locations condition than in the random or the fingers condition ($F_s > 6.5$, $ps < .05$). Learning in the locations condition was equivalent to learning in the both condition ($F < 1.0$). Thus, transfer of learning is excellent when the sequence of response locations is maintained; there is no cost to changing the sequence of finger movements, so long as the sequence of response locations is maintained. Maintaining the sequence of finger movements offers no benefits at transfer, however. The participants in this condition showed no more knowledge of the sequence than the participants who had not seen the sequence during training at all.

Figure 5. Summary learning measure at transfer for Experiment 2. Error bars are standard errors.

Accuracy. The accuracy data did not show a main effect of condition [$F(3,72) = 1.7$, $MS_e = 40.5$, $p = .16$], but did show a marginal effect of trial block [$F(5,360) = 2.2$, $MS_e = 4.3$, $p = .058$], although the mean accuracy across these blocks varied only between 95.6 and 96.3% correct. There was a reliable interaction [$F(15,360) = 2.2$, $MS_e = 4.3$, $p < .01$]. These accuracy data are shown in Figure 6. As can be adduced from the figure, this interaction was not easy to characterize.

Accuracy at transfer were the more crucial data, and they are also shown in Figure 6. The main effect of condition approached reliability [$F(3,72) = 2.4$, $MS_e = 29.2$, $p = .07$], but the effect of trial block and the interaction did not ($F_s < 1.5$, $p_s > .20$). As in Experiment 1, there were some marginal effects on accuracy, but these effects did not reflect sequence learning, nor did they indicate speed-accuracy tradeoffs with RT.

Explicit knowledge. The free recall test was scored as in Experiment 1, and the results are shown in Table 2. An ANOVA showed that there was not a reliable difference among the means of the four conditions [$F(3,71) = 0.7$, $MS_e = 6.6$, $p > .20$]. It is nevertheless possible that a few participants had substantial explicit knowledge. The analyses of RTs were therefore conducted a second time, excluding subjects who correctly recalled nine positions

or more of the sequence. The results of the analyses described above were qualitatively unchanged.

GENERAL DISCUSSION

In Experiment 1, when the response locations were changed, the participants showed little or no transfer of sequence knowledge even though the perceptual sequence of stimuli was retained. In Experiment 2, when the response locations were changed, the participants showed little or no transfer of sequence knowledge, even though the motor sequence of responses was retained. It would seem, then, that the sequence of response locations must be retained in order for implicit sequence knowledge to transfer.

What Is Learned?

An alternative explanation would be that implicit sequences are represented as stimulus-response bonds, a suggestion one of us made in an earlier paper (Willingham et al., 1989). This explanation is belied by other data, however. Willingham (1999, Experiment 2) found excellent transfer when the stimuli were changed from centrally presented digits to spatial cues (and the sequence of response locations was retained). That change in stimuli

Figure 6. Accuracy across training and transfer, separated by condition, for Experiment 2. Error bars are standard errors. R, random stimuli; S, sequenced stimuli.

would also entail a change in stimulus–response bonds. In another experiment (Willingham, 1999, Experiment 3), it was shown that sequence learning transferred even if the stimulus–response mapping was changed, as long as the sequence of response locations was retained. This change in stimulus–response mapping necessitates a change in the stimulus–response pairings at transfer.

One might note that training appeared to vary between the experiments. In Experiment 1, the participants used a single finger to make all responses, whereas in Experiment 2 they used one finger assigned to each response key. It may seem plausible that learning could differ depending on the effector used at training. Keele et al. (1995) examined this question, training participants on the sequence with either a single finger or four fingers, and either maintaining or changing the effector assignment at transfer. They reported complete transfer when effectors were changed, making it unlikely that the type of representation depended on the effector used during training.

Another possibility is that implicit sequence learning is not represented as a spatial sequence of response locations. Rather, it may be represented as a sequence of response selections. A response selection is a hypothetical

stage of processing in a motor task wherein the participant decides what to do in response to the stimulus after it has been identified (Welford, 1984). If one were to define this stage quite abstractly, one might propose that it would be possible to “decide what to do” in response to a stimulus without committing to a specific spatial nature of response. Such a hypothesis is a little difficult to put clearly, given that responses in the task seem to be defined largely by their spatial nature, so it is hard to separate such an account from the one that we propose. Nevertheless, an account of this sort may be consistent with an experiment reported by Keele et al. (1995).

Keele et al. (1995) reported transfer of implicit sequence learning when participants changed from making key responses (as in the present experiments) to making verbal responses. In their experiment, during the training phase, the participants performed the SRT task by making either keypress responses, or verbal responses. There were only three stimulus locations (unlike the four used here) and so the verbal responses were the words “left,” “right,” or “middle.” In addition, the participants were required to simultaneously perform a secondary task. After each stimulus, a high-pitched or low-pitched tone would

Table 2
Free Recall, Experiment 2

Positions Recalled	Condition			
	Locations	Fingers	Both	Random
0-2	1	0	3	2
3-5	5	6	7	8
6-8	10	11	7	7
9-12	2	3	3	2
<i>M</i>	5.8	5.8	4.9	5.1
<i>SE</i>	0.4	0.6	0.6	0.6

sound, and the participants were required to categorize it. If they were making keypress responses on the SRT task, they said "high" when the high-pitched tone sounded (and said nothing for the low-pitched tone). If they were making verbal responses to the SRT task, they pushed a key when the high-pitched tone sounded, and did nothing for the low-pitched tone. At transfer, all participants used verbal responses for the SRT task. The experimenters reported that the participants who maintained the same responses made during training showed a learning measure of about 100 msec. (Keele et al. defined a learning measure the same way it was defined here.) The participants who switched from keypresses to verbal responses showed a learning measure of 34 msec in one experiment and 47 msec in another.

