Are fingers special? Evidence about movement preparation from event-related brain potentials

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Abstract

Ulrich, Leuthold, and Sommer (1998) suggested that movement preparation at the level of the motor cortex, as indexed by the lateralized readiness potential (LRP), proceeds in a strongly hierarchical fashion, where parameters other than response hand are prepared only if all the movement parameters are known. These conclusions were based on an experiment where a precue provided information about response hand, direction of finger movement, and movement force. To assess the generality of these findings, we replaced the force parameter with response finger. LRP indicated that preparation of the required finger is possible even when preliminary information is incomplete. Therefore, movement preparation appears to follow different rules when anatomical relationships (hand and finger) are concerned as compared to functional parameters like movement direction. On the other hand, at a limb-unspecific level, as indicated by the contingent negative variation, we confirmed evidence for parallel programming of all movement parameters.

Descriptors: Lateralized readiness potential, Contingent negative variation, Movement preparation, Precuing

Even very simple movements involve different dimensions and, therefore, require the specification of values along these dimensions. For example, flexing a finger requires the specification of the finger, the movement direction, its force, and velocity. According to the theory of generalized motor programs (Schmidt, 1975), values on movement dimensions are conceived as parameters of abstract motor programs. The assembly of concrete motor commands requires the selection of the motor program as well as the specification of all its parameters. A crucial question for theories about movement preparation is the organization of parameter specification. In principle, all necessary parameters might be specified independently and in parallel. Alternatively, specification of the various movement parameters might proceed in a predetermined, strictly hierarchical order (cf. Rosenbaum, 1980). In the present experiments, the structure of parameter specification is analyzed by means of recording event-related brain potentials (ERPs).

Important headway in investigating the organization of movement preparation has been made by using the precuing technique developed by Rosenbaum (1980, 1983). Here, a number of possible responses differ with respect to parameter values, for example, an upward or downward movement with the right or left index finger. A precue prior to the response signal may provide none, some, or all of the defining parameters of the response, allowing for different degrees of advance movement preparation. Finally, a response signal is presented that specifies the required response. In many experiments, it has been shown that reaction time (RT) to the response signal decreases with the number of parameters provided by the precue. This so-called precuing effect is considered to be informative about questions like the order of movement parameter selection, whether the selection of response parameters occurs serially or in parallel, and the validity of the very idea of motor programs (Rosenbaum, 1983).

On the other hand, Goodman and Kelso (1980) questioned the validity of the precuing effect as reflecting advance response specification. They suggested that the RT savings due to precue information might merely relate to a reduction of response alternatives. However, recent experiments, using the lateralized readiness potential (LRP; Coles, 1989; De Jong, Wierda, Mulder, & Mulder, 1988), a brain potential signaling hand-specific motor preparation, have provided evidence that the precuing effect is at least to some extent motoric in origin. Leuthold, Sommer, and Ulrich (1996) required finger extensions or flexions with the left or right index finger to the response signal. A precue provided preliminary information about both movement dimensions, hand and direction, about only hand or only direction, or none of these dimensions. When the precue provided hand information, an LRP developed during the interval between the precue and the response signal, that is, the foreperiod LRP amplitude was larger when hand plus direction had been specified by the precue than when only hand was
known. In addition, by measuring the interval between LRP onset and the response, Leuthold et al. showed that the RT savings due to partial advance information about movement direction can be localized within those processing stages that occur after the LRP onset. Because the LRP is assumed to indicate the moment in time when the response hand becomes centrally activated, in information processing terms, advance precue information shortens the motoric portion of RT following response selection (cf. Müller-Gethmann, Rinkenauer, Stahl, & Ulrich, 2000).

LRP studies not only demonstrate that the precuing effect may be motoric in origin. They are also informative as to the possible neural substrate of qualitatively different levels of movement organization. On the one hand, with partial advance information about response hand, a foreperiod LRP is elicited even when other parameters are still unknown (e.g., Leuthold et al., 1996; Ulrich, Moore, & Osman, 1993). This finding indicates that partial movement preparation already invokes effector-specific neural activity in the corresponding primary motor cortex. On the other hand, in case of fully informative precues about direction and hand, the transition from incomplete to complete movement preparation is accompanied by an additional increase in LRP amplitude (Leuthold et al., 1996). Thus, the LRP seems to be sensitive both to partial and complete preparatory states of movements.

Most recently, Sangals, Sommer, and Leuthold (2002) demonstrated that this increase of foreperiod LRP amplitude with advance information is, in fact, informative about the organization of movement preparation per se. For example, it is conceivable that the precuing effect in foreperiod LRP amplitude relates to a strategy to focus preparatory efforts on those conditions that are most rewarding, that is, with the most informative precue. In contrast to this notion, Sangals et al. found a robust precuing effect in foreperiod LRP amplitudes even when subjects were forced by means of time pressure to maximize preparation in every single precue condition. Therefore it appears safe to conclude that the precuing effect reflects the limits of motor preparation determined by precue information rather than participants’ strategies.

