Motor programming of rapid finger sequences: Inferences from movement-related brain potentials

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Abstract

The present study investigated the predictions of two prominent models (Klapp, 1995, 2003; Rosenbaum, Inhoff, & Gordon, 1984) of programming of response sequences with the help of behavioral data, the foreperiod Contingent Negative Variation (CNV) and the Lateralized Readiness Potential (LRP). Participants performed one-key and three-key responses with their left or right hand in a precuing task. Sequence length was manipulated across blocks and precues provided either no information, partial information about hand or start finger, or full information about the response. A sequence length effect was indicated by reaction time when the precue provided partial or full information. The LRP data suggested that the duration of motor processes increases with sequence length. Foreperiod LRP and CNV revealed that participants preprogram only the first element of the sequence and prepare multiple responses if the precue provides only partial information. We discuss the implications of current findings for the two models.

Descriptors: Response sequence length effect, Contingent Negative Variation, ERP, Lateralized Readiness Potential, Response precuing, Motor programming

Sequential actions play a prominent role in achieving goal-directed behavior. Despite the apparent ease with which we perform such actions, the underlying functional and brain mechanisms are still not entirely understood. Functional neuroimaging, neuropsychological, and neurophysiological studies have been indicating a key role of the supplementary motor area (SMA) and the pre-SMA in the planning and timing of multi-element action patterns (e.g., Dick, Benecke, Rothwell, Day, & Marsden, 1986; Gerloff, Corwell, Chen, Hallett, & Cohen, 1998; Halsband, Ito, Tanji, & Freund, 1993; Harrington et al., 2000; Kennerley, Sakai, & Rushworth, 2004; Shima & Tanji, 1998, 2000). Psychological studies examining response sequences of different length (e.g., Henry & Rogers, 1960; Klapp, 1995, 2003; Magnuson, Wright, & Verwey, 2004; Rosenbaum, Inhoff, & Gordon, 1984; Sternberg, Monsell, Knoll, & Wright, 1978; Verwey, 1999) have provided evidence for the view that a central motor program, which consists of prestructured motor commands, controls the production of sequential actions (e.g., Keele, 1968; for a recent overview, see Rhodes, Bullock, Verwey, Averbeck, & Page, 2004).

In the present work, the major aim is to reveal the mechanisms underlying the programming of response sequences by combining the response precuing paradigm (Rosenbaum, 1980, 1983) with the recording of event-related brain potentials (ERPs). Whereas such a combined approach has allowed researchers to advance our understanding about the hidden mechanisms underlying the preparation of simple actions (e.g., Leuthold, Sommer, & Ulrich, 1996; Osman, Moore, & Ulrich, 1995; for a review, see Leuthold, Sommer, & Ulrich, 2004), to our knowledge, it has not yet been applied to study the programming of response sequences.

Models of Response Sequence Programming

Here we review the two main competing models of programming of short response sequences, namely the two-process model of Klapp (1995, 2003) and the hierarchical editor model (HED) of Rosenbaum et al. (1984). Figure 1 shows a schematic illustration of the programming processes assumed by the two models, respectively, for one-key and three-key responses in a simple reaction time (RT) task (and a precuing task) and a choice RT task.

Klapp (1995, 2003) has argued that two distinct parallel processes contribute to the programming of response sequences. This conclusion was initially based on the finding that sequence length and response duration produce differential effects on RT in a simple RT task as compared to a sequence choice RT task, in which participants have to choose between response alternatives differing in sequence length. Specifically, in the simple RT task,
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RT increases with the number of response elements but is uninfluenced by response duration. By contrast, in the sequence choice RT task, RT increases with increasing response duration but is uninfluenced by the number of response elements (see also Verwey, 1999). Klapp (1995) proposed a two-process model to account for these differential RT effects. The so-called INT process includes the programming of internal features of a single element (e.g., duration), whereas the so-called SEQ process relates to the programming of the overall sequence of response elements (e.g., single key presses) or chunks. This model explains the simple RT task pattern by assuming that the INT process is performed prior to the onset of the imperative stimulus, whereas the SEQ process must be performed after the imperative stimulus that involves response choice (e.g., the choice between different effectors). Therefore, we use the more specific term “sequence choice RT task” in order to refer to tasks including a choice between response sequences of different length.

Figure 1. Schematic illustration of the programming processes assumed by the original two-process model of Klapp (1995, left side) and the HED model of Rosenbaum and colleagues (1984, right side) for one-key and three-key responses in the simple RT task/sequence precuing task and in the sequence choice task. INT: process INT, SEQ: process SEQ, MP: motor program containing all features common to the possible responses, ED: edit pass, EX: execution pass, SP: sequence precue, WS: warning stimulus, IS: imperative stimulus, R1–3: responses 1–3.

Two-process model

HED model

Simple RT / Sequence Precuing Task

1-key

INT SEQ MP ED

SP IS R1

1-key

SEQ

INT MP ED

SP IS R1

3-key

INT SEQ MP ED

SP IS R1-R3

3-key

SEQ

INT MP ED

SP IS R1-R3

Sequence Choice Task

1-key

INT MP ED

WS IS R1

3-key

SEQ

INT MP ED

WS IS R1-R3

Note: In the simple RT task, the sequence precue is replaced by a warning stimulus. According to Klapp’s (2003) modified two-process model, in the simple RT task/sequence precuing task process INT corresponds to the establishment and uploading of an abstract time frame into a motor buffer and process SEQ to the scanning of the time frame until the starting point of the response sequence is found. Moreover, this model assumes that scanning in the sequence choice task is not required, as no abstract time frame is preloaded into the buffer. Hence, the processes INT and SEQ depicted for the sequence choice task would be replaced by a single selection/motor programming process that is unaffected in its duration by response sequence length.

However, in more recent experiments using the response precuing paradigm (Rosenbaum, 1980; Klapp, 2003; see also Khan, Mourton, Buckolz, & Franks, 2008) found evidence against the view that INT and SEQ processes operate in parallel. In this work, a precue provided partial advance information about sequence length (N = 1, 2, or 3) whereas the imperative stimulus specified the response element (syllable, vocal or manual response) that had to be repeated N times. Because the response element was not specified, according to the two-process model, the INT and SEQ process should both occur after the imperative signal. Hence, RT should be uninfluenced by sequence length as for the sequence choice RT task. In contrast to this prediction, RT in this precuing task increased with response sequence length.

To explain this finding, Klapp (2003) modified his original model by assuming that the initiation of each response element is controlled by a temporal framework, which specifies the time of initiation of each element in an abstract manner, that is, independent of the nature of individual response elements. When the response sequence is known in advance (as in simple RT and response precuing tasks), this abstract time frame is loaded into a motor buffer, while it is activated only after the presentation of the imperative stimulus. During the activation period, the time frame is scanned until the starting time point of the response sequence is found (see also Sternberg et al., 1978). As scanning time increases with the number of time points loaded, this explains the increase of RT with sequence length both in the simple RT task and when the number of response elements is precued. According to Klapp (2003), however, scanning is not required in the sequence choice tasks, because the time frame is retrieved just before responding without the need for scanning. Thus, RT is independent of response sequence length in this task.

