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Original Research Paper

Early behavioural facilitation by temporal expectations in complex visual-motor sequences

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In daily life, temporal expectations may derive from incidental learning of recurring patterns of intervals. We investigated the incidental acquisition and utilisation of combined temporal-ordinal (spatial/effector) structure in complex visual-motor sequences using a modified version of a serial reaction time (SRT) task. In this task, not only the series of targets/responses, but also the series of intervals between subsequent targets was repeated across multiple presentations of the same sequence. Each participant completed three sessions. In the first session, only the repeating sequence was presented. During the second and third session, occasional probe blocks were presented, where a new (unlearned) spatial-temporal sequence was introduced. We first confirm that participants not only got faster over time, but that they were slower and less accurate during probe blocks, indicating that they incidentally learned the sequence structure. Having established a robust behavioural benefit induced by the repeating spatial-temporal sequence, we next addressed our central hypothesis that implicit temporal orienting (evoked by the learned temporal structure) would have the largest influence on performance for targets following short (as opposed to longer) intervals between temporally structured sequence elements, paralleling classical observations in tasks using explicit temporal cues. We found that indeed, reaction time differences between new and repeated sequences were largest for the short interval, compared to the medium and long intervals, and that this was the case, even when comparing late blocks (where the repeated sequence had been incidentally learned), to early blocks (where this sequence was still unfamiliar). We conclude that incidentally acquired temporal expectations that follow a sequential structure can have a robust facilitatory influence on visually-guided behavioural responses and that, like more explicit forms of temporal orienting, this effect is most pronounced for sequence elements that are expected at short inter-element intervals.

1. Introduction

A lot of our behaviour entails complex patterns that unfold with characteristic temporal profiles. Examples of this can be found in speech, playing musical instruments or performing sports. Timing related to such non-isochronous sequential movement patterns is often acquired in an incidental manner, over long periods of time. In this study, we looked at the acquisition and utilisation of spatial-temporal structure in complex visual-motor sequences, in which the spatial and temporal structure of visual sequences are incidentally acquired and integrated over time, in order to guide adaptive behaviour.

Serial reaction-time (SRT) tasks are often used to investigate sequence learning and memory. In classic SRT tasks (see Nissen and Bullemer, 1987, for a first description of the task), participants have to follow the order of targets presented at four different locations on the screen by pressing the corresponding button whenever a target is presented. The button press either triggers the presentation of the next target, or alternatively, a fixed stimulus onset asynchrony (SOA) is used. Unknown to participants, the targets follow a repeating sequence, usually of length 8–12. In such tasks participants generally get faster over the course of the experiment, while it is unknown to them that they learned something. When 'probe blocks'—blocks containing a random or novel

Abbreviations: FMRI, functional magnetic resonance imaging; MEG, magnetoencephalography; PC, percentage correct; RSI, response-to-stimulus interval; RT, reaction time; SOA, stimulus-onset asynchrony; SRT, serial reaction time.

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sequence—are presented, reaction times are much slower, indicating that these effects are caused by the incidental learning of the sequence, instead of a general effect of training.

Sequence-learning paradigms have been used to investigate not only the acquisition of ordinal visual-motor sequences, but also how temporal aspects of such sequences are acquired (Buchner and Steffens, 2001; Gobel et al., 2011; Karabanov and Ullen, 2008; Kornysheva et al., 2013; O'Reilly et al., 2008; Salidis, 2001; Sanchez et al., 2015; Schultz et al., 2013; Shin and Ivry, 2002; Ullen and Bengtsson, 2003). Temporal learning in this type of task is said to be implicit, or 'incidental' (as we will refer to it). Incidental learning occurs as a by-product of non-temporal task goals, when stimuli or motor responses adhere to a strict temporal framework (see Coull and Nobre, 2008, for the proposed distinction between implicit and explicit timing). In such a situation, participants are not asked to time or recall the different intervals used in the task, but the temporal structure influences performance measures. Such incidental learning can be shown in the pattern of reaction times, which decrease over time in a manner consistently related to the temporal structure inherent to the task. SRT tasks containing a recurring sequence of temporal intervals show that learning of temporal sequences affect behavioural measures like reaction times, at least when they are combined with a stable ordinal sequence. However, it is not yet clear how the influence of learned temporal structure on behaviour and neural processing develops over time. From research on temporal orienting following explicit temporal cues, we know that explicit temporal cueing is most effective at short, compared to long intervals (Correa et al., 2006; Coull and Nobre, 1998; Miniussi et al., 1999; Nobre, 2010; Rohenkohl et al., 2014). This can elegantly be explained by the notion that, when an event has not yet occurred, the probability that it will still occur increases with time (also known as the hazard rate). Whereas at short intervals participants will be most engaged following short cues, at long intervals their engagement will have become largely independent of the cue, because once the early interval has passed, it is certain that the stimulus will thus occur late (making the cue information redundant). In other words, for events that are due to happen, knowledge about their expected timing will be most beneficial at early intervals. Based on this literature on temporal orienting following explicit cues, we hypothesise that incidentally learned temporal structure will also have the strongest impact on performance for targets that occur following short (as opposed to longer) intervals (with intervals referring to the intervals between the targets that comprise the sequence).

