Long-term training affects cerebellar processing in skilled keyboard players

Susan Koeneke,CA Kai Lutz, Torsten Wüstenberg[1] and Lutz Jäncke

Department of Neuropsychology, University of Zurich, Treichlerstrasse 10, CH-8032 Zurich, Switzerland; [1]Berlin Neuroimaging Center, Humboldt University Berlin, Germany

CACorresponding Author: s.koeneke@psychologie.unizh.ch

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We studied cerebellar hemodynamic responses in highly skilled keyboard players and control subjects during complex tasks requiring unimanual and bimanual finger movements. Both groups showed strong hemodynamic responses in the cerebellum during the task conditions. However, non-musicians showed generally stronger hemodynamic responses in the cerebellum than keyboard players. We conclude that, due to long-term motor practice a different cortical activation pattern can be visualized in keyboard players. For the same movements fewer neurons need to be recruited. The different volume of the activated cortical areas might therefore reflect the different effort necessary for motor performance in both groups. *NeuroReport* 15:1279–1282 © 2004 Lippincott Williams & Wilkins.

Key words: Bimanual coordination; Cerebellum; fMRI; Human motor cortex; Motor skill; Musicians

INTRODUCTION

Professional musicians constitute an ideal population for studying long-term plasticity within the sensorimotor system [1–4]. Following a lifelong, intense musical training they develop exceptional fine motor skills. Associated with these performance gains several anatomical and neurophysiological peculiarities have been reported. Recent fMRI studies have revealed unusual cortical activation patterns during music-related uni- or bimanual movements in highly skilled pianists and string players [5–8]. In general musicians show weaker hemodynamic responses within the motor system, including the primary motor area (M1), the premotor cortex (PMC), and the mesial motor wall (pre-supplementary motor area: pre-SMA, posterior part of the supplementary motor area: SMA proper, cingulate motor area: CMA), suggesting a more efficient way to control these movements. It was also shown that learning new motor paradigms is not only easier for musicians but is also accompanied by weaker hemodynamic responses than those seen in non-musicians. A further line of research revealed substantial differences in musicians with respect to macroanatomical measures of brain areas which are involved in musical training. For example, it has been shown that professional right-handed piano players have enlarged cortical hand motor regions compared to non-musicians. The between-group difference is larger for the subdominant motor cortex [9], resulting in reduced between-hemisphere asymmetries for the group of musicians. Further studies found larger anterior parts of the corpus callosum in professional pianists, indicating enhanced interaction between the motor areas of the two hemispheres [10,11] which is thought to be related to the excellent ability of pianists to integrate the action of both hands. An important finding is the correlation of the anatomical changes with the age at which musical training commenced suggesting that use dependent stimulation is the main aspect determining these anatomical peculiarities [9,11]. A recent elegant study using voxel-based morphometry to detect structural differences between pianists and non-musicians across the whole brain found larger grey matter volumes in the motor network of the musician group including M1, the somatosensory areas (S1), PMC, and the left cerebellum (CB) [12]. Another very recent study found a significant difference in absolute and relative cerebellar volume between male musicians and non-musicians [13]. While the findings regarding anatomical differences in classical motor regions (M1, S1, PMC) is somehow expected on the basis of previously published papers of our group, the finding with respect to the anatomical difference in the cerebellum is new and needs further theoretical and experimental elaboration. The cerebellum is known to be involved in the precise timing and temporal integration of movements (for a review see [14]) and motor learning [15,16]. Therefore, one could hypothesize that this structure has established a specific capacity to control skilled movements especially in musicians practicing skilled movements each day. As far as we know there is no study that has examined cerebellar activations in musicians during complex tasks requiring uni- and bimanual movements. Motivated by the new finding of Hutchinson *et al.* we looked more closely at cerebellar activations in musicians performing complex coordination tasks using a powerful statistical analysis. Generally we would expect less cerebellar activation since this structure is known to be particularly important during the early error-driven adaptation phase of motor skill learning, thus becoming less active with increasing skill [17,18]. It maybe that the finding of larger cerebellar grey matter volumes indicates a larger network housing more computational capacity to control extensively practiced movements.

