



Motor programming of finger sequences of different complexity

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ABSTRACT

In a response precuing task, we used behavioral and electrophysiological measures – Contingent Negative Variation (CNV) and the readiness potential (RP) – to investigate the programming of three-element response sequences of different complexity. Precuing effects on foreperiod CNV and RT indicated the use of advance information about response hand and response sequence. Crucially, with advance information about both hand and sequence, heterogeneous response sequences (e.g., 1 → 2 → 2) elicited larger foreperiod CNV activity over medial motor areas than homogeneous response sequences (e.g., 1 → 2 → 3), whereas CNV activity over lateral motor areas was not influenced by sequence complexity. It was only before response execution that lateral but not medial RP activity was stronger for heterogeneous than homogeneous response sequences. Both behavioral and electrophysiological measures indicated finger-order dependent influences on the duration of on-line response programming during response execution.

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1. Introduction

It is generally assumed that a central motor program, which consists of pre-structured motor commands, controls the production of sequential actions (e.g., Keele, 1968; for a review, see Rhodes et al., 2004). This view has received support in behavioral and electrophysiological studies examining the production of response sequences of different length (e.g., Hackley and Miller, 1995; Henry and Rogers, 1960; Klapp, 1995, 2003; Magnuson et al., 2004; Rosenbaum et al., 1984; Schröter and Leuthold, 2008; Sternberg et al., 1978; Verwey, 2003). However, little is known about the (brain) mechanisms underlying both the planning and execution of response sequences that differ in structural complexity, that is, response sequences for which only the relationship among response elements but not the number of response elements varies.

The main aim of the present study was to investigate motor programming of three-element response sequences that differ in structural complexity and finger order by analyzing event-related brain potentials (ERPs). Previous ERP studies examining response sequence effects have commonly analyzed the readiness potential (RP) (Kornhuber and Deecke, 1965; for a review, see Shibasaki and Hallett, 2006). Studies concerned with sequence programming revealed larger RPs before sequential, multi-element than single-element responses (e.g., Benecke et al., 1985; Kristeva, 1984;

Simonetta et al., 1991). To our knowledge, the ERP study of Prescott (1986) is the only one that examined the production of unilateral response sequences of different structural complexity. Specifically, in a forewarned RT (S1–S2) paradigm, participants were asked to produce in separate blocks of trials either homogeneous (1 → 2 → 3) or heterogeneous (1 → 3 → 2) response sequences consisting of index (1), middle (2) and ring finger (3) key presses. Most relevant for present purposes, Prescott found a larger response-locked RP preceding heterogeneous than homogeneous finger sequences. However, an analysis of the Contingent Negative Variation (CNV; Walter et al., 1964), which reflects preparatory motor activity (e.g., Brunia, 2003; Rohrbaugh and Gaillard, 1983), but also non-motoric anticipatory processes (e.g., Falkenstein et al., 2003; Van Boxtel and Böcker, 2004), was unaffected by structural complexity. The CNV and RP findings of Prescott seem to suggest that structural complexity influences mainly late execution-related motor processes in the brain. However, possible influences of structural complexity on preparatory brain processes are still relatively unknown, because functional neuroimaging and transcranial magnetic stimulation (TMS) studies examined mostly sequence execution (e.g., Chen et al., 1997; Gerloff et al., 1997, 1998; Haaland et al., 2004; Van Oostende et al., 1997; but see Elsinger et al., 2006).

Another open issue concerns the brain areas contributing to the execution of finger response sequences of different structural complexity. Thus, Kitamura et al. (1993) suggested that both the supplementary motor area (SMA) and bilateral sensorimotor areas contribute to sequence programming, based on their finding of a larger late RP over both midline and bilateral precentral electrodes before sequential as compared to simultaneous index

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and middle finger movements. In accord with Kitamura et al.'s proposal, neuroimaging, neurophysiological, and repetitive TMS studies demonstrated influences of structural complexity on both SMA and primary motor cortex (M1) (e.g., Colebatch et al., 1991; Gerloff et al., 1997, 1998; Lu and Ashe, 2005; Van Oostende et al., 1997; Wexler et al., 1997).¹ Yet, findings from Arunachalam et al. (2005) indicate that the control of finger sequences by SMA and M1 might depend on finger order. Thus, sequential taps with two fingers were found to be faster in the little-to-index finger direction (4 → 1) than the reverse direction (1 → 4), for both adjacent and non-adjacent fingers. Arunachalam and colleagues speculated that this tapping effect reflects the temporal gradient of finger programming in grasping objects. Moreover, when applying TMS to contralateral M1 after the first tap of a two-finger tapping sequence, disruption of the next tap was larger in the faster (2 → 1) than the slower tapping direction (1 → 2). The authors concluded that tapping in the faster direction is controlled by M1 and in the slower direction by SMA.

2. Objectives and rationale

The main objective of the present study was to investigate whether the preparation of heterogeneous as compared to homogeneous response sequences influences effector-unspecific and/or effector-specific levels of the motor system. Another goal was to determine the influence of finger-order on response sequence execution and its underlying brain processes. To this end, a response precuing (S1–S2) paradigm (cf. Rosenbaum, 1983) was employed, in which participants were to perform three-finger response sequences of different structural complexity (e.g., 1 → 2 → 3 and 3 → 2 → 1 vs. 1 → 3 → 2 and 3 → 1 → 2). Advance information (S1) about response sequence (homogeneous vs. heterogeneous) and response hand (left vs. right) was factorially manipulated, whereas the start finger (1 vs. 3) was specified only by the response signal (S2). This allowed us to investigate the nature of finger-independent preparation of response sequences of different structural complexity and of finger-order dependent differences on motor execution.

