Independent Processing of the Temporal and Ordinal Structure of Movement Sequences

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Ullén, Fredrik and Sara L. Bengtsson. Independent processing of the temporal and ordinal structure of movement sequences. J Neurophysiol 90: 3725–3735, 2003; 10.1152/jn.00458.2003. We investigated if the temporal and ordinal structures of sequences can be represented and learned independently. In Experiment 1, subjects learned three rhythmic sequences of key presses with the right index finger: Combined consisted of nine key presses with a corresponding temporal structure of eight intervals; Temporal had the temporal structure of Combined but was performed on one key; Ordinal had the ordinal structure of Combined but an isochronous rhythm. Subjects were divided into two groups. Group 1 first learned Combined, then Temporal and Ordinal; Group 2 first learned Temporal and Ordinal, then Combined. Strong transfer effects were seen in both groups. In Group 1, having learned combined facilitated the learning of the temporal (Temporal) or ordinal (Ordinal) sequence alone; in Group 2, having learned Temporal and Ordinal facilitated the learning of Combined, where the two are combined. This supports that subjects had formed independent temporal and ordinal representations. In Experiment 2, we investigated if these can be learned independently. Subjects repeatedly reproduced sequences with fixed temporal and random ordinal structure; random temporal and fixed ordinal structure; and random temporal and ordinal structures. Temporal and ordinal learning was seen only in the first and second sequences, respectively. In summary, we provide evidence for the existence of independent systems for learning and representation of ordinal and temporal sequences and for implicit learning of temporal sequences. This may be important for fast learning and flexibility in motor control.

INTRODUCTION

An important question in neuropsychology is how sequential movements are represented by the CNS. A traditional view in motor control theory has been that movement sequences are controlled by generalized motor programs (see e.g., Schmidt 1999). A key feature of this concept is that the ordinal structure (i.e., serial order) and the temporal structure (i.e., relative timing) of the movements remain constant once a particular sequence is learned, while other global parameters of the motor program, e.g., overall duration or overall force, can be varied depending on performance demands. That relative timing is an invariant feature of an overlearned movement sequence was indicated by several early studies. Summers (1975) taught subjects to perform a sequence of finger presses with a particular temporal structure; when subjects subsequently performed the same sequence at maximum speed, the rhythmical structure of the sequence was, to some extent, preserved. A fixed relative timing of the component movements during performance at different speeds and over long periods of time was also demonstrated for skills such as typing, piano playing, and handwriting (Armstrong 1970; Schmidt 1999; Shaffer 1980; Shapiro 1977; Viviani and Terzuolo 1980). These findings were taken as evidence for an integrated representation of ordinal and temporal sequential structures.

More recent studies have examined the learning of sequential information using the serial reaction-time (SRT) paradigm (Nissen and Bullemer 1987). This is a choice reaction-time task, where a sequence is presented as a series of stimuli, usually of visual modality. The correct response to each stimulus depends on some stimulus property, such as location or shape. When stimuli follow a fixed sequence, reaction times decrease as learning of the sequence progresses. Typically, the time interval between one response and the subsequent stimulus presentation (the response-stimulus interval, RTI) is kept constant, so that the time interval between two consecutive stimuli is the sum of the subject’s reaction time and the RTI (see e.g., Clegg et al. 1998; Nissen and Bullemer 1987). In a few studies, the RTIs have been varied systematically to study either the influence of timing on the learning of the ordinal structure of the sequence (Frensch and Miner 1994; Stadler 1993, 1995; Willingham et al. 1997) or the learning of temporal structures per se (Lee 2000; Shin and Ivry 2002). The SRT paradigm has proved extremely useful for studies of various questions related to the learning of ordinal information. However, results on the learning of temporal sequences have been less clearcut.