Of particular interest for present purposes is a study by Ulrich, Leuthold, and Sommer (1998), who assessed possible constraints on advance parameter specification in the precuing paradigm by recording the foreperiod LRP and the contingent negative variation (CNV), a vertex-negative potential appearing prior to a forthcoming significant event (Cui et al., 2000; Kutas & Donchin, 1974; Walter, Cooper, Aldridge, McCallum, & Winter, 1964). They asked participants to perform right- or left-hand index finger flexions or extensions with two levels of force, giving precue information about hand, hand plus movement direction, hand plus movement force, and hand plus direction and force. In the latter condition, the movement was fully specified. This design allowed for distinguishing between various views of advance movement preparation.

First, according to a nonhierarchical preparation view, all available parameters might be prepared independently and in parallel. In this case, the foreperiod LRP should increase as a function of the mere number of specifiable parameters, irrespective of their identity. Second, preparation might be hierarchical, allowing for the preparation of lower-order parameters only if all higher-order parameters are also known, for example, movement force can be prepared only when also the extensor and flexor muscles, that is, movement direction, are specified (Megaw, 1972; Rosenbaum, 1980). In this case, one would expect LRP amplitude to increase above the hand-alone condition only if additional parameters represent contiguous steps in the hierarchy, for example, hand plus direction, or hand plus direction and force, but not, for example, hand plus force. Third, in a stronger version of hierarchical preparation, it is even conceivable that information about parameters in addition to hand increases LRP amplitude only if the response is fully determined. For example, specification of appropriate muscle groups may be impossible unless information about both direction and force is available. In this case, one would expect foreperiod LRP amplitude to increase above the hand-alone condition only if the response is fully determined.

In fact, the LRP findings reported by Ulrich et al. (1998) directly support the strong version of hierarchical preparation, because the foreperiod LRP amplitude was the same for all partial precue conditions and increased only in the full precue condition. Accordingly, advance preparation at the level indexed by the LRP appears to require information about both response force and direction. This pattern contrasted with the precuing effect in RTs and in CNV amplitudes before the response signal. Thus, RTs decreased and foreperiod CNV amplitudes increased with the number of specified movement parameters even when information was still incomplete. On the basis of these and related findings (cf. Miller, Coles, & Chakraborty, 1996), the authors suggested dividing the motor processes into an early processing stage that is not limb specific and into a late stage that is limb specific. Accordingly, CNV amplitude modulations in the precuing paradigm were taken to reflect the actions of the earlier response programming system that may be responsible for the precuing effects on RT. In this system, programming of the movement parameters appears to be organized in parallel. In contrast it was suggested that the foreperiod LRP might index the implementation of the motor program on a subsequent limb-specific level—presumably the primary motor cortex. At this level, movement parameters appear to be organized hierarchically rather than independently.

In the study of Ulrich et al. (1998), only a subset of possible movement parameters was investigated. It is therefore of interest whether the hypothesis of strong hierarchical preparation—at the level reflected in the foreperiod LRP—generalizes also to other movement parameters. In the present study, we compared the specification of anatomical response effectors as compared to their function. The parameters movement direction and force, investigated by Ulrich et al., represent functional aspects of response preparation. Preparation of such parameters may differ in principle from the preparation of response effectors, for example hand and finger. It is conceivable that the preparation of effectors reflects the hierarchical organization of the underlying anatomy. That is, progressing from hand to finger may represent individual steps within the preparatory hierarchy that can be taken prior to preparing functional parameters like direction and force. In this sense, it may be possible to prepare both hand and finger if prespecified even when functional parameters like movement direction are still unknown. Accordingly, the strong version of hierarchical movement preparation may be specific for functional parameters such as direction or force, whereas it may not apply to the structural parameters response hand and finger.

It was therefore the main goal of the present study to assess whether the strong version of hierarchical preparation holds true when response hand and finger are independent movement dimensions. To determine this, we used the same basic design as
Ulrich et al. (1998) with three movement dimensions but replaced response force with response finger. In contrast to previous precuing studies where hands and fingers had not been varied independently, the present design allows us to differentiate possible contributions of finger-specific response preparation to both CNV and LRP. More specifically, the strong version of hierarchical preparation would receive further support if LRP amplitude for hand plus finger were the same as for hand alone. Alternatively, one can also expect that information about finger in addition to hand leads to an incremental limb-specific activation as shown in an increased foreperiod LRP. Finally, it is also conceivable that participants simultaneously prepare all possible fingers in question when this parameter is unspecified. According to such a multiple-preparation hypothesis, one should expect a larger foreperiod LRP for the hand-alone or the hand-plus-direction condition than for the hand-plus-finger or the fully informative precue condition.

A further aim of the present study was to reassess the effect of precue information on the CNV amplitude under the current precue conditions. If the CNV amplitude reflects limb-unspecific preparation processes (movement programming) as proposed by Ulrich et al. (1998), we expect the amplitude to increase with the number of precued parameters, independent of their identity.

