

Research report

Learning of spatial and temporal patterns in sequential hand movements

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Accepted 17 August 1999

Abstract

Speed and accuracy in performing a complex movement sequence improve with practice. To examine how the temporal and spatial patterns of movement sequence are learned, the sequence of target locations and the consistency in the timing of target presentation were manipulated independently while subjects produced a series of visually guided hand movements. When the sequence of target locations and the timing of target presentation followed a consistent pattern, performance for a particular movement sequence improved with practice for both temporal and spatial movement parameters. However, when the same temporal and spatial patterns were recombined with a phase shift, there was a small but consistent deficit in performance. These results suggest that whereas spatial and temporal patterns in a learned movement sequence can be recombined flexibly, optimal performance is obtained for a specific spatio-temporal pattern of movement sequence. Whereas subjects were largely aware of the spatial and temporal patterns, they were unaware of the phase-shift, suggesting that learning of a specific spatio-temporal pattern was implicit. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Human subject; Reaching; Sequence learning; SRT task

1. Introduction

Primates achieve most behavioral goals with a series of hand movements. Although initial performance of a particular movement sequence may be slow and clumsy, both speed and accuracy improve with practice. In a laboratory setting, the serial reaction time (SRT) paradigm [8] has been frequently used to investigate behavioral changes and underlying neural mechanisms associated with learning of sequential movements [1]. In a typical SRT task, subjects perform a choice reaction-time task by pressing a key indicated by one of several alternative targets. Reaction time (RT) decreases faster when a particular sequence of target locations is presented repeatedly than when each target location is randomly selected. This improvement in performance occurs independently of subject's ability to recall the sequence (i.e., implicit learning) [1,8]. In most studies of the SRT task, the interval between the response and onset of the next target (response–stimulus interval, RSI) was fixed, so effects of temporal predictability on learning could not be studied. However, more natural, complex sequences of movements tend to occur with stereotypical temporal, as well as spatial patterns. In fact, there is evidence that temporal factors exert a powerful

influence on the learning and performance of sequential movements. For example, a long RSI impairs performance of learned movement sequences, although it does not interfere with learning a new sequence [4,15]. In addition, performance is improved when the RSI is varied according to a fixed pattern, compared to when it is varied randomly [14,15].

There were two major goals of the present study. One was to determine whether performance improvement for a previously learned sequence of movements is influenced by the temporal pattern of the sequence. Another goal was to determine if spatial and temporal patterns of movement sequences are learned independently. This was examined by introducing a phase-shift between the spatial and temporal patterns of a learned movement sequence, which would not affect performance if spatial and temporal patterns are learned independently.

2. Materials and methods

2.1. Apparatus and stimuli

Visual stimuli were displayed on a computer monitor (32 × 24 cm) located approximately 90 cm away from the subject's eyes. Subjects, who were seated, controlled the

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position of a feedback cursor (0.25 cm radius) by moving their right hand in a fronto-parallel plane [7]. Hand movements were monitored with a 3D electro-optic sensor (Dyasight, Origin Instrument, TX) by tracking a reflective marker attached to the index finger. The measurement was updated and sampled at 64 and 200 Hz, respectively, with a spatial resolution of 0.1 mm. Nine gray circles (1.25 cm radius), arranged in 3×3 grid, were displayed on the monitor throughout the experiment and indicated potential target locations (Fig. 1, top). The distance between centers of adjacent circles was 6.0 cm.

2.2. Procedure

In each trial, the subject captured a series of 18 targets (1.0 cm radius) by locating the cursor on each target within 1 s after target onset. Each subject performed 200 trials (3600 movements) each day, equally divided into 20 blocks, and participated in this experiment for either 10 (Experiment I) or 8 (Experiment II) days. Three naive subjects with normal or corrected-to-normal vision participated in each experiment.