Lee (2000) found indications of an independent representation of temporal information when training three subjects to perform a sequence of 18 hand movements to different spatial targets with RTIs consisting of alternating long and short time intervals. When this temporal structure was phase-shifted one step in relation to the ordinal structure, deficits in performance were very small. This was taken as an indication that subjects had formed independent representations of the ordinal and the temporal structure (Lee 2000). However, an alternative explanation could be that the learning of this particular temporal pattern, which had only two intervals, was so rapid that no substantial decreases in performance were seen in the phase-shifted condition. That temporal and ordinal learning rather may be integrated processes was suggested by an extensive study of the learning of rhythmic sequences by Shin and Ivry...
(2002). They used sequences of visual stimuli, where the correct response — a key press on one of four different keys — was determined by the spatial location of the stimulus. Two parameters were manipulated: a temporal sequence of either RTIs or stimulus onset intervals was used and the temporal and ordinal structure of the stimuli were either correlated, i.e., of the same length and always with the same starting point, or uncorrelated, i.e., of different lengths. Significant learning of the temporal sequence was found only when stimulus onset intervals were controlled and even then only in the correlated condition. The learning of the ordinal and temporal structure of a sequence are thus not completely independent processes. As noted by the authors, the question of whether this learning can result in the formation of independent representations of serial orders and rhythms remained unresolved (Shin and Ivry 2002).

However, for temporal sequence learning the SRT paradigm has two distinct disadvantages. First, when a temporal sequence of RTIs rather than stimulus intervals is used, the exact temporal structure of the stimuli used to present the sequence cannot be controlled because it is influenced by the reaction time of the subject. Second, even when stimulus onset intervals are controlled, learning of temporal information is assessed by comparing reaction times on a probe trial with sequential temporal structure and random ordinal structure with reaction times on another probe trial where both temporal and ordinal structures are random (Shin and Ivry 2002). When the ordinal structure is random, the subject will be unable to prepare the next response in the sequence in advance even if the temporal structure of the sequence is learned because the identity of the next key press is unpredictable. Consequently, learning of temporal information could occur without significant decreases in reaction time, and thus be underestimated with this method.

Here, we performed two experiments to directly investigate the representation and learning of temporal and ordinal sequential structures, respectively. In Experiment 1, we used a learning transfer paradigm to test the hypothesis that independent representations of the temporal and ordinal structure of movement sequences can indeed be formed. This hypothesis leads to two predictions. First, having learned a sequence with a certain temporal and ordinal structure should strongly facilitate the subsequent learning of the same temporal structure alone, and the same ordinal structure using a regular rhythm. Second, having learned a ordinal structure and a temporal structure in isolation should strongly facilitate the subsequent learning of a sequence where the two are combined. We tested these predictions using explicitly timed sequences of key presses on a PC keyboard as a model behavior. A training paradigm where the subjects produced complete sequences from memory was used so that both ordinal and temporal accuracy could be measured from the subjects’ responses.

In Experiment 2, we investigated whether independent processes for learning of temporal and ordinal information exist. As in Experiment 1, subjects reproduced rhythmic sequences of key presses on the PC keyboard. Three types of sequential stimuli were used in three tasks: sequences with random temporal and fixed ordinal structure, sequences with fixed temporal and random ordinal structure, and sequences where both structures were random. The learning of temporal and ordinal information in each task was investigated. Furthermore, to investigate the role of conscious learning strategies, subjects were after each task given a questionnaire designed to evaluate their explicit knowledge of the ordinal and temporal structure of the sequences (see METHODS).

METHODS

This study includes two independent experiments. All subjects were right-handed (Oldfield 1971), and no subjects participated in both experiments. The experimental procedures were approved by the Ethical Committee of Karolinska Institutet (KI Forskningsetikkom­mitté Nord; Dnr 01-364).

In Experiment 1, 30 subjects participated. Of these, six were unable to learn at least one task within 60 min and therefore had to be excluded. Twenty-four subjects were thus used for analysis. These were 12 females and 12 males, aged between 20 and 46 yr, with a mean age of 26 yr. Twelve subjects participated in Experiment 2: six females and six males. All subjects were able to perform the task and were included in the analysis. Their age ranged from 21 to 35 yr, with a mean age of 30 yr.

Experiment 1

SEQUENCE TASKS. The experiment was performed using a conventional PC. Both sequence presentation and data collection were performed automatically using the E-Prime software package (Psychological Software Tools). Subjects performed rhythmic sequences of key presses with the right index finger on the keyboard of the computer. During the experiment, subjects were seated in front of the computer at a distance of ~1 m from the computer screen. The center key and the up, down, left, and right arrow keys of the numerical keypad were used for sequence production. During presentation of a sequence, these keys were schematically displayed on the computer screen (dimensions of each square: 6 × 6 cm; Fig. 1A). The sequences were presented audiovisually: the timing of a particular key press was marked by a brief (62 ms) drum sound, and the corresponding key was simultaneously displayed in red on the computer screen.