**EXPERIMENT 1**

**Method**

**Participants**

Six women and eight men \((M = 28 \text{ years}, \text{range} = 19–51 \text{ years})\) were tested in single 2.5-hour sessions. All participants were right-handed with mean handedness score (Oldfield, 1971) of 87 (range = 60–100), and had normal or corrected-to-normal vision. They received either payment (15 ) or course credits for participating.

**Stimuli and Procedure**

Participants were seated in a dimly lit, sound attenuated, and electrically shielded room with forearms resting on a table. They viewed the stimuli on a computer screen from a distance of approximately 1 m, provided by a fixed chinrest. Each hand grasped the horizontal bar of a manipulandum. The index and middle fingers were extended halfway and gently clamped in two thumb-like holders to register isometric flexion and extension forces.

As *precue signal*, the frame of two slanted parallel bars appeared in white on a dark background in the center of the screen (Figure 1). The stimulus size was \(21 \times 21 \text{ pixels}\) corresponding to viewing angles of 1°. Compatible with the position of the hands, clockwise and counterclockwise slant of the bars indicated responses with the left and right hand, respectively. The upper and lower bars corresponded to the middle and index fingers, respectively, the top and bottom half (shank) of each bar represented an upward (extension) or downward (flexion) movement. Depending on the precue condition, the shanks of the bars were filled in red. If both bars were completely filled, the slant of the bars provided preliminary information about response hand (hand, H). Filling just one of the bars provided additional information about response finger (hand plus finger, HF). Filling both upper or both lower shanks provided information about movement direction (hand plus direction, HD). Finally, full information about the required movement was provided by filling one shank of one bar (hand plus finger plus direction, HFD). The imperative response signal was similar to the precue except that just one shank of one bar was filled in green, providing specific movement information. On average, in one of nine trials (11%), a no-go signal was presented instead of the response signal in order to prevent premature responses. In this case, the frame of the precue signal and the fixation point turned red, requiring the suppression of any prepared response.

Each trial started with the presentation of the fixation cross in the center of the screen. After 450 ms, the fixation was superimposed by the precue for 1,400 ms. This precue provided preliminary information about the upcoming response. Preliminary information was given either about response hand (H), hand plus movement direction (HD), hand plus response finger (HF), or all three parameters (HFD). The precue was replaced by the response signal that was shown for 1,000 ms and that demanded a specific response unless it was a no-go signal. These signals were immediately followed by a feedback signal, consisting in a number displaying for 500 ms the points just earned (see below). After a warm-up block the experimental session started, which consisted of eight blocks of 72 trials each separated by participant-determined breaks. Within a given block, the four precue conditions and the eight response alternatives were equiprobable; presentation order was randomized.

In each trial, either three positive points could be achieved for a fast correct response, whereas correct but slow responses were fined with one negative point. This regime was introduced to create moderate time pressure, which increases foreperiod LRP without affecting the precuing effect. The criterion for fast responses was adapted individually after each trial block on the basis of the previous RT distribution (cf. Sangals et al., 2002). After an incorrect response, six negative points were given and

![Figure 1](image.png)

**Figure 1.** The temporal sequence of events in a single trial. In the example shown, a flexion movement with the index or middle finger of the left hand is precued. The response signal commands a left index finger flexion.
displayed on the screen together with information about the type of error committed (RT < 100 ms, missed response, or wrong movement). The next trial started 1,500 ms after feedback offset. Following each trial block, mean RT, error counts, and the total score were computed and displayed to the participant.

Written instructions were given to the participants advising them to use the precues in order to respond quickly and as correctly as possible. Participants were also asked to keep their eyes on the fixation point and not to blink except for the feedback and intertrial periods.

Response Recording
Reaction times were measured by means of force-sensitive keys for the index and middle fingers of each hand, mounted in a pistol-grip manipulandum. Leaf springs (150 by 20 by 2 mm) were held by clamps at one end, and the other end remained free. The thimble-like finger holders were attached on top of the free end of each spring. Strain gauges (Type 6/120 LY 41, Hottinger Baldwin Messtechnik, Darmstadt, Germany) were attached near the fixed end of the leaf springs. Any force applied to the leaf spring via the finger holders at the free end was reflected by an analogous signal, which was digitized along with the electrophysiological signals (see below). Force onsets were measured with 1-ms resolution as the point in time where a threshold was exceeded; the threshold was set at 23 and 19 cn for flexions and extensions, respectively, because flexions are performed more forcefully than extensions.

Electrophysiological Recordings
Electroencephalographic (EEG) and electrooculographic (EOG) activity was amplified with a bandpass of 0–40 Hz (−3 dB attenuation, 12 dB rolloff/octave) recorded continuously with 200 Hz sample rate by means of tin electrodes (Electrocap Co.) and impedance of less than 5 kΩ. The EEG potentials were measured with left mastoid as a common reference at Fz, Cz, and Pz (Jasper, 1958) and at the electrode sites C'3 and C'4, that is, 4 cm to the left and to the right of Cz, respectively. Vertical EOG was registered from above and below the left eye. Horizontal EOG was recorded 2 cm lateral of the left and right outer canthi. Offline, the EEG data were bandpass filtered with high and low cutoff frequencies set to 0.01 and 10 Hz, respectively, and all signals were separated into epochs of 3 s, starting 500 ms before precue onset.