The spatial pattern of target locations was determined by a sequence of 18 target locations, in which each of nine alternative locations was used twice, and was preceded by two different locations (Fig. 1, top). Denoting each of nine alternative locations as the letters “A” through “I”, “IHEDCBHFCGABEGIDAF” would be an example of such a sequence (e.g., “H” is preceded by “I” and “B”, as indicated by the underscores). This sequence was circular, so that for any given trial, the first target can be chosen from any point in the sequence. For each subject, a new pattern was generated and used throughout the experiment. A target is referred to as “grammatical”, when its location followed the order specified in the fixed sequence, and “ungrammatical” otherwise. Most targets were grammatical, but ungrammatical targets were also presented within the same block of trials to provide a measure of performance improvement specifically related to the fixed sequence throughout the experiment. There were two different types of ungrammatical targets. A first-order ungrammatical target was preceded by neither of the two alternative targets specified in the sequence (i.e., it violated the first-order conditional probability). A second-order ungrammatical target (used only in Experiment I) was preceded by one of the two alternative target locations, but the triplet of locations ending with a second-order ungrammatical target was not a part of the sequence (i.e., it violated the second-order conditional probability). In Experiment I, second-order ungrammatical targets were presented twice randomly between the 7th and 18th targets in each of seven trials in each block. In addition, in one trial of each block, all targets were first-order ungrammatical. All other targets were grammatical. In Experiment II, grammatical and first-order ungrammatical targets were presented in

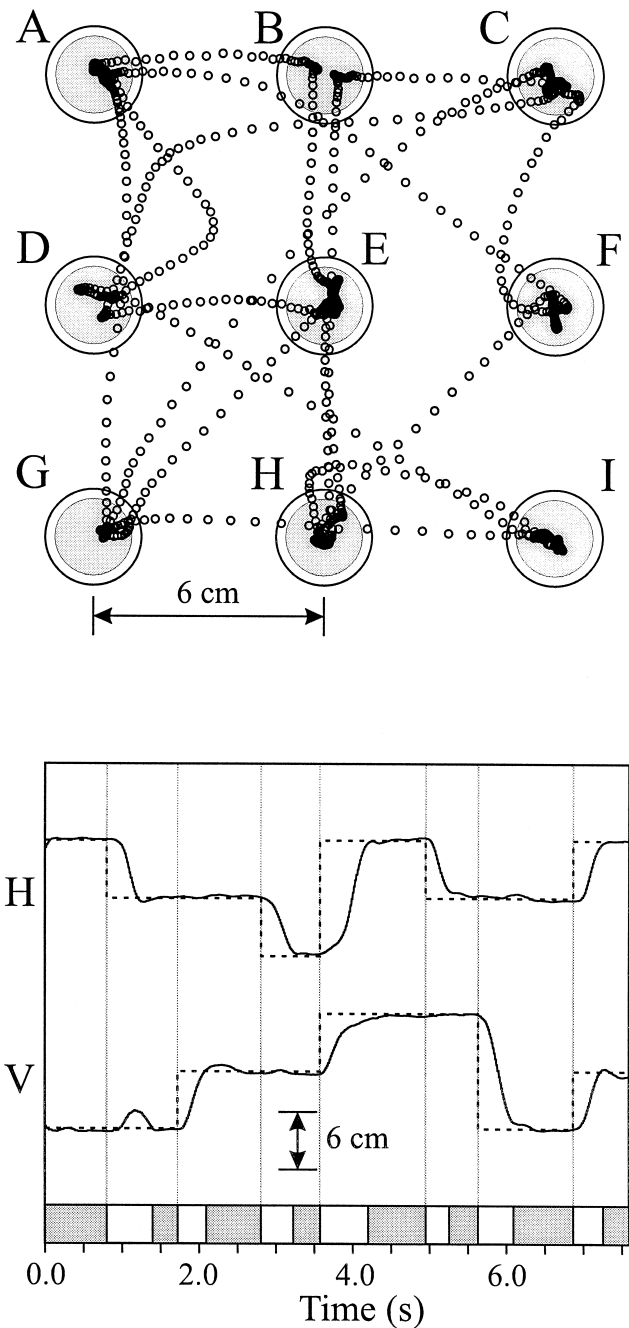


Fig. 1. (top) Layout of the targets (gray disks), and the auxiliary circles which were displayed constantly. An exemplary trajectory of hand movement for a single trial is also shown (Day 2, Experiment I). In this example, all the targets were grammatical according to the following pattern: IHEDCBHFCGABEGIDAF. (bottom) Temporal sequence of a rhythmic trial. Horizontal (H) and vertical (V) hand positions are shown in solid lines, and target positions in dashed lines. Gray-filled rectangles indicate RSI. Data are shown only for the first eight targets.

separate trials (referred to as grammatical and ungrammatical trials, respectively).