All subjects learned three different sequences, in different order for different groups of subjects (see EXPERIMENTAL PROCEDURE). These sequences are illustrated schematically in Fig. 1B. Three different temporal interval durations were used, all even multiples of 375 ms: 375, 750, and 1,125 ms. In Fig. 1, B and C, Arabic numerals (1–3) show the interval durations of the different sequences normalized to the duration of the shortest interval (375 ms). The first sequence, Combined, had an ordinal structure of a series of nine key presses and a corresponding temporal structure of eight temporal intervals. The second sequence, Temporal, had the same temporal structure as combined but was performed on the central key only, i.e., had an ordinal structure of one element. The third sequence, Ordinal, had the same ordinal structure as combined but a temporal structure of one element, i.e., a regular rhythm. In addition to these three sequences, 14 of the subjects learned a control sequence, Control, that had the same length of the temporal and ordinal structure as Combined (Fig. 1C; see next section).

EXPERIMENTAL PROCEDURE. Each sequence was learned in a single continuous session, without breaks, organized as depicted schematically in Fig. 1D. Before the session, subjects were given a brief instruction on the task and the experimental procedure. The session started with one presentation of the sequence. The subject subsequently tried to reproduce the sequence on the keyboard. The time point and identity of all key presses in the response were recorded on the computer hard disk. The number of temporal and ordinal errors in the response were thereafter calculated. The number of ordinal errors was defined as the number of instances where a wrong key was pressed. Before counting the number of temporal errors, all produced temporal intervals were normalized to the mean value of the shortest intervals in the sequence. In this way, only errors in relative timing, but not errors resulting from a too slow or too fast overall tempo, were taken into account. A temporal interval was counted as incorrect if its
normalized duration deviated >30% from the ideal value. In pilot experiments, we found that with this criterion all subjects were able to complete the task in reasonable time.

During the session, the subject was given feedback about his response by the computer program as follows. If the response contained at least one error, the subject was informed about the number of errors of each type and the sequence was presented again (Fig. 1D). If the sequence had been produced without any errors, temporal or ordinal, the subject was informed that the response was correct and instructed to reproduce the sequence again without a new sequence presentation (Fig. 1D). One such set of consecutive sequence reproductions, without an intervening sequence presentation, will be referred to as a block of reproductions. In the beginning of the learning session, each block typically consisted of a single erroneous reproduction. The learning session was terminated when the subject had produced 12 correct reproductions in a row.

To quantify transfer effects, subjects were divided into two groups, with 12 subjects in each group. Group 1 started by learning Combined and thereafter learned Temporal and Ordinal. The order of Temporal and Ordinal was balanced within the group, so that six of the subjects learned Temporal before Ordinal (i.e., task order Combined–Temporal–Ordinal), whereas the other six subjects learned Ordinal before Temporal (Combined–Ordinal–Temporal). Group 2 started by learning Temporal and Ordinal and thereafter learned Combined. Here too, the order of Temporal and Ordinal was balanced within the group: six subjects started with Temporal (Temporal–Ordinal–Combined), whereas the other six started with Ordinal (Ordinal–Temporal–Combined). In addition to these basic tasks, 14 of the subjects learned the additional sequence Control, to enable an estimation of nonspecific effects of training. Seven of these subjects learned Control first of all, i.e., before the three other sequences; the other seven learned Control as a final task after the other three sequences.

DATA ANALYSIS. The time points and identities of all key presses of all responses were recorded during the experiments. Statistical analysis was performed using Statistica (StatSoft). Learning transfer was estimated by between-group comparisons of the total number of failed reproductions before a particular sequence was learned, using the Mann-Whitney U test. Transfer effects were also analyzed within subjects by comparing the total number of failed reproductions required before learning of the different tasks, using the Wilcoxon matched-pairs test. Within-subject correlations of the duration of the same temporal interval, as performed in the temporal and combined tasks, were analyzed by calculating the Pearson product-moment correlation coefficient.
Experiment 2

