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Preparation of Mirrored Sequences Reflected in EEG.

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Abstract

The present study replicated the research by De Kleine and Van der Lubbe (in preparation) which found amongst others that the preparation of unfamiliar sequences requires more an abstract motor processing level. The transfer of learned motor skills to the other side of the body is thought to underlie abstract representations, as well. Hence, the original research was extended by examining the preparation of mirrored sequences. The results show that mirrored sequences were executed significantly faster than new sequences, indicating a transfer between hands as supposed by Verwey and Clegg (2005). The EEG measures were analyzed with the aid of the Contingent Negative Variation (CNV) as a general index of cortical motor preparation. The study replicated that learned sequences are prepared less on an abstract processing level which applies to mirrored sequences, too.

Preparation of mirrored sequences reflected in EEG

If we learn on the first day of skiing to turn to the right, we instinctively trust our ability to turn to the left without any specific instruction in the mirror-image task. Once we have learned to use the computer mouse with one hand, it is easier to handle it even with the opposite hand. The question is which underlying motor processing levels engage when sequences are executed in mirrored shape with the fingers, when playing keyboard instruments for example. Also the seemingly automatic ability to transfer a learned motor skill to the other side of the body is not well understood in terms of the underlying motor processing levels during preparation.

De Kleine and Van der Lubbe (in preparation) studied the differences in underlying processing levels of new and learned sequences during the preparation phase and claimed that sequence preparation develops from an attentive to an automatic phase and from a pre-motor to a more motor stage through practice. The preparation of unfamiliar sequences requires central motor and muscle specific motor preparation in contrast to familiar sequences, which only require a muscle specific motor processing level.

The present study replicates the study by De Kleine and Van der Lubbe (in prep.) with the goal to replicate the findings that new sequences are prepared at an abstract level in contrast to learned sequences. The study by De Kleine and Van der Lubbe (in prep.) does not take into account the processing levels of mirrored sequences during preparation. On the assumption that there are different processing levels for learned and new sequences, another aim was to examine whether mirrored sequences are prepared at an abstract level as unfamiliar sequences or with this component and more as familiar sequences.

A motor-driven sequence learning task was used to measure the reaction time and percentage of correct responses. Furthermore, measures were derived from the electroencephalogram (EEG) to study the underlying processing levels during the preparation of finger movements.

A paradigm to study motor sequence learning is the DSP task (Verwey, 1999), which is acquired from the serial reaction time (SRT) task (Nissen & Bullemer, 1987). In this task, participants are instructed to respond to a series of three to six key-specific stimuli that are presented in a fixed order. Through that, participants' responses are in a fixed series as well. Further, the beginning and the end of a sequence are clearly denoted. On this account participants are aware of the differently repeated sequences that they have to learn. During the DSP task, participants have to press fewer keys and sequences are repeated more often compared to the SRT task.

Verwey (1999) proposes that response selection and sequence execution are independent and can be separated in time. Sequence learning and transformation can be differentiated into the preparation and execution phase through the pre-cuing technique developed by Rosenbaum (1980) to study the processing levels during the different phases. The pre-cue gives information about the required forthcoming of a response and gives insight into the pre-programming of movements (Rosenbaum, 1980). To examine preparation in the present study, the pre-cue technique was used in a modified version of the DSP task. A preparation interval was given to the participants after the sequence was shown and before the go/no-go signal, to give the possibility for preparation of a hand movement. It is assumed that identical processes underlie the standard DSP task and the go/no-go DSP task. The DSP task was used to study the preparation of sequence planning and the execution of these finger movements (Verwey, 1999; Verwey & Wright, 2004) in contrast to the SRT task, where the preparation of each finger cannot be separated from the finger movement. In the original study (De Kleine and Van der Lubbe, in prep.), participants had to carry out six keystrokes in a fixed order as a sequence in a go/no-go DSP task with their left and right hand. Eight sequences were practiced with six keystrokes. The exercise and test trials varied in new and already learned sequences. In the present study, the sequences were reduced to five keystrokes because mirrored sequences were added which have to be learned, too. In comparison to the original study the test trials varied in four already learned, four mirrored and four new sequences.

Several studies support the idea that sequence learning develops through different phases with different levels of processing (Verwey, 2003; Keele, Ivry, Mayr, Hazeltine & Heuer, 2003). Various models have been proposed to explain the processing levels underlying sequence learning. It is shown that sequence learning develops from an initial attentive phase to an automatic phase (Fitts & Posner, 1967) through practice.

Verwey (1999) proposes that familiar and unfamiliar sequences are executed on different processing levels, because learned sequences are executed faster than new sequences. He proposes a model that underlies discrete sequence production. In this model, a cognitive and a motor component (movement of muscles) can be distinguished. Verwey (1999) argued that the cognitive processor plans and represents a symbolic goal structure of the action. With more practice, there are fewer demands on the cognitive component and the sequence is executed more automatically because a single representation (motor chunk) of the sequence is subsequently read and executed by the motor processor (Verwey, 2001). Therefore, the motor system organizes the movements appropriate to the goal, by reading and executing the symbol representation. For unfamiliar sequences, each element of a sequence has to be selected individually. Hence, the difference between familiar and unfamiliar sequences depends on the demands on the cognitive component. There are fewer loads on the cognitive component for familiar sequences during sequence learning. The movement execution does not change with practice; hence, the motor component does not change.

