Decreased load on general motor preparation and visual-working memory while preparing familiar as compared to unfamiliar movement sequences

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Abstract

Learning movement sequences is thought to develop from an initial controlled attentive phase to a more automatic inattentive phase. Furthermore, execution of sequences becomes faster with practice, which may result from changes at a general motor processing level rather than at an effector specific motor processing level. In the current study, we examined whether these changes are already present during preparation. Fixed series of six keypresses, either familiar or unfamiliar, had to be prepared and executed/ withheld after a go/nogo signal. Reaction time results confirmed that familiar sequences were executed faster than unfamiliar sequences. Results derived from the electroencephalogram showed a decreased demand on general motor preparation and visual-working memory before familiar sequences as compared to unfamiliar sequences. We propose that with familiar sequences the presetting segments of responses is less demanding than with unfamiliar sequences, as familiar sequences can be regarded as less complex than unfamiliar sequences. Finally, the decreasing demand on visual-working memory before familiar sequences suggests that sequence learning indeed develops from an attentive to an automatic phase.

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1. Introduction

Piano playing requires the accurate coordination of finger movements on both hands. Each finger movement has to be sequenced in the right order and executed with the right pace relative to finger movements on the same or the other hand. Skilled piano players can rapidly sequence these movements in case of playing a familiar piece, however, in case of an unfamiliar piece, their movements become slower, less precise and seem to require more attention (Drake & Palmer, 2000; Lotze, Scheler, Tan, Braun, & Birbaumer, 2003). Previous studies suggest that different processes underlie the execution of familiar as compared to unfamiliar sequences of movements (e.g. Hikosaka et al., 1999; Ivy, 1996; Verwey, 2001). These processes can be studied by using so-called discrete movement sequences, which are relatively short sequences of movements usually consisting of three up to six key presses with a clear start- and endpoint. The learning of these sequences has been described in several models, and is indeed thought to develop from an initial controlled attentive phase to a second automatic phase in which attention is no longer needed (e.g., Cohen, Ivy, & Keele, 1990; Doyon & Benali, 2005; Verwey, 2001). In our study, we examined whether these different processes underlying the execution of familiar and unfamiliar sequences of movements are already active while preparing these movements, by focusing on several measures derived from the electroencephalogram (EEG).

Sequence learning can be studied by using the discrete sequence production (DSP) task. In a typical DSP task discrete sequences are practiced by responding to series of three to six key-specific stimuli. All stimuli, apart from the first stimulus, are presented immediately after the response to a previous stimulus. Since sequences have a limited length and a clear beginning and end, the DSP task is especially suitable for studying hierarchical control and segmentation (Rhodes, Bullock, Verwey, Averbaek, & Page, 2004). Behavioral results of the DSP task show that execution gets faster with practice and that some keypresses within a sequence are executed consistently slower than other keypresses, which is assumed to index the segmentation of motor sequences (Verwey, 1996). As segments consolidate with practice, it is suggested that each segment involves the execution of a motor chunk (Verwey & Eikelboom, 2003). With practice, chunking can speed up the selection and initiation of familiar segments (Verwey, 1999).

In motor sequencing tasks like the DSP task, anticipation and programming of the next motor response may already start while executing the previous response (Eimer, Goschke, Schlaghecken, & Sturmer, 1996). In other words, motor preparation and motor execution occur in parallel in this task, which implies that it is
difficult to disentangle these processes. In order to get a clearer view on the precise function of the processes underlying familiar and unfamiliar sequences it seems better to separate motor preparation from motor execution. Therefore a modified version of the DSP-task was developed, inspired by the precuing paradigm of Rosenbaum (1980). In Rosenbaum’s paradigm precues (S1) provide specific information about the forthcoming movement. After a delay period an execution/withhold (go/nogo) signal (S2) is presented, which may provide missing information about the forthcoming movement in case of partial or non-informative precues or simply a go/nogo signal. Similar to the S1–S2 paradigm of Rosenbaum, a go/nogo version of the DSP task was designed in which six key-specific stimuli were presented in sequence, which after a preparatory interval were followed by a go/nogo signal. In case of a go signal, participants were to react as fast and accurately as possible by pressing the six corresponding keys in the indicated order, and in case of a nogo signal responses should be withheld. This modified DSP task allows us to study the preparation phase of sequence learning in isolation from motor execution.