Data Analysis
The influence of vertical eye movement activity on the EEG recordings was corrected with the method described by Elbert, Lutzenberger, Rockstroh, and Birbaumer (1985); if this was not possible, the trial was discarded. Also, all trials with incorrect responses were discarded from EEG analysis, as were all trials with signal drifts of more than 100 μV within the recording epoch or with other EEG artefacts.

As usual, the LRP was defined as the difference between the electrodes contra- and ipsilateral to the responding hand over the primary motor cortices (i.e., C'3 minus C'4 and C'4 minus C'3 for right- and left-hand responses, respectively) averaged across hands. For each condition, the difference waves were averaged first within and then across left- and right-hand responses. To assess possible contributions of ocular artefacts due to horizontal eye movements to the LRP, difference potentials were computed for the horizontal EOG in the same way as for the LRP. That is, the difference between the electrodes contra- and ipsilateral to the responding hand over the left and right outer canthi (i.e., left EOG minus right EOG and right EOG minus left EOG for right- and left-hand responses, respectively) was averaged across hands yielding the Lateralized hEOG (LhEOG). Average LRP and LhEOG amplitudes were analyzed for two adjacent time periods preceding the target by 400 to 200 and 200 to 0 ms, relative to a 100-ms baseline immediately before the precue.

Statistical analyses were performed by means of Huynh-Feldt corrected repeated measures analyses of variance (ANOVA). For performance and LRP/LhEOG data, the within-variable was precue condition (H, HD, HF, and HFD). For the analysis of midline ERPs (foreperiod CNV) the variable electrode (Fz, Cz, Pz) was added. Differences between conditions were compared with a test of critical differences (Scheffé test).

Results
Performance
Table 1 shows the percentage of errors and mean RTs for the different conditions. There were 9.6% anticipations in no-go trials. The overall error rate in go trials was 7.0%, comprising 2.1% movements with the incorrect finger on the correct hand, 2.2% direction errors, 1.5% hand errors, 0.1% misses, and 2.4% anticipations. Separate ANOVAs for percentage of errors were computed for go and no-go trials. For go trials, there was a significant main effect of precue condition, F(3, 39) = 92.2, p < .01. A Scheffé test (Diff crit, 1% = 2.7; Diff crit, 5% = 2.2) revealed significant differences between all four precue conditions (HFD = 3.5%; HD = 5.9%; H = 9.1%; HD = 16.0%). For no-go trials, a significant main effect for the variable precue was found, F(3, 39) = 22.4, p < .01, indicating the following ordering of precue conditions: HFD > HF > HD > H (2.2%).

Mean RT (Table 1) depended strongly on precue information, F(3, 39) = 107.2, p < .01. The following ordering of conditions was confirmed by a Scheffé test (Diff crit, 1% = 22.7 ms): HFD < HF < H < HD (426 ms).

Foreperiod LRP
The average LRP waveforms are shown in Figure 2. Under all four conditions, there was more negativity above the motor cortex contralateral to the responding hand than over the ipsilateral cortex elicitig a prestimulus LRP about 500 ms after precue onset, increasing monotonically towards target onset. For statistical analysis, mean foreperiod LRP amplitude was determined in two adjacent intervals from 400 to 200 and from 200 to 0 ms prior to response signal onset for each precue condition. Two-tailed t tests show that foreperiod LRPs for all

<table>
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<tr>
<th>Finger Condition</th>
<th>RT (ms)</th>
<th>Error (%)</th>
</tr>
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<tbody>
<tr>
<td>Hand (H)</td>
<td>426</td>
<td>9.1</td>
</tr>
<tr>
<td>Hand + Direction (HD)</td>
<td>389</td>
<td>16.9</td>
</tr>
<tr>
<td>Hand + Finger (HF)</td>
<td>371</td>
<td>5.9</td>
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<tr>
<td>Hand + Finger + Direction (HFD)</td>
<td>291</td>
<td>3.5</td>
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</table>

Table 1. Grand Means and Standard Deviations of RT and Error Rates of Experiment 1
four precue conditions deviated significantly from zero in both intervals, \( t(13) < -6.5, p < .001 \). Precue information affected the LRP amplitude in the interval between 400 and 200 ms prior to target presentation, \( F(3,39) = 3.3, p < .05 \). According to Scheffe’s critical difference (\(<0.54 \mu V\)), this effect was due to larger LRP amplitudes in the fully informative precue condition (\( M = -1.8 \mu V \)) as compared to the hand-alone condition (\( M = -1.2 \mu V \)), whereas HF (\( M = -1.5 \mu V \)) and HD (\( M = -1.3 \mu V \)) did not differ from any of the other conditions. During the final 200 ms of the foreperiod, the precue effect was somewhat smaller but remained a trend, \( F(3,39) = 2.7, p = .07 \).

To assess whether the effect of precue condition on the foreperiod LRP was mediated by horizontal eye movements, the LhEOG was statistically analyzed in the same way, as was the LRP. Because precue condition did not affect the LhEOG, it can be safely excluded that the effect of the precue conditions on foreperiod-LRP amplitude relates to systematic differences in horizontal eye movements.