The EEG results of the study by De Kleine and Van der Lubbe (in prep.) showed a preparation of unfamiliar sequences 200 ms before the go/no-go signal on an abstract level and in addition on a muscle specific one. These results indicate that only new sequences require a central motor processing level during the preparation. No differences in the motor component for familiar and unfamiliar sequences were found. These results are in line with the model of Verwey (1999), but it is still unclear what applies to mirrored sequences.

Recent research indicates that the transfer of a sequence from the practiced hand to the other is supported by the same underlying representation as the original sequence and additional processes are also involved to transform the sequence. Hence, a more abstract component engages for the transfer of sequences (Grafton et al. 2002). Verwey and Clegg (2005) support the idea that it is transfer of practice from one hand to the other hand that mirrored sequences are executed faster than new sequences in the DSP. The left and right keys of the sequences were reversed around the center key for the mirrored sequences in the task used by Verwey and Clegg (2005). They claimed for an effector-independent and effector-dependent learning which are both accounted for transfer. During the sequence learning, the motor representation allows an efficiently integrated series of hand postures. If this representation is available to the other hand as well, the same series of hand postures performed by the other hand will produce the mirror sequence. A spatial representation develops for transfer to mirror sequences, demonstrated by the fact that the transferred sequences are executed faster with the other hand compared to new sequences.

To study the underlying processing levels during preparation EEG measures are used. EEG is an inverse reflection of the performance measure, because the neural changes increase gradually but slowly with practice, whereas the reaction time decreases slowly (Anderson, 2005). The Contingent Negative Variation (CNV) is an electrophysiological, centrally distributed, negative motor index for abstract moving preparation and is measured on a central lying electrode (Leuthold, Sommer & Ulrich, 2004). In the present study, this index is measured after a warning stimulus and before the go/no-go cue. Its purpose is to reflect the level of pre-programming of finger-movements in the DSP task. Goal of the present study was to visualize the underlying processes during the preparation phase by means of learned, new and mirrored sequences with the CNV on the central electrode (Cz) as an index of preparatory motor processing (Leuthold, et.al, 2004).

Aim of the present study was to replicate the results of the study by De Kleine and Van der Lubbe (in prep.) and investigate whether the movement preparation of mirrored sequences is prepared on an abstract level with the aid of the CNV. It was hypothesized that there would be a more abstract processing of unfamiliar sequences as shown in the earlier study. Furthermore, it is hypothesized that mirrored sequences are processed with less demands on the abstract component because the processing levels described in sequence production suggest that the preparation of mirrored sequences, as it is in an automatic phase, is more at a motor-driven level.

Through practice, the sequence preparation should develop from an attentive to an automatic phase, indicated by a reduction in reaction time. The CNV is used as a general index of motor preparation, reflecting abstract movement preparation, which corresponds to the cognitive component of the model of Verwey (1999). The model of Verwey predicts that with unpracticed sequences the cognitive component is highly active, therefore, the CNV should be observed for unfamiliar sequences and less for mirrored sequences. Verwey and Clegg (2005) predict a reduction in reaction time for mirrored sequences compared to new sequences as an indication for transfer of practice from the learned to the mirrored sequences.

Method

Participants

Eighteen right-handed undergraduate students (14 women, 4 men) from the University of Twente participated in this study, with an average age of 22 years. The students had normal or corrected to normal vision and received course credits for their participation. Only right-handed participants were allowed to sign up for this study because the lateralization of skills in the brain is of a greater consistency compared with left-handed participants. The handedness was measured by the Annet Handedness Inventory (1970). This standardized questionnaire devoted an average handedness score of 18.94 indicating that all participating students can be considered as right-handed. All participants gave their written informed consent for the study and were unacquainted with the purpose of the experiment. The study was approved by the local ethics committee at the University of Twente.

Apparatus

The task was run on two different computers (Pentium 4) on the first and second day. The presentation of stimuli and the ensuring triggers of the EEG and EOG were recorded by Brain Vision Recorder (version 1.05) software, strengthened with a Quick-Amp (72 channels) amplifier and analyzed with Brain Vision Analyzer (version 1.05).

Stimuli

The task was a go/no-go version of a Discrete Sequence Production (DSP) task. On the computer screen, there were eight squares (2.5° each) shown horizontally, which were divided through a fixation cross (1.3°) at the center of the screen (see Figure 1).