To study movement preparation measures derived from the EEG appear especially useful (Dinnberger et al., 2000; Van der Lubbe et al., 2000; Verleger, Waschkuhn, van der Lubbe, Jaśkowski, & Trillenberg, 2000). Event related potentials (ERPs) are indeed suitable to track the time course of functional processes underlying movement preparation. In the present study, we employed the contingent negative variation (CNV), the lateralized readiness potential (LRP), and the contralateral delay activity (CDA) to study preparation of motoric sequences, since they give information about several different aspects of preparation.

The CNV is a negative going wave with mostly a central maximum that unfolds in the interval between a warning stimulus and an execution signal (e.g. a go/nogo signal) (Jentzsch & Leuthold, 2002; Verleger, Vollmer, Waschkuhn, van der Lubbe, & Wascher, 2000). The late CNV is typically maximal at the Cz electrode and is thought to reflect preparatory motor activity (cf. Brunia, 2004; Schröter & Leuthold, 2009). What exactly is represented in the CNV is unclear. Cui et al. (2000) suggest that the complexity of the prepared response is reflected in the CNV. In their study a simple and complex motor task were compared. During the simple movement task thumbs were opposing the index fingers three times in a row, by both hands. The complex movement task was the same, except that the second thumb opposition involved the little fingers instead of the index. An increased late CNV for complex movements as compared with simple movements was obtained, which suggests that more preprogramming is taking place before complex movements compared with simple movements. In contrast with Cui et al. (2000), Schröter and Leuthold (2009) suggest that the amount of prepared responses is reflected in the CNV. They found an increased CNV when preparing three-key compared with one-key responses, which suggests that motor programming increases with the length of the response sequence. In principle, however, this increased CNV could also be caused by the increased complexity of a longer sequence. Jentzsch, Leuthold, and Ridderinkhof (2004) and Wild-Wall, Sangals, Sommer, and Leuthold (2003) revealed that with more advance information (response hand, response direction and response finger) before an upcoming movement the amplitude of the late CNV increases, which may reflect more preprogramming. These studies all suggest that if more items have to be prepared or more parameters are specified before the upcoming movement then the CNV will increase. Thus, Cui et al. (2000) suggest that the complexity of a movement is represented in the amplitude of the CNV, whereas Schröter and Leuthold (2009) and others suggest that the amount of items or parameters that have to be prepared is represented in the amplitude of the CNV.

The source of the CNV is a point of discussion. Hultin et al. (1996) tried to locate the source of the CNV, by using magnetoencephalography (MEG), and suggested that the source of the CNV is located in the premotor cortex. Furthermore, based on ERP topography and on dipole source localization it has been proposed that the CNV originates from higher level motor areas such as the SMA and the cingulated motor area (Cui et al., 2000; Leuthold & Jentzsch, 2001). Overall, the idea appears to be that the CNV reflects general motor preparation, which is not effector specific, and results from activity at the supplementary motor cortex. Therefore we use the CNV to examine if there is a difference between familiar and unfamiliar sequences in general motor preparation.

A second ERP measure that can be derived from the EEG is the LRP, which is a deviation from baseline before the response, with a peak at the moment of response (De Jong, Wierda, Mulder, & Mulder, 1988; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). It is assumed that the LRP begins to deviate from baseline as soon as the response hand is activated (e.g. Kutus & Donchin, 1980). Verleger and Vollmer et al. (2000), using arrows as precues, could distinguish between a contralateral negativity before S2 (preparation related LRP) and a contralateral negativity beginning at movement onset (motor LRP). Source localization and magnetoencephalography studies strongly suggest that the LRP reflects activity in the primary motor cortex (M1) (Böcker, Brunia, & Cluitmans, 1994a, 1994b; Praamstra, Schmitz, Freund, & Schnitzler, 1999). In the present study we focused on the preparation related LRP, which is thought to originate from M1 and reflect effector specific motor preparation (Leuthold & Jentzsch, 2001). The LRP was used to examine whether there is a difference in effector specific preparation between familiar and unfamiliar sequences.

Another useful lateralized ERP measure is the contralateral delay activity (CDA), which has been considered as an index for the encoding and/or maintenance of items or locations in visual memory (Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; Vogel, McColough, & Machizawa, 2005). The CDA consists of a contralateral ipsilateral negativity relative to the relevant stimulus side. The CDA is maximal at posterior recording sites (P07 and P08) and is calculated by subtracting activity at ipsilateral electrode sites from the corresponding contralateral electrode sites. Most studies use bilateral stimuli in order to keep stimulation of both hemifields as comparable as possible. Thus, in agreement with Klaver et al. (1999) it may be argued that the CDA reflects the load on visual-working memory by spatial attention and can be used to examine if sequence learning develops from an attentive to an automatic phase.