MATERIALS AND METHODS

Subjects: Seven highly skilled keyboard players (three male, four female; mean age 24.0±3.4 years) and seven control subjects (three male, four female; mean age 24.3±5.6) took part in the study. The keyboard players received at least ten years of intense musical training and started before the age of 7 (mean duration of musical training 16.4 years). Control subjects were matched according to the demographic characteristics of the musicians and had not received any special musical training. All subjects were self-professed right-handers and used their right hand for writing and painting. Subjects gave written informed consent according to institutional guidelines (Ethics Committee of the University of Magdeburg). Data of these subjects will also be published in the context of a different research question.

Task: Subjects had to perform a task requiring coordinated movement of two fingers either of one hand or of both hands in order to manipulate the position of a cursor on a computer screen. This task was constructed according to a design that was originally introduced by Preilowski (for details see [19]). For the present study this task was modified to make it suitable for the fMRI environment. A channel that was formed by two parallel white lines of equal length was presented in the middle of a black computer screen. The channel was programmed to rotate around its own center according to different sine functions. Subjects were instructed to guide a small cursor, which moved at a pre-determined speed, through this rotating channel without touching or crossing its boundaries. If the cursor crossed the walls subjects needed to redirect the cursor back into the channel. Steering the cursor was done via two buttons. Pressing one button led to a movement change in the vertical direction, pressing the other button moved the cursor in a horizontal direction.

Each subject took part in three experimental conditions. During the bimanual condition (BIM) subjects were instructed to use the left index finger to control the vertical dimension and the right index finger to control the horizontal direction. In the unimanual conditions (left hand: UL, right hand: UR) subjects had to use middle and index fingers of one hand.

fMRI design: The motor task was presented within a classical fMRI box-car design with alternating rest (20 s) and activation (20 s) blocks. One session consisted of seven resting and six activation blocks. During the activation (ON) periods the task was presented. Prior to every session subjects were instructed as to which fingers they had to use. Single tasks that were carried out during the course of one session differed regarding the characteristics of the rotation course of the channel. During the resting (OFF) blocks subjects were required to fixate the cursor that was located at the start position of the channel. Subjects performed two sessions per task condition. The order of the sessions was pseudo-randomized for each subject.

Scanning procedure: fMRI was performed on a 1.5 T system (General Electric, Waukesha, WI, USA), equipped with gradient echo EPI (repetition time, TR=2.0 s; echo time, TE=40 ms; field of view=200 × 200 mm; flip angle=90°; matrix size=64 × 64 × 23; voxel size=3.125 × 3.125 × 6 mm). Initiation of each scan session was synchronized with stimulus presentation by a computer trigger.

Data analysis: Image analysis was performed on a PC using SPM99 running on MATLAB 5.3 (Mathworks Inc., Natiek, MA, USA). All images were realigned to the first volume, corrected for motion artifacts, normalized (4 × 4 × 4 mm) into standard stereotaxically space (EPI-template provided by the Montreal Neurological Institute), and smoothed using an 8 mm full-width-at-half-maximum Gaussian kernel. Activated voxels were identified using the general linear model approach. At the first level of analysis a statistical model for each subject was computed, applying a box-car model, convolved with the modeled hemodynamic response. Linear contrasts were employed for each subject and condition. To confirm the activation and compare the difference among the groups, a random effects analysis was employed using the contrast images obtained from the individual subjects separately for groups and conditions (contrasts: BIM > rest, UR > rest, UL > rest; height threshold: $p=0.001$, spatial extent: k=15 voxels). In order to test for between-group differences with respect to the hemodynamic responses Z-maps from the random-effects analysis were compared using the Cornish-Fisher expansion of the inverse distribution of a sum of random deviates [20] (contrasts: non-musicians > musicians, musicians > non-musicians separately for each task condition). To detect significant differences a conservative threshold was used (t=3; $p<0.05$, corrected for the cerebellar volume). This threshold effectively eliminates false-positive voxels from the functional maps.

Task performance: Performance data were recorded simultaneously with the task. This was done by calculating the mean deviation between real and ideal cursor position for each task (one ON block). This deviation parameter was averaged across all ON-blocks of a particular task condition. Thus, we got an overall performance parameter for each subject and each task condition. This performance parameter was subjected to a repeated measurement ANOVA with musician status (pianists *vs* non-musicians) and task condition (UR *vs* UL *vs* BIM) as independent variables to test for differences in performance across conditions and groups. To check for differences in performance accuracy across the entire experiment and to examine between-group differences regarding the learning profile an additional repeated measurement ANOVA was conducted using the mean error scores (mean distance between the current and the ideal cursor position) of each experimental session resulting in six error scores.