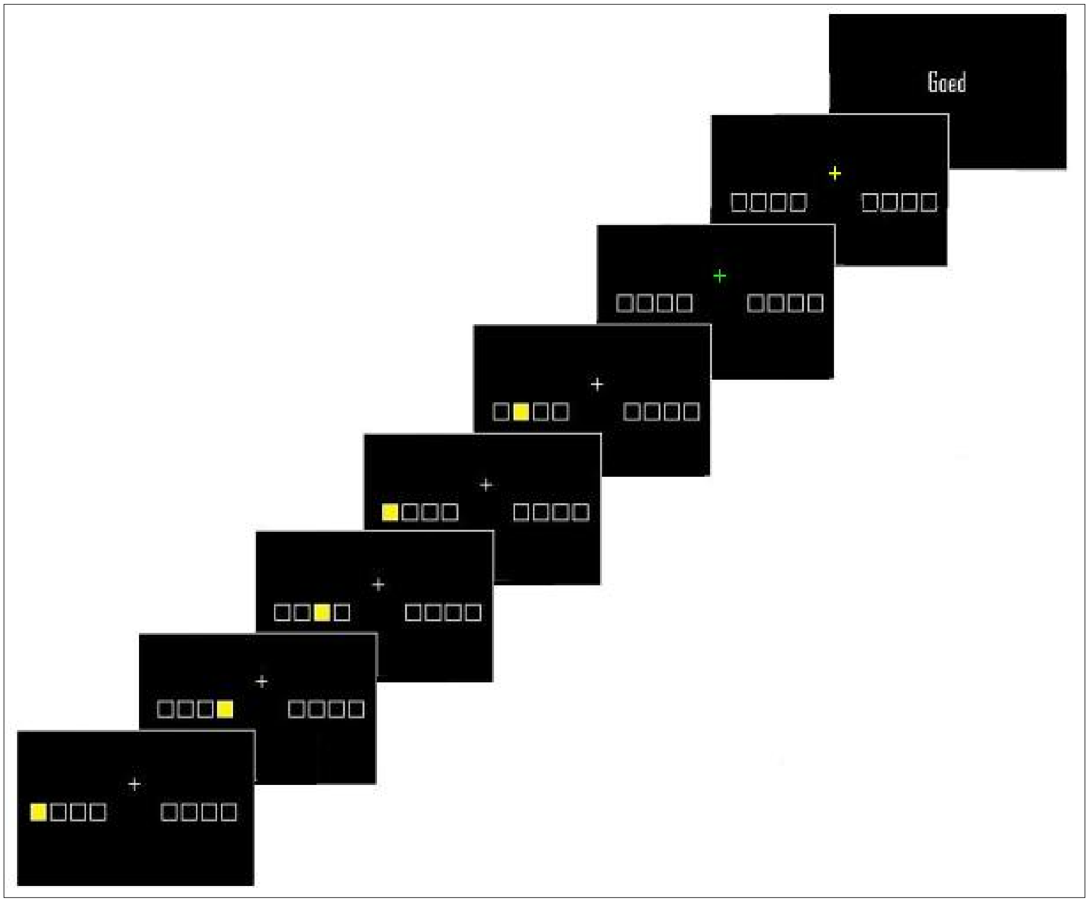

Figure 1. *An example of one sequence of the DSP task.*

The eight stimulus squares and the fixation cross were displayed in a gray line on a black background. This screen is the default setting in this task. All participants were instructed to use their little, ring, middle and index fingers of each hand and the keys: *a, s, d, f* for the left hand and the keys *j,k,l,;* of a standard English (QWERTY) keyboard for the right hand. The computer screen displayed the eight squares in the same spatial arrangement as the assigned key. The eight squares were divided in four squares each by a cross. The sequences appeared randomly for the left, as well as for the right hand on the computer screen. The task was designed with a total visual angle of 26.5°.

An event (stimulus) occurred when one of the squares turned yellow. A go stimulus was indicated by a green fixation cross, which indicated that the participants had to give their response by five keystrokes in the earlier seen order for the corresponding hand. Respectively, a no-go stimulus was indicated by a red fixation cross and required no action.

One trial can be considered as the time from offering the sequence of five flashing squares till the implementation of the response. This is equal to one sequence. During the test phase, the trials consisted of new, learned and mirrored sequences.

Participants were instructed to place their fingers on the corresponding keys and to hold their hands in this position during the whole task. Each sequence started with a foreperiod which had a duration of 1500 ms and was regarded as the interval between the warning signal and the presentation of the go/no-go stimulus to which the subject was expected to respond (Figure 2).

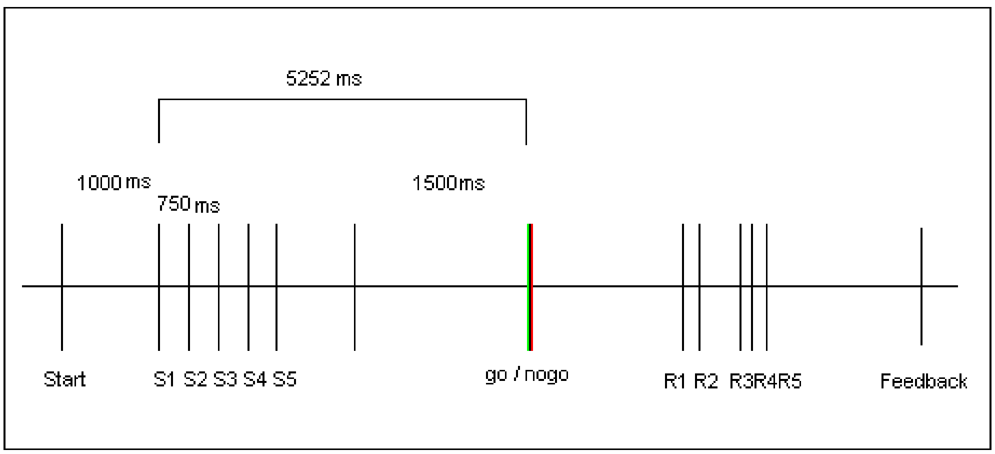

Figure 2. The *sequence of stimuli from the start of a trial until the go / no-go signal.*