In the present study, we examined whether differences between familiar and unfamiliar sequences are already present while preparing these sequences. We predicted familiar motor sequences to be executed faster and with fewer errors than unfamiliar motor sequences. When comparing familiar and unfamiliar sequences in terms of general motor preparation, reflected in the CNV, several possibilities can be distinguished. First, behavioral differences in speed and accuracy may be solely due to processes active during the execution phase and not during preparation. Therefore no difference in general motor preparation between familiar and unfamiliar sequences may be predicted to be observed. Second, if the CNV reflects the complexity of the sequences (Cui et al., 2000) then there may be more general motor preparation before unfamiliar sequences as compared with familiar sequences, since unfamiliar sequences can be regarded as more complex than familiar sequences. This second option would predict a larger CNV during the preparation of unfamiliar sequences than for familiar sequences. Third, if the CNV reflects the amount of prepared keypresses or parameters (Schröter & Leuthold, 2009) then there may be more general motor preparation before familiar sequences.
as compared with familiar sequences, as more keypresses can be prepared for familiar sequences than for unfamiliar sequences. This would be reflected in a larger CNV during the preparation of familiar sequences compared with unfamiliar sequences. Regarding effector specific preparation it may be argued that only the first keypress is prepared on an effector specific level (Schröter & Leuthold, 2009), which predicts no differences in LRP amplitude between familiar and unfamiliar sequences. The CDA is used to index visual-working memory. If more items are stored in visual-working memory during the preparation of unfamiliar sequences as compared with familiar sequences then the CDA may be enlarged for unfamiliar sequences. This could be related to the increased complexity of unfamiliar sequences, as with unfamiliar sequences individual items have to be kept in visual-working memory, whereas with familiar sequences segments of stimuli can be kept in visual-working memory. In contrast, if more items are stored in visual-working memory during the preparation of familiar sequences then the CDA will be increased for familiar sequences. Finally, the CNV, LRP and CDA are expected to be most pronounced just before the go/nogo signal.

2. Materials and methods

2.1. Participants

Sixteen students (seven males, nine females), aged 18–24 years (mean: 21 years) from the University of Twente served as participants. They had a mean handedness score of 20 (range: 13–24), measured by the Annett Handedness Inventory (Annett, 1970), signifying that all participants can be considered as right-handed (−24 to −9 indicates left-handed, −8 to 8 indicates ambidexter, 9–24 indicates right-handed). All participants gave their written informed consent and reported normal or corrected-to-normal vision. Participants were paid € 42 for their participation of maximally 7 h divided over 2 days. The study was approved by the local ethics committee of the Faculty of Behavioural Sciences of the University of Twente and was performed in line with the Declaration of Helsinki.

2.2. Stimuli and task

Participants placed their little finger, ring finger, middle finger and index finger of their left and right hand respectively on the a, s, d, f keys and the; l, k, j keys. A trial consisted of the presentation of six stimuli which, in case of a subsequent go stimulus, was to be followed by the execution of six spatially corresponding keypresses (one sequence). The presentation of the stimuli is displayed in Fig. 1. Each trial started with the presentation of a fixation cross (1.3°) in the center of the screen accompanied with eight horizontally aligned squares (2.5°), four on the left and four on the right side of the fixation cross (default screen). The alignment of the eight stimulus squares had a total visual angle of 26.5° and corresponded with the alignment of the eight response keys. The eight squares and the fixation cross were drawn with a silver color line on a black background. One thousand milliseconds after onset of the default screen, one square was filled yellow for 750 ms, next a second square, and so on until a sixth square was filled. Next, the default screen remained for another 1500 ms. Subsequently, the fixation cross was colored either red (8%) or blue (92%). The red fixation cross stayed on the screen for 3000 ms and indicated that no action should be executed (a nogo trial) whereas the blue fixation cross (presented for 100 ms) indicated that participants had to press the buttons corresponding to the presented sequence of yellow squares (a go trial). Participants were instructed to respond as fast and accurately as possible, and were requested to keep their eyes on the fixation cross from the moment when the last stimulus disappeared until the final response of the sequence was executed. Feedback was given after the end of a response sequence, but only when a participant reacted before the go/nogo signal, or when a false button press was conducted.

