

EXPERT PIANISTS DO NOT LISTEN: THE EXPERTISE-DEPENDENT INFLUENCE OF TEMPORAL PERTURBATION ON THE PRODUCTION OF SEQUENTIAL MOVEMENTS

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Abstract—Auditory information plays an important role in fine motor control such as speech and musical performance. The purpose of this study was to assess expertise-dependent differences in the role of temporal information of auditory feedback in the production of sequential movements. Differences in motor responses to the transient delay of tone production during musical performance between expert pianists and non-musicians were evaluated. Compared to expert pianists, non-musicians showed more pronounced movement disruptions following the delayed auditory feedback. For example, in response to a perturbation the inter-keystroke interval was prolonged and the key-press was longer in non-musicians, while the expert pianist marginally shortened both measures. These distinct differences between groups suggest that extensive musical training influences feedback control in sequential finger movements. Furthermore, there was a significant positive correlation between the age at which the expert pianists commenced their musical training and the amount of disruption. Overall, these findings suggest that expert pianists have a higher level of robustness against perturbations and depend less on auditory feedback during the performance of sequential movements. © 2014 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: auditory feedback, sequential movements, expertise-dependent differences, plasticity, fine motor control.

INTRODUCTION

Speech and musical performance such as singing and playing an instrument represent highly-sophisticated

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Abbreviation: IKI, inter-keystroke interval; CD, finger-key contact duration; VEL, keystroke velocity.

sensorimotor skills. Previous studies provided evidence for a salient role of auditory feedback in the precise control of the production of a tone by perturbing auditory feedback of motor actions such as shifting the pitch of a tone (Pfordresher, 2003, 2005; Purcell and Munhall, 2006; Tumer and Brainard, 2007; Munhall et al., 2009; Maidhof et al., 2010) and delaying the timing of a tone (Black, 1951; Yates, 1963; Howell and Archer, 1984; Hashimoto and Sakai, 2003). A key issue in sensorimotor control research is the neuroplastic adaptation of feedback control during movements. Several studies have investigated this topic by comparing the effect of pitch manipulation on vocalization (Jones and Keough, 2008; Zarate and Zatorre, 2008; Keough and Jones, 2009) and on piano performance (Pfordresher, 2005, 2012; Katahira et al., 2008) between skilled, unskilled musicians, and non-musicians. These studies have characterized distinct differences in behavioral and neurophysiological responses to the pitch perturbation between the individuals with different skill levels.

The rhythmic feature of acoustic information also plays a prominent role in fine motor control during speech and musical performance. Of particular importance in expressive musical performance is the fine-tuned control of the timing of tones (Bhatara et al., 2011; Furuya and Soechting, 2012; Furuya and Altenmüller, 2013). Evidence for a tight coupling between the temporal features of acoustic events and motor actions has been provided by studies that delayed the timing of the production of a tone in musical performance (Gates et al., 1974; Pfordresher and Palmer, 2002; Furuya and Soechting, 2010; Pfordresher and Dalla Bella, 2011). For example, it was shown that delayed auditory feedback during piano performance augmented temporal variability of movements (Pfordresher and Palmer, 2002; Pfordresher, 2003; Pfordresher and Dalla Bella, 2011). This suggests that skilled individuals use rhythmic information of tones to maintain the precise timing control of sequential movements. Similarly, temporal disruptions of movements caused by the delayed auditory feedback were evident during speech (Howell and Sackin, 2002). In contrast to pitch, however, to our knowledge, no study has examined the expertise-dependent role of timing information of auditory feedback in relation to the production of skilled motor actions.

Neuroimaging studies have demonstrated a specialized neural network that connects auditory and

motor regions in musicians' brains (Bangert and Altenmüller, 2003; Baumann et al., 2005; Baumann et al., 2007; Bangert et al., 2006; Lahav et al., 2007; Zatorre et al., 2007; Engel et al., 2012; Engel et al., 2013). Pianists showed neural activities at the motor region by merely listening to a short sequence of piano tones (Bangert et al., 2006). This motor activation occurred only when listening to a rehearsed piece (D'Ausilio et al., 2006). Overall, these studies suggest that in trained musicians auditory information evokes both activations in auditory areas as well as in brain areas related to the relevant movements. Perturbations of auditory feedback during musical performance might therefore, at least in trained pianists, automatically evoke motor action. This idea corroborates the neurophysiological findings of a larger and earlier neural response following the transient pitch perturbation in skilled pianists as compared to unskilled players (Katahira et al., 2008). In addition, untrained individuals may focus largely on movement execution with little listening to tones. Other research showed that motor action relies largely on sensory feedback information when performing a novel task (Kawato, 1999; Seidler et al., 2004; Lametti et al., 2012). This raises an alternative possibility in relation to the effects of perturbed auditory feedback, namely that the motor actions of less skilled individuals are more susceptible to auditory perturbation. Consistent with this, the pitch perturbation during vocalizing a single tone yielded smaller motor disruption in the trained singers than in the untrained individuals (Jones and Keough, 2008; Zarate and Zatorre, 2008).