After this, one square at a time filled yellow for 750 ms. In total, this took 3750 ms (5 x 750 ms). The default screen followed for 1500 ms. During this time, participants were instructed to fix on the fixation-cross in the middle of the screen. Next, the fixation cross was colored either green as a go stimulus (for 92% of the cases) or red (for 8% of the cases) as a no-go stimulus. The green fixation cross was displayed for 100 ms and the red one for 3000 ms. Every time the response of the participant was correct, the feedback “good” appeared on the screen for 1000 ms (all messages were written in Dutch). Pressing a wrong key resulted in an enumeration of wrong responses after the trial (e.g., “number 1 wrong”). Pressing a key during the no-go period was not allowed and the computer indicated this to the participant by displaying the message “wrong” for 5000 ms. When no key was pressed during the no-go signal, no feedback was displayed. The reaction time was defined as the time interval between the go signal and the first response of the participant. Participants were told to press the corresponding key to the target square as quickly and as accurately as possible after they saw the sequence and the go signal indicated by a green cross. While maintaining accuracy below 50 errors in each session, every student had to minimize the reaction time about 150 ms after the first session or to 200 ms. Feedback in terms of average reaction time and number of errors was presented on the screen after half of the block during a break of 20 ms and at the end of each block.

Procedure

Practice phase. The study was split up into two days. The students had different amounts of days between the practice and test phase but seven days at the most.

The major purpose of the practice phase was to give participants the possibility to accustom to the task and to learn the sequences. Having signed the informed accordance, the participant received a written instruction that was extended by oral explanation. Participants were told that they could obtain a comfortable posture. After the first three blocks of the practice day, the handedness questionnaire from Annet (1970) was presented to the participants. They had to complete five blocks during the practice phase and one more practice block in the beginning of the test phase. For this phase, two different versions were programmed within the experiment generator E-Prime 1.1 to counterbalance the five keystrokes over the four fingers. One sequence was executed with five keystrokes and four fingers (e.g., asfds, jlk;l). The sequences were evenly and randomly distributed over the left and right hand and over the fingers to eliminate finger-dependent effects. One block consisted of 96 sequences. In this practice phase participants had to learn 8 sequences over the five blocks.

Test phase. To remind of the instructions and the task, participants performed one further practice block on the second day. Accordingly, participants were prepared for the EEG measure and completed three test blocks. Participants had a pause of approximately 100 minutes between the last practice block and the first test block because of the implementation of the EEG equipment. After each block a break of approximately 10 minus was given. In these test blocks, the participant carried out three types of sequences:

already learned sequences in the practice phase, mirrored sequences from the trained hand to the untrained hand and new sequences. To get mirrored sequences, four sequences used in the trainings phase were mirrored at the first key (e.g., “fadsa” gets “j;kl;”). Four different versions, in which the five keystrokes per sequence were counterbalanced over the four fingers of each hand, were randomly counterbalanced among participants to eliminate finger-specific effects. During this phase, four already learned sequences were presented as well as four mirrored sequences, which were constructed from the remainder of the learned sequences during the practice phase. In addition, four new sequences were included. Participants had to learn twelve sequences in total. Having finished the test blocks, questionnaires were handed out to the participants, in which they were asked to recall and recognize the sequences that appeared during the test phase.

Data recording and processing

Electroencephalographic recordings. EEG signals were recoded from 61 ring electrodes on the scalp to the 10-20 system and were referenced online to the average of all electrodes. The resistance was kept below 5 kΩ. The level of impedance was checked after every session.

Electrooculographic recordings. The electrooculography (EOG) measures the resting potential for the retina and detects eye movement as well as winks. When the eye moves, one electrode detects the positive side of the retina and the other one the negative side, respectively. During the EOG measure a vertical and a horizontal bipolar ring electrode was placed above and below the left eye and at the outer regions of both eyes.

Data analysis

One participant did not follow the instructions and was removed from the analysis. Participants had correct keystrokes of 88% on average during the last block of the practice phase and 89% on average during the last block of the test phase. All sequences with at least one wrong keystroke were removed for the Reaction Time (RT) analysis. For the practice phase, 33.1% of the total sequences were removed and 26.5% of the sequences of the test phase. The first two trials of every block and sequences that were not carried out accurately because a wrong key was pressed were excluded from the reaction time analysis. The reaction time was measured from the go/no-go signal until the last keystroke. Average reaction time was calculated for remaining sequences per block, from the onset of the go signal and the five keystrokes. Furthermore, all blocks with a relative reaction time that deviated more than three standard deviations from the calculated mean were excluded. Therefore, 0.9% of the blocks were removed as outliers from the analysis for the practice and test phase, respectively. The correct keystrokes were calculated as percentages for the Percentage Correct (PC). For statistical analysis an alpha of .05 was adopted throughout. The between-subjects factor version did not reach the expected significance ($p > .50$) and was therefore excluded from further analysis. The Mauchly's test for sphericity tests whether the assumption that the pairs of treatments have an equal variance and thus, the level of dependence between pairs of groups is equal was hold. If the assumption of sphericity was not hold ($p < .05$) for independent variables, the appropriate correction was used to correct the degrees of freedom and enhance the probability of type 2 errors. If the estimate of sphericity (ε) was smaller than .75 then the Greenhouse-Geisser correction was used; for $\varepsilon > .75$ the Huynh-Feldt correction was adopted.