In the present experiment, participants executed eight familiar sequences during the learning phase, which were presented in random order. Every participant practiced four sequences with the left hand and four sequences with the right hand, which were mirror versions (a→d, s→f, l→k, j→l). This was done to reduce differences between left and right hand responses to make calculation of the LRP neater. In order to counterbalance across participants and across fingers four different structures of sequences were used; 134231, 142413, 124314, and 132413, 123413, and 132314. With each structure four sequences were created by assigning different keys to the numbers, thereby eliminating finger-specific effects. The first structure leads to the sequences adfasd, sfadfs, dasfad, and fsdasf, and so on for the three other structures. The four sequences of each hand started with a different key press and at the same time the four sequences had a different structure. This led to four different versions of sequences, which were counterbalanced across participants. During the test phase eight unfamiliar sequences were added. Again, four sequences were executed with the left hand and four sequences with the right hand, which were mirror versions. This resulted in the random presentation of eight familiar and eight unfamiliar sequences. Half of the sequences of each block were carried out with the left hand and the other half with the right hand. Sequences performed with the right hand were again mirror versions of the sequences executed by the left hand. The four versions were counterbalanced across the test phase and practice phase in such a way that the unfamiliar sequences of one group were the familiar sequences of another group. Thus, differences between familiar and unfamiliar sequences cannot be ascribed to the specific sequence employed or to finger-specific effects.

2.3. Procedure

Participants were tested on two successive days. On the first day, they performed six practice blocks and on the second day they
2.4. Recording and data processing

The experiment was run on a personal computer (Pentium 4) with a QWERTY keyboard. Stimulus presentation, response registration and production of external triggers were controlled by E-Prime, version 1.1. A 17 in. monitor was placed in front of the participants at a distance of about 45 cm. EEG and electro-oculogram (EOG) were amplified with a Quick-Amp amplifier (72 channels, DC) and recorded with Brain Vision Recorder (version 1.05) software. EEG was recorded from 61 Ag/AgCl ring electrodes located at standard electrode positions of the extended 10/20 system. An online average reference was employed. EOG was recorded bipolarly, both vertically from above and below the left eye and horizontally from the outer canthi of both eyes. Electrode impedance was kept below 5 kΩ. The EEG and EOG data were sampled at a rate of 500 Hz. Measured activity was digitally filtered online (low-pass 140 Hz, DC).

2.5. Data analysis

For statistical analyses, Greenhouse–Geisser epsilon correction for the degrees of freedom was applied whenever appropriate. One participant was left out from the final analyses because of the large number of errors (61% correct keypresses, while all other participants had a percentage of correct keypresses of 85% or higher), which suggested that this participant did not fully comply with the task instructions. Furthermore, EEG analyses were performed on all data without artifacts, because elimination of all trials with the task instructions. Furthermore, EEG analyses were performed on all data without artifacts, because elimination of all trials with artifacts from all electrodes. Statistical analyses were performed on Fz, Cz and Pz, as these electrodes represent the predominant distribution of the CNV (Leuthold & Jentsch, 2002). The LRP and CDA were determined in 200 ms intervals from −1200 to the go/nogo signal on which statistical analyses were performed. All analyses included the factors Time Interval (6) and Familiarity (familiar or unfamiliar), the CNV analyses additionally included the factors Hand (2) and Posterior-anterior axis (3). To exclude confounds in terms of volume conduction from PO7/8 to C3/4 electrodes for the LRP and vice versa for the CDA, we performed analyses in which PO7/8 and C3/4 electrodes were respectively treated as a covariate (for a comparable procedure see Van der Lubbe & Woestenburg, 1999).

3. Results

3.1. Behavioral measures

3.1.1. Practice phase

RTs and Percentage Correct (PC) as a function of Block and Hand are compiled in Table 1. Responses were faster with the right than with the left hand, \( F(1, 14) = 10.1, p = 0.007 \), participants became faster with practice, \( F(6, 84) = 63.5, \varepsilon = 0.35, p < 0.001 \), and there was an effect of Key, \( F(5, 70) = 15.6, \varepsilon = 0.41, p < 0.001 \). Furthermore, the difference in RT between keys decreased with practice.