Both the original and modified two-process model of Klapp (1995, 2003) challenges models that assume a serial programming of response sequences (e.g., Rose, 1988; Rosenbaum et al., 1984; Sternberg et al., 1978; for a review of these models, see Schröter & Leuthold, 2008). However, the parametric HED model of Rosenbaum and colleagues (1984; see also Rosenbaum, Van Hindorff, & Munro, 1987), which assumes a serial programming process of response sequences, can also account for the above reported pattern of response sequence length effects (Khan et al., 2008; Klapp, 1995, 2003). Specifically, according to the HED model, a hierarchically organized motor program that contains all the features common to the possible response sequences is established before the response signal is presented. After the imperative signal has been identified, two processing phases follow before the first element of the response sequence is

3Furthermore, this two-process model can also account for the fact that the sequence length effect on simple RT decreases with practice (Klapp, 1995; Verwey, 1999; Wright, Black, Immink, Brueckner, & Magnuson, 2004). According to Klapp (1995), participants optimize the SEQ process for longer response sequences by integrating the consecutive key presses into a single chunk (cf. Verwey, 1996, 2003; Verwey & Eikelboom, 2003).
executed. First, during the edit pass, all uncertain response features are specified in a serial manner from top to bottom of the program hierarchy. Crucially, editing of each response feature requires a certain amount of time. Second, the execution pass follows upon completion of the edit pass. Here, the motor program is traversed again from the highest to the lowest level of the hierarchy, and a response element is physically executed whenever a terminal response node is encountered. When response sequence length is known in advance, the number of editing steps involved in motor program specification increases with sequence length. As each editing step takes time, RT increases with response sequence length (cf. Figure 1, upper right panel). However, in a sequence choice task, the alternative responses are specified within the same motor program and, hence, RT is unaffected by sequence length (cf. Figure 1, lower right panel; see also Schröter & Leuthold, 2008).

To test the two-process model of Klapp (1995, 2003) against the HED model of Rosenbaum et al. (1984), we propose to study in a response precuing paradigm the programming of response sequences of different lengths in combination with the programming of other response features, namely, response hand and start finger. This procedure is motivated by the assumption that for the HED model the number of required editing steps depends on the to-be-specified parameters; hence, the sequence length effect would decrease with the amount of advance information provided. By contrast, the two-process model assumes that the response sequence length effect is determined by the duration of the SEQ or scanning process, which is not influenced by the specification of other response parameters. Accordingly, and in contrast to the HED model, the response sequence length effect should be independent of the amount of advance information provided. Importantly, as behavioral measures provide only indirect access to covert preparatory and online motor programming processes, we will supplement behavioral measures by the recording of ERPs. This is a particularly promising approach, as it builds on previous ERP studies concerned with the functional organization of motor programming (cf. Leuthold et al., 2004). It is worthwhile to briefly review the insights gained from these ERP studies before outlining the objectives and rationale of the present work.

**ERP Correlates of Advance Motor Programming**

The Contingent Negative Variation (CNV; Walter, Cooper, Aldridge, McCallum, & Winter, 1964) and the Lateralized Readiness Potential (LRP; Coles, 1989; Eimer & Coles, 2003) provide excellent tools to tap into the covert mechanisms involved in the programming of response sequences. The CNV is a sustained negativity that develops after the precue (S1) and before the imperative signal (S2), that is, during the foreperiod interval. The CNV during the late phase of the foreperiod, to which we refer hereafter as foreperiod CNV, is typically maximal at the Cz electrode and is assumed to reflect preparatory motor activity (cf. Leuthold et al., 2004; Rohrbaugh & Gaillard, 1983) originating mainly within higher-level motor areas (supplementary motor area, SMA, and cingulate motor area, CMA) but also within lower-level motor areas (primary motor cortex, MI) (cf. Leuthold & Jentzsch, 2001; Praamstra, Stegmann, Horstink, & Cools, 1996). Ulrich, Leuthold, and Sommer (1998), who showed the foreperiod CNV amplitude to gradually increase with the number of precued movement dimensions (see also Wild-Wall, Sangals, Sommer, & Leuthold, 2003), suggested that the foreperiod CNV reflects abstract programming at a higher motor level where all movement parameters are prepared independently. In addition, the foreperiod CNV might also relate to anticipatory cognitive processes (e.g., Brunia, 2003) and the degree of effort allocation (e.g., Falkenstein, Hoormann, Hohnsbein, & Kleinsorge, 2003).

The LRP is a relative measure of effector-specific activation within the MI cortices (Leuthold & Jentzsch, 2002) by which the time course of hand-selective motor activation can be traced (cf. De Jong, Wierda, Mulder, & Mulder, 1988; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988; Miller & Hackley, 1992). For example, in a response precuing task, Wild-Wall et al. (2003) found a foreperiod LRP when hand was precued. In addition, in line with a hierarchical preparation view (cf. Rosenbaum, 1980), foreperiod LRP amplitude increased in amplitude only when additionally precued parameters represented contiguous steps in the hierarchy (i.e., from hand to hand-plus-finger) but not when a lower-level parameter was additionally precued (hand-plus-direction precue) while a parameter at an intermediate level of the program hierarchy was missing (finger).

Most important for present purposes, analyzing LRP onsets obtained in waveforms time-locked to the onset of either the imperative signal or the overt response (cf. Leuthold et al., 1996; Osman & Moore, 1993) reveals that the time course and locus of experimental effects within the stream of information processing. Thus, the interval from response signal onset to stimulus-locked LRP onset (S-LRP interval) indicates the duration of premotoric (perceptual and response selection) processes, whereas the interval between response-locked LRP onset and the overt response (LRP-R interval) indicates the duration of late motor processes.

**Response Sequence Length Effects and ERPs**

ERP studies occasionally investigated the preparation of manual response sequences of different length. Using a S1-S2 paradigm, Prescott (1986) manipulated response sequence length between different experimental blocks of trials. He found foreperiod CNV to be unaffected by sequence length, whereas the asymmetry of the response-locked readiness potential (RP) was larger preceding three-key than one-key movements of the dominant hand, like in the study of Kristeva (1984; but see Lang, Zilch, Koska, Lingdinger, & Deecke, 1989; Simonetta, Clanet, & Rascol, 1991). In our view, these findings appear to suggest that programming demands of the forthcoming response influence the motor system at an effector-specific level rather than higher level of motor programming. Consistent with this view, more recent foreperiod LRP findings indicate an effect of response sequence length on effector-specific preparatory processes (Hackley & Miller, 1995; Stief, Leuthold, Miller, Sommer, & Ulrich, 1998). Participants in the study of Hackley and Miller were to produce one-key responses with their left or right index finger or three-key responses with the index, ring, and middle fingers. Sequence length was manipulated across blocks, and a precue specified response hand in each trial. The foreperiod LRP amplitude was considerably enhanced in the three-key as compared to the one-key condition (see also Stief et al., 1998; Experiment 2). Together, the aforementioned RP and LRP findings certainly agree with the recent neurophysiological evidence obtained in monkeys (Lu & Ashe, 1989).
2005) that points to a role of MI in the programming of action sequences.

