

Running Head: EFFECTS OF EXPERIENCE AND LEARNING IN A MELODIC
REPRODUCTION TASK.

**The effects of experience and learning on perception and response preparation in a
melodic reproduction task.**

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Abstract

The current study used a melodic reproduction task to investigate underlying processes that separate musicians from non-musicians in the ability to play by ear. It was hypothesized that musicians are better able to extract movement related information from the notes in target melodies. It was predicted that this process would be reflected by the auditory evoked potential (AEP) and in the preparation of upcoming responses, measured by the contingent negative variation (CNV). It was found that musicians out-performed non-musicians in playing by ear and that overall learning was reflected by different processing of target melodies. Evidence for upcoming response preparation was not found which seems to disconfirm the original hypothesis. Instead, it is suggested that musicians are better in the encoding of melodies into working memory.

The effects of experience and learning on perception and response preparation in a melodic reproduction task.

One of the most striking abilities of trained musicians is the ability to reproduce melodies or pieces of music by 'ear'. With accumulated practice on an instrument comes the ability to reproduce a piece of music or a melody after a single hearing. The aim of this study is to investigate what cognitive abilities sets musicians apart from non-musicians in reproducing melodies by ear. To answer this question the current paper focuses on the effects of experience and learning on auditory perception and preparation of upcoming responses.

There is evidence to support the idea that as a result of training, the brains of musicians change. In a study by Schneider, Scherg, Gutschalk, & Rupp (2002) it was found that the grey matter concentration of the Heschl's gyrus could be correlated to musical aptitude. In a study by Gaser & Schlaug (2003) an increased volume of the auditory cortex and an increased amount of grey matter in the motor cortex was found in musicians compared to non-musicians. Evidence that these differences are caused by extensive practice on a musical instrument and not by innate predispositions present from birth come from an earlier study by Elbert, Pantev, Wienbruch, Rockstroh, & Taub (1995). In this study it was found that expert violin players showed larger cortical representations of the digits of the fingers of the left hand. Size of the cortical representation was found to be correlated to the age one started their musical training. Another study (Schlaug, Jancke, Huang, Staiger, & Steinmetz, 1995) found the size of the corpus callosum to be increased in musicians. This increase in size was also related to the onset of musical training.

Musical ability may not only be reflected by auditory and motor systems becoming more specialized by themselves, but also by a stronger coupling between these systems. Neuroimaging studies using fMRI (Baumann, Koeneke, Meyer, Lutz, & Jäncke, 1995; Bangert et al., 2006) scanned trained pianist while either hearing a well known piece without making any movements or while playing the same piece without any auditory feedback. They found that in both conditions auditory and motor regions became activated. This finding is in line with earlier results found by a MEG study (Haucheisen, & Knösche, 2001) where professional pianists showed activation of the primary motor cortex when they listened to a familiar piece of music. This pairing of auditory and motor systems is

not only restricted to highly trained musicians but has also been discovered for non-musicians learning in a musical context. In a study by Lahav, Saltzman, & Schlaug (2007) non-musicians were taught to learn a simple melody on a keyboard. On hearing the learned melody, in addition to activation of the auditory cortex, they showed activation of pre-motor areas. Activity in the pre-motor and supplementary motor area has also been found in studies in which musicians and non-musicians had to imagine music (Zatorre & Halpern, 2005), and in studies in which musicians imagined musical performance (Meister et al., 2004).

In light of the above it was reasoned that ability to play by ear is mediated by differences in auditory and motor processing and that experience and learning will affect them both. Considering the evidence that both auditory and motor systems are tied together in music performance (Zatorre, Chen, & Penhune, 2007), it was reasoned that ability to reproduce a melody on a musical instrument relies on making transformations from the auditory to the motor domain. Therefore to determine what underlying processes set musicians apart from non-musicians it was considered necessary to develop a task that allows investigation of both perceptual and motor related processes.

To study perception and preparation of upcoming movements these processes have to be set apart from the motoric processes related with making actual movements. The study of movement preparation has most commonly used response pre-cueing tasks (Leuthold, Sommer, & Ulrich, 2004; Rosenbaum, 1980). In such a pre-cueing task, a visual, tactile or auditory stimulus presents complete or partial information about an upcoming response. The response is made after the presentation of a Go or no-Go signal. Advance information about a response can be used for response preparation. The more informative a pre-cue is, the better the preparation of an upcoming movement, which results in a decrease in reaction time after the go (Leuthold, & Jentzsch, 2002).

The learning of movement sequences has been studied using the discrete sequence production (DSP) task (for a review see: Rhodes, Bullock, Verwey, Averbach, Page, 2004). In a DSP task, sequences of button presses are practiced by responding to key-specific stimuli. Presentation of these stimuli happens, with exclusion of the first key, after each response. After sufficient trials participants learn to recognize certain sequences by the first couple of stimuli and finish reproduction without further need for the other stimuli.

In the modified task, dubbed a melodic reproduction task, elements of the pre-cueing and the DSP task are combined. The pre-cues used are auditory presentations of tones in a musical scale. A presentation of five note sequences is separated from reproduction by a preparation period and a Go signal. By using cues with a musical organisation, it is reasoned that this task taps the ability of a participant to play by 'ear'. By separating sequence presentation and sequence execution by a preparation period it is possible to study perception and preparation of upcoming movements separate from movement execution. By dividing the experiment into a number of separate blocks it is reasoned that task-specific learning can be assessed. To assess short term melody-specific learning each block of the experiment is comprised of two different sets of melodies. One set is the same for every block, allowing participants to become familiar with these melodies. The other set consists of melodies which are replaced by novel ones in each block.

Concerning the performance on this task a number of predictions were made. First, if learning influences performance it is predicted that both groups will show task-specific and melody-specific learning. Task-specific learning will be reflected by an increase in overall task performance in each consecutive block. Melody-specific learning will be reflected by a greater increase in performance for familiar compared to novel melodies. Second, if experience influences performance it is expected that musicians will generally out-perform non-musicians on this task. Additionally, it is predicted that the effects of task-specific learning and melody-specific learning are larger for musicians compared to non-musicians.

Using measures derived from electroencephalography (EEG) it is possible to investigate, early sensory processing and working memory during the presentation of target melodies. To investigate the perceptual processing of the presented tones, the auditory event related potential (AEP) is used. The AEP is a series of positive and negative peaks occurring at the vertex after the presentation of an auditory stimulus. Most predominant within the AEP is the negative N1, occurring approximately 100ms after stimulus presentation, and the positive P2, occurring approximately 200ms after stimulus presentation. Often these two peaks are studied together and referred to as the N1-P2 complex. The N1 component of the AEP has been considered as an index of early sensory memory (Näätänen, & Picton, 1987) and is sensitive to differences between tone frequencies and stimulus repetition

(Näätänen et al., 1988). A study Baumann, Martin Meyer, Lutz & Jäncke(2008) using a pitch discrimination task found the N1 to be larger for musicians than for non musicians. In contrast to this effect of experience on the N1 other studies failed to find an effect of learning (Atienza, Cantero, & Dominguez-Marin, 2002). The P2 component is related to the processing of certain task-specific sound features as it is influenced by training in acoustic discrimination in non-musicians (Tremblay, Kraus, McGee, Ponton, & Otis, 2002; Atienza et al. 2002). Training non-musician subjects in frequency discrimination also results in an enhancement of the P2 (Bosnyak, Eaton, Roberts, 2004). In musicians the P2 is sensitive to the spectral complexity of musical tones, as it is found to be larger for tones containing more harmonics (Shahin, Roberts, Pantev, Trainor, & Ross, 2005). In a study by Shahin, Bosnyak, Trainor, & Roberts, (2003) highly trained violinist listened to pure, violin and piano tones and showed a larger P2 in comparison to non-musicians. The P2 component was largest for violin tones. In addition this study found the same effects for a right temporally occurring N1c, but not for the N1. The above findings suggest that the AEP is sensitive to remodeling by experience and learning. It was predicted that musicians would show larger N1 and P2 components in response to the tones of the target melody. In addition it was expected that effects of task-specific learning would manifest themselves at the P2 component.

To assess preparation of upcoming responses the contingent negative variation (CNV) is used. The CNV is a slow negative shift in the EEG occurring over the vertex in the time course between stimulus presentation and stimulus execution (Verleger, Vollmer, Wauschkuhn, Van der Lubbe, & Wascher, 2000; Leuthold et al., 2004). Interpretation of the CNV varies from stimulus-response binding (Verlger et al., 2000) to contribution of non-motoric processes like anticipation and visuo-spatial working memory (Ruchkin, Johnson, Grafman, Caoune, & Ritter, 1996). The CNV is also thought to reflect the level of pre-programming of upcoming responses. This has been demonstrated in a study by Cui et al. (2000) in which an increased CNV for more complex movements as compared to more simple movements was found. Additionally, studies by Jentsch, Leuthold, & Ridderinkhof (2004) and Wild-Wall, Sangals, Sommer, & Leuthold (2003) revealed that with more advance information before an upcoming movement the amplitude of the late CNV increases.

It is hypothesized that better perceptual processing is what sets musicians apart from non-musicians in reproducing melodies. It is reasoned that musicians will be able to extract more relevant information from the target melody to use for response preparation. Therefore it is predicted that the CNV will be larger for musicians compared to non-musicians. Furthermore, it is hypothesized that superior processing capabilities in musicians rely on the ability to discriminate between pitch, encoding of information into working memory and the ability to make auditory-motor transformations. It is predicted that with respect to pitch discrimination and extraction of task-relevant information N1 and P2 components of the AEP will be larger in musicians compared to non-musicians. In addition it is predicted that amplitudes and latencies of the P2 component is sensitive to learning effects in both musicians and non-musicians.

Methods

Participants

A group of fourteen musicians (10 male, 4 female) mean age 21.3 years ($SD=2.5$) were recruited from the city's university and conservatory student population. All musicians started playing an instrument before their thirteenth birthday, $M=7.6$ years, $SD=2.1$ years, and had on average 13.3 ($SD=3.3$) years of combined musical experience. Thirteen of the musicians played more than one instrument. All musicians had experience playing the piano. A group of fourteen non-musicians (4 male, 10 female) mean age 21.2 years ($SD=1.2$) were recruited from the university population. This group had on average 0.7 years of experience ($SD=0.9$) with a musical instrument.