<table>
<thead>
<tr>
<th>Hand</th>
<th>Sequence</th>
<th>Practice phase</th>
<th>Test phase</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Block 1</td>
<td>Block 2</td>
</tr>
<tr>
<td>RT</td>
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<td>289</td>
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<tr>
<td></td>
<td>Familiar</td>
<td>355</td>
<td>312</td>
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<tr>
<td></td>
<td>Unfamiliar</td>
<td>354</td>
<td>287</td>
</tr>
<tr>
<td>PC</td>
<td>Left</td>
<td>91.1</td>
<td>94.4</td>
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<td></td>
<td>Familiar</td>
<td>85.0</td>
<td>89.2</td>
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<tr>
<td></td>
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<td>Right</td>
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<td></td>
<td>Unfamiliar</td>
<td>90.8</td>
<td>93.9</td>
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2.6. Response parameters

Response time (RT) was defined as the time between onset of the go-signal and depression of the first key and as the time between the onsets of two consecutive key presses within a sequence. The stimulus–response interval was always 0 ms. The first two trials of every block and after every break and trials with errors were excluded from RT analyses. Trials in which the total RT, the sum of all RTs in one sequence, deviated more than 3 SD from the overall mean total RT per block across participants were additionally eliminated from the RT analysis (cf. De Kleine & Verwey, 2009a, 2009b). This procedure removed 1.4% of the trials. The Percentage Correct (PC) was calculated as the percentage correct keypresses. The mean RTs and mean PC were evaluated statistically by analysis of variance (ANOVA) with repeated measures, with in the practice phase Block (7), Key (6) and Hand (2) as within subject factors and in the test phase Block (3), Key (6), Hand (2) and Familiarity (2: familiar or unfamiliar sequence) as within subjects factors.

2.7. EEG parameters

The CNV was computed by averaging EEGs for all trials without artifacts from all electrodes. Statistical analyses were performed on Fz, Cz and Pz, as these electrodes represent the predominant distribution of the CNV (Leuthold & Jentsch, 2002). The LRP and CDA were determined by application of the double subtraction technique to obtain the contralateral minus ipsilateral difference to the response/stimulus side. As a consequence, more negativity at the site contralateral to the required response/stimulus than ipsilateral results in a negative difference wave. Averaged activity was determined in 200 ms intervals from −1200 to the go/nogo signal on which statistical analyses were performed. All analyses included the factors Time Interval (6) and Familiarity (familiar or unfamiliar). The CNV analyses additionally included the factors Hand (2) and Posterior-anterior axis (3). To exclude confounds in terms of volume conduction from PO7/8 to C3/4 electrodes for the LRP and vice versa for the CDA, we performed analyses in which PO7/8 and C3/4 electrodes were respectively treated as a covariate (for a comparable procedure see Van der Lubbe & Woestenburg, 1999).
as was shown by the significant interaction between Block and Key, $F(30, 420) = 2.8$, $p < 0.008$, see Fig. 2.

More correct responses were made with practice, $F(6, 84) = 26.8$, $e = 0.28$, $p < 0.001$, and there was an effect of Key, $F(5, 70) = 15.1$, $e = 0.35$, $p < 0.001$. Furthermore, the increase in the number of correct responses differed between keys, as was shown by the interaction between Block and Key, $F(30, 420) = 5.0$, $p < 0.001$ (see Fig. 2). In sum, participants became faster and made more correct responses during the practice phase, which indicates that the sequences were learned.

3.1.2. Test phase

Responses were faster when executing familiar sequences than when executing unfamiliar sequences (281 vs. 324 ms), $F(1, 14) = 23.1$, $p < .001$. Participants became faster during the test phase, $F(2, 28) = 32.5$, $p < 0.001$ (see Table 1), and there was an effect of Key $(368, 285, 306, 313, 320, 225$ ms respectively for Key 1–6), $F(5, 70) = 11.8$, $e = 0.50$, $p < 0.001$. The decrease in RT as a function of Block was larger for unfamiliar sequences than for familiar sequences, as was shown by a significant interaction between Familiarity and Block, $F(2, 28) = 8.8$, $p = 0.001$. The interaction between Familiarity and Key is shown in Fig. 3, $F(5, 70) = 5.4$, $p < 0.001$. Post-hoc tests showed that especially key fourth and fifth key were executed faster in the familiar sequence as compared to the unfamiliar sequence, $F(1, 11) < 21.3$, $p = 0.001$.