To determine the locus of the response sequence length effect within the stream of information processing, two previous ERP studies analyzed S-LRP and LRP-R onsets (Schröter & Leuthold, 2008; Smulders et al., 1995). Both studies reported a longer LRP-R interval, but not S-LRP interval, for three-key than one-key responses, suggesting that the duration of late motor processes increases with sequence length. As Schröter and Leuthold (2008) pointed out, these LRP findings are at variance with the two-process model and the HED model, because both assume that response hand is activated only once the sequence has been fully programmed and hence predict a response sequence length effect on the S-LRP rather than the LRP-R interval. Therefore, to accommodate the sequence length effect on the LRP-R interval, both the two-process model and the HED model need to be slightly modified by assuming, respectively, that the SEQ process occurs only after response hand activation and that the first response element (hand) is immediately activated during the edit pass but only executed once the execution pass has reached the terminal node for this element.

**Objectives and Rationale**

The main objective of the present study was to discriminate between the two major accounts of response sequence length effects, namely, Rosenbaum's HED model and Klapp's two-process model, as mentioned earlier, by examining whether the sequence length effect is modulated by the amount of advance information provided. To this end, we employed a response precuing paradigm in which participants were to perform nonrepetitive manual responses that differed in sequence length (one-key and three-key responses) and advance information about different response features (i.e., response hand, start finger) was manipulated. The analysis of RT was complemented by that of S-LRP and LRP-R intervals to advance our inferences concerning the locus of precuing and response sequence length effects within the S-R processing stream, although this was possible only for conditions in which response hand was available (finger precise and uninformative precise) and, hence, the LRP was at baseline before the imperative signal (cf. Leuthold et al., 1996).

In addition, to reveal possible influences of advance information on perceptual processing stages, as in Leuthold et al. (1996), we analyzed the peak latency of the P300 component. P300 latency has been shown to be a sensitive index of perceptual processes and to reflect changes in stimulus evaluation time while being largely unaffected by motor-related processes (e.g., Leuthold & Sommer, 1998; McCarthy & Donchin, 1981; for a review, see Verleger, 1997). Thus, if the duration of perceptual processing is influenced by the precue category, this should be indicated by P300 latency. Figure 2 illustrates the programming processes assumed by the two models, respectively, for one-key and three-key responses in the four precue conditions.

The original and modified two-process model of Klapp (1995, 2003) accounts for the response sequence length effect in terms of a specific SEQ or abstract time frame scanning process, whereas the programming of other response features produces an additive effect (cf. Khan et al., 2008). As sequence length is manipulated between blocks in the present experiment, participants can preload an abstract time frame. Therefore, this model predicts a response sequence RT effect of equal magnitude in all precue conditions (cf. Figure 2A–D, left side). In addition, like in previous LRP studies (Schröter & Leuthold, 2008; Smulders et al., 1995), the LRP-R interval but not the S-LRP interval should be longer for three-key than one-key responses.

Unlike the two-process model of Klapp (2003), the HED model of Rosenbaum et al. (1984) is quite specific regarding the specification of response parameters during the edit pass. Most importantly, this model assumes that only undefined response parameters need to be specified during the edit pass (cf. Rosenbaum, 1990). Consequently, the HED model predicts that precise information modulates the sequence length effect, because advance information about the forthcoming response (hand, start finger) reduces the number of required editing steps (cf. Figure 2, right side). For example, with full information, all hand and terminal finger nodes can be specified, and hence editing is not needed after the imperative stimulus. Conversely, time-consuming editing steps are necessary if only partial and even more so if no advance information about the forthcoming response is available. As a result, the sequence length effect in RT should be smallest with full advance information (cf. Figure 2A) and largest with no advance information (cf. Figure 2D). For partial precue conditions, one should expect intermediate response sequence length effects, although of larger magnitude when response hand (cf. Figure 2B) rather than start finger (cf. Figure 2C) is precued, because in the former condition more
program nodes (three finger nodes) must be specified during the edit pass than in the latter condition (one hand node). Crucially, for the same reason, a smaller response sequence length effect in the LRP-R interval is predicted for the finger precue than the uninformative precue (cf. Figure 2C,D).

Of course, the above predictions about the modulation of the sequence length effect by advance information apply only if participants utilize precue information and indeed preprogram the respective response parameters. Therefore, to demonstrate the specification of response parameters at a higher programming level, together with other preparatory influences like effort allocation, we measured foreperiod CNV amplitude, whereas foreperiod LRP amplitude was measured to reveal motor programming and its possible constraints at an effector-specific level—presumably MI. Utilization of precue information would be indicated, like in previous studies (e.g., Khan et al., 2008; Rosenbaum, 1980; Ulrich et al., 1998; Wild-Wall et al., 2003), by RT decreases and foreperiod CNV amplitude increases with increasing amount of advance information, reflecting the associated reduction of S-R alternatives and advance movement programming. In addition, effector-specific preprogramming would be indicated by larger foreperiod LRP amplitude when both response hand and start finger are known than if only hand is known, like in the study of Wild-Wall et al. (2003). Finally, for the full precue condition, which closely resembles those employed by Hackley and Miller (1995), we expect to replicate the finding of a larger foreperiod LRP for three-key responses than for one-key responses.

Method

Participants

Thirteen women and three men (mean age: 25.1 years; range: 19 to 43 years) volunteered in a single 2.5–3-h experimental session as partial fulfillment of a course requirement or in return of €20. All participants were recruited at the University of Tübingen, had normal or corrected-to-normal vision, and had a mean handedness score (Oldfield, 1971) of .82 (range = .65 to 1.0).

Apparatus and Stimuli

The presentation of stimuli and recording of responses and RTs were controlled by the Experimental Run Time System (ERTS) running on a DOS computer. White letter and digit stimuli were presented at the center of the display against the blue background of a color monitor. A plus sign of 0.5° visual angle presented in white at screen center 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 80 cm. Figure 3 shows a schematic illustration of a sample imperative stimulus and the response pads.

Two response pads were used to register the 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 hand 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 hand; the other half of the participants received the reverse assignment. The order of response conditions was manipulated between blocks. Half of the participants responded with a one-key response in the first half of the experiment and with a three-key response in the second half. The order of response sequences was reversed for the other half of the participants.