EXPERIMENTAL PROCEDURE. Sequence presentation and data collection were performed as in Experiment 1: subjects were instructed to reproduce sequences, presented on the computer, with the right index finger on the numerical keypad. However, the experimental procedure and the sequential tasks were different in several respects. All sequences consisted of seven key presses separated by six temporal intervals. Only three different keys were used: the left and right arrow keys and the center key. The sequences were presented audiovisually as in Experiment 1 except that the timing of a particular key press was marked, not by a drum sound, but by a brief (62 ms) tone with different frequency depending on the key: left arrow key, 349 Hz; center key, 440 Hz; and right arrow key, 554 Hz. The same three different temporal interval durations were used as in Experiment 1: 375, 750, and 1,125 ms. Three different tasks were included in the experiment. For each task, the subject performed a session of 50 trials without a break. Each trial consisted of a sequence presentation and a subsequent reproduction by the subject. No feedback was given to the subject. The only instruction to the subject before each session was to repeat both the temporal pattern and the key sequence as accurately as possible in each trial.

In the first task, Fix Temporal, the sequences in all 50 trials of the session had a constant temporal structure (750–375–375–1,125–375–750; all in ms), while the ordinal structure was varying. The second task, Fix Ordinal, had a constant ordinal structure (left–right–center–right–left–center–left) but varying temporal structure. Random, the third task, had both varying temporal and varying ordinal structure. In Fix Ordinal and Random, the temporal structure of the sequence was set, in each trial, to a random permutation of the temporal intervals. Similarly, the varying ordinal structure of Fix Temporal and Random consisted of random permutations of the key sequence of Fix Ordinal with the constraint that the same key must not occur two or more times in a row. The order of the three tasks was balanced among the 12 subjects so that each of the total six possible task orders was used with two subjects.

DATA ANALYSIS. To quantify learning, the median number of correct key presses and correct temporal intervals were calculated for each trial in the different tasks, using data from all subjects. The same criterion for a correct temporal interval was used as in Experiment 1 (see preceding text). Correlations between trial number and number of correct responses were analyzed by calculating the Pearson product-moment correlation coefficient. In addition, within-subject comparisons (Wilcoxon matched-pairs test) were made of the median number of correct responses in the first five and the last five trials of each session to investigate if there was an improvement of performance in the temporal or ordinal dimension in each task.

To evaluate if subjects had explicit awareness of the structure of the different sequences, subjects filled out a brief questionnaire after each session, where they were asked if they noticed any pattern in the sequences and, if so, what pattern. This information was used to investigate if learning took place in those subjects that reported that they detected no regularities in the stimuli.

RESULTS

Experiment 1

LEARNING OF COMBINED IN NAIVE AND PRETRAINED SUBJECTS. To investigate if having learned Temporal and Ordinal would facilitate the subsequent learning of Combined, the number of trials required to learn combined was compared in subjects from Groups 1 and 2. Subjects in Group 1 learned Combined as first task. A typical example of a learning curve from one subject in Group 1 is illustrated in Fig. 2A. For each block of reproductions following a sequence presentation (see METHODS), the mean number of ordinal errors, i.e., erroneous key presses, and the mean number of temporal errors, i.e., too long or too short intervals, are plotted separately. Typically, these two parameters improved irregularly in parallel. In the illustrated example, the first correct reproduction of the sequence occurred in block 10 (Fig. 2A). In all subjects (n = 12), the ordinal structure was learned faster than (n = 10) or as quickly as (n = 2) the temporal structure (Fig. 2A). The mean number of additional failed reproductions, before the temporal structure was also learned, was 5.2. In most subjects, during the final phase of the training, the temporal structure thus continued to change, while coupled to a constant ordinal structure (see DISCUSSION).

The number of failed reproductions before Combined was learned in Group I subjects varied between 5 and 80 (M = 18). Learning of the same task in Group 2, which before that had learned Temporal and Ordinal, was significantly quicker (M = 4.5; P = 0.0003; Mann-Whitney U test; Fig. 2B). Two of the subjects in Group 2 could immediately perform Combined without errors (0 failed reproductions). For the remaining subjects (n = 10), some training was necessary to combine the previously learned ordinal and temporal structures.
LEARNING OF TEMPORAL AND ORDINAL IN NAIVE AND PRETRAINED SUBJECTS. Strong transfer effects were seen also on the Temporal and Ordinal tasks. Subjects in Group 2 learned these two tasks before Combined. Between 0 and 66 failed reproductions were seen before Temporal was learned in the Group 2 subjects ($M = 12.5$; Fig. 3A). Two subjects could immediately perform the task (0 failed reproductions). Group 1 subjects, which had learned Combined first, showed significantly quicker learning of Temporal ($M = 1; P = 0.015$; Fig. 3A). Notably, 11 of these 12 subjects had three or fewer failed reproductions with five subjects requiring no additional training at all (0 failed reproductions).

