Acquisition of the Temporal and Ordinal Structure of Movement Sequences in Incidental Learning

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Submitted 17 October 2007; accepted in final form 28 February 2008

INTRODUCTION

Skilled actions often incorporate a precise temporal pattern—for example, in speech, and in playing a musical instrument, timing is crucial. Even when the temporal structure of an action is not essential to meaning, the timing with which learned actions are executed tends to be invariant, revealing the importance of temporal structure in learned motor behaviors. For example, the typical timing of pen strokes determines individuals’ handwriting (Wright 1993), whereas skilled typists develop invariant temporal patterns for common words (Terzuolo and Viviani 1980).

In the field of motor learning, the acquisition of temporal patterns of movement has been relatively neglected while research has traditionally focused on the learning of ordinal sequences of movements (Hikosaka et al. 2002; Tanji and Shima 1994; Toni et al. 1998) or spatial visuo-motor contingencies (Shadmehr and Holcomb 1997; see Doyon and Benali 2005 for review). Functional imaging literature suggests that temporal and nontemporal (ordinal) sequences are encoded in different regions of motor association cortex. Schubotz and von Cramon have reported such a dissociation in both medial (Schubotz and von Cramon 2001b) and lateral (Schubotz and von Cramon 2001a; Schubotz et al. 2003) premotor cortex when participants encoded sequence information (pre-SMA and ventral premotor cortex (PMv) were associated with temporal sequences, whereas supplementary motor area (SMA) proper and dorsal premotor cortex (PMd) were associated with ordinal sequences). To what extent are temporal and ordinal representations of movement separable? To address this question, we developed a modified version of the serial reaction-time (SRT) task (4).

The SRT is a useful model for real-world skill acquisition because learning is incidental—participants are simply instructed to respond to incoming information, and regularities in the pattern of inputs or responses are “picked up” by the brain and used to facilitate performance. This kind of bottom-up or unsupervised learning mimics motor-skill acquisition in which people are often unable to verbalize or even recognize consciously their motor strategies. In contrast, those studies that have so far addressed the temporal aspect of motor learning have generally involved explicit memorization of the temporal sequence (Bengtsson et al. 2004; Ramnani and Passingham 2001; Sakai et al. 2002; Ullen and Bengtsson 2003). The use of explicit training raises the possibility that temporal learning is underpinned by sensory rather than motor representations, a hypothesis supported by engagement of auditory cortex in the temporal tasks, but not nontemporal control tasks, in the cited studies. Intuitively it seems that a sensory route would not underlie the acquisition of the temporal parameters of movement in general (for example in typing) but may be a strategy employed when participants explicitly memorize a rhythm.

We developed a modified version of the SRT task designed to assess the relationship between temporal and ordinal motor learning when these develop incidentally. In our between-subjects design, the stimuli/responses were governed by one of three types of sequence: ordinal (a fixed order of finger movements, temporal (a fixed sequence of stimulus onset asynchronies (SOAs); i.e., a rhythm), or combined (parallel fixed

1 The SRT task is a classic model for skill acquisition. In the SRT task, participants learn a sequence of finger movements incidentally as they respond to a series of visual targets. The visual targets can appear at one of four locations; responses are made with the corresponding one of four fingers of the right hand. Unknown to the participant, there is a repeating sequence of targets/responses embedded in the task, such that the participant makes the same series of movements over and over throughout the task. Learning for this sequence is assessed using “probe blocks” in which the repeating sequence of movements is switched for a random ordering; the reaction-time cost of switching from sequence to random (probe cost) equates to the proportion of reaction-time improvement that was specific to learning of the sequence rather than general training.

2 Note that in Ullen and Bengtsson (2003), although memorization of the rhythm on each trial was deliberate, participants also showed cumulative improvements in performance when the rhythm across trials remained the same. Participants reported no awareness of this cross-trial regularity, so knowledge of the repeated rhythm could be said to be implicit despite deliberate memorisation on each trial.

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ordinal and temporal sequences). Note that the classic SRT task is a type of combined ordinal and temporal sequence, where a constant temporal interval is typically used for all stimuli.

This design allowed us to address two specific questions. First: does adding temporal structure to a sequence of movements facilitate learning of that sequence? If so, we should see a greater learning effect in the combined condition, when the ordinal sequence was combined with regular timing, than in the ordinal condition in which the same sequence of finger movements was used but with random timing. Second, can a sequence of movement timings be learned independently of the ordinal sequence of movements itself? That is, do people form an abstract representation of timing of actions, even when the temporal sequence is not presented in the context of a fixed ordinal movement sequence?