The EEG measurements of all eighteen participants were included in the EEG analysis. The EEG was referenced to an average reference calculated from all electrodes. The interval between the off-set of the last stimulus and the go/no-go signal was 1500 ms. Therefore, the data were segmented starting 1600 ms before the go/no-go signal until 600 ms after the go/no-go signal. Baseline was set -1600-1500 before the go/no-go signal during which the last stimulus was presented. Trials with artifacts (an amplitude difference larger than 100µV within 50 ms) and out of range values (values larger than +/- 250µV for pre-frontal electrodes, +/- 200 µV for frontal electrodes, +/- 150 µV for central electrodes and +/- 100 µV for parietal electrodes) were excluded from further analysis. The EEG was corrected for EOG artifacts. To correct eye-movement related contaminations the Gratton & Coles procedure was applied for vertical and horizontal EOG.

Results

Behavioral analysis

Practice phase. A hand (2) x block (6) x key (5) ANOVA on reaction time revealed no significant main effect of the hand, [$F(1, 11) = 38.3$, $p = .97$]. A block (5) x hand (2) x key (5) on percentage correct also showed no significant difference for the left (86%) and right hand (88%) with $F(1, 14) = 0.1$, $p = .81$. The six blocks differed significantly in RT, $F(5, 55) = 35.6$, $p < .001$, indicating a reduction in RT over the first five blocks. The comparison of the sixth block, which was carried out on the second day of the experiment, to the first block still showed a significant reduction in RT compared to the first block, $F(1, 11) = 41.1$, $p < .001$. Furthermore, significantly less errors over the blocks were made with practice, [88.4% correct vs. 67.1% and 88.3% vs. 63.2%] $F(5, 70) = 21.4$, $p < .001$ (Table 1).

Table 1. Reaction Times and Percentages Correct

	Hand	*Sequence*	*Practice phase (ms)*						*Test phase (ms)*		
			Block 1	*Block 2*	*Block 3*	*Block 4*	*Block 5*	*Block 6*	*Block 1*	*Block 2*	*Block 3*
RT	Left	Learned	426	337	306	288	278	302	310	294	280
		Mirrored							342	314	291
		New							361	326	312
	Right	Learned	412	342	310	290	277	308	315	287	272
		Mirrored							328	299	280
		New							348	308	295
PC	Left	Learned	67.1	79.6	85.8	86.4	87.8	88.4	89.5	89.1	90.2
		Mirrored							84.4	89.1	91.9
		New							76.7	81.8	82.7
	Right	Learned	63.2	78.4	84.2	88.1	88.9	88.3	89.8	92.8	90.3
		Mirrored							84.8	89.6	89.1
		New							81.3	85.7	90.1

Throughout the task, the RT and PC decreased as an effect of practice. There was a significant main effect in RT for key, $F(4, 44) = 9.8$, $p < .001$. Significant differences in RT were found for the hand x key, $F(4, 44) = 10.8$, $p < .001$ interaction. According to percentage correct, the block x key interaction was significant, as well; $F(20, 280)= 4.0$, $p < .05$. To summarize the results, participants became faster and made fewer errors over the blocks.

Test phase. A sequence (learned, mirrored, new) x hand (2) x block (3) x key (5) ANOVA on reaction time confirmed the expected significant differences in RT between the three sequences: trained, mirrored and new, $F(2, 34) = 12.0$, $p < .001$ (Figure 3)

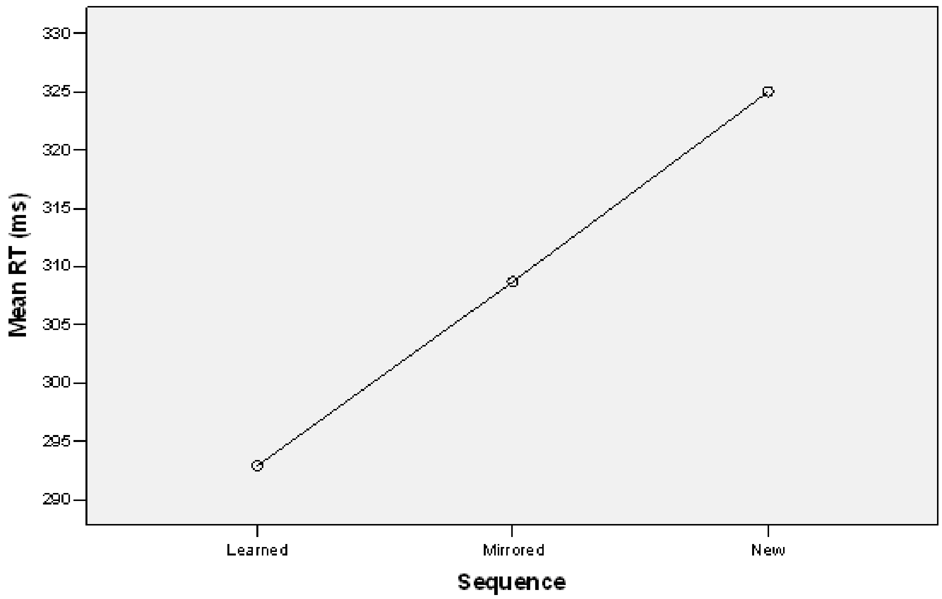

Figure 3. *Mean reaction time per sequence. From left to right: familiar sequences, mirrored and unfamiliar sequences.*