The number of failed reproductions required before Ordinal was learned in Group 2 subjects varied between 6 and 37 ($M = 13$; Fig. 3B). Here too, learning was significantly quicker in Group 1 subjects ($P = 0.0002$), which had between 0 and 13 failed reproductions ($M = 2$; Fig. 3B) before learning was complete. Four of these subjects could immediately perform the task correctly.

WITHIN-SUBJECT TRANSFER EFFECTS. The transfer effects revealed in the previous between-group analyses were also reflected in the amount of training required for each individual subject to learn the different tasks. Group 2 subjects first learned the Temporal and the Ordinal tasks and after that the more demanding Combined task where the temporal structure of Temporal had to be combined with the ordinal structure of Ordinal. In fact, learning of the more difficult Combined task was faster than the mean learning time for Temporal and Ordinal, in all Group 2 subjects, except one (Fig. 4A). For the whole group, the number of failed reproductions required to learn both Temporal ($M = 12.5$) and Ordinal ($M = 13$) was significantly higher than the number of reproductions required to subsequently learn Combined ($M = 4.5; P = 0.002$ for both comparisons, Wilcoxon matched-pairs test).

Similar transfer effects were seen in Group 1 subjects, who learned Combined first (Fig. 4B). The number of failed reproductions required to learn Combined in this group ($M = 18$) was significantly higher than for Temporal ($M = 1; P = 0.02$) and Ordinal ($M = 2; P = 0.002$). Learning of Temporal and Ordinal was faster than learning of Combined for all subjects in this group (Fig. 4B).

FIG. 3. Transfer effects on the Temporal and Ordinal tasks. A: the number of failed reproductions before temporal was learned in all naive (Group 2) and pretrained (Group 1) subjects. Pretraining with Combined resulted in a faster ($P = 0.015$) learning of Temporal. B: the same data for the Ordinal task. Pretraining with Combined resulted in a faster ($P = 0.0002$) learning of Ordinal.

FIG. 4. Transfer effects within subjects. A: the number of failed reproductions before Ordinal and Temporal (mean value) and Combined were learned by all individual subjects in Group 1. For all subjects except one, learning of the more demanding Combined task was faster ($P = 0.002$) than the previous learning of Temporal and Ordinal. B: the number of failed reproductions before Combined, and Temporal and Ordinal (mean value), were learned by all individual subjects in Group 2. For all subjects, learning of Temporal and Ordinal was faster ($P = 0.02$ and $P = 0.002$, respectively) than the preceding learning of Combined.
SPECIFICITY OF THE TRANSFER EFFECTS. To estimate how specific the observed transfer effects were to the particular temporal and ordinal structures employed, 14 subjects learned an additional Control task (see Fig. 1C), either before (n = 7) or after (n = 7) the other three tasks (see Methods). A faster learning of the Control task in the latter group should reflect improvements in the general ability to learn tasks of the studied type. However, learning of Control was significantly faster (P = 0.01; Mann-Whitney U test) in the group that trained this task at the beginning of the experiment, than in the group that trained it at the end (Fig. 5). The number of failed reproductions varied between 2 and 5 (M = 3) in the former group and between 3 and 56 (M = 16) in the latter one. The previously discussed transfer effects thus appear highly dependent on the fact that Combined, Temporal, and Ordinal share a particular temporal or ordinal structure and not due to general improvement of sequence learning ability (see Discussion).