The white imperative signal (3.29°) was composed of one digit (1 or 3) and three dashes (—). The digit 1 indicated a one-key response and the digit 3 indicated a three-key response. The digit was displayed at one of four possible display positions arranged in a vertical column along the center of the monitor and the dashes were presented at the remaining three positions. The two upper positions and the two lower positions were located 1.43° above and below the fixation cross, respectively. The position of the digit determined the start finger. That is, the upper top position indicated a response to start with the ring finger and the lower top position indicated a response to start with the index finger of the one hand, whereas the lower top position demanded a response to start with the ring finger and the lower bottom position to start with the index finger of the other hand. The one-key response consisted of either a single key press with the index or ring finger of either the left or right hand, and three-key responses consisted of three consecutive key presses with the index, ring, and middle finger or with the ring, index, and middle finger of either the left or right hand.

Precues were composed of two letters from the stimulus set R, L, Z, V, and X, with each letter subtending approximately 0.5° of visual angle. To prevent horizontal eye movements, the precue elements were located about 0.5° of visual angle above and below the fixation cross, respectively. For half of the participants, information about the start finger 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 other half of the participants. The letters L (left) or R (right) provided advance information about response hand and

Figure 3. Schematic illustration of the imperative stimulus presented on the computer screen (upper panel) and the response pads (lower panel) for a participant with the left response pad positioned above the right key pad. The sample imperative signal would require a one-key response with the left index finger as start finger (black response key). Digit identity determined the response sequence length (one-key or three-key). The position of the digit (1 or 3) determined the start finger (left ring, left index, right ring, or right index finger). The dashes served as placeholders for the alternative start fingers (gray response keys). As the response always started with an index or ring finger, the imperative stimulus did not include dashes to indicate the positions of the middle fingers (white response keys).
the letters Z (index finger) or V (ring finger) about the start finger. The letter X served as noninformative filler when the precue consisted of less than two informative letters.

There were four precue categories. First, the hand and finger precue (full precue) unambiguously signaled the required response. In this case, one letter indicated the response hand and the other letter indicated the start finger. For example, the letters Z and L presented above and below fixation in the three-key response sequence condition signaled a three-key response sequence of the left hand starting with the index finger. Second, the hand precue provided advance information about the response hand (left vs. right hand) but no information about the start finger. If the left (right) hand was prespecified, the letters L (R) and X were displayed. Third, the finger precue specified the start finger but not response hand. If the index (ring) finger was the start finger of the upcoming response the letters Z (V) and X were presented. Finally, the no-information precue (no precue) was composed of two X’s. There were 32 trial types resulting from the factorial combination of precue category by response alternative. A session included 20 replications of each trial type. With the exception of the blocked manipulation of response sequence, all other trial types were randomized across the experiment.

**Procedure**

In both the one-key and the three-key response conditions each participant was tested in two practice blocks of 32 trials followed by eight test blocks of 40 trials each, resulting in a total of 640 test trials. Participants were instructed about the meaning of the precues and were asked to utilize precue information to shorten RT but not to initiate a movement before response signal presentation. Each trial started with the presentation of the fixation cross, followed 650 ms later by the additional display of the precue. After a foreperiod of 1400 ms the precue was replaced by the response signal, which was presented until response onset or a maximal duration of 2100 ms, respectively. Then visual feedback about the correctness of the response was provided. One of the following messages was displayed: (a) “Korrekt” (Correct) if the response was correct; (b) “Fehler” if a wrong response alternative was used, if the participant responded with both hands, did not release a key before the next key press (three-key responses) or did not release the last key (both one-key and three-key responses), or responded too early or too late. Feedback information was displayed for 800 ms and after 2000 ms the next trial started with the presentation of the warning signal. Blocks of 40 trials each were separated by a break. Here, total mean RT and percentage of correct responses, computed for the preceding block, was provided as feedback. Participants controlled the duration of the break, as the next block started only once the lowest response key was pressed. They were asked to perform the required response as quickly as possible while avoiding response errors, to keep their eyes on the fixation cross, and not to blink as long as it was visible.

**Electrophysiological Recordings**

Electroencephalographic (EEG) and electrooculographic (EOG) activity was continuously recorded using a Neuroscan amplifier system. EEG was measured from midline electrodes Fz, Cz, and Pz, over the left hemisphere from electrode C3, and over the right hemisphere from electrode C4 (Jasper, 1958). The right mastoid was used as reference and the Fpz electrode as ground. Vertical EOG (vEOG) was registered from above and below the right eye and the horizontal EOG (hEOG) from the left and right outer canthi. Electromyographic activity (EMG) was recorded with a bipolar derivation that approximately trisected the wrist–elbow distance on both the left and the right ventral forearm. EEG, EOG, and EMG recordings were made with Ag/AgCl electrodes. All signals were sampled at 250 Hz. Electrode impedances were kept below 5 kΩ on the scalp and face and below 10 kΩ on the forearms.

The analysis epoch for the stimulus-locked data started 200 ms prior to precue onset and lasted for a total duration of 2800 ms. For response-locked analyses epochs started 2000 ms before the response and lasted for 2500 ms. EEG, EOG (both band-passes: 0.05–30 Hz), and EMG (bandpass: 0.10–30 Hz, cf. Osman et al., 1995) activity was filtered and averaged time-locked to the onset of the imperative stimulus (S-locked data) or to response onset (R-locked data) like in the study of Schröter and Leuthold (2008). Trials in which EOG activity exceeded an absolute value of 100 μV during the epoch were excluded from analysis.

The LRP was computed from average ERPs at C3 and C4 using standard procedures (cf. Coles, 1989; Eimer & Coles, 2003). For each condition the difference between the contralateral and the ipsilateral activation was computed (C3’ minus C4’ for trials requiring a right hand response and C4’ minus C3’ for trials requiring a response with the left hand) to eliminate any ERP activity unrelated to hand-specific motor activation. In addition, the computations to derive the LRP were also applied to hEOG and rectified EMG data to determine response-related lateralization in these measures (cf. Miller & Hackley, 1992; Osman et al., 1995).

**Data Analysis**

Only trials with correct response, with RT between 100 ms and 1200 ms, and without EEG or EOG artifacts were included in RT and EEG data analysis. All signals were averaged separately for experimental conditions. CNV and LRP waveforms were aligned to a 200-ms baseline before precue onset. Mean foreperiod CNV and LRP amplitudes were analyzed in a 200-ms interval immediately preceding the onset of the imperative signal. P300 waveforms were aligned to a 200-ms baseline that started 200 ms before the onset of the imperative stimulus. P300 latency was determined at Pz, using a computerized peak-picking procedure, at the time point after the onset of the imperative signal at which the largest ERP positivity occurred in the time interval from 250 to 600 ms.