**CNV**

The grand mean ERPs for each precue condition at midline recording sites are depicted in Figure 3. The CNV preceding the response signal during the last 200 ms showed a centroparietal scalp distribution (Fz to Pz = -2.8, -9.9, and -10.0 \mu V), resulting in a significant effect of electrode, \( F(2,26) = 20.3, p < .01 \). Figure 3 shows that foreperiod CNV increased with the number of movement parameters specified in the precue. This is reflected in a main effect of precue condition in the ANOVA, \( F(3,39) = 41.3, p < .01 \). The impression that the precuing effect on the CNV is more pronounced at Cz than at the other sites was confirmed by a Precue × Electrode interaction, \( F(6,78) = 5.0, p < .01 \). A Scheffé test at the Cz electrode (Diff_crit,1% = 2.1), where the precuing effect was most pronounced, indicated the following ordering: HDF (-12.4) < HF (-10.0 \mu V) = HD (-9.7 \mu V) < H (-7.5 \mu V).

**Discussion**

In many respects, this experiment indicates that the findings of Ulrich et al. (1998) generalize to a condition where preliminary information is given about the dimensions hand, finger, and movement direction. The present results showed the usual precuing effect, with RTs being slowest when only one movement parameter was precued, intermediate for two movement parameters, and fastest when three movement parameters were precued.

A very similar pattern as in RTs was seen in the CNV amplitude. Here, the amplitude was smallest for the one-parameter precue, intermediate for the two-parameter precues, and largest for the full precue condition. Also in line with the findings of Ulrich et al. (1998) is the discrepancy between the RT and CNV results on the one hand and of the foreperiod LRP on the other hand. The LRP was significantly different from zero in all four conditions, but a reliable precue information-dependent increase was only observed for the full information condition. Together, the present findings do not contradict a strong version of hierarchical movement preparation according to which the next level of preparation after hand information within the hierarchy can only be activated when the movement is completely specified.

Yet, as always, a conclusion based on the absence of a significant difference between conditions can only be tentative —especially when the differences found in other conditions are less than impressive. Although the crucial hand-plus-finger condition was not different from hand alone, it was also not
different from the fully specified movement, which it should be, according to the interpretation of Ulrich et al. (1998). In fact, Figure 2 shows the LRP in the critical hand-plus-finger condition to be intermediate between the fully informative condition and the others. In addition, half the participants showed larger foreperiod LRP amplitudes for hand-plus-finger than for hand-alone precues. This observation argues against an intrinsic limitation in terms of the strong version of hierarchical movement preparation, which precludes finger preparation on a limb-specific level unless the response is fully specified. Therefore, before accepting generalizability of the results of Ulrich et al. (1998) to finger as a movement dimension independent of hand, it seemed necessary to replicate the findings in an experiment with an improved task context. In the first experiment, the conditions for obtaining finger-specific preparation might not have been optimal. In particular, subjects might have been reluctant to use the precues because of the no-go trials or because of the large number of conditions. Therefore, in Experiment 2, omitting the fully informative precue condition reduced the number of conditions. Because now information was partial in all conditions, the no-go trials—the precaution against premature responses in fully informative conditions—could be dropped as well, increasing the number of trials per condition from 128 to 240. The general validity of the strong hierarchical movement preparation view would be supported by the finding of a foreperiod LRP that is of identical amplitude for hand, hand-plus-finger, and hand-plus-direction precue conditions. In contrast, the special role of fingers would be supported if the hand-plus-finger condition yields larger LRPs than the two other conditions. In addition, Experiment 2 used a multichannel recording of the EEG to obtain a more complete view of the precue effect on the CNV.

**EXPERIMENT 2**

**Method**

**Participants**

Nine women and three men ($M = 23$ years, range = 19–31 years) were tested in single 2.5-hour sessions. The mean handedness score (Oldfield, 1971) was 83 (range = 38–100). All participants had normal or corrected-to-normal vision and received either payment (15) or course credits.

**Stimuli and Procedure**

The experimental setup and the procedure were the same as for Experiment 1 with the following exceptions. The number of 72-trial blocks was increased to 10 and both the fully informative and the no-go conditions were dropped, leaving just the partial precue conditions H, HF, and HD. For these conditions, the EEG was recorded and analyzed in the same way as in Experiment 1, with the exception that now a multichannel recording was used in order to analyze the topography of the CNV. The additional electrodes according to the international 10-20 system were FP2, F3, F4, F7, F8, FC1, FC2, T7, T8, P3, P4, P7, P8, PO9, PO10, O1, O2, and the right mastoid.

**Data Analysis**

Statistical analyses were performed as in Experiment 1, except that the within-variable precue condition involved three levels (H, HD, and HF). For topographical analysis, the EEG data were calculated to an average reference derivation and vector scaling (McCarthy & Wood, 1985) was performed to remove amplitude differences between the precue conditions. The grand mean amplitudes and the scaled values were submitted to an ANOVA with factors precue and electrode sites, respectively. In the case of significant interactions, additional ANOVAs were performed with adjusted significance levels and factor precue including only two levels.