PRESERVATION OF THE DETAILED TEMPORAL CHARACTERISTICS OF A SEQUENCE AFTER TRANSFER. In the analysis of the temporal structure of the subjects’ responses during training, only intervals that deviated >30% from the ideal value were counted as erroneous (see Methods). A certain amount of variability in temporal performance was thus permitted. The previously described transfer effects may be explained by the fact that the subjects formed and recombined independent representations of the temporal and ordinal structure of the sequences (see Discussion). If this is the case, one would predict that each subject's characteristic deviations from the ideal temporal pattern would be highly similar during performance of Temporal and Combined, regardless of which sequence was learned first, because the same representation would be used for the control of the temporal structure in both cases.

To investigate this, the temporal structure of the 12 responses in the last block of reproductions (i.e., the responses after the last presentation of the sequence; see Methods) during performance of Temporal and Combined, was analyzed for all subjects. While the detailed characteristics of the temporal structure varied substantially between subjects, individual subjects showed a remarkable consistency in these two tasks. Figure 6, A and B, shows the mean duration of all eight intervals in the sequence, during performance of Temporal and Combined, for two subjects that differed considerably from each other in their pattern of rhythmic deviations. The temporal patterns of Temporal and Combined, however, were highly similar within both subjects.

When pooling data from all subjects, high positive within-subject correlations were found for the duration of all individual temporal intervals of the sequence during performance of Temporal and Combined. Scatter plots of the mean duration of each of the eight intervals of the sequence, as performed by individual subjects in Temporal and Combined, are shown in Fig. 7. The correlation coefficients for different intervals varied between r = 0.65 and r = 0.86. All correlations were significant at P < 0.0001, except for interval 5, which was significant at P = 0.001 (Pearson product-moment correlation).

FIG. 5. Specificity of the transfer effects. The number of failed reproductions before the task Control was learned is shown for subjects that learned this task before and after the experimental tasks. A slower (P = 0.01) learning of Control was seen in the latter group.

FIG. 6. Rhythmic patterns performed by two subjects in the Temporal and Combined tasks. A and B: the mean durations of all eight intervals in the sequence during the last block of reproductions is shown for two subjects that showed large differences in the exact temporal pattern performed. Within each subject, however, the temporal pattern produced in the two tasks was highly consistent.
information could be learned in *Fix Temporal* and *Fix Ordinal*, respectively, although the other parameter was varying. First, the median number of correct key presses and correct temporal intervals were calculated for each trial in the different tasks, using data from all subjects (Fig. 8, A–D). A significant correlation (Pearson product-moment correlation coefficient) between trial number and number of correct responses was observed only in two cases: for number of correct temporal intervals in *Fix Temporal* (*P* < 0.00001; *r* = 0.73; Fig. 8A) and for number of correct key presses in *Fix Ordinal* (*P* < 0.01; *r* = 0.55). The relatively weaker correlation in the latter case is due to the fact that the ordinal structure of the sequence was learned very rapidly, so that the learning curve reached an early plateau, and the relationship with trial number was curvilinear (Fig. 8B); for the same reason, no regression line is plotted in the diagram. Correlations between trial number and number of correct key presses in *Fix Temporal*, and number of correct temporal intervals in *Fix Ordinal* were not significant (*P* = 0.90 and *P* = 0.31; Fig. 8A and B). In *Random*, neither parameter correlated with trial number (*P* = 0.86 and *P* = 0.84; Fig. 8C).

These findings suggest both that information about temporal
The results of this analysis confirmed the correlational analysis after the sessions (see METHODS). All subjects except one could sequence in these two tasks, a brief questionnaire was given to investigate the subjects’ awareness of the regularity of the sequences. Fix five trials and the last number of correct temporal intervals or key presses in the fixed the amount of learning by comparing the median quantification is unsuitable to analyze learning. For this reason, we also rapidly reached a plateau (Fig. 8). In this case, linear regression was highly specific to the particular temporal and ordinal structures employed. In fact, somewhat surprisingly, no general learning effects could be demonstrated: learning a combined sequence strongly facilitated the subsequent learning of sequences that consisted of the same temporal structure on a single key or the same ordinal structure with an even rhythmic pulse (Group 1 subjects). Learning a temporal and an ordinal structure separately strongly facilitated the subsequent learning of a sequence where the two are combined (Group 2 subjects). Both these transfer effects were highly specific to the particular temporal and ordinal structures employed. In fact, somewhat surprisingly, no general learning effects could be demonstrated: learning the control task was significantly slower in the group that had previously learned the experimental tasks (see Fig. 5). Probably, this strong interference effect is related to the high similarity of the tasks. Two other findings provide additional evidence for the fact that independent representations were used: in most subjects, the ordinal structure of the sequence was established before the temporal structure, implying that substantial changes in the representation of the temporal pattern could occur while the ordinal structure remained constant. Finally, a remarkable similarity in the details of the temporal pattern was observed when the same subject performed the temporal pattern alone (Temporal) and coupled with a complex ordinal structure (Combined). Taken together, these findings — the magnitude and specificity of the transfer effects and the close similarity of the temporal pattern in temporal and combined, in particular — appear difficult to explain without assuming that independent representations of the temporal and ordinal structures were utilized.