More correct responses were made for familiar than for unfamiliar sequences (95 vs. 88%), $F(1, 14) = 34.3$, $p < 0.001$. The number of correct responses increased during the test phase, $F(2, 28) = 13.5$, $p < 0.001$, and there was an effect of Key, $F(5, 70) = 6.9$, $e = 0.39$, $p = 0.002$. The effect of Key showed that participants made increasingly more errors towards the end of the sequence except for the last key, which was probably due to a recency effect (mean PC for key 1–6 respectively: 95%, 93%, 91%, 90%, 88%, 91%). Although the interaction between Familiarity and Key was not significant ($F(5, 70) = 2.3$, $p = .104$), this effect can mainly be attributed to unfamiliar sequences as most errors were made in this condition (mean PC for key 1–6 for familiar sequences respectively: 97%, 95%, 96% 94%, 93%, 94% and for unfamiliar sequences respectively: 93%, 91%, 87%, 85%, 84%, 88%). There was a larger increase in the number of correct responses for unfamiliar sequences compared to familiar sequences, as was shown by the interaction between Familiarity and Block, $F(2, 28) = 5.5$, $p = 0.01$. Finally, on 6.4% of the no-go trials a response was given. In sum, participants became faster and made more correct responses during the test phase, especially with unfamiliar sequences. This indicates that participants still learned the sequences during the test phase, especially unfamiliar sequences. Furthermore, execution was faster for familiar than for unfamiliar sequences, which is probably related to the faster initiation and execution of chunks in familiar sequences.

3.2. EEG analyses

3.2.1. CNV

The CNV at Fz, Cz, and Pz electrodes for left and right hand sequences and the topographic maps for activity averaged across the 200 ms interval before the go/no-go signal are displayed in Fig. 4.1 Fig. 4 reveals an increased CNV for unfamiliar sequences at Cz, a comparable CNV for familiar and unfamiliar sequences at Pz, and an increased positivity at Fz (increased for familiar sequences with left hand sequences and increased for unfamiliar sequences with right hand sequences). Inspection of the topographic maps shows a parietal negative maximum for familiar and unfamiliar sequences, preceding both left and right hand responses. Statistical analyses performed on the 1200–0 ms interval relative to the go/no-go stimulus showed a main effect of Electrode, due to positivity at Fz and negativity at Cz and Pz, $F(2, 28) = 36.1$, $e = 0.71$, $p < .001$. The interaction between Time and the Posterior-anterior axis, $F(10, 140) = 31.3$, $e = 0.25$, $p < .001$, showed that positivity at Fz and negativity at Cz and Pz increased over time (see Fig. 4). Planned comparisons showed that the increasing negativity was larger for Pz than for Cz, $F(1, 14) = 10.0$, $p = .007$. Furthermore, a three-way interaction between Hand, Familiarity and the Posterior-anterior axis was observed, $F(2, 28) = 7.0$, $p = .003$. Fig. 4 shows that familiarity had the largest effect on Cz and Pz, therefore planned comparisons were performed on these electrodes. An increasing negativity was shown for unfamiliar sequences compared with familiar sequences at Cz both for left hand and for right hand trials ($F(1, 14) = 15.73$, $p = .001$ and $F(1, 14) = 12.85$, $p = .003$).
3.2.2. LRP

The LRP as a function of Familiarity, and topographic maps for averaged activity within the 200 ms interval before the go/nogo signal as a function of Familiarity, are displayed in the upper panel of Fig. 5. Fig. 5 reveals an increasing negativity during the preparation of familiar and unfamiliar sequences. The data in the topographic maps were arranged such that the electrodes at the right in Fig. 5 represent the lateralized ERP activity and the left electrodes represent the mirror version of the right electrodes. Inspection of the topographic maps shows lateral activation at central sites for unfamiliar and familiar sequences, which may reflect motor related activity for unfamiliar and familiar sequences. Statistical analyses performed on the 1200 ms prior to the go/nogo interval revealed that the LRP increased over time, $F(5, 70) = 7.1$, $\varepsilon = 0.33$, $p = 0.006$. Furthermore, results showed that overall the LRP deviated from zero, $F(1, 14) = 11.5$, $p = .004$, but there was no difference in LRP amplitude between familiar and unfamiliar sequences, $F(1, 14) = 0.2$, $p = .7$. Volume conduction from posterior to central sites does not seem probable, as indicated in Fig. 5. However, we performed an additional analysis on the LRP to check for possible volume conduction from posterior to central sites. An ANOVA was performed in which we included activity at the PO7/8 electrodes as a covariate. The effect of Time-interval was still evident when correcting for volume conduction from posterior sites, $F(5, 69) = 9.75$, $p < .001$. This indicates that the LRP was not caused by volume conduction from posterior sites.