**Results**

**Performance**

Table 2 shows the percentage of error trials and mean RTs for the different conditions. The overall error rate was 9.2%, comprising 4.5% misses, 0.4% premature responses, 2.3% keypresses with the wrong finger, 1.2% keypresses with the wrong hand, and 0.8% direction errors. There was no effect of precue condition on overall error rates, $F(2,22) = 1.4, p = .26$.

ANOVA revealed a strong effect of precue condition on mean RT, $F(2,22) = 93.5, p < .01$. The Scheffé test confirmed the following ordering of conditions: HF ($M = 389$ ms) < HD ($M = 408$ ms) < H ($M = 447$ ms), $ps < .001$.

**Foreperiod LRP**

Figure 4 displays the LRP waveforms for each precue condition of Experiment 2 with the same left-mastoid reference as used in Experiment 1. Two-tailed $t$ tests showed that mean prestimulus LRP for all three precue conditions HF, HD, and H deviated significantly from zero, $t$s($11) > -5.8, ps < .001$. According to the ANOVA, precue condition affected the prestimulus LRP amplitude during the 200-ms interval preceding the response signal, $F(2,22) = 4.0, p < .05$. A Scheffé test (Diff$_{crit,5%} = 0.62 \mu V$) indicated a reliable difference of 0.66 $\mu V$ between precue conditions H and HF ($-0.95 \mu V$ vs. $-1.61 \mu V$) during this period, but no differences between H and HD ($-0.95 \mu V$ vs. $-1.36 \mu V$) and between HD and HF ($-1.36 \mu V$ vs. $-1.61 \mu V$). In the interval between 400 and 200 ms before the precue, the effect of precue condition was somewhat smaller but remained a trend, $F(2,22) = 2.8, p = .08$.

**CNV**

The average ERP along the midline for the precue conditions is shown in Figure 5. The statistical analysis of the average amplitude during the 200 ms prior to response signal onset indicated a centrotemporal scalp distribution of the foreperiod CNV, $M(\text{Fz, Cz, and Pz}) = 0.01, -3.46$, and $-5.19 \mu V$, $F(2,22) = 10.9, p < .01$. The precue condition affected the mean CNV amplitude, $F(2,22) = 12.4, p < .01$, but did not interact with electrode site, $F(4,44) < 1$. A Scheffé test at the Cz electrode (Diff$_{crit,1%} = 1.41$), where the precuing effect was most pro-

<p>| Table 2. Grand Means and Standard Deviations of RT and Error Rates of Experiment 2 |
|---------------------------------|-----------------|-----------------|</p>
<table>
<thead>
<tr>
<th>Precue condition</th>
<th>RT</th>
<th>Error (%)</th>
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<tr>
<td>Hand (H)</td>
<td>446</td>
<td>46.7</td>
</tr>
<tr>
<td>Hand + Direction (HD)</td>
<td>407</td>
<td>45.4</td>
</tr>
<tr>
<td>Hand + Finger (HF)</td>
<td>389</td>
<td>43.6</td>
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</table>
nounced, indicated the following ordering: HF (−4.1 µV) = HD (−4.0 µV) < H (−2.3 µV).

**Topographical Analysis**

Figure 6 depicts for each precue condition the average reference topography of the CNV amplitude during the 200-ms interval before the response signal for the full set of electrodes as well as the difference maps calculated between the conditions. Looking at the midline electrodes, there is a similar anterior/posterior voltage distribution as for analysis reported above. In addition, Figure 6 shows that the activity added to the CNV above that seen for hand alone by giving precue information for both hand and finger (i.e., HF minus H) has a marked central topography, whereas the activity for hand alone (H) is characterized by an anterior positivity/posterior negativity. The additional activity provided by the direction information (HD minus H) appears qualitatively similar to the finger-precue (HF minus H) elicited activity.

ANOVA of the CNV amplitudes measured at the full set of electrodes confirmed the significant effect of the precue condition as an interaction with electrode sites, $F(56,616) = 5.3$, $p < .01$. For pairwise comparisons, ANOVAs were repeated with only two precue conditions, showing significant differences between H and HF, $F(28,308) = 6.37$, $p < .01$; H and HD, $F(28,308) = 7.24$, $p < .01$; but not between HF and HD, $F(28,308) = 2.33$, $p = .21$.

The overall ANOVA was repeated after normalization of the CNV amplitudes in order to assess whether the precue conditions differ in their scalp topographies; this is indeed the case, as indicated by a significant interaction of precue condition and electrode site, $F(56,616) = 2.8$, $p < .01$. Pairwise comparisons between precue conditions (see Figure 6, bottom), revealed differences in scalp topography only between conditions H and HF, $F(28,308) = 4.9$, $p < .01$, but not between conditions H and HD, $F(28,308) = 2.5$, $p = .15$, and between HD and HF, $F < 1$.