2.1. Preparation of response sequences

To examine whether the planning of heterogeneous as compared to homogeneous response sequences involves contributions of medial as well as lateral motor areas (e.g., Kitamura et al., 1993), we analyzed foreperiod motor activation (foreperiod CNV) over these areas (cf. Jentzsch et al., 2004). Because surface ERP waveforms provide a spatially blurred picture of the underlying brain activity due to volume conduction effects, like in other EEG studies concerned with motor programming (e.g., MacKay and Bonnet, 1990; Vidal et al., 1995), we estimated surface Laplacian waveforms to increase the spatial resolution of the EEG (Nunez et al., 1994). As in similar previous studies (e.g., Schröter and Leuthold, 2009; Ulrich et al., 1998; Wild-Wall et al., 2003), we expected that RT decreases and foreperiod CNV amplitude increases with increasing amount of advance information, reflecting the associated reduction of S–R alternatives and advance movement preparation. Most importantly, if structural complexity influences motor planning

¹ In the one fMRI study that controlled for the number of fingers included (Harrington et al., 2000) larger activation was found for heterogeneous than homogeneous sequences within premotor and parietal lobe areas. However, responses in this study were externally cued by a visual signal, thereby minimizing motor programming demands considerably in comparison to conditions in which the response sequence must be internally pre-structured, presumably under the involvement of SMA and M1 (e.g., Dassonville et al., 1998; Van Oostende et al., 1997). As a result, the generality of Harrington et al.'s findings awaits further empirical tests.

only at a higher, effector-unspecific level when response sequence is precued, foreperiod CNV amplitudes over medial but not lateral motor areas should be larger for heterogeneous than homogeneous sequences. In addition, structural complexity should not influence effector-specific motor activation, as indicated by the hand-related foreperiod CNV asymmetry over lateral motor areas when hand is precued.

2.2. Finger-order effects

To reveal possible complexity effects on execution-related motor activity we analyzed the amplitude of response-locked surface Laplacian waveforms over lateral and medial motor areas immediately preceding key press onset. Building on the findings of Arunachalam et al. (2005), we predicted that homogeneous sequences are produced faster in the ring-to-index finger direction (3 → 2 → 1) than the reverse direction (1 → 2 → 3). For heterogeneous response sequences, due to the change in direction after the second key press (e.g., 1 → 3 → 2), we predicted that the finger order effect for the first part of the response sequence (e.g., 1 → 3) is different from that for the second part (e.g., 3 → 2), as each part should be produced faster in the ring-to-index finger direction. To reveal such finger order effects, we analyzed inter response intervals (IRIs). Crucially, finger order might also modulate the extent to which response sequences are controlled by SMA and M1, which should be reflected by surface Laplacian waveforms over medial and lateral motor areas.

3. Method

3.1. Participants

Nine females and seven males ($M = 25.3$ years; range = 21–42 years) volunteered in a single 2-h experimental session in return of £12. All participants were recruited at the University of Glasgow, had normal or corrected-to-normal vision, and were mainly right-handed as indicated by a mean handedness score (Oldfield, 1971) of 47.6; there were four left-handed participants.

3.2. Apparatus and stimuli

The presentation of stimuli and recording of responses were controlled by a DOS computer. Letter and digit stimuli were white characters presented centrally against the blue background of a colour monitor. A plus sign of 0.5° visual angle presented in white served as warning stimulus and fixation cross. Ambient light was kept at a low level. A fixed chin rest provided a constant viewing distance of 60 cm. Fig. 1 shows a schematic illustration of a sample S2 and of the response pads.

Responses consisted of a sequence of three key-presses with the index, middle and ring finger of either the left hand or the right hand. Two response pads were used to register these sequential finger responses. On each response pad, three keys were mounted about 1.25 cm (from edge to edge) apart. The two response pads were aligned to the body's midline. Index, middle, and ring fingers of the left and right hands operated the three keys on each response pad, respectively. For half of the participants, the left hand was assigned to the upper response pad and the right hand was assigned to the lower response pad, the other half of the subjects received the reverse assignment.

Precues were composed of two letters from the stimulus set R, L, S, C, and X, with each letter subtending approximately 0.5° of visual angle. To prevent horizontal eye movements, the centers of both precue elements were located 0.5° above and below the fixation point, respectively. The letters "L" (Left) vs. "R" (Right) provided advance information about response hand and the letters "S" for Straight (Homogeneous) vs. "C" for Crossed (Heterogeneous) about the response sequence. The letter "X" served as non-informative filler when the precue consisted of less than two informative letters. For half of the participants, information about response sequence was always provided above the fixation point and information about response hand was always presented below the fixation point. This assignment was reversed for the remaining half of participants.

The white S2 (3.25°) was composed of one digit (1, 2, or 3) and three dashes (–). The digit was displayed at one of four possible display positions arranged in a vertical column along the centre of the monitor and the dashes were presented at the remaining three positions. The centers of the two upper positions and the two lower positions were located 1.5° and 3.0° above and below the fixation cross, respectively. If the S2 appeared in one of the two upper (lower) positions, then the response sequence was performed with the hand operating the upper (lower) response pad. Digit position determined in a spatially compatible manner the start finger of the

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