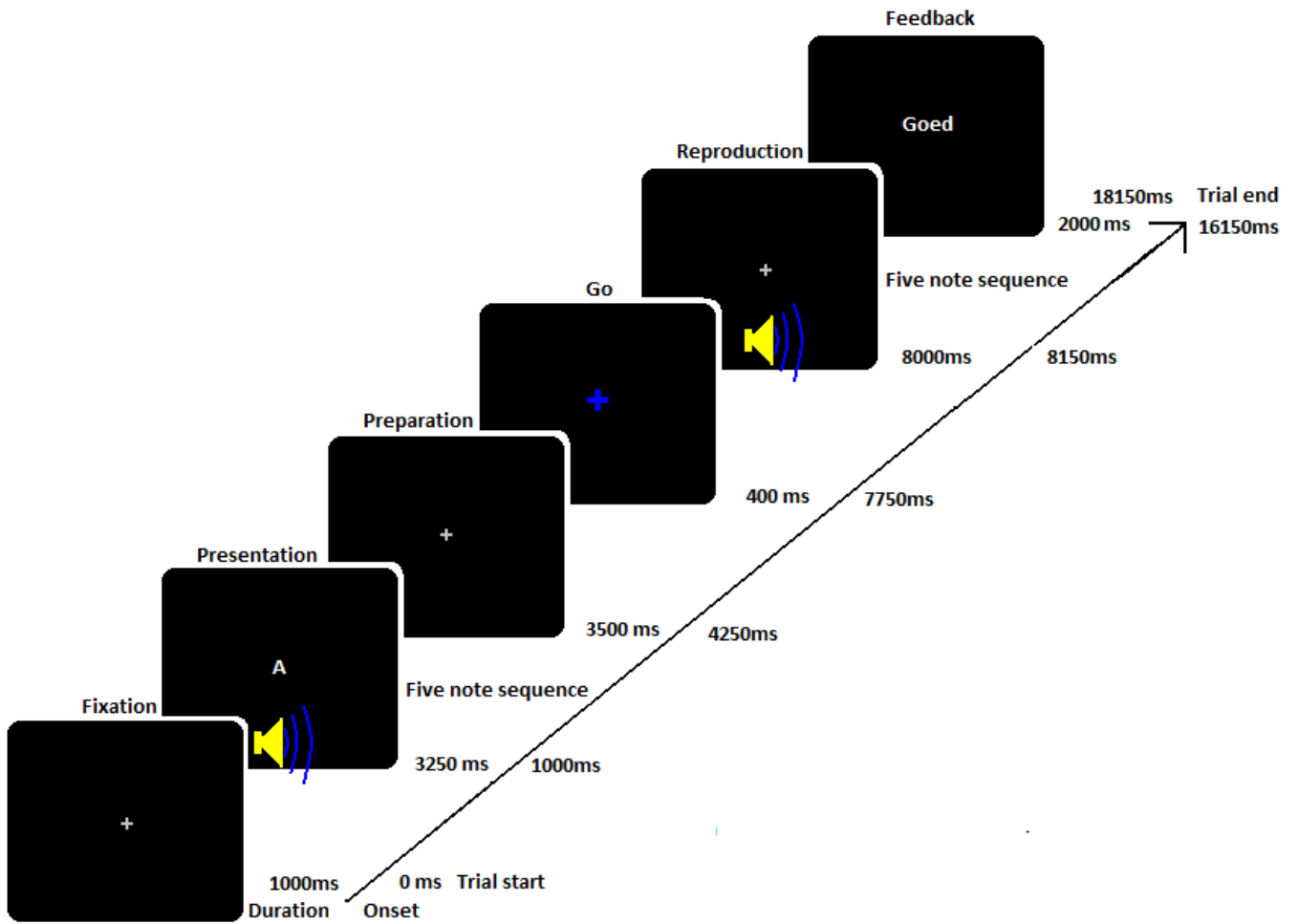
Prior to the start of the experiment participants answered a questionnaire, asking them about several aspects of their musical experience and music consumption. Participants were also submitted to a short verbal test to measure working memory capacity (Fawcett, Nichols, 2005). Both groups had a mean handedness score of 20 ($SD=7$), measured with the Annett Handedness inventory (Annett, 197) signifying that all subjects could be considered right handed. Groups showed no significant difference in age and handedness. Self reported daily consumption of music, obtained through the questionnaire, did not differ significantly between groups. A significant difference between groups on the raw scores of the test for working memory was found $F(1, 26)=4.2$, $p<0.05$. The average for musicians was 7.5 ($SD=1.2$) and for the non-musicians 6.6 ($SD=1.2$).

All participants gave their written informed consent and reported normal or corrected-to-normal vision, normal hearing and an absence of neurological disorders. 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. Participants from inside the faculty were recruited from the faculty's pool for test-subjects. Participants recruited from outside the faculty received €24,- for participation.

Task and Stimuli

Participants placed the little, ring, index and middle finger of the left hand on the a, s, d, f keys of the keyboard and the index, middle, ring and little finger of their right hand on the j, k, l, ; keys of a computer keyboard. Participants were instructed to keep their eyes on a fixation cross (1.5°) in the centre of the screen. Target melodies were presented through a pair of Apple earplugs and kept at a fixed volume level throughout the experiment. Each trial, see Figure 1, consisted of the presentation of a melody, a preparation period and a reproduction period. During presentation participants heard a five note sequence in which each note had the same duration. At the same time in the middle of the screen the letter of the key corresponding to the first note of the sequence was presented. This was done to give participants an explicit motor reference as a starting point from which to complete the whole sequence. Each letter was mapped to a corresponding note. The a, s, d, f, j, k, l, ; keys were mapped to G3, A3, B3, C4, D4, E4, Fis4, G4 notes respectively. This created a mapping analogous to that of a piano in which keys on the left correspond with low pitches and those on the right correspond with high pitches. After presentation a fixation cross was presented for duration of 3500ms in the middle of the screen. Participants were instructed to begin target reproduction after presentation of a 'go', represented by a blue cross (2.0°) appearing in the middle of the screen. Any responses made before the 'go' did not produce auditory feedback and resulted in a warning displayed on the screen. During the response period participants were required to make five key presses for a trial to come to an end; irrespective whether these presses were right or wrong. At the end of each trial participants received feedback about their performance, indicating if reproduction was right or wrong. If one of the reproduced notes was wrong reproduction as a whole was considered erroneous.

Figure 1, Trial time course. Reproduction of the target melody was finished when five key presses were obtained. Only during reproduction did key presses result in immediate auditory feedback. Pressing keys during other events did not generate auditory feedback.



Melodies used were five notes in length, and were constricted to a four note range. To this end the eight note G major scale was divided into a four note range for each hand (G3, A3, B3, C4 for the left hand and D4, E4, Fis4, G4 for right hand). Each note was formed by combining three pure sine waves: One for the pitch of the note itself, one an octave above and another for an octave below this pitch. The sine waves of the added octaves had half the amplitude of the sine wave of the original pitch. All audio was high pass filtered at 62 Hz 48dB/oct and low pass filtered at 984 Hz 48dB/oct. Individual notes were 500ms in length and note amplitude was familiar over the course of note duration. This resulted in auditory stimuli that had an immediate onset and offset.

The complete experiment consisted of five blocks. During the experiment, participants were presented with a set of melodies that would be repeated for each of the five blocks, and with sets of melodies that would only be repeated within a specific block. This created the experimental conditions; familiar and novel. To control for possible confounding effects of specific sets of melodies six different sets of eight melodies each were created. Using a Latin square, sets of melodies were assigned to different conditions for each participant. To ensure that sets of melodies were compatible on a stimulus and on a motor level all notes, and therefore all fingers, were used the same amount of time for each set. This was achieved by using two underlying templates for each group. By offsetting these templates to the different fingers, all eight sequences were created (See Appendix A for details) Differences between the used templates were maximized to ensure that possible learning effects for one set would not easily transfer to another set. As a result of these procedures each finger was used once as the starting point of a melody within each set and each of the eight possible notes was used 30 times within each set.

The resulting creation of the 48, 24 for each hand, distinct five note sequences was further constricted by the following rules aimed at creating sequences that were comparable in difficulty: First, no direct repetition of a previous note, second, all possible notes within the range were used in one sequence, third, all notes were used an equal amount of times as the first note of a melody.

Procedure

In order for participants to familiarize themselves with the task, participants practiced two trials where they reproduce an ascending eight note scale (Gmajor) and 24 trials with two note sequences,

exhausting all possible combinations without repetition of the same note. The test phase consisted of a total of 5 blocks of 96 trials each. After each block participants were allowed five minutes of rest.

Each participant was assigned a familiar set of eight (4 for the left and 4 for the right hand) sequences presented six times within each block, totaling 48 trials. For the 48 trials that remained in each block, a set of eight novel sequences (4 for the left hand and 4 for the right hand) were presented six times. Within a block novel and repeated sequences were presented intermixed. Assignment of novel and repeating sequences was counterbalanced across subjects.

Recording and data processing

The experiment was run on a personal computer (Pentium 4) with a QWERTY keyboard. Auditory stimuli were presented using a set of Apple stereo earplugs, set to a fixed volume level. Stimulus presentation, response registration and production of external triggers were controlled by E-Prime, version 1.1 (for a list of markers recorded alongside EEG data see Appendix B). A 17 inch monitor, refresh rate of 75 Hz, was placed in front of the participants at a distance of about ± 70 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 64 active Ag/AgCl electrodes (ActiCap) located at standard electrode positions of the extended 10/20 system. Using passive Ag/AgCl ring electrodes EOG was recorded bipolarly, both vertically from above and below the left eye and horizontally from outer canthi of both eyes. Electrode impedance was kept below 20 k Ω during the experiment. To filter out interference from electronic devices and head movements the active shield sub-mode of the ActiCap system was used for all participants. The EEG and EOG data were sampled at a rate of 1000 Hz. Measured activity was digitally filtered online (low-pass 140Hz, DC and notch 50Hz) and on-line referenced by means of an electrode placed at the left mastoid.

Data analysis

For a detailed description of EEG analysis see Appendix C. Before segmentation all data was referenced to the mean of all electrodes. Because of their susceptibility to drift and muscle artifacts FT9, FT10, PO9, PO10 were not included in determination of the common reference. Trials were segmented into intervals that lasted from -100ms to 8000ms on the basis of trial markers (indicating

the current block and condition). Trials in which participants responded before the GO signal were excluded from further analysis.

On the basis of trial markers the presentation interval was separated into segments containing the first note and segments containing the last four notes. The part of the presentation interval containing the last four notes was on the basis of individual note markers further segmented into -100 to 500ms intervals. The baselines for these segments were set at -100 to 0ms.