The present study aimed at addressing the role of expertise-dependent differences in the processing of temporal information of auditory feedback during the production of sequential movements. Toward this goal, differences in motor responses to the transient delay of the production of a tone during musical performance between expert pianists and non-musicians were compared. Musical performance is an ideal task to approach this issue with several advantages over vocalization. First, this task provides technical possibility for transiently manipulating the timing of a single tone (Furuya and Soechting, 2010; Pfordresher, 2014). A transient sensory perturbation allows for purely probing sensory feedback control, compared to often-applied permanent manipulation of auditory feedback that can cause adaptation to the perturbation (Houde and Jordan, 1998; Jones and Keough, 2008). Second, a comparative study

of musical performance between skilled and unskilled individuals enables the assessment of the effects of training (Münste et al., 2002; Zarate and Zatorre, 2008; Kleber et al., 2013), without a possible confounding aging-effect as a result of development, which may be the case in vocalization (MacDonald et al., 2012).

EXPERIMENTAL PROCEDURES

Participants

Ten expert pianists (10 female, 25.2 ± 4.83 yrs, nine right-handed, one bimanual) and 10 non-musicians (six female, 26.6 ± 5.48 yrs, all right-handed) participated in the study. The expert pianists studied piano playing at music conservatories, whereas the non-musicians have no or very little experience of studying piano playing. All expert pianists had at least 12 years of extensive piano training (range 12–26; mean 20.2; sd 5.16). Six of the non-musicians had some sort of musical education in playing an instrument (e.g., recorder/guitar). These six participants had on average 2.67 years (sd = 1.34) of experience. The experimental protocol was approved by the local ethics committee of the Hannover Medical University. All participants gave written informed consent prior to the experiment.

Experimental design

Participants were asked to play a sequence of seventeen tones requiring the use of all five digits of the right hand (Fig. 1). The target inter-keystroke interval (IKI) was 400 ms. The participants played on a digital piano (MP 9000; Kawai, Krefeld, Germany) that was connected to a Windows computer. They were provided with the musical score on a computer screen in front of them and were allowed to practice to familiarize themselves with the piano and the music selection. The practice session prior to the experimental trials required the completion of five correct trials, judged by the experimenter. During practice, participants played with a metronome (150 beats per minute, IKI = 400 ms) in order to play consistently and accurately at the target tempo without erroneous keystrokes. Because some of the non-musicians could not read a score, the experimenter demonstrated how to play the sequence. Furthermore, the start position of the thumb was highlighted on the keyboard, in order to make sure participants used the desired fingering during the experiment.

metronome
• • • •

index delay
ring delay

1 2 3 4 5 4 3 2 1 2 3 4 5 4 3 2 1

1: thumb, 2: index, 3: middle, 4: ring, 5: little

Fig. 1. Musical score that was available for the participants during the trials indicating the sequence and appropriate fingering. For explanation purposes only, the events during which the manipulations could occur are indicated by the dashed ovals. The latter information was not available to the participants.

Following the practice session, participants played the target melody in either *delayed* or *normal* conditions, presented in a randomized order. In *delayed* conditions, there was a delay of the timing of the tone production of either the 10th or the 12th tone, corresponding with the stroke of the index, or ring finger, respectively (Fig. 2A). Tone production was delayed by 120 ms using a custom-made script written in JAVA, running at 1 kHz for control and recording of MIDI data from the keyboard. In the *normal* condition, the participant played the melody without any auditory perturbation. The design consisted of three conditions (delay at the strike with the index or ring finger, and no delay), times 15 trial repetitions for each condition, being randomly provided. The randomized order of the 45 trials made it impossible for the participants to know whether and when a delay would occur.

During the experiment, each trial started with the presentation of four successive tones of a metronome (tempo = 150 beats per minute) as a cue of the target tempo. The metronome was turned off automatically after the participant started to play. The participants were instructed to play as accurately as possible in the target tempo. They were also asked to look at the musical score that was displayed on the computer screen in front of them in order to have them instead of looking at their hands on the piano keys.

Data analysis

During the experiment, the time each key was depressed and the time it was released were recorded. In addition, we also recorded the speed with which each key was depressed. Here, MIDI velocities (indicating loudness of

the tone) provided by the interface ranged from 1 to 127. Using these data, the mean and standard deviation of the inter-keystroke interval (from key depression to key depression), of the keystroke velocity, and of the finger-key contact duration (from key depression to key release) per trial were computed (Fig. 2B, C). The changes in keystroke timing and loudness in response to the delay were defined as the difference in the average values of each measure between the delayed and normal conditions. The trials of the normal condition functioned as a baseline. Possible effects of exposure to the delay during the experiment were assessed by computing the difference between the mean of the first and last five trials for both perturbed fingers. Again the trials of the normal condition functioned as a baseline.