This conclusion has several implications. First, it appears that independent representations of temporal and ordinal structures can be formed both of a complex task, where both these parameters consist of a sequence of many elements (Combined), as well as of simpler tasks, where one of the parameters consists only of one repeated element (Temporal

**DISCUSSION**

**Independent representations of the temporal and ordinal structure of the sequences**

That subjects can form independent representations of the temporal and ordinal structure of explicitly learned motor sequences is supported by a number of results in Experiment 1. For example, our two initial predictions were confirmed: learning a combined sequence strongly facilitated the subsequent learning of sequences that consisted of the same temporal structure on a single key or the same ordinal structure with an even rhythmic pulse (Group 1 subjects). Learning a temporal and an ordinal structure separately strongly facilitated the subsequent learning of a sequence where the two are combined (Group 2 subjects). Both these transfer effects were highly specific to the particular temporal and ordinal structures employed. In fact, somewhat surprisingly, no general learning effects could be demonstrated: learning the control task was significantly slower in the group that had previously learned the experimental tasks (see Fig. 5). Probably, this strong interference effect is related to the high similarity of the tasks. Two other findings provide additional evidence for the fact that independent representations were used: in most subjects, the ordinal structure of the sequence was established before the temporal structure, implying that substantial changes in the representation of the temporal pattern could occur while the ordinal structure remained constant. Finally, a remarkable similarity in the details of the temporal pattern was observed when the same subject performed the temporal pattern alone (Temporal) and coupled with a complex ordinal structure (Combined). Taken together, these findings — the magnitude and specificity of the transfer effects and the close similarity of the temporal pattern in temporal and combined, in particular — appear difficult to explain without assuming that independent representations of the temporal and ordinal structures were utilized.

This conclusion has several implications. First, it appears that independent representations of temporal and ordinal structures can be formed both of a complex task, where both these parameters consist of a sequence of many elements (Combined), as well as of simpler tasks, where one of the parameters consists only of one repeated element (Temporal
and *Ordinal*. Second, it appears that once temporal and ordinal representations are established, they can be combined to a complex sequence with relatively little further training. In this regard, it is notable that slightly more training was required for subjects in *Group 2* to combine the previously learned temporal and ordinal structures, than for subjects in *Group 1* to extract the temporal and ordinal structure of the combined sequence they already had mastered.

**Learning of temporal and ordinal structures**

The results of *Experiment 1* suggest that independent mechanisms may be used also during the learning of temporal and ordinal sequential structures. The data from *Experiment 2* support this idea. An ordinal structure could be learned from repeated presentations with a random temporal structure, and, vice versa, a constant temporal structure could be extracted from stimulus sequences with random ordinal structure. The latter result is the more striking one because it shows that the learning of temporal structures is not necessarily incidental to the learning of ordinal information as has been suggested (Shin and Ivry 2002). The discrepancy between the present study and that of Shin and Ivry (2002), which did not find independent learning of temporal structures, is most likely explained by the fact that these authors employed the SRT paradigm, which as discussed (see **INTRODUCTION**) may be less optimal for studies of temporal learning: When the duration of RTIs is controlled, the temporal structure of the stimuli will not be consistent. In addition, subjects will be unable to predict responses, regardless of their knowledge of temporal structure, when the ordinal structure is random.