For analysis of the preparation interval segments were created, lasting from -1600 to 100ms, on the basis of the marker for the Go signal. A baseline for the analysis was set at 1600 to 1500ms before the marker for the Go signal. Setting a baseline earlier, 100ms before trial onset, proved to be impractical due to baseline drift on EOG electrodes which, after artifact removal, left too few (<70% trials) trials for further analysis

For all participants PO4 electrode position had to be replaced with the average of surrounding channels. For two participants, due to excessive high frequency artifacts, the T8 channel had to be replaced with the average of surrounding channels. For one participant, the AF4 channel had to be replaced with the average of surrounding channels. The hEOG channel was first filtered with a high-cut-off filter at 12 Hz with a 24db/oct slope before marking trials with horizontal eye movements using a level trigger(-80 negative and 80 positive threshold). Channels with artifacts (an amplitude difference larger than 100 μ V within 50ms) and out of range values (values larger than +/- 200 μ V for frontal electrodes, +/- 150 μ V for central electrodes, and +/- 100 μ V for parietal and occipital electrodes) were excluded from further analyses. Next, trials with horizontal eye movements were excluded from further analysis and the EEG data was corrected for vEOG artifacts using Ocular Correction (Gratton, Coles & Donchin, 1983). For three participants EEG could not be corrected using this method therefore trials containing vEOG artifacts were excluded from further analysis using a level trigger(-100 negative and 100 positive threshold). After ocular correction baselines were reset. For calculating the averages single channel mode was used. This procedure left between 70% and 90% of all the trials for each participant.

Response parameters

For the calculation of the percentage correct (PC), instead of the amount of correct reproductions of whole melodies, individual responses were used. This allowed the determination of the PC of each position within a melody. Furthermore correct responses were used up until the first incorrect response during melody reproduction. This was done because the direct auditory feedback caused a substantial number of participants to correct their mistakes directly after making them. In spite of instructions a number of participants were unable to suppress this urge. This subsequent switch of strategy after a mistake renders interpretation of subsequent correct and incorrect responses impossible and would add unnecessary noise to PC scores. The mean response time (RT) was defined as the time between the onset of the GO signal and the onset of the first response. In addition an inter response RT was defined as the time between responses.

The first cue during melody presentation was intended to give an explicit reference and as consisted with the presented tone accompanied with the correct response. Because of this analysis of the first and the last four responses was separated. For the first response the mean RTs and mean PC were evaluated statistically by analysis of variance (ANOVA) with repeated measures, with Block (5), Condition(2: familiar, novel) as within subject factors and Group as a between subjects factor. For the last four responses the mean RTs and mean PC were evaluated statistically by ANOVA with repeated measures, with Block (5), Condition (2: familiar, novel), Position (5) as within subject factors and Group as a between subjects factor.

To analyze the influence of a specific pitch of a note on performance an ANOVA with repeated measures analysis of the PC for each different note was conducted. This analysis used Block(5), Condition(2), Note(8) as the within subjects factors and Group as a between subjects factor. Responses to the first note were not used in this analysis. Greenhouse-Geisser correction was applied where appropriate.

EEG parameters

For the AEP trials without artifacts were used. The AEP was computed by averaging the segments of the last four notes of each target melody. In each experimental condition all possible pitches were equally represented. Using this method confounding influences of a specific note or the introduction of cognitive processes related to the processing of the first note of the target melody are prevented. Averaged activity was determined in fifteen 20ms intervals from 100ms to 400ms after stimulus onset. For the N1 component the factors Time(3), Block(2), Condition(2) as within subjects variables and Group as the between subjects variables. For the P2 and p300 components the factors Time (6), Block (2), Condition (2) were used as within subjects variables and Group was used as between-subjects variables.

The CNV was computed by averaging EEG's for all trials without artifacts from Fz, Cz and Pz, as these electrodes represent the predominant distribution of the CNV (Leuthold & Jentsch, 2002). To obtain sufficient trials for each condition trials from experimental Blocks 2, 3, 4 and 5 were taken together to calculate the averages. Averaged activity was determined in 200ms intervals from -600 to the Go signal on which statistical analyses were performed. All analyses included the factors Time (3) and Condition (2) as within subjects variables and Group as the between subjects variables.

Results*Behavioral Measures*

Analysis of PC and RT, using all 28 participants, did not reveal a between subjects effect for a specific set of melodies. With $F(5,15)=0.7$, $p=0.66$ and $F(5,15)=0.4$, $p=0.85$ for PC and RT respectively. Specific sets were created to counter-balance the experimental design with respect to confounding influences of a specific set of melodies. Because no significant effect of a specific set of melodies was found all 28 participants were used, to raise statistical power, in subsequent analysis of Behavioral and EEG measures.

During presentation of the melody the first note presented was accompanied, on screen by the correct response key. This was done to give participants an explicit reference from where to start melody reproduction. An analysis of the response PC of the first position revealed a significant effect for Block $F(4,104)=7.4$, <0.001 . The mean PC for the first position in the first Block was 91.0% (SD=3.4%) and for the fifth and last block it was 97.0% (SD=2.3%). However, because significant

group differences were found on the short task assessing working memory capacity it was considered appropriate to do an additional analysis introducing the raw score of the working memory task as a covariate. Analysis carried out this way removed the effect of Block leaving $F(4,100)=1.3$, $p=0.2$, indicating that increase in performance in each subsequent block could be accounted for by individual differences in raw score on the test for working memory. However, a between subjects effect for the working memory task failed to reach significance $F(1,25)<1$. Further analysis, with and without a covariate, did not reveal an effect for Group or Condition. This indicated that both groups did most probably not differ in their ability to make correct responses on the basis of this first cue. Further analysis of PC involved the second, third, fourth and fifth positions and used the score on the working memory task as a covariate.

A graph containing the PC for Group Block and Condition can be seen in Figure 2. Analysis of PC correct revealed a between subjects effect of Group $F(1,26)=28.7$, $p<0.001$. This indicated that overall task performance was better for musicians than for non-musicians. Additional analysis revealed an effect for Block $F(4,108)=21.5$, $p<0.001$ and Block*Group $F(4,108)=3.4$, $p<0.05$. Analysis of separate groups found significant effects of Block with $F(4,52)=17.2$, $p<0.001$ and $F(4,52)=6.3$, $p<0.001$ for musicians and non-musicians respectively. This indicated that task-specific performance increased with each consecutive block and that this increase was highest for musicians. Further analysis revealed an effect of Condition $F(1,26)=29.5$, $p<0.001$ and Condition*Group $F(1,26)=16.3$, $p<0.001$. Separate analysis of both groups revealed this effect to be present for musicians $F(1,13)=32.0$, $p<0.001$ but not for non-musicians $F(1,13)=1.6$, $p=0.23$. This indicated that only for musicians, performance in familiar conditions was better compared to performance in novel conditions. In addition an effect of Block*Condition $F(4,104)=3.7$, $p<0.05$ was found. In separate groups this effect failed to reach significance in musicians $F(4,52)=2.5$, $p=0.77$ and non-musicians $F(4,52)=1.4$, $p=0.26$. Using raw scores of the working memory task in as a covariate in the same analysis removed the significant effect of Block $F(4,100)=1.3$, $p=0.279$ but not the significance of the effect for Block*Group $F(4,100)=3.2$, $p<0.05$ and Condition*Group $F(1,25)=14.3$, $p<0.001$.

A graph containing the position PC for Group Position and Condition can be seen in Figure 3. Analysis of PC in respect to effect of positions revealed an effect of Position $F(3,78)=187.7$, $p<0.001$

and an effect of Position*Group $F(3,78)=6.4$, $p<0.05$. Separate analysis of groups revealed this effect to be present for musician $F(3,39)=65.2$, $p<0.001$ and non-musicians Position $F(3,39)=65.2$, $p<0.001$. This indicated that reproduction performance declined with each increasing position in the melody. This decline of performance with each successive melody position was more pronounced for non-musicians than for musicians. In addition an effect for Condition*Position $F(3,78)=7.2$, $p<0.01$ was found. This indicated that the decline in performance with each successive position was less for familiar than for novel conditions. Further analysis of separate groups revealed this effect to be present for musicians $F(3,39)=10$, $p<0.001$ but not for non musicians $F(3,78)=0.9$, $p=0.40$.

The PC for each Note and Group can be seen in Figure 4. Analysis of PC for specific notes revealed an effect for Note $F(7,182)=7.2$, $p<0.001$. This indicates, as can be seen in Figure 4, that general performance is slightly better for the higher notes (F#4, G4). Significant interactions of Note with Group, Condition or Block were not found. This indicates that, most probably, musical experience and learning did not influence the ability to respond to a specific note.

A graph containing the RT as for each Group, Position and Condition can be seen in Figure 4. An analysis of the RT after the Go can be made but Interpretation of inter-response RT is difficult due to the high number of incorrect responses on subsequent positions in both groups. To analyse the RT after Go the only the first position was considered. This analysis revealed an effect of Group $F(1,26)=4.3$, $p<0.05$ both no effects of Block or Condition. This indicated that the first responses, and therefore initiation of melody reproduction, were faster for musicians, mean 506 ms (SD=108), compared to non-musicians, mean 713(SD=186).

Additional analysis inter-response RT for all positions revealed an effect of Condition $F(1,26)=12.5$, $p<0.05$ and an effect of Condition*Group $F(1,26)=7.3$, $p<0.05$. Separate analysis for each group revealed that there was an effect of Condition $F(1,13)=14.3$, $p<0.01$ present for musicians but not for non-musicians $F(1,13)=0.5$, $p=0.48$. This indicated that for musicians that responses were generally faster for the familiar set of melodies than for the novel melodies. In addition for musicians an effect of Position $F(4,52)=4.7$, $p<0.05$ was found. This indicated that responses were generally fastest for the first position and slowest for the second becoming increasingly faster with each subsequent position.

Figure 2. Mean PC's as a Function of Block, Condition and Group. The first response is not used in determining the mean PC.