**Discussion**

Experiment 2 was designed to reassess the critical precue conditions of Experiment 1 with fewer conditions—omitting the fully informative precue condition and the no-go trials—and an increased number of trials per condition. Again both the RT results and the CNV amplitudes in the midline confirmed the findings of Ulrich et al. (1998). The performance data revealed a similar pattern as in Experiment 1, with RTs being slower in the hand precue condition than in the two other conditions. The only notable difference is that here, the HF condition was somewhat faster than the HD condition.
Also very similar to Experiment 1 was the finding that the CNVs of the two-parameter partial conditions were indistinguishable but more negative by about 2 μV than for the hand-only condition.

In contrast, the present findings for the LRP differed from Experiment 1. Now, foreperiod LRP amplitude increased significantly in conditions that precued finger in addition to hand, whereas in Experiment 1 (see Figure 2), there had only been an unreliable tendency in this direction. This result is clearly at variance with the strong version of hierarchical movement preparation, which predicts that the finger-plus-hand condition would not be significantly different from hand alone. The same prediction should also hold for the direction-plus-hand condition. However, looking at Figure 4, the curve of this condition is intermediate between the two other conditions. Therefore, along the same lines as for the hand-plus-finger condition in Experiment 1, one might argue that possibly the amplitude difference is just too slight to reach statistical significance under the conditions used here. This LRP finding might be taken as tentative evidence for the view that, at least sometimes, participants were able to prepare index and middle fingers simultaneously.

The analysis of the scalp topographies showed that the scalp distribution found for the midline recordings is quite robust when more electrodes and an average reference montage is used. The analysis of normalized data indicated that there is not only an amplitude difference but also a difference in topography between conditions. Interestingly, the contribution to the CNV provided by hand plus finger was quite different from the CNV distribution for hand alone. The foreperiod CNV of the hand-alone condition presumably not only reflects the preparatory activity for the hand, but most likely reflects a multitude of other processes as well, such as expectancy for the stimulus, general preparatory processes, or even arousal. Therefore the effects of movement programming should be seen most clearly in the differences between precue conditions. The fact that the hand-plus-finger condition differs in topography from the hand-alone condition indicates that the amplitude increase is due to the additional involvement of a specific process rather than to an increase of all those processes that are already active for the hand-alone condition. This finding is in line with the suggestion of Ulrich et al. (1998) that the precuing effect in the CNV reflects the assembly of a central motor program. Also in line with this idea is the observation that the specific contribution of the hand-plus-direction condition shows a qualitatively similar topography as the specific contribution of the hand-plus-finger condition (see Figure 6). Unfortunately, this observation is merely suggestive, because, after correction, the topography of this and the hand-alone condition was—at best—a trend.

General Discussion

The main purpose of the present experiments was to assess the generality of the results of a previous precuing study of Ulrich et al. (1998) about the organization of movement programming and preparation. Ulrich et al. had drawn two important conclusions from their findings. Because the LRP did not increase above the level attained for precuing hand unless the movement was fully specified, they favored a strong version of hierarchical movement preparation. According to this hypothesis, limb-specific movement preparation as indexed by the LRP progresses above hand only if the response is fully specified. The pattern that Ulrich et al. observed for the CNV was quite different. Here CNV amplitude increased monotonically with the number of response parameters specified, much the same way as did RT. The authors suggested that CNV amplitude in the precuing paradigm might reflect limb-unspecific preparation of movement, organized in parallel. Although the current experiments replicated results of Ulrich et al. at the level of performance and limb-unspecific movement preparation, an important difference was found in the organization of movement preparation at the level indicated by the LRP.

The present studies tested the generality of the findings of Ulrich et al. (1998) by uncoupling response hand and finger precues and omitting the force dimension. In both experiments, the RTs showed the usual precuing effect, with RT decreasing as a function of the number of movement parameters conveyed by the precue, indicating that our design was basically sound, including the effects of the new parameter. Just as RT, the CNV findings were fully consistent with the results of Ulrich et al. CNV amplitude was a mere function of the number of prespecified parameters, increasing from one parameter (hand) over two (hand plus direction or hand plus finger) to all three parameters. The pattern for one- and two-parameter precues was the same even when the fully informative condition was omitted in Experiment 2, demonstrating that the effect is robust.

In contrast to the RT and CNV findings, which replicate and confirm the results of Ulrich et al. (1998), the LRP findings regarding the new response dimension finger are clearly different. Although Experiment 1 did not find a significant increase of LRP amplitude above hand information alone for the hand-plus-finger condition, the LRP waveshapes indicated weak and transient effects. Therefore, the experimental context was simplified and the number of trials per condition was raised in Experiment 2 by sacrificing the fully informative condition and the no-go trials. This time, the foreperiod LRP for hand plus finger was clearly larger than for the hand-alone condition. This finding is in line with the strong version of the hierarchical preparation hypothesis put forth by Ulrich et al. On the other hand, the hypothesis is at least partially supported by the present findings about hand and direction information. Therefore, the present findings suggest that the movement parameters response finger and movement direction are qualitatively different. Whereas strong hierarchical preparation appears to hold when parameters like movement direction or force are involved (Ulrich et al., 1998; this study), other principles have to be invoked for the relationship of hand and fingers.

