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Sequences show rapid motor transfer and spatial translation in the oculomotor system

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ABSTRACT

Every day we perform learnt sequences of actions that seem to happen almost without awareness. It has been argued that for learning such sequences parallel learning networks exist – one using spatial coordinates and one using motor coordinates – with sequence acquisition involving a progressive shift from the former to the latter as a sequence is rehearsed. When sequences are interrupted by an out-of-sequence target, there is a delay in the response to the target, and so here we transiently interrupt oculomotor sequences to probe the influence of oculomotor rehearsal and spatial coordinates in sequence acquisition. For our main experiments, we used a repeating sequences of eight targets in length that was first learnt either using saccadic eye movements (left/right), manual responses (left/right or up/down) or as a sequence of colour (blue/red) requiring no motor response. The sequence was immediately repeated for saccadic eye movements, during which the influence of on out-of-sequence target (an interruption) was assessed. When a sequence is learnt beforehand in an abstract way (for example, as a sequence of colours or of orthogonally mapped manual responses), interruptions are immediately disruptive to latency, suggesting neither motor rehearsal nor specific spatial coordinates are essential for encoding sequences of actions and that sequences – no matter how they are encoded – can be rapidly translated into oculomotor coordinates. The magnitude of a disruption does, however, correspond to how well a sequence is learnt: introducing an interruption to an extended sequence before it was reliably learnt reduces the magnitude of the latency disruption.

1. Introduction

Many events in daily life consist of automated – and essentially deterministic – sequences (Land, Mennie, & Rusted, 1999; Schneider, Dumais, & Shiffrin, 1984). For example, the regular work-day routine of rising, showering, eating breakfast and driving to work are all actions that proceed in a prescriptive sequence. It has been proposed that such habitual sequences are generated by relatively automatic parts of the motor system (Hikosaka et al., 1999). Such automisation frees cognitive processes for other, non-habitual tasks.

Some researchers have suggested that sequences of actions are learnt in spatial coordinates. With such learning, participants are able to transition between different modes of response to a sequence without loss of response speed and accuracy as long as the response locations are kept the same (Willingham, Wells, Farrell, & Stemwedel, 2000). However, other researchers have found conflicting results – that disrupting the spatial mapping of a sequence does not matter as long as the motor response itself is kept constant (Richard, Clegg, & Seger, 2009). How can we resolve the contrasting evidence that in some studies spatial representations appear to be the dominant sequence encoding form, while in others sequences seem coded in motor response representations? One solution might be to consider sequence learning within the dual-pathway framework for sequence learning proposed by Hikosaka et al. (1999). The authors propose that there are two mechanisms for learning sequences – one spatial and one motor. Early in sequence learning, spatial mechanisms are dominant. As a sequence becomes automatic, motor mechanisms become increasingly important, with areas implicated in motor function becoming increasingly recruited as a sequence is learnt (Hikosaka & Isoda, 2008; Rand et al., 2000; Sakai et al., 1998).

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One way that we might be able to explore the spatial and motor aspects of sequence acquisition is by examining what happens when a sequence is interrupted. We have previously described a simple oculomotor model for sequenced actions (Anderson & Carpenter, 2010; Anderson, Stainer, Brotchie, & Carpenter, 2014), wherein targets appearing out of sequence (an *interruption*) cause an elevation in the latency of saccades for looking at these targets (a *disruption*). This disruption reflects, at least in part, a time-cost involved in reprogramming the direction of the upcoming saccade (Anderson et al., 2014). However, our previous sequence interruption experiments deliberately used very simple sequences already known to the participant, and excluded from analysis any trials at the very beginning of a run to avoid any influence of sequence learning.

Here we use three experiments that involve more complex sequences, and analyse early trials where sequence acquisition is likely still occurring. In Experiment 1, participants pre-learnt a previously unknown sequence, after which we measured the effect of a sequence interruption when the sequence was performed with saccadic responses. Pre-learning was either via making saccades, or by making manual button pushes. If disruption effects are principally caused by inhibition of an automated saccadic motor response, we would expect that sequences learnt by making manual responses (without eye movements) should show less disruption when the learnt sequence is then continued with eye movements (i.e. the eyes would have to 're-learn' the sequence). However, oculomotor sequence interruption may be due to the inhibition of an *expected* response to a spatial location, in favour of an unexpected response to another location. If this is the case, learning should 'transfer' from motor responses to oculomotor responses, and interruptions would be met as though the sequence had been learnt using saccades from the start. This transfer would be facilitated by the reasonably long foreperiod in our sequence interruption task, which is approximately a second on average (Anderson & Carpenter, 2010). In a variation of this experiment, subjects learnt the sequence using orthogonally mapped vertical switch-button responses movements. Participants were not instructed of the mapping between the vertical responses and the directions of the subsequent oculomotor testing. Because of this, only a spatially abstracted version of the sequence could be learnt. A second experiment further abstracted the sequence by presenting it as a sequence of coloured dots (red and blue) during the learning phase. This allowed us to consider whether sequences that contained no spatial elements at all can be rapidly translated to spatial coordinates.