In the current study we used an adapted version of the SRT task used by O'Reilly et al. (2008) that used blocks containing learned and pseudorandom sequences. O'Reilly and colleagues exposed participants to blocks of trials that had a repeating ordinal sequence, a repeated temporal sequence, or both. In this study having predictable temporal information greatly facilitated learning of the ordinal sequence, but temporal information was not learned when presented in isolation (see also Buchner and Steffens, 2001; Gobel et al., 2011; Sanchez et al., 2015; Shin and Ivry, 2002). However, because our study was part of a larger magnetoencephalography (MEG) and functional magnetic resonance imaging (fMRI) investigation, several changes were made with respect to the O'Reilly et al. (2008) task, of which we now highlight the most important ones. We only used conditions where either both temporal and ordinal information were repeated, or where both types of information were changed. We used longer intervals between events to ensure reliable hazard rate effects, and used intervals between responses and stimuli (response-to-stimulus intervals; RSIs) as opposed to between stimuli intervals (stimulus onset asynchronies; SOAs) in order to strictly separate responses and stimuli in time. Shin and Ivry (2002) have reported comparable learning effects for SOA and RSI manipulations in a spatial-temporal RT task. Finally, we used new sequences, instead of pseudorandom sequences for the probe blocks, to ensure comparable second-order conditional probabilities between blocks (see Reed and Johnson, 1994). Reed and Johnson showed that it is important to keep a number of parameters the same between repeated and probe sequences. These parameters are (A) location frequency: how often each location occurs within the sequence; (B) transition frequency, how often each possible transition between locations occurs; (C) reversal frequency: how often back and forth movements occur (e.g. Position 1 – Position 2 – Position 1, see also Vaquero et al., 2006); (D) rate of full coverage: how many targets occur before each location has at least occurred once; (E) rate of complete transition usage: average number of targets before each possible location transition has occurred at least once. In addition to these constraints, we ensured that each of the three RSIs occurred once with every location, with the same RSI never occurring twice in a row.

The main goal of the current report was to evaluate the hypothesis that incidental sequential temporal orienting effects (like more explicit temporal orienting effects) are most effective at short intervals. Moreover, given our experimental set-up, we are able to address two additional points. First of all, we aimed to replicate and extend the results found by O'Reilly et al. (2008) by establishing a spatial-temporal SRT task that can be used flexibly in a behavioural setting, as well as in neuroimaging settings. We therefore optimised our task parameters for neuroimaging analysis, that benefits from sufficiently long temporal intervals and a strict separation between responses and subsequent stimuli, by virtue of the use of RSIs instead of SOAs. Second, since this study contained three different sessions, taking place over the course of two weeks, this study allows us to look at whether (and, if so, how) these incidental learning effects change with time.

2. Methods

2.1. Participants

Twenty-one young, healthy volunteers (aged 24.7 ± 3.9 (SD), 9 males) participated in this study. All were right handed according to self-report and all had normal or corrected-to-normal vision. All participants gave informed consent and the study was approved by the Central University Research Ethics Committee of the University of Oxford (MSD-IDREC-C2-2014-036). Participants received money for their participation (£10 per hour). Each participant completed three experimental sessions. The first session consisted of just the behavioural experiment; the second session, one or two days later, and the third session, taking place within two weeks subsequently, included a magnetoencephalography (MEG) and a functional magnetic resonance imaging (fMRI) scan. This manuscript will focus on the behavioural results from each of these three sessions. One participant was excluded from the main analysis because of extreme fatigue during all three experimental sessions, causing a high number of mistakes and long gaps where the sequence was interrupted, especially during the second session (percentage correct was smaller than the mean minus 3 times the standard deviation across participants). Another participant was excluded because of a very slow mean reaction time (larger than the mean plus 3 times the standard deviation across participants). Results of nineteen participants (aged 22.6 ± 4.0 (SD), 9 males) were therefore included in the final analysis, on which we here report.

2.2. Apparatus

The sessions were all run in rooms with similar (normal) illumination. Stimuli were created with MATLAB (The MathWorks, Inc.,