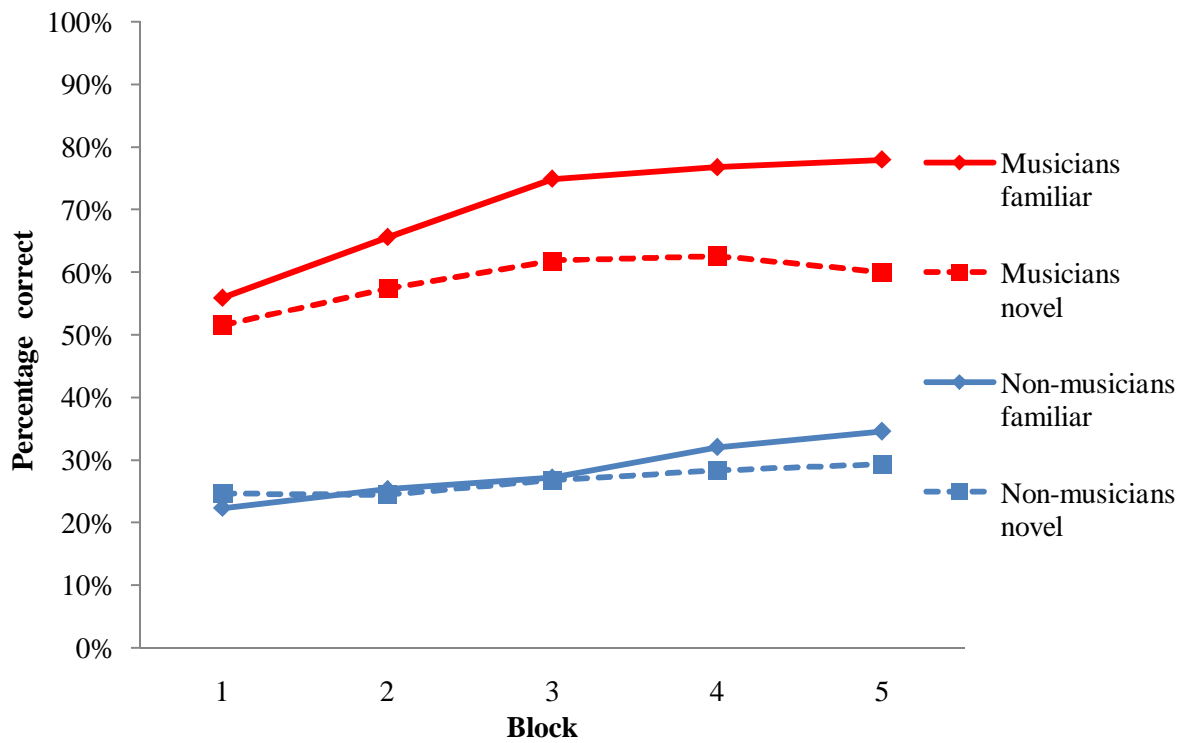


Figure 3. Mean PC's as a Function of Group, Condition and Position.

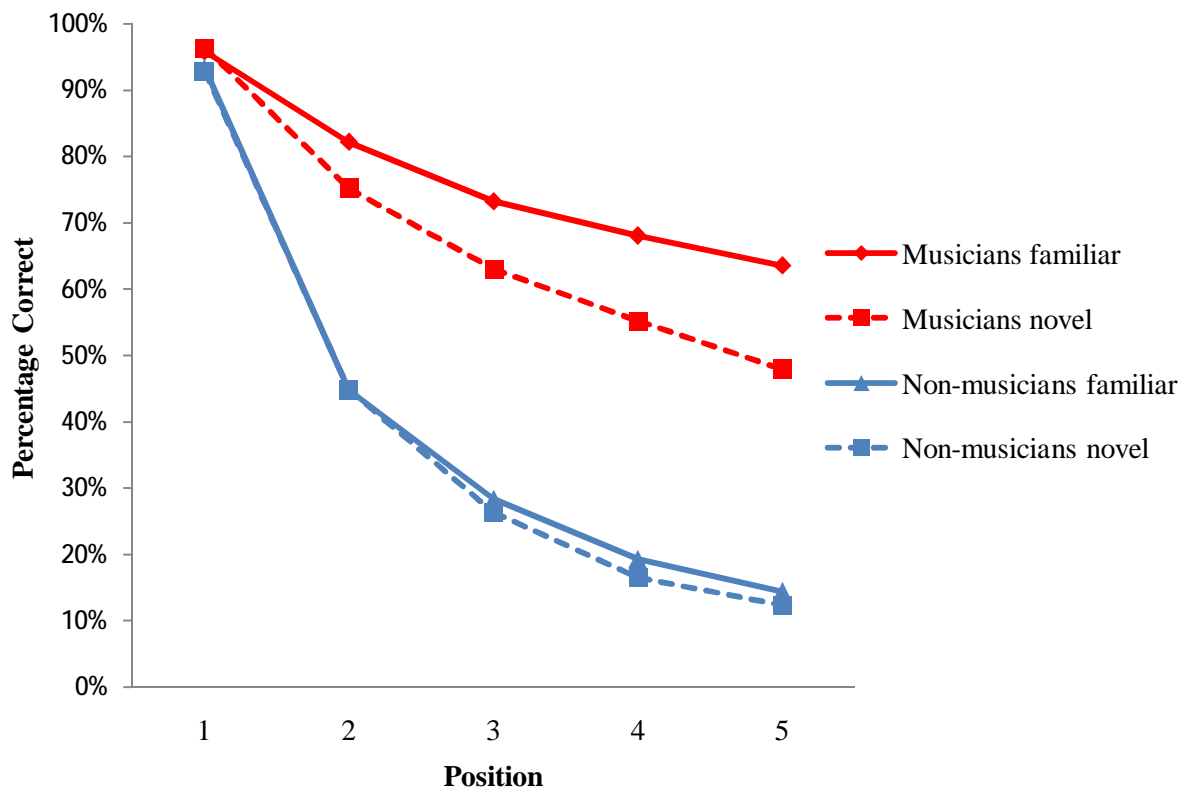


Figure 4. Mean RT's (in ms) as a Function of Group, Condition and Position.

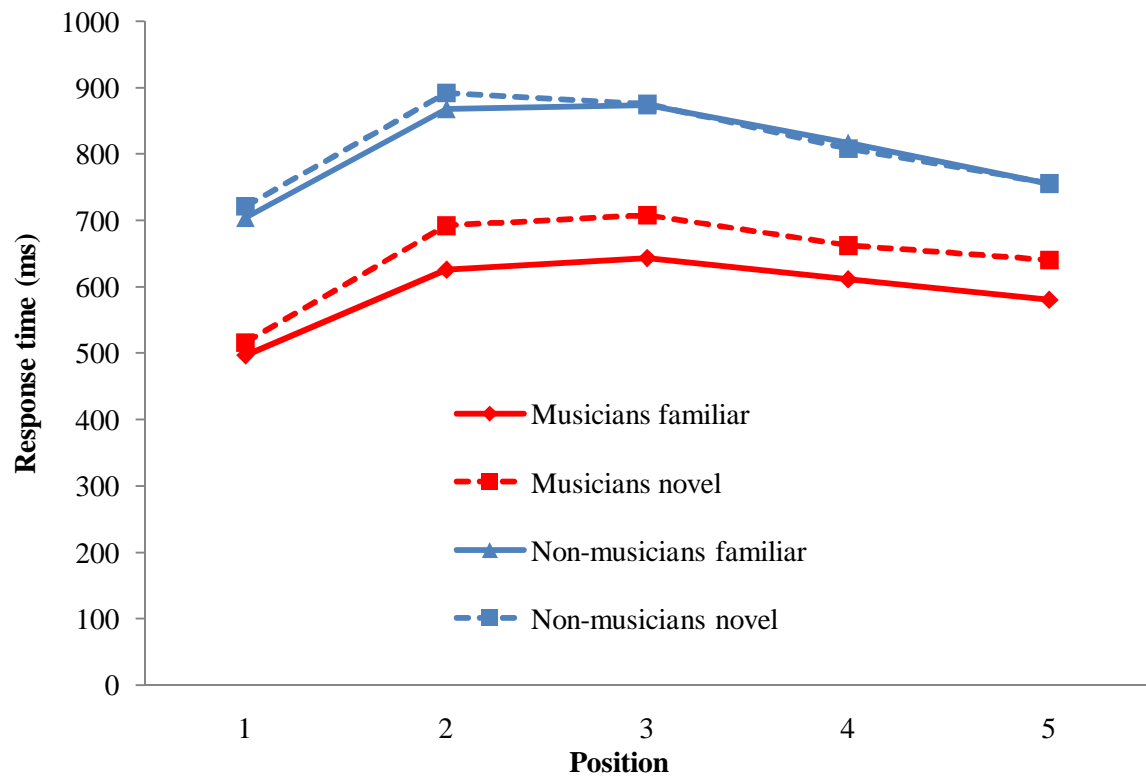
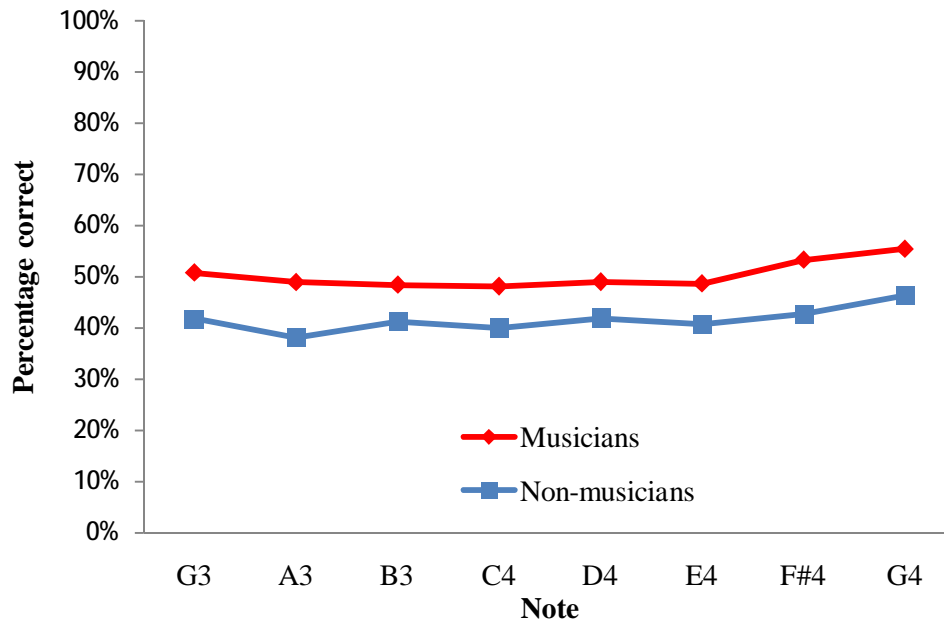


Figure 5. Mean PC's for each note. The first response was not used to calculate the PC.