For most trials, RSI alternated between two possible values, and these trials are referred to as rhythmic (Fig. 1, bottom). For all subjects, the long RSI was 800 ms. For two subjects in each experiment, the short RSI was 400

ms, whereas it was 200 ms for the third subject. Trials in which either RSI was randomly selected for each target are referred to as arrhythmic. In Experiment I, effects of temporal pattern were examined by altering the phase of the temporal sequence relative to the spatial sequence after 6 days of training with one of their two possible combinations. After 2 days of additional training with this new combination (days 7 and 8), all trials became arrhythmic (days 9 and 10). In Experiment II, effects of temporal predictability were assessed within the same block of trials. In every block, rhythmic ungrammatical, arrhythmic grammatical and arrhythmic ungrammatical trials were each presented once. The other seven trials were rhythmic and grammatical, and these were of two varieties. Targets followed by the short RSI in one variant were followed by the long RSI in the other. One arbitrarily chosen variant (referred to as primary) was presented six times, and the other (referred to as syncopative) was presented only once.

Subjects were informed of the temporal pattern before the experiment, but not of the spatial pattern, and their explicit knowledge of the spatial pattern was assessed after the experiment using a generation task [8]. In this task, subjects were required to press a key on a computer keyboard according to the location in which they thought the next target would be presented. Subjects were also queried whether they noticed a phase-shift, at the end of the experiment on day 7 (Experiment I) or at the end of the entire experiment (Experiment II).

2.3. Data analysis

For each movement, three parameters were measured: RT, movement duration (MT), and directional error at movement onset [7]. Initial direction of movement was defined as the direction of the velocity vector when the velocity threshold (10 cm/s) was crossed. In Experiment I, movements to the first six targets in each trial were excluded from analysis, since they did not include any second-order ungrammatical targets. Statistical significance was determined with analysis of variance (ANOVA), and all effects described below were significant at the level of 0.01.

3. Results

In Experiment I, for 10% of trials, all targets were randomly chosen, first-order ungrammatical. For these trials, both RT and MT decreased gradually, although most of the RT decrease occurred within the first two days (Fig. 2, left). In the other 90% of trials, most movements were to grammatical targets, and RT and MT were substantially smaller than for the first-order ungrammatical targets. In addition, directional error for movements to grammatical targets decreased gradually, whereas it increased for first-order ungrammatical targets. A small fraction of targets were second-order ungrammatical, requiring the same

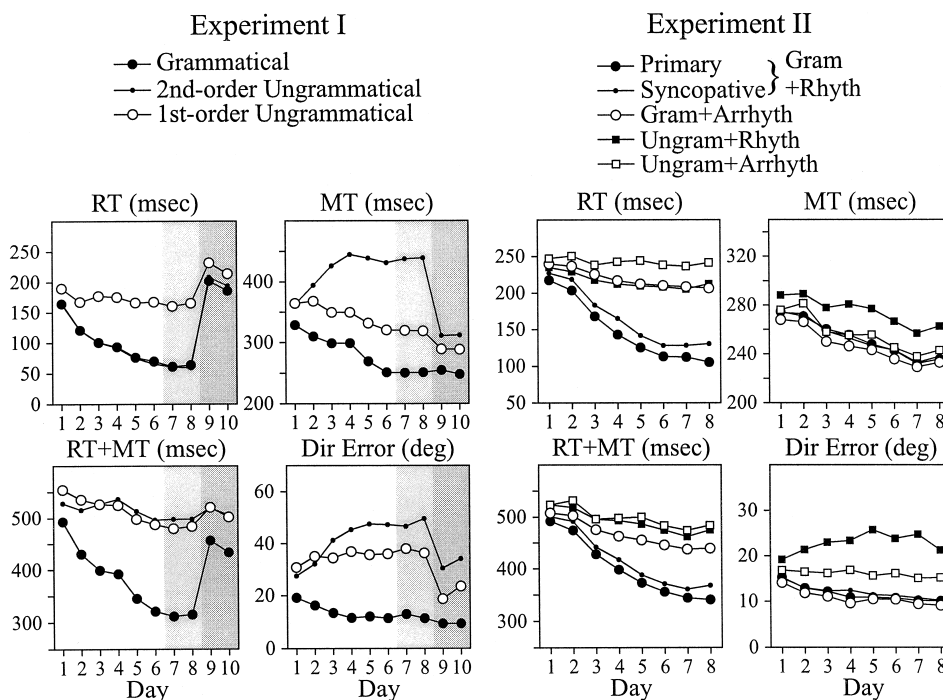


Fig. 2. Effects of practice on multiple movement parameters. For Experiment I, the days in which the temporal pattern was phase-shifted and abolished are indicated by light and dark gray backgrounds, respectively. In Experiment II, grammatical (Gram) and ungrammatical (Ungram) refer to the presence or absence of a consistent spatial pattern, whereas rhythmic (Rhyth) and arrhythmic (Arrhyth) refer to the presence or absence of a consistent temporal pattern. The particular combination of temporal and spatial pattern that was practiced most frequently is referred to as primary, and its phase-shifted counterpart as syncopative.