LRP onsets were measured and analyzed by applying the jackknife-based procedure suggested by Miller, Patterson, and Ulrich (1998) and Ulrich and Miller (2001). Sixteen different grand average LRPC’s for each of the experimental conditions were computed by omitting from each grand average the ERP data of another participant. Off-line, each grand average was low-pass filtered (4 Hz) and LRP onsets were determined in the waveform of each grand average. Stimulus-locked and response-locked LRP waveforms were aligned to a 200-ms baseline that started 200 ms before the imperative signal and 800 ms before the response, respectively. LRP onsets were measured with both absolute and relative onset criteria to demonstrate the robustness of effects. S-LRP onsets (for calculating the length of the S-LRP interval) were measured at the point in time, respectively, when LRP amplitude reached 1.8 μV and 40% of maximal LRP amplitude within 500 ms after stimulus onset in that specific condition. Effects in the LRP-R interval were obtained using, respectively, an absolute LRP onset criterion of 2.0 μV and a
relative LRP amplitude criterion of 40%, with waveforms referred to a 200-ms baseline. Response-locked EMG onsets were measured analogously to the response-locked LRP (cf. Osman et al., 1995) but with an onset criterion of $-5 \mu V$. To check for potential influences of horizontal eye movements on LRP onsets, we calculated the average signed hEOG activity in stimulus-locked hEOG and response-locked hEOG waveforms in the 500-ms interval following stimulus onset and in the 500-ms interval preceding response onset, respectively.

**Design**

Statistical analyses were performed by means of Greenhouse–Geisser corrected repeated measures analyses of variance (ANOVA). A preanalysis of the data revealed no systematic effects of the within-subject factors response hand and start finger on RT. Therefore, data were collapsed across hand and start finger.

For the analysis of behavioral data (movement time [MT], RT, error rate), foreperiod LRP, and P300 latency, the within-subject variables were precue category (full precue, hand precue, finger precue, no precue) and response sequence (one-key, three-key). The analysis of foreperiod CNV amplitude included the additional factor electrode (Cz, Fz, Pz). LRP onset measures, response-locked EMG onset, and hEOG amplitudes were submitted to ANOVA with variables precue category (FP, NP) and response sequence (one-key, three-key). For LRP onset measures and response-locked EMG onset, the F values (as well as the t values of planned contrasts) were corrected as follows:

$$F_C = F(n-1)^2$$

where $F_C$ denotes the corrected $F$ value and $n$ the number of participants. This correction is necessary as the mean squares for the error terms of the experimental effects and their interactions are too small by a factor of $(n-1)^2$ when applying the jackknife-based ANOVA procedure (cf. Ulrich & Miller, 2001). Tukey post hoc comparisons were performed where applicable for both behavioral and psychophysiological measures.

**Results**

**Movement Time**

Movement time for one-key responses (three-key responses) was defined as the interval from the start of the first key press up to the release of the first key (third key). As one should expect, the ANOVA for MT revealed a significant effect of response sequence, $F(1,15) = 635.36, MSE = 9.487, p < .001$, reflecting a longer MT for three-key (611 ms) than for one-key responses (177 ms). No other effects were significant (all Fs $< 1$).

**Reaction Time**

Figure 4 shows the mean reaction times and percentage of errors as a function of precue category and response sequence.

RT was not reliably shorter for one-key than three-key responses (547 vs. 563 ms), $F(1,15) = 1.80, MSE = 4460, p > .05$, whereas the effect of precue category was significant, $F(3,45) = 134.67, MSE = 3.778, p < .001$. Post hoc contrasts (critical value: 41.00 ms, $p < .05$) revealed the following order of mean RT for the different precue conditions: full precue (388 ms) $<$ hand precue (572 ms) $<$ finger precue (566 ms) $<$ no precue (695 ms). The interaction of precue category and response condition was significant, $F(3,45) = 6.97, MSE = 379.69, p < .01$.

Pair-wise $t$ tests revealed the following order of the sequence length effect for the different precue conditions: full precue (38 ms) $<$ hand precue (15 ms) $<$ finger precue (17 ms) $<$ no precue ($-7$ ms). However, the sequence length effect differed significantly from zero only in the full precue condition, $t(15) = 2.17, p < .05$, but failed to reach significance for the hand precue, $t(15) = 1.14, p > .05$, finger precue, $t(15) = 1.54, p > .05$, and for the no precue, $t(15) = -0.67, p > .05$, conditions.

**Error Rate**

An ANOVA was performed for arc-sine transformed error rate data, which comply better with the assumption of normally distributed error components (Winer, 1971). This analysis revealed a significant effect of response sequence, $F(1,15) = 32.26, MSE = 0.03, p < .001$, due to nearly twice as many error responses in the three-key (6.9%) than in the one-key response condition (3.7%). A more specific analysis of errors, however, revealed that this difference was caused by execution but not initiation errors within the three-key response sequence. The error rate for the first key press was virtually identical for three-key (3.3%) and for one-key responses (3.6%), $F < 1$. Precue category also had a significant effect on error rate, $F(3,45) = 3.46, MSE = 0.03, p < .05$. Contrasts revealed that error rate did only differ significantly between no precue (6.7%) and hand precue (4.0%) conditions. The interaction of precue category and response sequence was not significant, $F(3,45) = 1.02, MSE = 0.02, p > .05$.

**Foreperiod CNV Amplitude**

Figure 5 shows grand average ERP waveforms during the foreperiod as a function of response condition (one-key vs. three-key) and precue category and Figure 6 depicts foreperiod CNV amplitude values.

As can be seen in Figure 5, the centroparietal foreperiod CNV, $F(2,30) = 50.12, MSE = 36.60, p < .001$, was of larger amplitude for three-key ($-4.39 \mu V$) than for one-key responses ($-3.03 \mu V$), $F(1,15) = 5.85, MSE = 30.76, p < .05$. The effect of precue category was significant, $F(3,45) = 8.66, MSE = 16.03, p < .01$, indicating a smaller foreperiod CNV amplitude in the

![Figure 4](image-url)

**Figure 4.** Mean reaction times (upper panel) and percentage of errors (lower panel) as a function of precue category and response sequence. HFP: Hand+Finger Precue; HP: Hand Precue; FP: Finger Precue; NP: No Precue.
no-precue condition (−1.94 µV) than in the other precue conditions: full precue (−4.01 µV) = hand precue (−4.28 µV) = finger precue (−4.61 µV). This foreperiod CNV amplitude pattern was more prominent over frontocentral electrodes than over the parietal electrode (cf. Figure 5), resulting in a significant interaction of electrode position and precue category, $F(6,90) = 3.35$, $MSE = 2.12$, $p < .05$. The interaction of precue category and response sequence was significant, $F(3,45) = 3.76$, $MSE = 5.45$, $p < .05$. Foreperiod CNV amplitude was significantly larger for three-key responses than one-key responses in the full precue condition (−5.03 vs. −2.99 µV, $p < .01$) and the no precue condition (−3.09 vs. −0.80 µV, $p < .05$). However, foreperiod CNV amplitude did not differ between three-key and one-key responses in the hand precue condition (−4.60 µV vs. −3.96 µV) and the finger precue condition (−4.86 vs. −4.36 µV), both $ps > .05$. The interaction of electrode position, precue category, and response sequence was not significant, $F(6,90) = 1.01$, $MSE = 1.07$, $p > .05$.