METHODS

Participants

Thirty-six young adults (15 male and 21 female) participated in the experiment: 12 in each of the three conditions: timing, ordinal, and combined. All participants were right handed. They were paid £10 in cash. The study was conducted in accordance with Central Oxford Research Ethics Committee guidelines.

Task

The task was a modified SRT paradigm. In the ordinal condition, the position of the target (and hence the order in which fingers were selected) was repeated in a 12-element cycle (ABACDBCADCBD), where A is the first index finger, B is the second position/middle finger, etc. The SOA on each trial took one of four values selected) was repeated in a 12-element cycle (ABACDBCADCBD), where A is the first index finger, B is the second position/middle finger, etc. The SOA on each trial took one of four values randomly: 500, 750, 1,125, or 1,687 ms.1 The SOA values were related by a scalar factor of 1.5. In the timing condition, it was the SOA that followed a repeating cycle of 12: SQRSPQRSRQPQ, where letters correspond to SOAs: (P = 500 ms, Q = 750 ms, R = 1,125 ms, S = 1,687 ms). In the combined condition, both the position of the target and the SOA followed a repeating sequence of 12 elements (ABACDBCADCBD and SQRSPQRSRQPQ, respectively). The sequences, described at this abstract level, were isomorphic in that the rhythm sequence was simply the ordinal sequence backward. Therefore the sequences were equated for “simple event frequencies” (Reed and Johnson 1994). Note that the mapping between fingers and intervals was only at the level of the 12-element cycle, that is, no one finger was associated with a particular interval. In all conditions, participants completed 25 blocks of 84 trials (7 loops of the sequence per block). Of these, blocks 15, 20, and 25 were probe blocks, in which the temporal or ordinal structure of the sequence (or both) was altered to assess learning.

For the random dimensions (timing in the ordinal condition, finger order in the timing condition), and in probe blocks, we used a nonrepeating pseudo-random set of 84 SOAs/fingers in each block, controlled to exclude repetitions of elements (e.g., AA).

The response buttons were keys H, U, I, and L on a standard computer keyboard, which could be reached comfortably by the four fingers of the right hand. Stimuli were presented on a CRT monitor at a distance of 1 m. All participants responded with their right hand.

3 We selected these intervals in line with the Scalar Property of timing (the increase between intervals is always proportional to the interval). This gave rise to a non-metrical rhythm. It is possible that learning may have been facilitated by the use of a metrical rhythm, although the temporal sequence we used was learned successfully in the combined condition.

Probe blocks

Of the 25 blocks, blocks 15, 20, and 25 were probe blocks in which one or both dimensions of the stimulus sequence were altered to assess learning. In the combined condition, there were three types of probe block: 1) in probe change timing, the repeating cycle of 12 SOAs was replaced by a pseudorandom set of 84 SOAs, while the cycle of 12 positions/fingers was retained. 2) In probe change order, the sequence of positions/fingers was replaced with a pseudorandom set of 84 button-presses, but the repeating cycle of SOAs was maintained. 3) In probe change both, both repeating cycles were replaced. The order of probe blocks was completely counterbalanced between subjects. All three probe-block types were included in all three conditions, but note that the logic was slightly different in the timing and ordinal conditions, as in one of the probed dimensions (order or timing, respectively) there was no sequence to abolish—one random set of 84 stimuli was switched for another random set. Therefore in these conditions the probe block in which the untrained dimension was abolished acted as a negative control.

RESULTS

Data cleaning

Only trials with an accurate response (“hits”) were included in the reaction-time analysis. The first correct response in the reaction-time range −250 to 500 ms (where stimulus onset time was 0) was treated as the response for that trial. We included anticipatory responses in the analysis because in the combined version in which participants could predict the exact response and timing, anticipatory responses were common and to exclude them would have artificially masked the learning effect.