3.2.3. CDA

The CDA as a function of familiarity and the topographic maps for averaged activity within the 200 ms interval before the go/nogo signal as a function of Familiarity are displayed in the lower panel of Fig. 5. Fig. 5 reveals an increasing negativity when preparing unfamiliar sequences as compared to familiar sequences. The topographic maps, showing the time-interval at which the difference between familiar and unfamiliar sequences was maximal, indicate lateral activation at posterior sites for the unfamiliar sequence, but not for familiar sequences. This may reflect memory related activity for unfamiliar sequences but not for familiar sequences. Statistical analyses performed on the 1200 ms prior to the go/nogo interval showed a main effect of Time-interval, $F(5, 70) = 3.5$, $\varepsilon = 0.44$, $p = 0.039$. The main effect of Familiarity showed that the amplitude of the CDA was larger for unfamiliar sequences than for familiar sequences, $F(1, 14) = 4.6$, $p = .05$. Furthermore, results showed that overall the CDA deviated from zero, $F(1, 14) = 9.8$, $p = .007$. Extra analyses in which we included activity at C3/4 as a covariate showed that the CDA remained larger for unfamiliar sequences as compared to familiar sequences, $F(1, 13) = 4.94$, $p = .045$.

4. Discussion

With practice the execution of discrete sequences becomes faster and learning develops from an initial controlled attentive phase to a more automatic inattentive phase. This may result from changes at a general motor processing level rather than at an effector specific motor processing level. The goal of the present study was to investigate if the differences between familiar and unfamiliar sequences are already present while preparing these sequences. To this aim participants performed a go/nogo DSP task in which, in case of a go-signal, familiar and unfamiliar sequences were to be executed. We used the late CNV, LRP and CDA to index general motor preparation, effector specific motor preparation and visual-
working memory, respectively. We predicted familiar motor sequences to be executed faster and more accurately than unfamiliar motor sequences. With regard to the CNV there are several possibilities. If the CNV reflects the complexity of the sequence (Cui et al., 2000) an increased CNV-amplitude for unfamiliar sequences can be expected, as unfamiliar sequences can be regarded as more complex than familiar sequences. If the CNV reflects the amount of prepared keypresses (Schröter & Leuthold, 2009) an increased CNV-amplitude for familiar sequences can be expected, as more keys can be prepared for familiar sequences than for unfamiliar sequences. Furthermore, we predicted an equal load on effector specific preparation before familiar and unfamiliar sequences, as it is suggested that only the first response in prepared on an effector specific level (Schröter & Leuthold, 2009). Finally, we predicted that sequence learning develops from an attentive to an automatic phase (e.g., Cohen et al., 1990; Doyon & Benali, 2005; Verwey, 2001), which would be reflected in an increased CDA for unfamiliar sequences.

Behavioral results showed that during practice participants became faster and made more correct responses (see Fig. 2) and that in the test phase familiar sequences were executed faster than unfamiliar sequences. This indicates that the familiar sequences were learned during the practice phase. Results derived from the EEG showed an increased central CNV (see Fig. 4) and CDA (see Fig. 5) for unfamiliar sequences as compared to familiar sequences. No difference in LRP amplitude was found between familiar and unfamiliar sequences (see Fig. 5). This implies that the difference between the preparation of familiar and unfamiliar sequences concerns the involvement of general motor preparation and the load on visual working memory, being enlarged for unfamiliar sequences.

The differences between familiar and unfamiliar sequences were already present during preparation. This suggests that behavioral differences between familiar and unfamiliar sequences are not only due to execution, but also to preparation. Regarding the interpretation of the CNV several options were posed in the introduction. Schröter and Leuthold (2009) suggested that the CNV reflects the amount of prepared keypresses or parameters. This was not confirmed by the present results, as there was no increased CNV for familiar sequences. In contrast, we observed an increased CNV before unfamiliar sequences as compared with familiar sequences. Therefore we interpret the CNV effect as a reflection of the difference in preparation of unfamiliar (complex) and familiar (simple) responses (Cui et al., 2000). The complexity of the sequences per se was identical for familiar and unfamiliar sequences, as these were counterbalanced. However, during preparation of familiar sequences segments of responses could be presetted, which is less demanding as compared with unfamiliar sequences where each individual response has to be presetted. Thus, we suggest that with practice the complexity of preparation decreases, as segments of responses can be presetted instead of individual responses.