RESULTS

Performance data: The comparison of the error score across experimental groups and conditions revealed no significant effect (all $p > 0.10$). Subjecting the mean error scores for each of the six experimental sessions to a repeated-measures ANOVA (with each session as repeated factor) revealed a significant reduction of error scores during the course of the fMRI experiment (F(5,8)=53.47, $p < 0.001$, ETA^2=0.87). However, there was neither a significant group main effect nor an interaction between error rate and group indicating that the error rates and learning profiles are similar for both groups.

Brain activation data: The comparison of hemodynamic responses obtained during the three conditions with a resting baseline showed activations in the expected motor areas (M1, SMA proper, pre-SMA, parietal lobes, and cerebellum). The activation patterns were similar for uni- and bimanual conditions. The two unimanual conditions differed with respect to the fact that right-handed movements were associated with stronger activations on the left M1 and right cerebellum, while movements with the left hand caused stronger activations on the right M1 and left cerebellum. We will not discuss these patterns of activation in detail since the focus of this paper is placed onto the evaluation of differences between musicians and non-musicians with regard to cerebellar activations.

The SPM analysis for the entire brain volume revealed no significant difference between pianists and non-musicians in either task for the conservative statistical tests (p=0.05, corrected for the entire volume). However, when restricting the analysis to the *a priori* defined cerebellar volume we revealed a significant difference between pianists and non-musicians for all three movement conditions (Fig. 1). Between-group differences were evident within the vermis (X=−10 to 10) and in the cerebellar cortices. The lateral activations are located within the vicinity of the intermediate zone of the anterior cerebellar lobe. Activation differences in the cerebellar nuclei were not evident. For BIM the non-musicians showed stronger activations in the left cerebellar hemisphere (peak at −32, −58, −32, t=5.45), the vermis (peak 3, −64, −32, t=5.07), and within the right cerebellar hemisphere (peak 25, −62, −32, t=5.1). In contrast, keyboard players showed stronger hemodynamic responses in a slightly more lateral area of the right cerebellar hemisphere (peak 33, −64, −32, t=5.1). For the UR condition non-musicians showed two peaks of stronger hemodynamic responses in the cerebellum (left hemisphere: −38, −53, −32, t=4.3; vermis: 5, −63, −32, t=6.5; right hemisphere: 32, −62, −32, t=5.3). For the UL condition the keyboard-players showed stronger hemodynamic responses in the left cerebellar hemisphere (−20, −56, −32, t=6.6).

DISCUSSION

This work was motivated by the very recent finding of larger cerebellar volumes [13] and increased grey matter densities within the cerebellum [12] in a larger sample of keyboard players than in non-musicians. The authors argue that these anatomical peculiarities are due to life-long practice of hand skill associated with keyboard playing. If these anatomical differences are indeed related to piano playing we expect that there should also be differences between piano players and non-musicians with respect to hemodynamic responses in the cerebellum during complex finger movement tasks. In fact we found between-group differences regarding the cerebellar activation pattern.

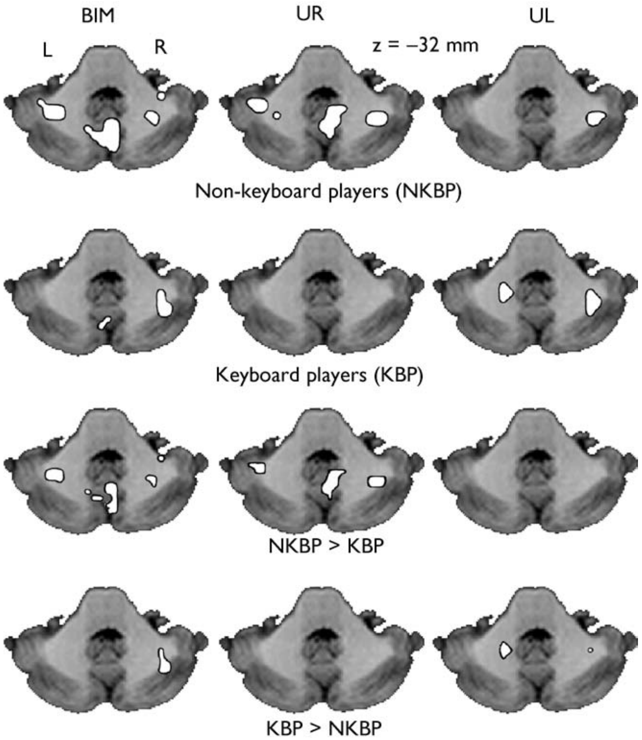

Fig. 1. Significant hemodynamic responses in the cerebellum during the different tasks (BIM, UR, UL) broken down for non-keyboard players (NKBP) and keyboard players (KBP). The lower two rows represent activation differences between the two groups.