movements as their twin grammatical targets. RT for movements to second-order ungrammatical targets was indistinguishable from that to grammatical targets. In contrast, MT and directional error increased gradually for second-order ungrammatical targets, suggesting that after practice these movements were initiated before information about target location was fully analyzed [5,7], and that corrections were made during the movement.

On the seventh day of Experiment I, the phase of the temporal pattern was shifted relative to that of the spatial pattern. This did not produce any significance impairment in performance for any movement parameters (Fig. 2, left, light gray bands), suggesting that information about spatial and temporal patterns of movement sequence was learned independently and can be recombined flexibly. However, when the temporal pattern was eliminated (Fig. 2, left, dark gray bands), RT for grammatical targets increased dramatically.

In Experiment I, the phase shift between the temporal and spatial patterns was introduced only once. Therefore, the results of Experiment I did not exclude completely the possibility that such a phase shift produces only momentary and relatively minor performance impairment. To test this possibility, in Experiment II, two alternative combinations of the same spatial and temporal patterns were presented with different frequencies within the same block. For RT, there was a small (~ 20 ms), but consistent difference between these two conditions, suggesting that movement initiation is delayed when the previously learned spatial and temporal patterns have to be recombined (Fig. 2, right). For MT, there was no difference between these two conditions. Compared to the condition without any consistent spatial or temporal patterns, RT decreased slightly when either a consistent spatial or temporal pattern was introduced. These effects were relatively small (~ 30 ms) and reached asymptotic levels by the fourth day. On the other hand, MT and directional error increased when only a temporal pattern was introduced, suggesting that a consistent temporal pattern shifts a balance in the speed–accuracy tradeoff. When both spatial and temporal patterns were consistent, performance improved throughout the experiment, eventually displaying effects much larger than the sum of the effects of introducing either a spatial or temporal pattern alone.

At the end of these experiments, subjects displayed explicit knowledge of most of the spatial sequence. On the average, subjects correctly predicted the next target location with 78% accuracy. However, none of the subjects became aware of the phase-shifts introduced in these experiments.

4. Discussion

These data demonstrate that the effects of practice on a particular sequence of movements are manifested in both

spatial (e.g., directional error) and temporal (e.g., RT and MT) parameters of movement. Optimal performance was obtained when both the location and timing of targets followed a consistent pattern. In this case, the asymptotic level of RT (about 60 and 105 ms, for Experiments I and II, respectively) was substantially smaller than the normal RT for reaching movements in a reaction time task (> 200 ms) [7,13], suggesting that after intensive practice, movements can be initiated based on prior knowledge about the location and timing of the target. The performance deficit was substantial and similar for spatial and temporal pattern violations, suggesting that efficient planning of sequential movements requires information in both spatial and temporal dimensions. Analogous results have been obtained in the standard reaction time task, in which a consistent foreperiod shortens RT to a much larger extent when movement direction can be also anticipated [11,12].

As long as previously learned spatial and temporal patterns remained unchanged, the cost associated with recombining them was relatively small. This suggests that information about movement metrics (direction and amplitude) and timing of movement are acquired independently [5,7,13] and that these two types of information can be recombined flexibly. However, a small but consistent deficit in performance following such a phase-shift indicates that a specific spatio-temporal pattern of movement sequence is also learned. The fact that subjects were unaware of the phase shift suggests that this knowledge was implicit.

Learning of a specific spatio-temporal pattern of movement sequence demonstrated in this study may be a function of a distributed network of various brain areas including both cortical and subcortical regions. It has been demonstrated that a recurrent network equipped with multiple time constants can acquire a specific spatio-temporal pattern [2]. In addition, neuroimaging studies have implicated common regions of the brain, such as prefrontal cortex and the supplementary motor area, for learning of spatial and temporal sequences [3,6,9,10]. These cortical areas may be a part of the network involved in learning of specific spatio-temporal patterns of movement sequences.

Acknowledgements

I thank Dr. Joseph Malpeli for advice on the manuscript. This work was supported by the National Institute of Health Grant MH 59216.

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