To test for potential parallel response preparation (Jentzsch, Leuthold, & Ridderinkhof, 2004; see Discussion for details), we performed an additional analysis of foreperiod CNV activity contralateral and ipsilateral to the responding hand as recorded over electrodes C3 and C4. First, for the electrode site contralateral to the responding hand, a priori contrasts revealed no reliable influence of precue category on foreperiod CNV amplitude, $M$(full precue, hand precue, and finger precue) = −4.5, −4.7, and −4.4 µV, all $Fs < 1$. Second, foreperiod CNV amplitude at the electrode site ipsilateral to the responding hand was larger for the finger precue condition (−4.5 µV) in comparison with both the full precue condition (−2.6 µV), $F(1,15) = 14.6$.
p < .01, and the hand precue condition (−3.5 μV), F(1,15) = 10.4, p < .01. Third, the full and the hand precue conditions elicited a hand-related lateralization (comparison ipsi vs. contra) in foreperiod CNV amplitude, F(1,15) = 27.4, p < .001, whereas the finger precue condition showed no such effect, F < 1.

**Foreperiod LRP Amplitude**

Figure 7 shows the grand average foreperiod LRP, hEOG, and EMG waveforms as a function of precue category and response sequence.

The ANOVA of foreperiod LRP amplitude revealed a significant effect of precue category, F(3,45) = 29.65, MSE = 1.22, p < .001, with contrasts using the Tukey procedure (critical value: 0.53 μV, p < .05) revealing the following order of precue conditions: full precue (1.92 μV) > hand precue (1.20 μV) > finger precue (0.22 μV) > no precue (0.03 μV). Neither the effect of response sequence, F < 1, nor the interaction of the two factors, F(3,45) = 1.19, MSE = 0.57, p > .05, was significant.

**P300 Latency**

The three-way ANOVA with factors precue category and response sequence indicated a reversed response sequence length effect, as P300 latency was shorter for three-key than one-key responses (453 vs. 476 ms), F(1,15) = 7.19, MSE = 2.510, p < .05. The significant effect of precue category, F(3,45) = 6.50, MSE = 6.136, p < .01, was due to shorter P300 latency (critical value: 52.3 ms, p < .05) in the full precue condition (419 ms) as compared to the hand precue condition (492 ms) and the no precue condition (493 ms). P300 latency in the finger precue condition (455 ms) was of intermediate length but did not differ significantly from the other precue conditions, ps > .05. The interaction of precue category and response condition was not significant, F < 1.

**LRP Onset Latency**

In the following we first report effects on the S-LRP interval and the LRP-R interval as measured by applying the absolute onset criterion followed by those obtained for the relative onset criterion. Figure 8 shows the stimulus-locked LRP, hEOG, and EMG waveforms as a function of precue category and response sequence.

Although the S-LRP interval was numerically shorter for the three-key (310 ms and 281 ms) than the one-key (329 ms and 300 ms) response conditions, ANOVAs of the S-LRP interval revealed no significant effect of response sequence, F(1,15) = 2.47, MSE = 9.98, p > .05 and F(1,15) = 2.34, MSE = 11.98, p > .05. The effect of precue category was significant, F(3,45) = 6.75, MSE = 24.65, p < .05 and F(3,45) = 7.42, MSE = 11.32, p < .05, respectively, reflecting a shorter S-LRP interval in the finger precue condition (295 ms and 273 ms) than in the no precue condition (344 ms and 308 ms). Interestingly, the interaction of the two factors was also significant in both measures, F(1,15) = 5.11, MSE = 9.32, p < .05 and F(1,15) = 6.99, MSE = 4.65, p < .05. Post hoc t tests revealed that in the finger precue condition the duration of the S-LRP interval did not differ significantly between the one-key and three-key response conditions.
conditions (292 ms vs. 299 ms and 274 ms vs. 274 ms), $t_{C}(15) < 1, p > .05$. Unexpectedly, there was a reliable reversed sequence length effect of 45 ms (one-key: 366 ms and 328 ms, three-key: 321 ms and 287 ms) on the duration of the S-LRP interval in the no precue condition, $t_{C}(15) = 2.36, p < .05$ and $t_{C}(15) = 2.73, p < .05$.

Figure 9 shows the response-locked LRP, hEOG, and EMG waveforms as a function of precue category and response sequence. The corresponding ANOVA for the LRP-R interval revealed a main effect of response sequence, $F_{C}(1,15) = 4.58, MSE = 19.18, p < .05$ and $F_{C}(1,15) = 4.89, MSE = 13.85, p < .05$, reflecting a longer LRP-R interval for the three-key than for the one-key response condition (261 vs. 226 ms and 254 vs. 223 ms). The effect of precue category was significant, $F_{C}(1,15) = 10.87, MSE = 16.12, p < .01$ and $F_{C}(1,15) = 16.49, MSE = 17.05, p < .01$, reflecting a longer LRP-R interval in the no precue condition (269 ms and 270 ms) than in the finger precue condition (219 ms and 207 ms). The interaction of the two factors was not significant ($F_{C} < 1$).

**HEOG Activity**
Both S-hEOG, $F(1,15) = 1.10, MSE = 3.63, p > .05$, and R-hEOG activity, $F(1,15) = 2.01, MSE = 0.71, p > .05$, were low and did not differ significantly from zero. Furthermore, the ANOVA for stimulus-locked hEOG activity revealed no significant effect of response sequence, precue category (both $Fs < 1$), or the interaction of the two factors, $F(1,15) = 1.31, MSE = 5.60, p > .05$. The same was true for the ANOVA of the response-locked hEOG activity (all $Fs < 1$). Therefore, the observed latency differences cannot be explained by differential eye activity in the different conditions.

**Response-Locked EMG Latency**
The ANOVA of response-locked EMG onset latency revealed no significant results, all $F_{C} < 1$. This suggests that the duration of processes following muscle activation did not differ between the experimental conditions (cf. Osman et al., 1995).

**Discussion**
The present experiment investigated the organization of motor programming of one-key and three-key responses in a precuing paradigm. Response sequence length was blocked and a precue provided advance information about both response hand and start finger, partial information about either response hand or start finger, or no information. We combined the measurement of behavioral responses with that of ERPs in order to assess as fully as possible covert preparatory and online motor programming processes. This approach allowed us to test the predictions made by two-process model of Klapp (1995, 2003) and the HED model of Rosenbaum et al. (1984) regarding the influence of advance information about response parameters on the response sequence length effect. Before discussing the implications of the present behavioral and ERP results for the two competing models of the response sequence length effect, as mentioned in the introduction, it is first important to demonstrate that participants followed instructions and utilized precue information to optimize their performance. Then we will evaluate the two models in the light of relevant behavioral and ERP results.