Thus, Keele et al. (1995) reported that transfer was not perfect when participants switch from manual responses to verbal responses, but there was some transfer. The hypothesis proposed here predicts that there should have been no transfer at all. Why was there partial transfer? We disagree with Keele et al.'s statement that the transfer represented knowledge tied to the stimuli, because that explanation appears inconsistent with other data, as described earlier. One possible explanation is that some participants might have had some explicit knowledge of the sequence, which was recruited to improve RTs (Curran & Keele, 1993). Keele et al. used a dual-task paradigm, and the secondary task should have significantly reduced the likelihood that participants would become aware of the sequence. Nevertheless, a number of factors make it plausible that these participants did learn some of the sequence explicitly. Keele et al. used a rather short sequence—just 5 units long, as opposed to the 12-unit sequence used here. The sequence was repeated 160 times during training (as opposed to 40 times in the present experiments). The experimenters did test for explicit knowledge, but their test may not have been the most sensitive possible. The participants were asked whether or not they noticed a sequence, and only if they answered positively were they asked to reproduce it. Therefore, a participant who had some explicit knowledge, but lacked the confidence to say so, would have been classified as having no explicit knowledge. We believe that this undetected explicit knowledge in some of the participants might have led to what appeared to be transfer of implicit knowledge across response modalities.

Another recent experiment by Grafton, Hazeltine, and Ivry (1998) appears inconsistent with the present position.

Participants learned a sequence using a small keyboard similar to that used here and then were asked to respond to stimuli using large response paddles that were farther apart. This result is, in a sense, not surprising. Translations of scale for motor skill are well known, the most commonly observed being that handwriting, which is practiced at a small scale on paper, readily transfers to a much larger scale when written on a chalkboard, with little or no cost. One possible explanation is that sequences are coded in egocentric space, but that this space maintains only ordinal representations, not precise metric ones. Another possibility is that the metric representations can be scaled, as long as they maintain their relative positions. This issue remains to be investigated.

Egocentric and Allocentric Space

The hypothesis proposed here should not be interpreted to mean that sequence learning can never rely upon knowledge of perceptual sequences. Recently, one of us (Willingham, 1998) has proposed that when sequences are learned implicitly, they are learned in terms of response locations, which are coded in egocentric space, a spatial frame that codes the locations of objects relative to part of the body. When sequences are learned explicitly, they are coded in allocentric space, a spatial frame in which the locations of objects are coded relative to one another. Allocentric space is not a fixed spatial frame; there is not a set of world-wide landmarks that fix the spatial frame. For example, the location of a pencil can be located relative to the boundaries of a room (it's in the back-right corner), or relative to a desk (it's in the front-left corner). Thus one object may be located within multiple allocentric frames. One would be likely to locate the pencil relative to the room if it was necessary to walk to the pencil to get it, and one would be likely to locate the pencil relative to the desk if one were sitting at the desk and wanted to grasp the pencil.

Other researchers have proposed that allocentric representations support conscious perception, whereas egocentric representations are privileged to the motor system (Bridgeman, 1991; Jeannerod, 1994; Paillard, 1991). Willingham (1998) suggested that this distinction extends to motor-skill learning as well; allocentric representations support explicit, conscious learning, and egocentric representations support implicit learning, which is privileged to the motor system. We propose that explicit learning can be coded in terms of stimuli, response locations, or body movements, as a matter of strategy for the participant. Nevertheless, if the participant codes the sequence in terms of response locations, it will still be coded in allocentric space, unlike the egocentric representation we argue is used here. These predictions remain to be tested.

Neuropsychological Implications

The interpretation offered here is broadly consistent with existing neuropsychological data. Lesion studies show that patients with basal ganglia abnormalities—patients with Huntington's and Parkinson's diseases (HD and PD)—are impaired in learning the sequence in the SRT

task (Jackson, Jackson, Harrison, Henderson, & Kennard, 1995; Willingham & Koroshetz, 1993), and these same patients also have problems sequencing motor acts. HD and PD patients also show signs consistent with frontal lobe damage (see, e.g., Salmon, Pow, Heindel, Butters, & Thal, 1989), and indeed, patients with lesions restricted to the frontal lobe also show sequencing deficits on certain tasks, such as temporal memory (Shimamura, Janowsky, & Squire, 1990), just as basal ganglia patients do (Sagar, Sullivan, Gabrieli, Corkin, & Growdon, 1988). Nevertheless, this deficit in frontal patients may not extend to implicit motor sequencing, since at least some patients seem to be minimally impaired on the SRT task (Marks, Cermak, & Grafman, 1998; Marks, Wild, Higgins, Massaquoi, & Grafman, 1998). Neuroimaging data also support the contention that sequence learning is rooted in the motor system. Studies using positron emission tomography (Grafton, Hazeltine, & Ivry, 1995) implicate the basal ganglia and primary and secondary motor cortices in sequence learning.

Thus, the behavioral data from the neurologically intact participants presented here are in line with the neuropsychological data because both have a basis for learning rooted in the motor system—motoric not in the sense of muscle movements, but in the sense of selecting targets for motor movements. Future work may be directed at determining whether or not they are represented in egocentric space, and if so, on what part of the body the egocentric spatial frame is centered.

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