Participants had an average RT of 299 ms for the learned, 309 ms for the mirrored and the longest RT for the new sequences (325 ms) over all blocks. Post Hoc tests indicated significant differences in RT between the learned and new sequences ($p < .001$) and between the mirrored and new sequences ($p < .05$). According to a post hoc test, there was no significant difference in RT between the learned and mirrored sequences ($p = .14$). A block (3) x sequence (learned, mirrored, new) x hand (2) x key (5) ANOVA on percentage correct confirmed significant differences between the three sequences, $F(2, 32) = 7.8$, $p < .05$. Post-hoc tests revealed that the learned sequences differed significantly from the new one in terms of RT ($p < .001$). Also, the mirrored sequences were significantly faster executed than the new ones ($p < .05$). The familiar sequences were executed with an average PC of 90.3; 88.2% of the mirrored sequences and 83% of the unfamiliar sequences were executed correctly. Hence, more errors were made with the unfamiliar sequences compared to the mirrored and familiar one. The analysis revealed neither significant differences in reaction time [$F(1, 17) = 3.4$, $p = .08$] nor PC between the left (86.2) and right (88.2) hand [$F(1, 16) = 2.2$, $p = .18$] in this phase. All participants were right-handed and more trained to use their right hands. Furthermore, there was a significant decrease in RT over the blocks, $F(2, 34) = 38.7$, $p < .001$, and an increase in percentage correct (84.4, 88, 89). This is an indication that the participants still learned the sequences during the practice phase. Reaction time decreased over the three blocks from primarily 334 ms down to 288 ms. There was a significant main effect for key, $F(4, 68) = 7.8$, $p < .001$, whereupon the second finger with an average RT of 297 ms was executed significantly faster ($p < .02$) than the third one with an average RT of 336 ms as the post-hoc test showed. This result indicates a chunking of the sequence in two parts (Verwey, 2001). The significant interaction between the three sequences and the three blocks, $F(4, 68) = 3.1$, $p < .05$, can be explained by the fact that the RT decreases with the blocks per sequence because of practice. In addition, there is an interaction between hand and key, $F(4, 68) = 3.0$, $p < .05$. Furthermore, analyses of behavioral effects educed a three-way interaction between sequence x hand x key, $F(8, 136) = 11.3$, $p < .001$ that is of no further interest here. Participants reacted faster to familiar and mirrored sequences than to unfamiliar ones and with fewer errors regardless of which hand was used. These findings are completely in line with the experimental predictions.

Questionnaire

In general, participants were able to recall down 2-3 sequences correctly (s.d. = 1.7). The participants were moderately able to recognize the sequences with an average correct recognition of 5-6 sequences (s.d. = 2.7) of 12 sequences in total. The variance (7.5) for the first and second (3.9) questionnaire indicated large individual differences in the ability to recall and recognize the sequences. The third questionnaire examined the used strategy by the participants to recall and recognize the sequences. One-third of the participants combined a motor strategy with an abstract one where they ticked the sequences on the board and in memory.

EEG analyses

The CNV at electrode Cz that lies on the central-midline site, is displayed in figure 4 for -1200 ms until go/no-go signal. Figure 4 shows the CNV amplitudes for the three different sequences: learned, mirrored, new in µV.

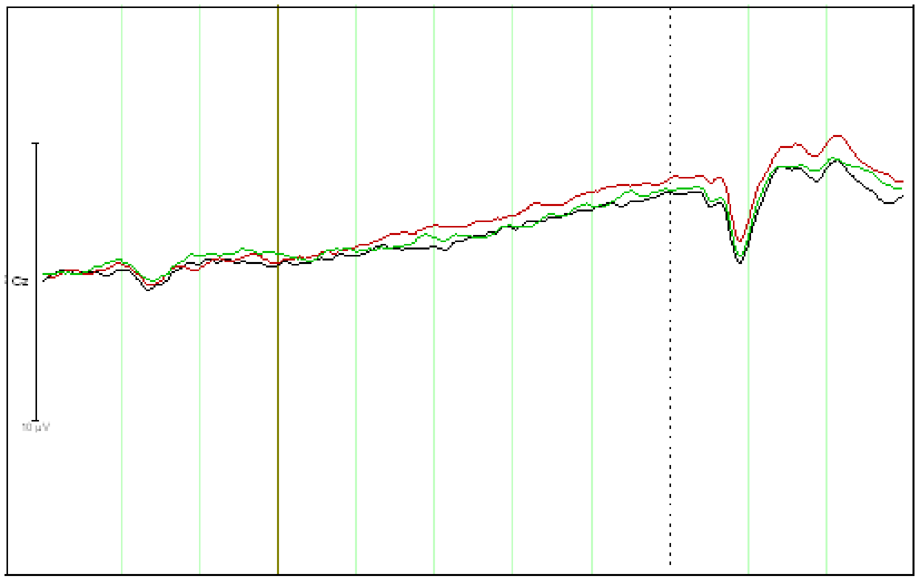

Figure 4. CNV at Cz from -1200 till 0 (go / no-go: interrupted line). Average amplitude for learned sequences (black), mirrored (green) sequences and new sequences (red).