Learning effects

Mean reaction time by block is shown in Fig. 1. Reaction times in the standard (non-probe) blocks decreased significantly over the course of the experiment in the ordinal and combined conditions. Data were analyzed block-wise using a repeated-measures ANOVA, with the three conditions as between-subjects variables and block (the 22 standard blocks) as the within-subjects variable. There was a significant block-by-condition interaction \(F(42,672) = 4.18, P < 0.001\). There was a main effect and a linear contrast of block (learning effect) in the ordinal condition \(F(21,231) = 4.99, P < 0.001; F(1,11) = 9.84, P = 0.009\) and in the combined condition \(F(21,231) = 8.14, P < 0.001; F(1,11) = 18.91, P < 0.001\), suggesting that learning occurred in these conditions. No significant learning occurred in the timing condition [main effect of block: \(F(21,231) = 0.36, P = 0.996\); linear interaction of block: \(F(1,11) < 0.001, P = 0.99\)]. The difference in reaction time between the first and last (22nd) standard blocks, which gives a sense of the learning effect, was much larger in the combined condition (mean RT decreases from block 1 to 14 = 85 ms) than for the ordinal condition (38 ms). In the timing condition, it was negligible (4 ms). The learning effect over the series of 22 blocks was quantified as the linear regression of RT on block and differed significantly between conditions. In an ANOVA, the effect of condition on slope of linear regression was significant \(F(2,33) = 8.66, P < 0.01\). The learning effect (slope) was significantly greater in the combined condition than the ordinal condition \(t(22) = 2.09, P = 0.05\).
0.048, independent samples $t$-test), while in the timing condition the learning effect was not significantly different from zero ($t_{12} = 0.19, P = 0.985$).

**Probe costs**

The probe cost is defined as the increase in reaction time in the probe blocks when the order or timing of stimuli, or both, was changed. We calculated the probe cost as the difference between mean reaction time in each probe block and the mean reaction time for the preceding three standard blocks for each participant, to account for individual differences in reaction times and rate of learning. Probe costs were compared statistically with zero, using one-sample $t$-test, Bonferroni corrected for multiple comparisons.

Probe costs for the three types of probe blocks are shown in Fig. 2. Size and significance of the costs (comparison against zero with a 1-sample $t$-test) are shown in Table 1. Note that in the case of the timing condition, the change order probe block is a negative control in that there was no ordinal sequence to change: one block of 84 nonrepeating stimuli was exchanged for another. The converse was true for the ordinal condition.

The probe costs were much higher in the combined condition than in either the timing or ordinal condition. This is in accordance with the much greater learning effect in that condition. Note that where SRT paradigms have been used in the
In the combined condition, there were significant probe costs for changing the temporal sequence and the ordinal sequence separately as well as for changing both. The cost of changing the ordinal sequence was as high as the cost of changing both the ordinal and timing sequences (the difference was 6.7 ms; $t = 0.85$, $P = 0.41$, paired samples $t$-test). There was a cost of changing the timing, but this was significantly lower than the cost of changing both the rhythm and the ordinal sequence (difference = 48 ms, $t = 3.72$, $P = 0.003$, paired samples $t$-test).

In the timing condition, the probe cost in all three probe blocks was very small, reflecting the lack of learning in this condition. None of the probe costs was significantly different from zero (1-sample $t$-test; see Table 1).

In the ordinal condition, there was a significant cost of changing the order of fingers. There was no significant difference in probe costs between the change-order and change-both probes (the difference of 6.5 ms was not significant: $t = 1.1$, $P = 0.32$, paired samples $t$-test) in accordance with the fact that these were equivalent (because there was no rhythm to change in the change-both probe). There was no RT cost in the change-timing probe, in accordance with the fact that there was no temporal sequence to change in this condition.

In a de-briefing questionnaire, we asked participants to rate their awareness of the sequence in ordinal and temporal domains on a 5-point scale. However, we were unable to find a reliable effect of condition on the relative awareness of the temporal and ordinal sequences due to high intersubject variability in confidence.

**DISCUSSION**

The results suggest that in motor learning, timing information must be incorporated into a concrete motor plan to be used. When participants were exposed to a temporal sequence in isolation (in the timing condition), there was no evidence of learning. In contrast, timing information was learned in the context of a specific motor (ordinal) sequence and this significantly improved performance: The learning-related decrease in reaction times was much greater when a sequence of movements with regular timing was used (in the combined condition) than when the sequence of movements was fixed but the timing was random (in the ordinal condition).