Our findings also contrast with early experiments that suggested that the relative timing and the serial order of movement sequences are normally represented in an integrated way (see **INTRODUCTION**). However, the independence of ordinal and temporal information was not tested directly using a transfer design in these early investigations. The observed temporal invariance could be due to a spontaneous tendency to use the same rhythm as during training, when not explicitly instructed to do otherwise, while the representation of the temporal structure is still independent. Summers (1975) and Shapiro (1977), however, found that traces of the original relative timing remained even when subjects were instructed to perform at maximum speed. This does suggest that integrated spatiotemporal representations of movement sequences can also be...
formed, although it should be noted that the temporal pattern at maximum speed only showed a relatively weak resemblance of the original rhythm (Summers 1975).

Can learning of temporal sequences occur implicitly?

In Experiment 2, learning of the temporal sequence occurred in subjects that, after the learning session, verbally reported having detected no regularities in the stimuli. Similar results for ordinal sequence learning have been found in a number of studies (see e.g., Shanks and St. John 1994; Stadler and Frensch 1997 with commentaries for reviews).

Implicit learning has usually been defined as learning taking place without concurrent conscious awareness of what is being learned (Shanks and St. John 1994). While verbal report is an arguably a good index of subjective awareness (Dienes and Perner 1994; Lindsay and Gorayska 1994; Reber and Winter 1994), the sensitivity and exhaustiveness of the employed awareness measurement has been a major concern in studies of implicit learning (Shanks and St. John 1994; Stadler and Roediger 1997). Thus while the subjects’ reported lack of awareness of any stimulus regularity in the present study is remarkable, we cannot exclude the possibility that some relevant conscious knowledge remained undetected by our questionnaire.

Recently, Stadler and Roediger (1997) have suggested defining implicit learning as learning occurring without intention to learn. Here, subjects were only given explicit instructions to reproduce each stimulus not to learn regularities in successive stimuli. This together with the fact that the temporal regularities of the patterns remained unnoticed suggests that, although conscious strategies were presumably used to reproduce each individual stimulus, intentional learning may have played little role for the observed improvement over repeated trials.

A separate question, not addressed in the present study, is whether there exist independent neural systems for implicit and explicit learning of temporal sequences. This could be investigated, e.g., by dissociation experiments where one system is selectively manipulated or by neuroimaging techniques. Interestingly, different neural correlates for implicit and explicit learning of ordinal sequences have recently been demonstrated (Willingham et al. 2002).

Neural control of temporal and ordinal aspects of sequences

The present findings raise the question of whether a corresponding segregation can be found at a neural level between brain regions that contain representations of the temporal and ordinal structure of motor sequences. Specific activations of the dorsal premotor cortex and the posterior parietal cortex have earlier been observed in several studies of tasks requiring movements to targets in extra-personal space (see e.g., Deiber et al. 1991; Kawashima et al. 1995; Roland et al. 1980). Tasks including the reproduction of rhythmic patterns have typically been accompanied by activity in the cerebellum, the superior temporal cortex, the ventral premotor cortex, and the presupplementary motor area (Penhune et al. 1998; Ramman and Passingham 2001; Schubotz and von Cramon 2001). Interestingly, recent functional MR experiments (S. L. Bengtsson, H. H. Ehrsson, H. Forssberg, and F. Ullen, unpublished data), where the same subjects performed the same type of sequences as in Experiment 1 of the present study, show that different brain regions are predominantly involved in the control of the temporal and the ordinal aspects of the movements. Brain regions involved in the control of the temporal aspect included the presupplementary motor area, the bilateral superior temporal cortex, the cerebellum, and the right ventral premotor cortex. In contrast, brain regions controlling the ordinal structure of the sequences included the bilateral dorsal premotor cortex, the bilateral superior parietal cortex, the putamen, and the left inferior frontal gyrus. Independent representations of the temporal and ordinal structure of explicitly timed motor sequences may thus be largely stored in different brain areas that control the exact timing of the movements and their spatial structure, respectively.

It is easy to imagine functional advantages for the presently demonstrated ability to represent temporal and ordinal structures independently. In some situations, the temporal structure of a movement sequence may be crucial, whereas the exact choice of effectors and their spatial movement pattern may be of subordinate importance to reach a particular goal. In other situations, the correct serial order may be essential, whereas the rhythmic pattern of the movements is less critical. Independent access to the rhythmic and ordinal structures of learned movement sequences would in either case enable rapid learning of alternative behavioral strategies to reach a certain result. In general, it appears likely that the ability to represent motor sequences in multiple ways is an important factor behind flexibility and adaptability in human motor control.

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