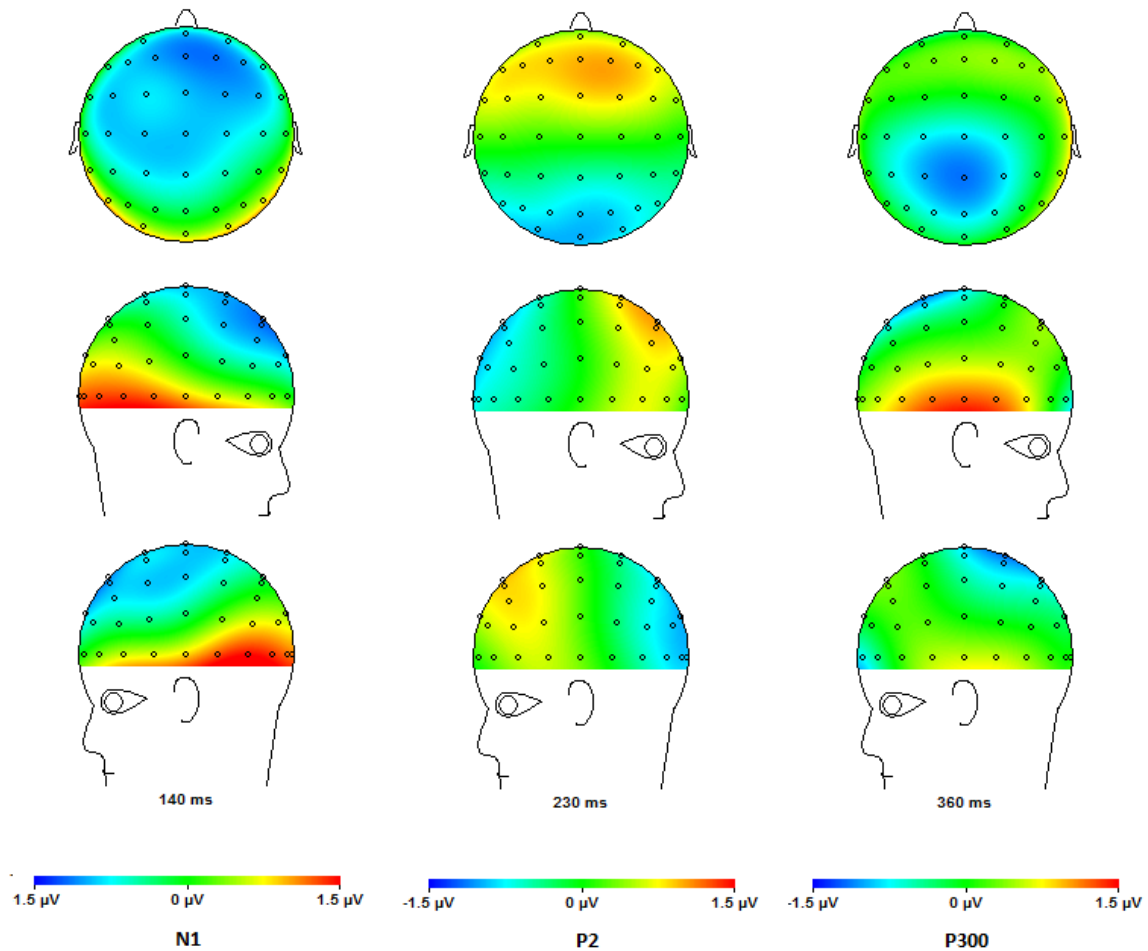
EEG results

See Figure 6 for the average AEP scalp voltage distribution of negative and positive peaks during tone presentation. Visual inspection of relevant time windows revealed a frontal distributed N1 and P2 and a late right temporal positivity,. The amplitude of the N1 component was found to be greatest over Fz electrode position and was reached at approximately 140ms. The p2 component was showed to be more diffusely distributed across fronto-lateral electrode positions, favouring the right hemisphere. Inspection of the AEP at Fz Electrode position revealed the latency of peak amplitudes of the P2 component to vary between 185ms and 280ms. A temporal positivity, indicative of a p300, was observed over right temporal positions. Inspection revealed peak amplitude to be reached at approximately 360ms at T8 electrode.

See Figure 7 and 8 for the AEP's above Fz electrode for Musicians and Non-musicians for each condition. Analysis of the N1 at Fz electrode position in time interval 100-160 ms revealed an effect of Time $F(2,52)=23.4$, $p<0.001$ indicating that voltages differed significantly from each other within the 100-160ms interval containing the peak of the N1 components. In addition an effect of Block $F(1,26)=12.9$, $p<0.001$ was found. These results indicate that the peak of the N1 amplitude was highest during the first block and lowest during the last. An effect of Block*Group $F(1,26)<1$ was not found.

Analysis of P2 at Fz electrode position in the 160-300ms time window revealed an effect of Time $F(3,78)=34.6$, $p<0.001$ indicating that voltages in different time windows differed significantly from each other. In addition an effect for Time*Block $F(6,156)=7.7$, $p<0.001$ was found. As can be seen in figure 4 and 5 the peak of the P2 occurs earlier and has smaller amplitude in the last block compared to the first block. In addition an effect for Time*Block*Condition $F(3,78)=3.8$, $p<0.05$ was found. Indicating that within the 160-300ms interval differences between conditions differed between the beginning and the end of the experiment. An effect for Time*Group could not be established $F(5,130)=2.0$, $\epsilon=0.33$ $p=0.14$.

Figure 6. The average scalp voltage distribution of N1, P2 and p300-like components obtained by averaging activity of all participants in the first block.



The observed right temporal positivity, approximately 360 ms, post-stimulus was considered to reflect a p300. Additional analysis of activity at T8 and T7 electrodes, with Hemisphere(2) as an extra within subjects factor, in the 300-400 time interval using 20ms windows was conducted. This analysis revealed an effect for Hemisphere $F(1,26)=25.2$, $p<0.05$, Hemisphere*Block $F(1,26)=7.3$, $p<0.05$, Hemisphere*Condition $F(1,26)=5.0$, $p<0.05$ and Hemisphere*Block*Group $F(1,26)=4.4$, $p<0.05$. This indicated the p300 above the right temporal cortex was larger for the last block in comparison to the first. These differences between the first and the last block were greatest for non-musicians. The interaction between hemisphere and condition indicated notes in familiar melodies evoked a smaller p300 than notes in novel melodies

Figure 7. AEP at Fz electrode position for notes in familiar melodies separated for Group (Blue and Red) and Block (solid and dotted lines)

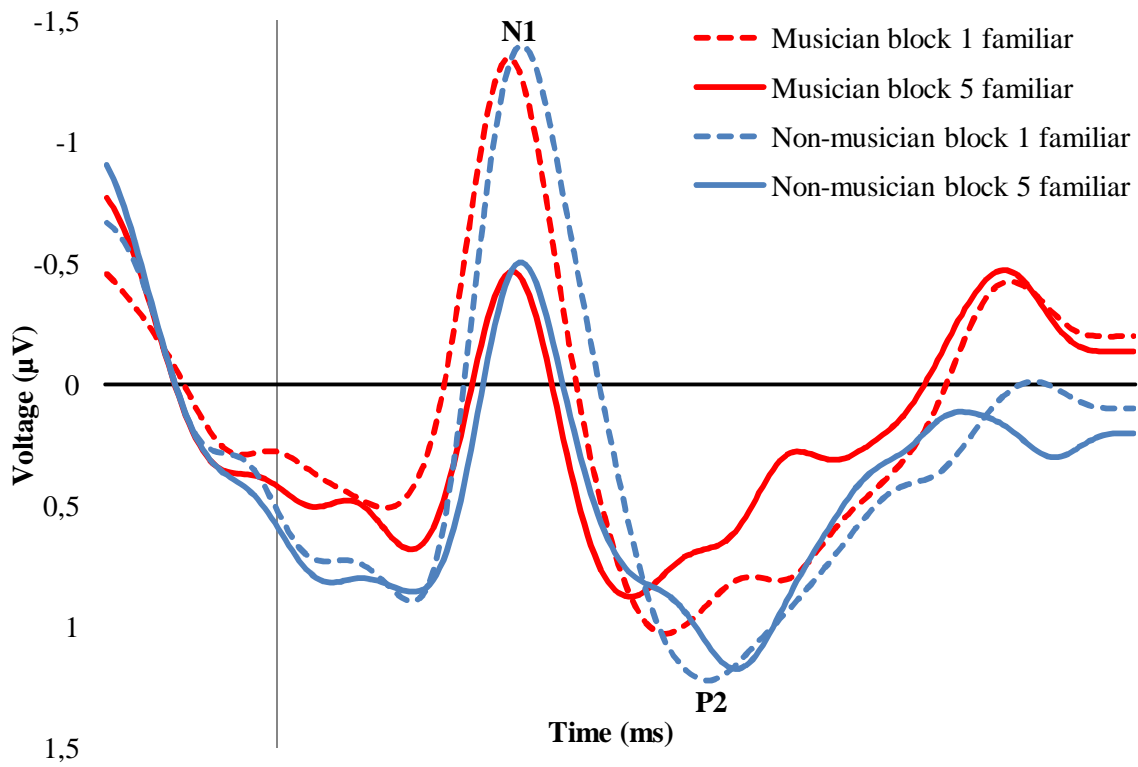
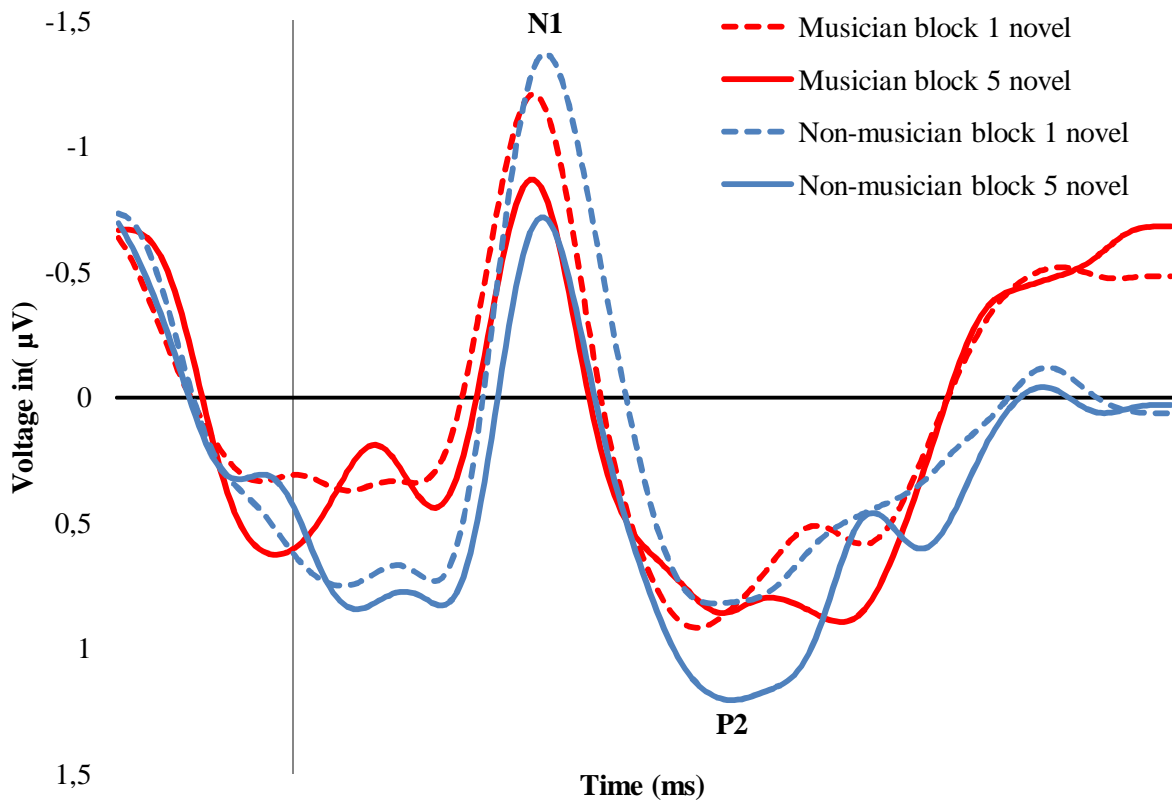