During bimanual and unimanual movements with the dominant right hand non-musicians show stronger hemodynamic responses bilaterally in the cerebellar cortices and in the vermis. However, the converse contrast of musicians > non-musicians also revealed some significant activation clusters within the cerebellar hemispheres indicating that there is no simple difference between keyboard players and non-musicians.

What are the underlying causes for this pattern of activation difference? Currently, there are various models of cerebellar functions, which are not mutually exclusive but address specific aspects of the multifunctional nature of this particular structure. Our task has characteristics that can be related to different aspects of cerebellar function. In short, the task involves the planning and execution of a sequence of movements which are considerably more difficult for the subdominant than for the dominant hand [21]. In addition, bimanual movements demand more cortical resources than unimanual movements because the motor cortices of the two hemispheres have to communicate in order to accomplish the coordination between hands. To the extent that the task is more difficult for bimanual movements, one can expect more emphasis on monitoring and attention to feedback for this condition [22]. The model by Thach *et al.* [23] emphasizes the role of the lateral cerebellum and dentate nuclei in the coordination of movement across several joints and it is possible that the task of coordinating movement across the two hands (bimanual task condition) is dealt with in a manner similar to the coordination of multiple joints within a limb.

Consistent with this hypothesis we suggest that the increased activations in the cerebellum during bimanual movements for non-musicians reflect the increased processing demands in this group. In other words, skilled pianists rely on less cerebellar processing demands for this particular task. Similarly, the activation pattern found for unimanual movements with the dominant hand also reflects reduced processing demands in the musicians group compared to non-musicians. Interestingly, there was no significant cerebellar activation for keyboard players during this task (UR). However, the lack of significant activation does not necessarily mean that there is no cerebellar involvement during this task in keyboard players. Perhaps fMRI is too crude to detect subtle hemodynamic responses driven by weak electrophysiological activation. A further problem is that the exact relationship between the BOLD response and electrophysiological activation is still a matter of dispute [24,25]. Further methodological studies are needed to clarify the general issue of interpreting fMRI data especially in the context of cerebellar activation.

However, we also found significant hemodynamic responses for the contrast musicians > non-musicians during the bimanual and unimanual movement condition with the subdominant left hand. During bimanual movements there were stronger hemodynamic responses in a small cluster within the right cerebellar hemisphere. It seems that non-keyboard players involve both cerebellar hemispheres in the control of bimanually coordinated movements, whereas in highly skilled keyboard players the dominant right cerebellar hemisphere takes the lead – indicating a strategic inter-group difference. Thus, the stronger activation of the right cerebellar hemisphere in keyboard players might simply be the result of the lateralization of neural control resources for this kind of bimanual movement. In contrast non-musicians seem to recruit a distributed bilateral cerebellar network in order to accomplish the task requirements. We suggest that the expansion of the cerebellum in keyboard players is associated with a relocation of neural networks and with an increased efficiency in controlling bimanual movements. Given the fact that it is a common phenomenon in keyboard players that the dominant right hand (usually playing the melody) takes the lead during piano playing it becomes conceivable that the neural control of bimanual movements might be preferably lateralized to the dominant motor cortices (ipsilateral cerebellum).

A different picture emerged for the unimanual condition with the subdominant left hand. During this condition non-musicians activated the right cerebellum only, while keyboard players showed bilateral cerebellar activation. We believe that keyboard-players use different cerebellar control modes for movements that involve their dominant right hand (BIM, UR) and left-handed finger movements (UL).

CONCLUSION

The reported pattern of activation supports the idea that intensive and long-lasting motor practice affects cerebellar functions a very peculiar manner. Thus, this paper complements recent anatomical studies in musicians in showing peculiar cerebellar functional adaptations.

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