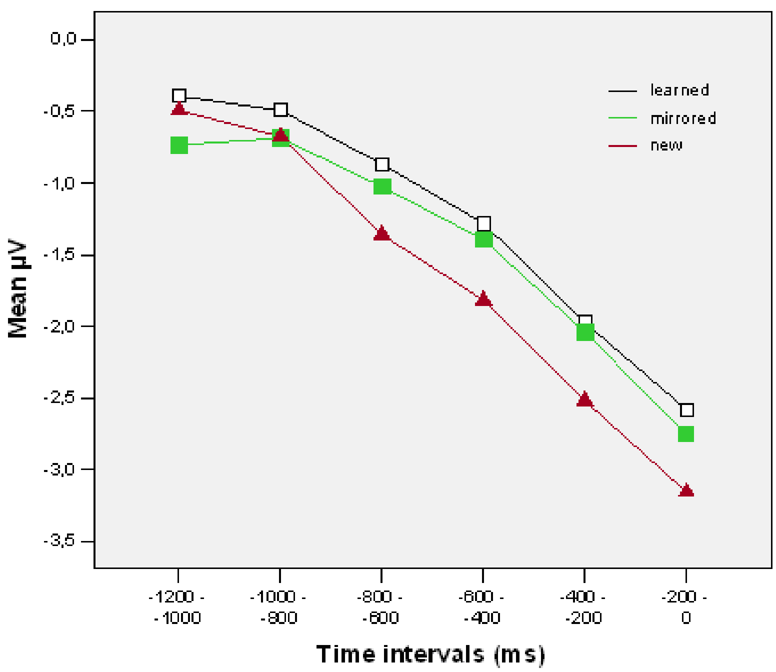

Figure 5. *Mean µV over the six time intervals for the sequences: learned, mirrored, new*

For the statistically generated figure 5 and further analysis, six time intervals before the go/no-go signal were examined: -1200 – -1000 ms, -1000 – -800 ms, -800 – -600 ms, -600 – -400 ms, -400 – -200 ms and -200 – 0 ms. As indicated by Figure 4, differences in the negativity for the three sequences: learned, mirrored and new are observable. The largest differences in the CNV are between the unfamiliar sequences compared to the mirrored and familiar sequences on the central electrode. However, statistical tests do not confirm this. There was no main effect of sequence found, $F(2, 34) = 1.1$, $p = .34$. A sequence (learned, mirrored, new) x time (6) ANOVA indicated the expected interaction of sequence x time, $F(10, 170) = 2.8$, $p < 0.05$. Analyses of within-subjects contrasts showed a significant difference between mirrored and new sequences between -800 ms - -600 ms and -1000 ms - -800 ms; $F(1, 17) = 4.6$, $p < 0.05$. Analyses revealed that negativity increased over time. Hence, the amplitude increased from -2.83 µV to -0.54 µV. between -200-0 ms and -1200 - -1000 ms after the no-go signal. Table 2 shows an overview of multiple one-way ANOVAs per time interval. It lists the average µV magnitude of the amplitude per time interval and sequence.

Table 2. Amplitude Means in µV of CNV from Cz Over Time Intervals

Sequence	*Time (ms)*					
	-200 – - 0	-400 – -200	-600 – -400	-800 – -600	-1000 – -800	-1200 – -1000
Learned	-2,58	-1,97	-1,28	-0,87	-0,49	-0,4
Mirrored	-2,75	-2,04	-1,4	-1,03	-0,69	-0,73
New	-3,16	-2,52	-1,82	-1,36	-0,68	-0,49

To summarize the results, a slight difference in tendency of sequences the three sequences were visible on the CNV at the central-midline located Cz electrode. The unfamiliar sequences have a more negative tendency than the familiar and mirrored sequences.

Discussion

The major impetus for starting the research described in this article was interest in the processes underlying the ability to transfer a learned motor skill to the other hand. An earlier study by De Kleine and Van der Lubbe (in prep.) at the University of Twente showed that pre-motor stages are presented during preparation of unfamiliar sequences and less for familiar sequences. Furthermore, it was concluded that sequence preparation developed from an attentive to an automatic phase. Goal was to replicate earlier findings of De Kleine and Van der Lubbe in terms of the underlying abstract motor processing levels of familiar and unfamiliar sequences and to investigate the underlying processing levels of mirrored sequences, as well. To study whether movement preparation differed between familiar, mirrored and unfamiliar sequences a go/no-go DSP task, in which participants had to accomplish sequences of five keystrokes to achieve sequence learning, was used. Behavioral analysis of the reaction times and correct percentages were used as well as an EEG-analysis at the Cz electrode, to examine the underlying processes.

Sequence learning was reflected in a decrease in RT and PC for all sequences. The results show a bigger decrease in RT and PC for familiar sequences and mirrored sequences compared to unfamiliar sequences. These findings correspond with the results of De Kleine and Van der Lubbe (in prep.).

Fewer errors were made and there was a significant benefit in reaction time for mirrored sequences compared to the new sequences, indicating that learned representations of the familiar sequences were transferred to the mirrored sequences as assumed by Verwey and Clegg (2005).