Figure 8. AEP at Fz electrode position for notes in novel melodies separated for Group (Blue and Red) and Block (solid and dotted lines)



See Figure 9 for scalp distribution of P2 related positivity for each group, and condition in the first and the last block of the experiment. Visual inspection of separate averages of the 180 to 300ms interval indicates an asymmetric distribution of P2 related positivity across blocks, group and time. Therefore, analysis of the 180-300ms interval using 20ms time windows with F8, F7, F4, and F3 electrodes was conducted. This analysis also included the extra factors Hemisphere (2), Medial-Lateral (2). This analysis revealed an effect of Group $F(1,26)=6.1, p<0.05$, indicating an overall difference in activity between groups. In addition, effects of Time $F(5,130)=13.5, p<0.001$ and Time*Hemisphere $F(5,130)=14.6, p<0.00$ were found. This indicated that during the 180-300ms interval positivity became more expressed the right hemisphere. The interaction between Group*Hemisphere $F(1,26)=3.3, p=0.08$ failed to reach significance.

Further analysis revealed an effect of Time*Lateral-Medial*Block $F(5,130)=6.5, p<0.05$ and an effect of Lateral-Medial*Block*Group $F(1,26)=4.5, p<0.05$. Indicating that positivity in this interval became more lateralised with each consecutive block. Separate analysis for musicians revealed an effect of Time*Lateral-Medial(5,65)=5.6, $p<0.05$ and Time*Lateral-Medial*Condition $F(5,65)=3.0, p<0.05$. For musicians positivity was expressed more laterally in novel conditions. The same effect for condition was not found for non-musicians $F(5,65)<1$.

. Analysis of the preparation interval revealed an effect for Condition*Group $F(5,26)=5.1, p<0.05$. See Figure 10 for a graph containing both groups and conditions. A statistically significant effect for Condition when both groups are analysed separately could not be established. In addition, the CNV did not significantly from zero, intercept $F(1,26)=2.0, p=0.2$. Which makes a clear interpretation of the Condition*Group interaction difficult.

Figure 9. Average scalp voltage distributions of P2 related positivity for group, block and conditions.

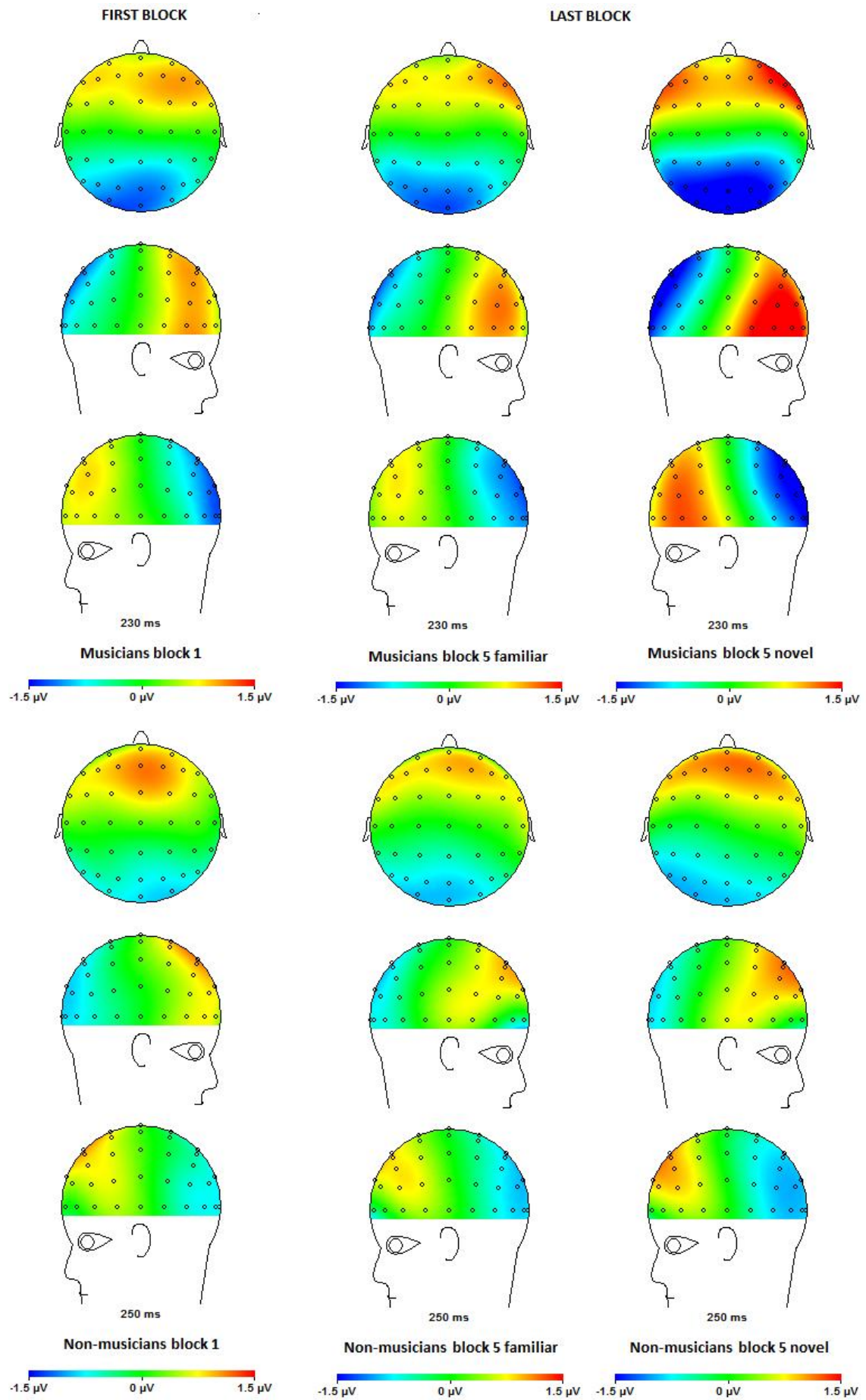
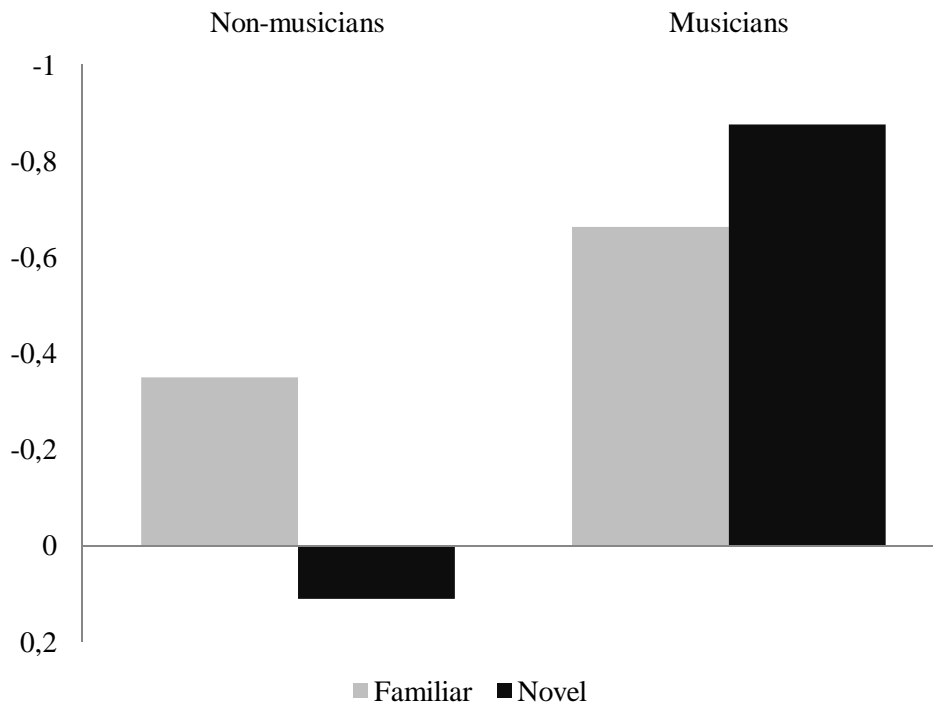


Figure 10. Mean CNV for familiar and novel conditions for musicians and non-musicians in the interval lasting -600ms until the Go.



Discussion

The goal of the experiment in this paper was to investigate what underlying processes set musicians apart from non-musicians in the ability to play by ear. It was hypothesized that differences in perceptual processing would govern this ability. It was predicted that the ability to extract information during perception of target melodies would be reflected by larger N1 and P2 in musicians compared to non-musicians. In addition it was predicted this ability would influence the preparation of upcoming movements reflected by CNV amplitude in the preparation interval before the Go.

In line with expectation, behavioral data indicated that musicians outperformed non-musicians in reproducing short melodic sequences by ear. From behavioral measures it can be inferred that the task was difficult. For non-musicians task performance was especially poor. In spite of this big performance difference, task specific learning, reflected by an increase in performance in each consecutive block, was present in both groups. An effect of learning of the familiar set of melodies could only be observed in musicians. Non-musicians did not show an increase in performance on familiar melodies.

In contrast to findings in studies using pitch discrimination tasks (Baumann et al., 2008; Shahin, Bosnyak, Trainor, & Roberts, 2003) the N1 and N2 amplitudes were not influenced by experience in the current study. These findings are backed up by behavioral data concerning performance on specific notes. Performance was influenced by the pitch of the note itself, which was slightly better for high notes, but not affected by musical experience or learning. This is considered an indication that musicians and non-musicians did probably not differ in their ability to discriminate between different notes. The effect of block and condition on the amplitude of the N1 and P2 suggest a role for melody recognition. The N1 and P2 were smaller for the last Block in comparison to the first. In addition, the amplitude of the P2 evoked by notes in familiar melodies is attenuated more in the last block compared to those notes of novel melodies. A possible explanation for these results is that further perceptual processing of individual notes is attenuated because the whole melody is recognized. Recognition of a melody is more likely as the number of instances such a melody is encountered increases. In addition to the P2 at Fz being smaller in the last compared to the first block of the experiment, the P2 related positivity in the last compared to the first block was found to be more spread out over lateral electrodes positions. In general the p2 was slightly more pronounced in the right hemisphere. These results seem to be in line with right hemispheric dominance in pitch processing (Zatorre, Evans, & Meyer, 1994; Zatorre, 2000), and studies by Halpern, (2001) and Zatorre, & Samson, (1991) that demonstrated activity of temporal and right frontal areas in the scanning and mental retrieval of melodies.