In our final experiment, we examined the timecourse of acquiring oculomotor sequences by manipulating the length of the sequence to be learnt. If the magnitude of disruption caused by a sequence interruption continues to increase after a sequence can be performed without errors, this would suggest that disruptions reflect suppression of an automated motor response that develops more gradually than sequence learning *per se*. Such a finding would be inline with the dual-pathway framework for sequence learning proposed by Hikosaka et al. (1999).

2. Methods

2.1. Participants

Experiment 1 included six participants (four female) with normal or corrected-to-normal (i.e. with glasses or contact lenses) vision. In Experiment 2, there were six participants (four female). Six participants (3 female) took part in Experiment 3. The authors MS and AA took part in all experiments, with different naive participants being used in each experiment. All procedures were approved by the University of Melbourne Human Research Ethics Committee, and conducted in accordance to the Declaration of Helsinki. The participants gave written informed consent before taking part.

2.2. Apparatus

Stimuli were controlled with Cambridge Research systems ViSaGe (Cambridge Research Systems, Kent, UK) and were presented on a calibrated monitor (Diamond Pro 2070SB monitor, Mitsubishi, Tokyo, Japan; frame rate 100 Hz) subtending 23 × 17 degrees at the 1 m viewing distance. Horizontal eye position was recorded using an Ober Oculometer (Ober et al., 2003), which is an infrared reflection oculometer that is symmetrically linear to 7% within 30 degrees, has a bandwidth of 250 Hz, with an internal noise of approximately 0.1 degree. The ViSaGe ensuring precise synchronization between the samples from the oculometer, taken every 10 ms, and the presentation of each frame. Participants used a chin-rest to minimise head movements. Saccades were automatically detected by SPIC software (Carpenter, 1994), using velocity thresholds optimised for each observer so that our comparatively large saccades (4 degrees) could be reliably differentiated from involuntary microsaccades (<0.5 degrees). Example traces of saccades to the left and right following a target presentation can be seen in Fig. 1. The data were manually screened to eliminate all saccadic responses contaminated by blinks, head movement or other artefacts. Participants were asked to try to blink following their saccadic responses on the return to the central target position to attempt to minimise blinks contaminating saccadic recordings. Blinks that overlapped the recording period showed up as prominent artefacts in the trace. Latencies were binned in 10 ms intervals with latencies <80 ms and >600 ms being removed. Saccades where participants looked in the incorrect direction were uncommon in both sequences (0.2% removed) and interruptions (0.4% removed), but were also removed from the analysis. The total mean number of saccadic responses removed for all participants in

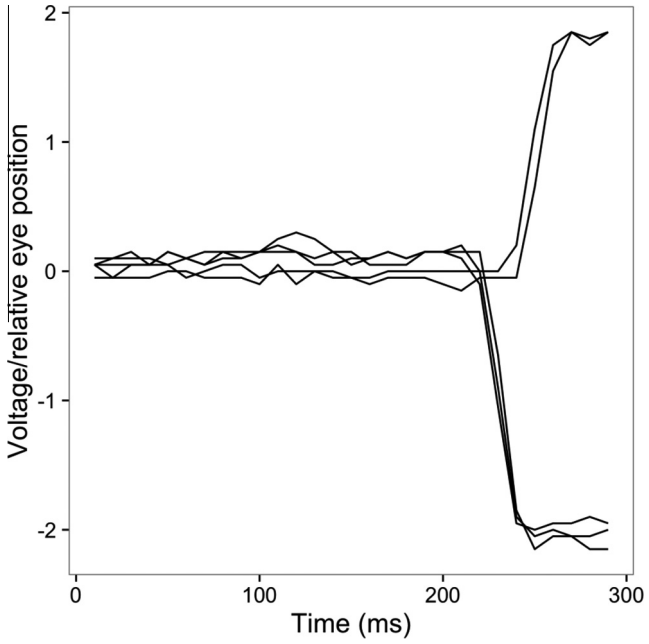

Fig. 1. Example of raw voltages from the Ober oculometer, sampled at 10 ms intervals. Traces for a participant making 5 saccades to a target appearing RRLRL. Voltages move positively for leftward saccades, and negatively for rightward saccades. Time 0 represents the time at which the saccadic target appeared.