What role does timing information play? In the combined condition, we included probe blocks in which the timing, order of fingers, or both was altered. This allowed us to ask whether the timing and order of movements were learned independently or as an integrated representation—if there was some degree of independence between the representations, some of the performance advantage should be retained when only one aspect of learning was altered compared with when both were changed. In fact, we found an asymmetrical relationship between temporal and ordinal sequences: in probe blocks when the order of stimuli was retained (with random timing), the probe cost was lower than when both the order and timing were abolished, but in probe blocks when the timing was retained (with random order of movements), performance was as bad as if both timing and order had been abolished. In other words, the ordinal sequence learned with a certain timing could be expressed with different timing (albeit at some cost in reaction time), but the temporal sequence could not be expressed with a random order of finger movements. This is in accordance with findings by Shin and Ivry (2002), who showed that if participants are exposed to interfering temporal and ordinal sequences (when the sequences had a different number of elements and were therefore “out of synch”), only the ordinal sequence is learned.

Had the representation of the rhythm been completely independent of (or superordinate to) effector selection, we would have expected an additive effect of temporal and ordinal regularity on learning and an additive cost in the probe blocks in the combined task. This was clearly not the case, suggesting that the representation of the temporal pattern was subordinate to the representation of the effector sequence. Had any representation of the temporal pattern been formed in the temporal condition, we would have expected at least a modest reduction in reaction time across training blocks, as temporal orienting experiments have shown that people can use temporal predictions to improve performance in discrimination tasks in an effector-independent way (Nobre et al. 2007).

It seems, then, that an abstract representation of timing, which could be executed with any response effector, was not formed. In the case of the timing condition, this meant that no representation of timing was formed, whereas in the combined condition, it meant that no benefit of learning the temporal sequence was retained when the ordinal sequence was changed (that is, the probe cost was as large in the change-order probe as the change-both probe). However, real life experience might cause us to question the generality of this finding because people clearly can form effector-independent representations of rhythms and express these through motor behavior—for example, people can tap their fingers to the rhythm of a tune that they have only experienced perceptually and indeed can express a given rhythm through different response effectors (e.g., tapping fingers on a desk, tapping a foot, dancing, or playing the tune on a musical instrument) without training each effector system separately. What is the difference between these examples and our experiment?

Perhaps the crucial difference is, as described in the preceding text, between explicit training and incidental pick-up of information: the use of sensory-imagery strategies. In inciden-

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**TABLE 1.** Probe block reaction time costs and significance

<table>
<thead>
<tr>
<th></th>
<th>Change Both</th>
<th>Change Timing</th>
<th>Change Order</th>
</tr>
</thead>
<tbody>
<tr>
<td>Combined version</td>
<td>111</td>
<td>63</td>
<td>104</td>
</tr>
<tr>
<td></td>
<td>$&lt;0.001^*$</td>
<td>$&lt;0.001^*$</td>
<td>$&lt;0.001^*$</td>
</tr>
<tr>
<td>Timing version</td>
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<td>2</td>
<td>11</td>
</tr>
<tr>
<td></td>
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<td>1.000</td>
<td>0.191</td>
</tr>
<tr>
<td>Ordinal version</td>
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<td>43</td>
</tr>
<tr>
<td></td>
<td>$&lt;0.001^*$</td>
<td>1.000</td>
<td>$&lt;0.001^*$</td>
</tr>
</tbody>
</table>

$P$ values are for one-sample $t$-tests against zero. The $P$ values were adjusted for multiple comparisons using a Bonferroni correction (number of comparisons = 9). $^*$Significant effect at $P < 0.05$ with correction for multiple comparisons.
tal learning paradigms such as the SRT, participants are unlikely to use sensory imagery as an effector-free representation of timing because no sensory representation need be formed. Hikosaka and colleagues (2002) have proposed a model of skill acquisition in which separate, parallel associations are formed between successive sensory cues and between successive motor actions (although sensory representations can also be used to guide action, as with the song heard on the radio). They suggest that in motor learning tasks such as the SRT, direct associations may be formed between action representations (action-action associations). Timing may be represented as a property of these action-action associations and would therefore be specific to learned pairs of actions. Taken with the present results, this would imply that, if timing is incorporated into a purely motor sequence representation, then it is at a level that is specific to the ordinal sequence of effectors with which that temporal pattern was learned.

In conclusion, our results suggest that in motor-skill acquisition under incidental learning conditions, timing is represented at a level specific to the ordinal sequence of movements rather than as an independent temporal template. Further research might address the question of whether temporal representations are specific at the level of effector preparation, or are also specific to action sequences performed by a single effector.

GRANTS
This work was funded by a Wellcome Trust 4-Year PhD scholarship awarded to J. O’Reilly.

REFERENCES