Habituation to the stimuli could be an explanation for the found reduction in the N1 component. It is known that the N1 amplitude decreases by repetition of the auditory stimulus (Näätänen, & Picton, 1987). This effect has been explained in the past as habituation to the stimulus but later studies have indicated this to be a refraction process of the neural generators underlying the N1 (Budd, Barry, Gordon, Rennie & Michie, 1998) sensitive to the length of the interval between stimuli. In this task the time interval between each note after the first note is the same, therefore differences in refraction cannot explain these results.

The different distribution of the P2 in musicians compared to non-musicians suggests musicians are better able to extract relevant information of a specific note for the formation of a melody

representation. An alternate interpretation for these findings is that selecting necessary responses happens during melody presentation. Such an interpretation is backed up by the fact that a CNV could not be established and therefore preparation might not have occurred. The right anterior areas, more specifically Brodmann area 44, have been proposed as the location of a key to note map (Bangert, & Altenmüller, 2003). Furthermore, it is known that this area together with the ventral pre-motor cortex contains a dense population of mirror neurons. It has been shown that mirror neurons can be activated by sound associated with an action Keysers et al., (2003). Application of source dipole modeling on the current data might help to establish the source of the P2 related activity.

It was predicted that movement preparation as reflected by the CNV would be better for musicians compared to non-musicians. However testing this prediction proves problematic. Results indicate an effect of group on differences between familiar and novel sets of melodies. Such a result is very difficult to interpret because the CNV in both groups was not found to differ significantly from the intercept. These findings suggest that preparation of upcoming movements did not take place in the current task. In defence of movement preparation it can be argued that methodological limitation in this study might have resulted in an underestimation of the CNV. Considering the findings by previous studies (Lahav, Saltzman, & Schlaug, 2007; Zatorre & Halpern, 2005) on auditory-motor interactions in music performance, setting the baseline at the beginning of the trial 100ms prior to onset of the first stimulus would have been preferred. This method would have taken into account the fact that preparation of upcoming movements might already start during melody presentation. The choice to put the baseline for the CNV at -1600ms before onset of the go was made out of methodological considerations. An implication of this approach for interpretation of the CNV is that it assumes no CNV is present before this time. This would result in an underestimation of seen effects rather than an over-estimation. Previous studies (Leuthold & Jentzsch, 2009) found a CNV indicative of movement preparation using simple pre-cues. In this study, the first presented note was accompanied with full information about the required response. PC and RT data suggest this upcoming information was used to prepare the first response. On this basis a CNV in this task would have been expected (Wild-Wall, Sangals, Sommer, & Leuthold, 2003). Using the current analysis, the presence of a CNV, and movement preparation, for musicians and not for non-musicians can only be

inferred from the underestimation of CNV negativity in current analysis and the found interaction of Group with Condition. However it cannot be concluded, on the basis task performance differences alone that upcoming response preparation is present for musicians and not for non-musicians.

Because of the difficulty of the current task for both musicians and non-musicians it is possible that instead of preparing movements beforehand, at least some participants adopted a different strategy. In this alternate strategy participants would reproduce the first note quickly, as the correct response for this note was already given, and continued with melody reproduction using the first note as a starting point for recall of the target melody. This implies that auditory feedback during reproduction was used to determine each subsequent response and that necessary auditory-motor transformation are made on the basis of memory during recall and not during perception or preparation.

The positivity found over right temporal sites at approximately 350ms has the envelope and latency consistent with that of a p3b but deviates in topography from the p3b reported in the literature (for a review see: Polich, 2007). The p3b is generally believed to relate to working memory and the updating of information in working memory. The p3b in this study was found to be larger for the last block in comparison to the first. In combination with the findings that task-performance was better in the last block it is reasoned that as a result of learning the ability to encode relevant information into working memory became better. The difference between blocks was greater for non-musicians compared to musicians. This might indicated that task-specific learning in non-musicians was mediated by an increased ability to encode information into working melody, whereas this was not the case for musicians. In addition it was found that tones of a novel melody evoked a larger p300 in comparisons to those of familiar melodies. It is reasoned that the processing of novel melodies places an increased demand on working memory compared to familiar melodies. It is reasoned that in novel melodies each note has to be kept active in working memory to allow for encoding of relative pitch distances into a melody-specific contour.

The interpretation of results found on the p3b component and the fact that musicians had a higher score on the short test for working memory indicates that working memory capacity might explain task performance differences between musicians and non-musicians. There is evidence that increased

working memory capacity is a side effect of musical training (Ho, Cheung, Chan, 2003; Chan, Ho, Cheung, 1998; Franklin, Moore, Yip, Jonides, Rattray, Moher, 2008). The scores on the working memory test explained some variance found in the data. Most notably, the effect of task specific learning failed to reach significance after the introduction of these scores as a covariate.

What sets musicians apart from non-musicians in the ability to play by 'ear'? Answering this question in terms of perception and response preparation proves to be difficult. Findings on the AEP in combination with behavioral measures suggest that attenuation of notes in target melodies can be attributed to melody recognition. Musicians showed a more diffuse distribution of the P2 component across lateral-frontal areas, possibly reflecting differences in the encoding of melodies. Task-specific learning was present and musicians generally out-performed non-musician, but the behavioral data also indicates that the reproduction of melodies in this task was difficult for both groups. In addition, the presence of a CNV, reflecting preparation of upcoming responses could not be established. It is proposed that instead of preparing upcoming responses beforehand, participants use the first tone as a reference for recall of a target melody. This interpretation is backed up by the influence of working memory capacity on task-specific learning. In addition a late memory related, p3b like, positivity was found to increase with each consecutive block. Different approaches to the same data set, like dipole source modeling, or separate analysis of the AEP's for correct and incorrect target melody reproduction might further clarify what sets musicians apart from non-musicians. Answering how musicians encode melodies into their short-term memory might provide a more definite answer to the initial question.

References

- Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology*, *61*, 303-321.
- Atienza, M., Cantero, J.L., Dominguez-Marin, E. (2002). The time course of neural changes underlying auditory perceptual learning. *Learning and Memory*, *9*, 138–150.
- Bangert, M. & Altenmüller, E. (2003). Mapping perception to action in piano practice: a longitudinal DC-EEG study. *BMC Neuroscience*, *4*, 26.
- Bangert, M., Peschel, T., Schlaug, g., Rotte, M., Drescher, D., Hinrichs, H., Heinze, H.J. & Altenmüller, E. (2006). Shared networks for auditory and motor processing in professional pianists: evidence from fMRI conjunction. *Neuroimage*, *30*, 917–926.
- Baumann, S., Koeneke, S., Meyer, M., Lutz, K. & Jancke, L. (1995). A network for sensory-motor integration: what happens in the auditory cortex during piano playing without acoustic feedback? *Annual New York Academy of Sciences*, *1060*, 186–188.
- Bosnyak, D.J., Eaton, R.A., Roberts, L.E. (2004). Distributed auditory cortical representations are modified when non-musicians are trained at pitch discrimination with 40 Hz amplitude modulated tones. *Cerebral Cortex*, *14*, 1088–99.
- Budd, T.W., Barry, R.J., Gordon, E., Rennie, C., Michie, P.T. (1998). Decrement of the N1 auditory event-related potential with stimulus repetition: habituation vs. Refractoriness. *International Journal of Psychophysiology*, *31*, 51-68.
- Chan, A.S., Ho, Y.C., Cheung, M.C., (1998). Music training improves verbal memory. *Nature*, *396*, 128.

- Cui, R.Q., Egkher, A., Huter, D., Lan, W., Lindinger, G., & Deecke, L. (2000). High resolution spatiotemporal analysis of the contingent negative variation in simple or complex motor tasks and a non-motor task. *Clinical Neurophysiology*, *111*, 1847-1859.
- Fawcett, A.J., Nicolson, R.I., Dutch translation: Kort, W., Schittekatte, M., Van den Bos, K.P., Vermeir, G., Iutje Spelberg, H.C., Verhaeghe, P. & van der Wild, S. (2005) DST-NL Dyslexie Screening Test. *Pearson-NL*
- Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B. & Taub, E. (1995). Increased cortical representation of the fingers of the left hand in string players. *Science*, *270*, 305–307.
- Franklin, M.S., Moore, K.S., Yip, C.Y., Jonides, J., Rattray, K., Moher, J. (2008). The effects of musical training on verbal memory. *Psychology of Music*, *36*, 353-365.
- Gaser, C. & Schlaug, G. (2003). Brain structures differ between musicians and non-musicians. *Journal of Neuroscience*, *23*, 9240–9245.
- Gratton, G., Coles, M.G.H., & Donchin, E. (1983). A new method for the off-line removal of ocular artefact. *Electroencephalography and Clinical Neurophysiology*, *55*, 468–484.
- Halpern, A.R. (2001) Cerebral Substrates of Musical Imagery. In: *The Biological Foundations of Music. Annual New York Academy of Sciences*, *930*, 179-192.
- Haueisen, J. & Knösche, T. R. (2001). Involuntary motor activity in pianists evoked by music perception. *Journal of Cognitive Neuroscience*, *13*, 786–792.
- Ho, Y. C., Cheung, M.C., Chan, A.S., (2003). Music Training Improves Verbal but Not Visual Memory: Cross-Sectional and Longitudinal Explorations in Children. *Neuropsychology*, *17*, 439-450.

- Jentzsch, I., Leuthold, H., & Ridderinkhof, K.R. (2004). Beneficial effects of ambiguous precues: Parallel motor preparation or reduced premotoric processing time? *Psychophysiology*, *41*, 231-244.
- Keysers, C., Kohler, E., Umiltà, M.A., Nanetti, L., Fogassi, L & Gallese, V. (2003). Audiovisual mirror neurons and action recognition. *Experimental Brain Research*, *153*, 628–636.
- Lahav, A., Saltzman, E. & Schlaug, G. (2007). Action representation of sound: audiomotor recognition network while listening to newly acquired actions. . *Journal of Neuroscience*, *27*, 308–314.
- Leuthold, H., & Jentzsch, I. (2002). Distinguishing neural sources of movement preparation and execution: An electrophysiological analysis. *Biological Psychology*, *60*, 173-198.
- Leuthold, H., Sommer, W., & Ulrich, R. (2004). Preparing for Action: Inferences from CNV and LRP. *Journal of Psychophysiology*, *18*, 77-88.
- Lotze, M., Scheler, G., Tan, H.R.M., Braun, C., & Birbaumer, N. (2003) The musician's brain: functional imaging of amateurs and professionals during performance and imagery. *NeuroImage*, *20*, 1817- 1829.
- Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*, 2128–2148.
- Meister, I. G., Krings, T., Foltys, H., Boroojerdi, B., Müller, M., Töpper, R., & Thron, A. (2004). Playing piano in the mind—an fMRI study on music imagery and performance in pianists. *Cognitive Brain Research*, *19*, 219–228.