The present findings partly support the model of hierarchical preparation of movement parameters as suggested by Rosenbaum (1980). According to this hypothesis, not all precue parameters are equally beneficial. A hierarchical ordering is assumed with hand being the first parameter to be specified, followed by finger preparation, and direction. Thus, our LRP results indicate a hierarchical relationship between finger and direction. In the absence of finger information, direction precues do not increase its amplitude above the level attained for hand information alone. However, present findings do not exclude the possibility that hand and finger are prepared independently and in parallel (cf. Osman, Moore, & Ulrich, 1995). Our data are uninformative for this question because hand was available in all conditions as a prerequisite to measure foreperiod LRP.

How are we to explain the qualitatively different effects of parameters like movement direction and force on the one side
and response finger on the other side? One might suggest that the preparation of finger movements has a privileged role because, like the hands, fingers are effectors of the human body. In contrast, movement direction and force are functional properties of effectors. The results of the present experiments indicate that if hand is known, it may be possible to prepare the response finger even if the final movement is not yet completely specified. In contrast, hand-specific preparation appears not to progress for other (functional) parameters like direction and force even if logically possible as, for example, when hand and direction are known but not response finger.

Interestingly, little evidence was obtained in the present experiments for multiple response preparation. This hypothesis predicts that the LRP for hand alone or hand plus direction is larger than the LRP for hand plus finger or full advance information, because in the former conditions participants might prepare all possible alternatives for the unspecified parameter (finger) in parallel. However, there was virtually no sign of such a possibility in the data collected here except to the slightly enhanced foreperiod LRP for the hand-plus-direction precue as compared to hand precues in Experiment 2. It is, however, very unlikely that multiple response preparation occurs in all choice-reaction conditions. If this were the case, the foreperiod LRP amplitude in partial precue conditions should always exceed or at least equal the full precue condition, which was clearly not found by Leuthold et al. (1996) and Ulrich et al. (1998). Although synchronous preparation of two fingers is not necessarily accompanied by increased neural activity (e.g., Kitamura, Shibasaki, & Kondo, 1993; Woolsey, Erickson, & Gilson, 1979), the LRP is larger before complex movements involving different fingers, as compared to a simple response, apparently due to parallel preparation of multiple effectors (Hacksley & Miller, 1995; Stief, Leuthold, Miller, Sommer, & Ulrich, 1998).

Although not in the focus of the present study, we should briefly mention two issues relating to discrepancies with reports of others. Ulrich et al. (1998) noted that the increase of CNV amplitude with increasing precue information is at variance with observations of van Boxtel and colleagues (van Boxtel & Brunia, 1994a, 1994b; van Boxtel, van den Boogart, & Brunia, 1993). In these studies, the CNV had been smaller when the precue informed about the response mode than when it did not. As mentioned by Vidal, Bonnet, and Macar (1995), however, these studies employed a strict RT deadline where responses after 400 ms were rejected. It is conceivable that in conditions without precue, subjects can only meet this criterion if they keep a high arousal level causing a larger CNV amplitude. The present experiments replicate the relationship between precue information and CNV reported by Ulrich et al. (see also MacKay & Bonnet, 1990), as do observations by Leuthold et al. (1996) and by Sangals et al. (2002). Because Sangals et al. had observed the same relationship whether precue information was varied blockwise or on a trial-by-trial basis, one can probably rule out that the blocking of conditions can account for the discrepant results of van Boxtel and colleagues, as had been suggested by Ulrich et al. It remains to be determined whether the discrepancy relates to the strict RT deadline employed, to the duration of the foreperiod (4 s in the experiments of van Boxtel and colleagues as compared to 1.5 s in our experiments), or to the kind of preliminary information given.

The second issue was raised by Verleger, Wauschkun, von der Lubbe, Jaskowski, and Trillenberg (2000), who noted that in their experiments, the CNV was more frontally distributed than in the data of Ulrich et al. (1998) and Gaillard (1977). We agree with Verleger and colleagues that the difference between their and our experiments may relate to the selection between effectors, that is, eye versus hand in their report and various kinds and combinations of movement parameters for hands in our series of studies (Leuthold et al., 1996; Sangals et al., 2002; Ulrich et al., 1998; this study). However, whereas Verleger et al. propose a differential involvement of a parietal motor system to be responsible for the differences in scalp distributions, we consider projections from the supplementary motor area to be just as plausible as long as no systematic modeling of brain sources has been made (Roland, Larsen, Lassen, & Skinhoj, 1980; but see Leuthold & Jentzsch, 2001).

In conclusion, the present experiments have provided corroborative evidence that the CNV reflects the assembly of a motor program at a central level where different movement parameters can be specified in parallel. The LRP indicated that the strong version of hierarchical response preparation at a more peripheral level does not hold in all cases. At least for preliminary information about the response finger, movement preparation may progress beyond the level of response hand even when the movement is not yet completely specified.

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(Received August 13, 2001; Accepted April 26, 2002)