Previous studies in monkeys (e.g. Shima & Tanji, 1998) and humans (e.g. Ashe, Lungu, Basford, & Lu, 2006) indicated that higher order movement areas like the premotor area and the supplementary motor area (SMA) are involved in abstract movement preparation. More specifically, Nachev, Kennard, and Husain (2008) relate the function of the supplementary motor complex to the complexity of actions. It was suggested that the pre-SMA is more active during complex or cognitive situations, whereas the SMA is more tightly related to actions (Nachev et al., 2008). In the present study...
we suggest that sequence preparation becomes less complex with practice, as segments of responses can be preset instead of individual responses. Therefore it may be argued that with practice activity related to general motor preparation shifts from pre-SMA to SMA.

In our study the CNV displayed a parietal maximum, whereas other studies revealed a central maximum (e.g., Schröter & Leuthold, 2009). This suggests that the CNV is a mix of different processes with different topographies. The parietal CNV may be used to index visual-spatial processes, whereas the central CNV may be used to index general motor processes. In the present study the visual-spatial format of the stimuli is highly important and therefore the contribution of the parietal component is large. However, the visual-spatial format of the stimuli is identical for familiar and unfamiliar sequences, as in both cases six key-specific stimuli are presented, and therefore the parietal maximum of the CNV is constant. The difference between the preparation of familiar and unfamiliar sequences is seen at the central CNV, which reflects general motor processes. Thus, with practice the preparation of sequences changes at a general motor level, but not on a visual-spatial level.

In the introduction we indicated that the CDA can be used to index visual-working memory. Results showed that the CDA was enlarged for unfamiliar sequences as compared with familiar sequences. The increased load on visual-working memory for unfamiliar sequences suggests that more items are stored in visual-working memory during the preparation of unfamiliar sequences as compared with familiar sequences. This could be related to the increased complexity of unfamiliar sequences, as with unfamiliar sequences individual items have to be kept in visual-working memory, whereas with familiar sequences segments of items can be kept in visual-working memory or visual-working memory may even be no longer involved. Since the load on visual-working memory decreases with practice, it can indeed be concluded that sequence learning develops from an attentive to a more automatic phase (e.g., Cohen et al., 1990; Doyon & Benali, 2005; Verwey, 2001).

Finally, as stated in the introduction the LRP was used to indicate effector specific preparation. As predicted the effector specific preparation was similar for familiar and unfamiliar sequences. This agrees with a recent paper of Schröter and Leuthold (2009) which showed that only the first element of a response sequence is prepared on an effector specific level. Since M1 is thought to be involved in effector specific preparation (e.g. Leuthold & Jentzsch, 2001), we suggest that activity during the preparation of a sequence is identical at the level of M1 for familiar and unfamiliar sequences.

Our results may be related to a model proposed by Verwey (2001). In this model it is proposed that a cognitive and a motor processor underlie performance in tasks in which discrete motor sequences are produced. The cognitive processor is thought to initially select a representation of a sequence, based on a symbolic representation, and subsequently this sequence is read and executed by the motor processor. The model of Verwey (2001) predicts that the difference between familiar and unfamiliar sequences only concerns the demand on this cognitive processor, which reduces when the load on planning and organization diminishes. The loading of the motor buffer and the execution of the sequence is thought to be independent of learning, so the demand on the motor processor should be the same for familiar and unfamiliar sequences. In the present study we showed an increased load on general motor preparation and visual-working memory for unfamiliar sequences, whereas effector specific preparation was identical for familiar and unfamiliar sequences. This suggests that general motor processing and visual-spatial memory is reflected in the cognitive processor, whereas effector specific preparation is reflected in the motor processor.

Concluding, differences between familiar and unfamiliar sequences were already present during the preparation of sequences.

More specifically, the load on general motor preparation and visual-working memory is increased during the preparation of unfamiliar sequences, as compared with familiar sequences. The load on general motor preparation is suggested to decrease with practice as there is a shift from preparation of individual movements to segment of movements. In line with this, the load on visual-working memory is suggested to decreases with practice as segments of responses can be kept in visual-working memory instead of individual responses. This suggests that sequence learning indeed develops from an attentive to a more automatic phase.

References