- Nätäänen, R., Picton, T. (1987). The N1 wave of the human electric and magnetic response to sound: a review and analysis of the component structure. *Psychophysiology*, 24, 375–425.
- Nätäänen, R., Sams, M., Alho, K., Paavilainen, P., Reinikainen, K., Sokolov, E.N., (1988). Frequency and location specificity of the human vertex N1 wave, *Electroencephalographic Clinical Neurophysiology*. 69, 523-531.
- Pantev, C., Oostenveld, R., Engelien, A., Ross, B., Roberts, L.E., Hoke, M. (1998). Increased auditory cortical representation in musicians. *Nature*, 392, 811–4.
- Rauschecker, J. P. & Tian, B. (2000). Mechanisms and streams for processing of ‘what’ and ‘where’ in auditory cortex. *Proceedings of the National Academy of Sciences*, 97, 11800–11806.
- Rhodes, B.J., Bullock, D., Verwey, W.B., Averbeck, B.B., Page, M.P.A., (2004) Learning and production of movement sequences: Behavioral, neurophysiological, and modeling perspectives *Human Movement Science*. 23, 699–746.
- Ruchkin, D.S., Canoune, H.L., Johnson, R.J., & Ritter, W. (1996). Working memory and preparation elicit different patterns of slow wave event-related brain potentials. *Psychophysiology*, 32, 399-410.
- Shahin, A., Roberts, L. E., Pantev, C., Trainor, L. J., & Ross, B. (2005). Modulation of P2 auditory-evoked responses by the spectral complexity of musical sounds. *NeuroReport*, 16, 1781–1785.
- Shahin, A., Bosnyak, D.J., Trainor, L.J. & Roberts, L.E. (2003). Enhancement of Neuroplastic P2 and N1c Auditory Evoked Potentials in Musicians. *The Journal of Neuroscience*. 23, 5545–5552.

Schneider, P., Scherg, M., Dosch, H.G., Specht, H.J., Gutschalk, A., Rupp, A. (2002). Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. *Nature Neuroscience*, 5, 688–694.

Schlaug, G., Jancke, L., Huang, Y., Staiger, J. F. & Steinmetz, H. (1995). Increased corpus callosum size in musicians. *Neuropsychologia*, 33, 1047–1055.

Tremblay, K., Kraus, N., McGee, T., Ponton, C., Otis, B. (2001). Central auditory plasticity: changes in the N1–P2 complex after speech–sound training. *Ear and Hearing*, 22, 79–90.

Ulrich, R., Leuthold, H., Sommer, W. (1998). Motor programming of response force and movement direction. *Psychophysiology*, 35, 721-728.

Verleger, R., Vollmer, C., Wauschkuhn, B., van der Lubbe, R.H.J., & Wascher, E. (2000). Dimensional overlap between arrows as cueing stimuli and responses? Evidence from contralateral differences in EEG potentials. *Cognitive Brain Research*, 10, 99-109.

Wild-Wall, N., Sangals, J., Sommer, W., & Leuthold, H. (2003). Are fingers special? Evidence about movement preparation from event-related brain potentials. *Psychophysiology*, 40, 7-16.

Zatorre, R.J., Samson, S. (1991). Role of the right temporal neocortex in retention of pitch in auditory short-term memory. *Brain*, 114, 2403-2417.

Zatorre, R. J., Evans, A. C., & Meyer, E. (1994). Neural mechanisms underlying melodic perception and memory for pitch. *Journal of Neuroscience*, 14, 1908-1919.

Zatorre, R. J. (2000). Neural specializations for tonal processing. *Presented at the NYAS conference 'The biological foundations of music'*, Rockefeller University, New York, NY, May 21, 2000.

Zatorre, R. J. & Halpern, A. R. (2005). Mental concerts: musical imagery and auditory cortex.

Neuron, 47, 9–12 .

Zatorre, R.J, Chen, J.L., & Penhune, V.B. (2007). When the brain plays music: auditory–motor

interactions in music perception and production. *Nature Reviews Neuroscience* 8, 547-558.

Appendix A. Melodies, Sequences and underlying Templates used in Experiment.

Hand		Set 1 (1 to 8)	Set 2 (9 to 16)	Set 3 (17 to 24)	Set 4 (25 to 32)	Set 5 (33 to 40)	Set 6 (41 to 48)
Left hand	1	1 2 4 3 2	1 3 2 1 4	1 4 3 4 2	1 2 1 3 4	1 3 4 2 3	1 4 2 3 1
	Key	a s f d s	A d s a f	A f d f s	A s a d f	A d f s d	A f s d a
	Note	G3 A3 C4 B3 A3	G3 B3 A3 G3 C4	G3 C4 B3 C4 A3	G3 A3 G3 B3 C4	G3 B3 C4 A3 B3	G3 C4 A3 B3 G3
	2	1 2 3 2 4	1 3 4 2 1	1 4 2 3 4	1 2 4 1 3	1 3 2 4 3	1 4 1 3 2
	Key	s d f d a	S f a d s	S a d f a	S d a s f	S f d a f	S a s f d
	Note	A3 B3 C4 B3 G3	A3 C4 G3 B3 A3	A3 G3 B3 C4 G3	A3 B3 G3 A3 C4	A3 C4 B3 G3 C4	A3 G3 A3 C4 B3
	1	1 2 4 3 2	1 3 2 1 4	1 4 3 4 2	1 2 1 3 4	1 3 4 2 3	1 4 2 3 1
	Key	d f s a f	D a f d s	D s a s f	D f d a s	D a s f a	D s f a d
	Note	B3 C4 A3 G3 C4	B3 G3 C4 B3 A3	B3 A3 G3 A3 C4	B3 C4 B3 G3 A3	B3 G3 A3 C4 G3	B3 A3 C4 G3 B3
	2	1 2 3 2 4	1 3 4 2 1	1 4 2 3 4	1 2 4 1 3	1 3 2 4 3	1 4 1 3 2
	Key	f a s a d	F s d a f	F d a s d	F a d f s	F s a d s	F d f s a
	Note	C4 G3 A3 G3 B3	C4 A3 B3 G3 C4	C4 B3 G3 A3 B3	C4 G3 B3 C4 A3	C4 A3 G3 B3 A3	C4 B3 C4 A3 G3
Right Hand	1	1 2 4 3 2	1 3 2 1 4	1 4 3 4 2	1 2 1 3 4	1 3 4 2 3	1 4 2 3 1
	Key	{ } l j k l	{ } k l { } j	{ } j k j l	{ } l { } k j	{ } k j l k	{ } j l k { }
	Note	G4 F#4 D4 E4 F#4	G4 E4 F#4 G4 D4	G4 D4 E4 D4 F#4	G4 F#4 G4 E4 D4	G4 E4 D4 F#4 E4	G4 D4 F#4 E4 G4
	2	1 2 3 2 4	1 3 4 2 1	1 4 2 3 4	1 2 4 1 3	1 3 2 4 3	1 4 1 3 2
	Key	L k j k { }	L j { } k l	L { } k j { }	L k { } l j	L j k { } j	L { } l j k
	Note	F#4 E4 D4 E4 G4	F#4 D4 G4 E4 F#4	F#4 G4 E4 D4 G4	F#4 E4 G4 F#4 D4	F#4 D4 E4 G4 D4	F#4 G4 F#4 D4 E4
	1	1 2 4 3 2	1 3 2 1 4	1 4 3 4 2	1 2 1 3 4	1 3 4 2 3	1 4 2 3 1
	Key	K j l { } j	K { } j k l	K l { } l j	K j k { } l	K { } l j { }	K l j { } k
	Note	E4 D4 F#4 G4 D4	E4 G4 D4 E4 F#4	E4 F#4 G4 F#4 D4	E4 D4 E4 G4 F#4	E4 G4 F#4 D4 G4	E4 F#4 D4 G4 E4
	2	1 2 3 2 4	1 3 4 2 1	1 4 2 3 4	1 2 4 1 3	1 3 2 4 3	1 4 1 3 2
	Key	J { } l { } k	J l k { } j	J k { } l k	J { } k j l	J l { } k l	J k j l { }
	Note	D4 G4 F#4 G4 E4	D4 F#4 E4 G4 D4	D4 E4 G4 F#4 E4	D4 G4 E4 D4 F#4	D4 F#4 G4 E4 F#4	D4 E4 D4 F#4 G4

Appendix B. List of Markers sent out by E-prime and recorded alongside EEG Data.

Marker	Meaning
<hr/>	
Procedural	
<hr/>	
S98	Begin Experiment
S99	Start five minute break between blocks
S255	Initialization, Used for debugging purposes only
S209	Indicates practice trials.
S30	Onset of GO signal indicates start of reproduction period.
S97	Indicates a responses made by participant before GO signal.
S50	Erroneous reproduction by participant
S51	Correct reproduction by participant
<hr/>	
Conditions	“Appears at start of trial. 1000ms before presentation of the first note”
<hr/>	
S210	Block 1 Familiar Condition
S211	Block 1 Novel Condition
S220	Block 2 Familiar Condition
S221	Block 2 Novel Condition
S230	Block 3 Familiar Condition
S231	Block 3 Novel Condition
S240	Block 4 Familiar Condition
S241	Block 4 Novel Condition
S250	Block 5 Familiar Condition
S251	Block 5 Novel Condition
<hr/>	

S100 to S147	Particular melody presented (48 in total)
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Stimuli

S21	Presentation of G3 Note
S22	Presentation of A3 Note
S23	Presentation of B3 Note
S24	Presentation of C4 Note
S25	Presentation of D4 Note
S26	Presentation of E4 Note
S27	Presentation of F#4 Note
S28	Presentation of G4 Note

Responses

S41	Reproduction of G3 Note by pressing A key
S42	Reproduction of A3 Note by pressing S key
S43	Reproduction of B3 Note by pressing D key
S44	Reproduction of C4 Note by pressing F key
S45	Reproduction of D4 Note by pressing J key
S46	Reproduction of E4 Note by pressing K key
S47	Reproduction of F#4 Note by pressing L key
S48	Reproduction of G4 Note by pressing ; key
S49	Indicates pressing of any other key, considered wrong and does not produce any auditory feedback.

Appendix C. Brain Vision EEG analysis tree with operations and their parameters.