**Effects of Precuing on Preparatory Processes**
Behavioral and ERP findings clearly indicate the utilization of precue information for advance preparation. Thus, responses were fastest for the full precue that specified both response hand and finger, intermediate for the partial hand and finger precue conditions, and slowest for the uninformative precue condition. This precuing effect in RT replicates the standard finding of decreasing RT with increasing amount of advance information obtained in previous studies (e.g., Leuthold et al., 1996; Rosenbaum, 1980; Ulrich et al., 1998). The present precuing effect in RT can be explained in terms of a reduction of S-R alternatives influencing perceptual and response selection stages and advance movement programming.

The foreperiod LRP and foreperiod CNV clearly indicate that participants used advance information to prepare for the forthcoming response already during the foreperiod. That is, the foreperiod LRP amplitude was larger when hand and finger than when only hand was precued, like in the study of Wild-Wall et al. (2003). This finding suggests that advance information about hand and finger influenced motor programming at an effectorspecific level. In addition, foreperiod CNV amplitude was larger in full and partial precue conditions than the no precue condition. Again, this finding provides converging evidence for the assumption that participants utilized advance information about hand or finger to improve their performance.

**Effects of Precuing on Processes Following the Imperative Signal**
To distinguish between premotor and motoric loci of the precuing effect, we analyzed stimulus-locked and response-locked
LRP onsets together with P300 latency. The S-LRP interval was longer in the no precue condition than the finger precue condition, indicating a shorter duration of either perceptual or response selection processes in the finger precue condition, most likely due to the reduction of response alternatives by the precue (e.g., Zelaznik, 1978). The finding of a precuing effect on P300 latency accords with the S-LRP effect and more generally suggests that the duration of perceptual processes was influenced by the nature of the precue. That is, P300 latency was shortest for the full precue condition but longest for the hand precue and the no precue conditions, for both of which the start finger was unknown. Importantly, however, advance information about the start finger additionally reduced the time demands of late motor processes, as indicated by the shorter LRP-R interval in the finger precue condition than in the no precue condition. This is a novel finding and extends previous reports that demonstrated that motor processing time is shortened by advance information about movement direction (e.g., Jentsch et al., 2004; Leuthold et al., 1996).

Whereas the chronometric ERP findings provide support for the influence of advance information on the time demands of S-R processing, there is a potential concern regarding the motoric locus of the finger precuing effect. As the evaluation of the HED model depends to a large extent on the interpretation of LRP-R interval effects, it is important to elaborate this concern in some detail. As pointed out by Osman et al. (1995) and Leuthold et al. (1996), the interpretation of LRP-R latency effects becomes less clear when premotoric and motoric stages overlap in time. In terms of such an overlap hypothesis, one might assume that it was easier to retrieve information about the required response hand than about the required start finger in the no precue condition. Accordingly, if there is asynchronous output of hand information from the response selection stage to the motor stage, the response hand would already become activated (and the LRP start to deviate from baseline) while the selection of the appropriate start finger would be still ongoing. That is, in the no precue condition, finger information would be available and transmitted from the response selection stage to the motor stage only after the LRP onset, thereby delaying the LRP-R interval. This phenomenon has been documented in a task in which finger selection was much more difficult than in the present study (Huckley & Valle-Inclán, 1999). By contrast, such asynchronous output to the motor system would be absent when the start finger is precued. As a result, the longer duration of the LRP-R interval in the no precue condition as compared to the finger precue condition would result from the nonmotoric selection process that temporally overlaps with the motor stage (cf. Leuthold et al., 1996; Osman et al., 1995).

On the basis of present LRP findings it is not possible to completely rule out this overlap hypothesis. However, we believe that the present chronometric and foreperiod ERP findings provide little support for it. On the one hand, both the finger precue condition and the no precue condition require the selection of the correct response hand. As a result, if hand information is easier to retrieve and hand is also initially activated as implied by the overlap hypothesis, the S-LRP interval should be uninfluenced by advance finger information. Contrary to this prediction, the S-LRP interval was shorter with advance finger information than when no advance information was available. In our view, this result clearly suggests that the time course of hand activation depends on advance specification of the start finger. In addition, the overlap account is also not very plausible in light of the present foreperiod CNV and LRP findings, which indicated that precue information influenced motor preparation already before the imperative signal, with this preparatory activity likely contributing to savings in RT (cf. Leuthold et al., 2004). Therefore, we assume that the LRP-R interval indeed reflects influences on the duration of late motor processes, hence allowing us to evaluate the predictions of the two-process model and the HED model.

**Models of Response Sequence Programming**

According to the HED model, the number of required editing steps depends on the number of to-be-specified response parameters. For the present experiment, this means that the time demands for the specification of three-key as compared to one-key responses within the edit pass should become increasingly larger. Hence, we hypothesized that the sequence length effect on RT increases with decreasing amount of advance information provided. Alternatively, the two-process model assumes that the response sequence length effect for present task conditions is determined by the duration of the SEQ or scanning process of an abstract time frame. This process is separate from that involved in the specification of individual response elements (see also Khan et al., 2008). Hence, this model predicts a constant response sequence length effect on RT across precue conditions, that is, independent of the amount of advance information provided.

It is evident that present RT results are at variance with both the HED model and the two-process model. Thus, a reliable response sequence length effect on RT of about 38 ms was observed only for the full precue condition, replicating previous similar findings in studies using simple RT tasks (e.g., Klapp, 1995; Verwey, 2003) and the precuing paradigm (Khan et al., 2008; Klapp, 2003). When the precue provided partial advance information (hand precue and finger precue conditions), a numerical, though not statistically reliable, sequence length effect of about 16 ms was observed. It is worth mentioning, however, that the sequence length effect for the partial precue conditions was not reliably different from that for the full precue condition. Additionally, the finger precue condition closely resembles conditions (with fixed instead of precued start finger) for which two previous studies reported a significant sequence length effect of about 25 ms (Schröter & Leuthold, 2008; Smulders et al., 1995). We therefore assume that statistical power in the present study was insufficient to reliably detect the present 16-ms effect. For example, it is possible that in the present response precuing paradigm, due to the more complex precuing procedure, participants did not prepare the forthcoming response sequence as well as in a standard choice RT task. This might also be indicated by the fact that the response sequence length effect on RT was completely abolished in the uninformative precue condition, a finding that is otherwise inconsistent with the predictions of both the HED model and the two-process model.