Electroencephalogram (EEG) measures were derived with the aid of the contingent negative variation (CNV) as a general index of cortical motor preparation, which corresponds to the cognitive component of the model compiled by Verwey (1999). It was hypothesized on the basis of earlier results by De Kleine and Van der Lubbe (in prep.) that the CNV would be less pronounced for the learned and mirrored sequences. The present data of the CNV on the Cz electrode show a tendency for the increase in negativity over the time. There are slight indications for the expected results, that the unfamiliar sequences are prepared less on an abstract processing level. Results of this study agree with those of De Kleine and Van der Lubbe in terms of the tendency of the CNV, which is more negative for new sequences. Follow up analyses of other electrodes and indexes, as the Laterized Readiness Potential (LRP) for effector specific motor preparation, should give further insight. To compare topographic changes, amplitudes should be determined at the same time at the frontoparietal midline, for example by averaging EEGs of the Fz, FCz, Cz, Cpz and Pz for all trials. The LRP should be examined in further research to show, if there is a motor processing level reflected during preparation of learned, mirrored and new sequences. Hikosaka et al. (1999) set up a second model about the underlying processing levels. They hold that a spatial component acts during the initial stage on the sequence learning and a motor component occurs at a later, more automatic stage of learning sequences. It is suggested, that the spatial component is more pronounced during execution of unfamiliar sequences. In contrast to the model presented by Verwey (2001), Hikosaka et al.(1999) claim that the motor component is more pronounced during familiar sequences. An analysis of the posterior contralateral negativity (PCN) analysis, as an index of spatial attention, should give more insight in whether the sequence preparation develops from an attentive to an automatic phase. Yet, the results do not validate the model proposed by Verwey (2001), because the results do not show in sufficient degree, if there are differences between in sequences in reference to a central processing level and motor processing level. Further research should investigate whether transfer to mirrored sequences is based on familiar hand postures and thus on motor representations.

The present study indicates the tendency that unfamiliar sequences require a central motor processing level. This suggests that with practice, the central motor processing level is no longer needed and even less for mirrored sequences. The results do not make clear if there is a motor processing level for the learned, mirrored and new sequences. Further studies should investigate further indexes of the EEG to find further processing levels.

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Samenvatting

Vele complexe bewegingen kunnen wij zonder grote mentale inspanning uitvoeren, omdat wij bewegingen automatiseren en onbewust kunnen uitvoeren. Wij zijn zelf in staat om gespiegelde bewegingen, bijvoorbeeld met de andere hand zonder veel meer mentale inspanning uit te voeren.

De huidige studie is een replicatie van het onderzoek van De Kleine en Van der Lubbe (in preparation). De Kleine en Van der Lubbe hebben onderzocht of de abstract versus motor specifiek leren al zichtbaar zijn tijdens de preparatie van de geleerde en nieuwe sequenties. Bovendien wordt het onderzoek uitgebreid door de preparatie van gespiegelde sequenties te onderzoeken.

De huidige studie gebruikt evenals in het eerdere onderzoek een go/no-go versie van de *Discrete Sequence Production* (DSP) taak (Verwey, 1999). De proefpersonen moeten vijf toetsen op een toetsenbord indrukken, nadat zij de sequentie gezien hebben. In tegenstelling tot de *Serial Reaction Time* (SRT) taak (Nissen & Bullemer, 1989) wordt de sequentie in zijn geheel gepresenteerd. Het begin en het eind van de sequentie zijn dus duidelijk gedefinieerd. In de testfase van de taak wordt onderscheid gemaakt tussen geleerde, gespiegelde en nieuwe sequenties. Om de onderliggende processen tijdens de preparatie, wordt de preparatie van een handbeweging met behulp van elektro-encefalografie (EEG) metingen onderzocht. Hiervoor werd de *Contingent Negativity Variation* (CNV), een *general motor index*, gebruikt om na te gaan of er preparatie op een abstract niveau plaatsvindt. Verwey (2001) beschrijft in zijn model een cognitieve component die voor nieuwe sequenties zichtbaar is en een motorische component die voor geleerde en nieuwe sequenties gelijk is, omdat de uitvoer van de sequenties door het oefenen niet verschilt. Dit model van Verwey (2001) werd door De Kleine en Van der Lubbe (in prep.) bevestigd. Het werd de preparatie op een abstract niveau voor nieuwe sequenties gevonden en een motorische component voor geleerde en nieuwe sequenties. Zoals De Kleine en Van der Lubbe (in prep.) al gevonden hebben, laat het interactie-effect tussen sequentie (geleerd, gespiegeld, nieuw) x tijd voor de CNV in de huidige studie zien, dat de preparatie van nieuwe sequenties in tegenstelling tot geleerde sequenties gepaard gaat met meer aandacht en op een abstract niveau voorbereid wordt. Een kleinere tendens van de CNV voor gespiegelde en geleerde sequenties laat zien, dat de voorbereiding van

deze twee sequenties, zoals verwacht, niet op een abstract motorisch niveau plaatsvindt. Verdere statistische analysen van andere EEG indexen zouden deze resultaten nog kunnen bevestigen. Het huidige onderzoek liet zien, zoals door Verwey en Clegg (2005) beweerd, dat een transfer van de geleerde sequenties naar de andere hand plaatsgevonden heeft. Dit is aangetoond door een verminderde reactietijd voor de gespiegelde sequenties, vergeleken met de nieuwe sequenties.

Verder onderzoek zou na gaan of de *Lateralized Readiness Potential* (LRP), een *effector specific motor index*, zoals bij De Kleine en Van der Lubbe (in prep.) voor de geleerde en nieuwe sequenties gelijk is. Is dit het geval, dan is het model van Verwey (2001) bevestigd dat stelt, dat nieuwe en motorische sequenties niet in de motorische component verschillen. Verder zal deze analyse meer inzicht kunnen geven in de preparatie van gespiegelde sequenties.