Most important, the analysis of ERP measures advanced our understanding of the response sequence length effects on RT. A first, yet unexpected, key finding is the reversed sequence length effect on the duration of the S-LRP interval (and numerically also on P300 latency) in the uninformative precue condition, indicating a longer duration of premotoric processes for one-key responses than three-key responses. Whatever caused this effect, it clearly counteracted the standard sequence length effect on motor processing time, resulting in the zero effect on RT in the no precue condition. Hence, the RT findings for the uninformative
The major finding then is that of a longer LRP-R interval for three-key than one-key responses in both the finger precue condition and in the no precue condition. These LRP-R findings replicate and extend those of previous studies in which the start finger (index finger) was fixed and hence known in advance (Schröter & Leuthold, 2008; Smulders et al., 1995), indicating that the duration of late motor processes is influenced by response sequence length. As we pointed out previously (Schröter & Leuthold, 2008), the effects on the LRP-R interval also strongly suggest that the required response hand is selected and activated before all response features are fully programmed. This is in line with the assumption that response elements within the motor program or subprograms can be activated before the program is fully established (e.g., Khan, Lawrence, Buckolz, & Franks, 2006; Portier, van Galen, & Meulenbroek, 1990; Verwey, 1994). Both the HED model and the two-process model have to be slightly modified to account for the sequence length effect on the LRP-R interval (cf. Schröter & Leuthold, 2008). In the framework of the HED model, one has to assume that during the edit pass the first response element is activated but only executed once the execution pass has reached the terminal node for this element. In the framework of the two-process model one has to assume that the SEQ process occurs after the activation of response hand.

Most crucial, however, is the fact that the response sequence length effect on the LRP-R interval was independent of the amount of advance information. This finding is consistent with the two-process model of Klapp (2003), whereas the HED model of Rosenbaum et al. (1984) has problems accounting for this. This is because, according to the HED model, advance information about start finger permits participants to specify all terminal finger nodes, whereas this is not possible when no advance information is available. As a result, fewer editing steps are required in the finger precue condition than the no precue condition, which should be reflected by the length of the LRP-R interval. In contrast to this prediction, the sequence length effect upon the LRP-R interval was found to be uninfluenced by advance information about start finger. In summary, the present LRP findings appear to be better accord with Klapp’s two-process model than Rosenbaum et al.’s (1984) HED model. Additional support for this interpretation is provided by the results of a precueing study of Khan et al. (2008). In their study, participants had to respond with manual aiming movements differing in amplitude and number of elements. Consistent with the findings of the present study, Khan et al. (2008) reported a sequence length effect on RT of equal size when the precue provided information about both amplitude and element number and when it provided information about element number only. The HED model, however, would again predict a larger sequence length effect for the latter condition.

Possible Limitations of the Present Study

So far we have argued that the present findings on the LRP-R interval are at variance with the predictions of the HED model. However, proponents of the HED view might raise the objection that participants did not specify all terminal finger nodes with advance finger information but only the start finger node. Clearly, such a preparation strategy could have contributed to the fact that we did not observe a larger sequence length effect on the LRP-R interval for the finger precue as compared to the no precue condition. In the following, we will discuss the evidence for such a strategy in the light of present forperiod LRP and foreperiod CNV findings.

The foreperiod LRP does not allow us to directly assess the possibility that participants specified only the first finger node when the precue provided partial finger information, because it reflects only hand-selective motor activation and is hence absent when hand is unknown in advance. However, the foreperiod LRP in the full precue condition can provide tentative information regarding this issue. Interestingly, we observed an equally large foreperiod LRP for three-key and for one-key responses in full precue and hand precue conditions. This result contrasts with forperiod LRP amplitude findings of previous studies in which the start finger (index finger) of the response sequence was fixed (Hackley & Miller, 1995; Stief et al., 1998, Experiment 2), whereas it accords with previously reported absences of a larger foreperiod LRP for three-key than one-key responses (Stief et al., 1998, Experiment 1) and of an increased RP asymmetry preceding complex as compared to simple movements (Lang et al., 1989). Thus, as effects of response sequence length are not observed under all conditions and appear to depend on procedural factors (Stief et al., 1998, Experiment 1), we can only speculate as to the reasons for the present zero effect. Assuming that the three-key response involves the specification of more fingers than the one-key response, and thus presumably activation of a larger number of muscle groups, this should be reflected by a larger foreperiod LRP in the former condition. One speculation for the absence of the sequence length on the foreperiod LRP then is that participants did not preprogram the complete finger sequence during the foreperiod (cf. Stief et al., 1998). Thus, despite the fact that all elements of the response sequence were in principle known when hand and start finger were precued in the present experiment, participants might have prespecified and activated only the start finger during the foreperiod, at least at the effector-specific level of motor programming. Only after the imperative stimulus, while executing the first finger response, will the remaining fingers then have become activated. This line of argument can of course be extended to the finger precue condition. Hence, the finger precue condition and the no precue condition would differ only with respect to the time demands required to edit the start finger, thereby potentially minimizing the chances to detect a modulation of the response sequence length effect on the LRP-R interval by precue information.

The issue is further complicated as foreperiod CNV amplitude did not further increase in amplitude from the partial precue conditions to the full precue condition, which might suggest that participants have prepared multiple responses when the precue provided partial information about either response hand or response finger. As a result, there would be little difference in the duration of the edit pass in partial and full precue conditions. It is, hence, important to more specifically examine whether parallel response preparation occurred in the present experiment. Importantly, as outlined in detail by Jentzsch et al. (2004), a multiple motor preparation makes clear-cut predictions regarding the influence on ERP activity over motor cortices contralateral and ipsilateral to the responding hand. For the present precue conditions, first, this view predicts that the foreperiod CNV is of equally large, if not larger, amplitude immediately preceding the imperative signal for the hand precue and finger precue conditions as compared to the full precue condition. That is, if participants activate in parallel either the two start fingers in the hand precue condition or the two hands in the finger precue condition, one would expect a similar level of activity in motor
areas contralateral to the appropriate response hand in these precue conditions like in the full precue condition, in which the appropriate hand and start finger is activated. Second, the multiple motor preparation view predicts that ERP activity over ipsilateral motor areas is larger for the finger precue condition than full precue and hand precue conditions, as only in the former case are both hands prepared in parallel and, hence, contralateral MI cortices should be activated to the same extent. For the same reason, a hand-related asymmetry in terms of larger contralateral than ipsilateral ERP activity should be obtained only for the full precue and hand precue conditions but not the finger precue condition.

These predictions were fully supported by the present CNV findings indicating that participants prepared multiple responses when only partial precue information was available. This might have made it hard to detect a sequence length effect that depends in its size on the amount of advance information provided.

Conclusions

Our results provide evidence for the assumption that the duration of motor programming processes increases with the length of the response sequence when the number of response elements is specified before the onset of the imperative signal. The longer duration of programming processes for three-key than one-key responses is reflected by the duration of the LRP-R interval. Furthermore, our results are in line with the notion that response elements (e.g., the response hand) within the motor program or subprograms can be activated before the program is fully established. Overall, the chronometric data are in better agreement with the two-process model of Klapp (1995, 2003) than the HED model of Rosenbaum and colleagues (1984). However, given that foreperiod ERP activity suggested the specification of multiple responses in partial precue conditions and only of start finger rather than the whole three-finger sequence in full and partial precue conditions, future studies should aim at providing a stronger test of the HED model’s predictions regarding the duration of the edit pass in interaction with precuing information. Importantly, the present study illustrates that, ultimately, a better understanding of the mechanism underlying the motor programming of action sequences of different length can be achieved through the combination of psychophysiological and behavioral approaches.

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