Statistical analysis

To test for effects of the delayed auditory feedback on the subsequent movement production, several three-way mixed-design analyses of variance (ANOVA) ($\alpha < 0.05$) with group (expert pianists and non-musicians) as between subject variable, and perturbed finger (index and ring), and event (strikes or intervals before, during and after the delay, see Fig. 2) as within subject variables were run. If the assumption of sphericity was violated, the Greenhouse–Geisser correction was applied. *T*-tests with Bonferroni correction were performed as post hoc tests. In addition, one-tailed *t*-tests (adjusted $\alpha = 0.0125$) were performed to test which level significantly differed from zero (=no change). Furthermore, Pearson's correlations between the age at which the expert pianists commenced their musical training and the different outcome measures

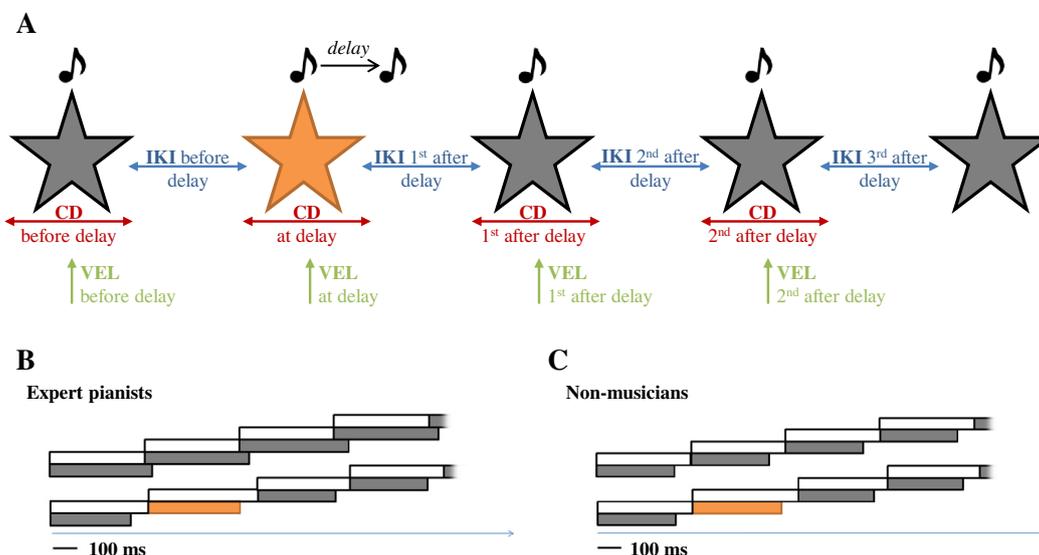


Fig. 2. (A) Schematic representation of the different events. Stars reflect key-presses. During the orange key-press delayed auditory feedback could occur. IKI = inter-keystroke interval; CD = finger-key contact duration; VEL = keystroke velocity. Schematic representation of the group mean of the inter-keystroke interval (open rectangles) and finger-key contact duration (filled rectangles) of the index finger perturbation for the expert pianists (B) and the non-musicians (C). The upper staircase reflects the normal condition that functioned as a baseline. The lower staircase shows the delayed condition (orange rectangle). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

were calculated to investigate the consequence of early musical training on the effect of the delayed auditory feedback. The analyses were performed with SPSS (IBM SPSS Statistics 21).

RESULTS

Effect of delayed auditory feedback

The mean change in the inter-keystroke interval, the finger-key contact duration, and the velocity at different events related to the delay-manipulation (Fig. 2) were calculated for both the index and ring finger perturbations in order to investigate the effect of delayed auditory feedback on the accuracy of the subsequent movement production. The change in standard deviation of all variables was used to assess the effect of the delayed feedback on the variability, i.e., consistency of the same measures. Although the fingering during the events differed (depending on the index or ring finger manipulation) for all measures the events resemble

values related to the strikes before and after the delay (Fig. 2A). The value related to the keystroke before the delay functions as a base line of normal movement production, the other events show the effect of the delay on the movement production.

Results showed significant main effects of group ($F_{(1,18)} = 16.29, p = 0.001$), and event ($F_{(1.30;23.29)} = 38.731, p < 0.001$) for the mean inter-keystroke interval change. Pairwise comparisons as post hoc tests (all $p < 0.001$) revealed that the difference in group mean between the delayed and normal conditions was smaller for expert pianists compared to non-musicians and that the first inter-keystroke interval after the applied delay was longer compared to the other intervals. The interaction effect between these two independent variables ($F_{(1.30;23.29)} = 22.81, p < 0.001$) showed that this latter effect was most pronounced for non-musicians (Fig. 3A). The one-tailed t -tests revealed that for the non-musicians the change in mean inter-keystroke interval at the first inter-keystroke interval after the

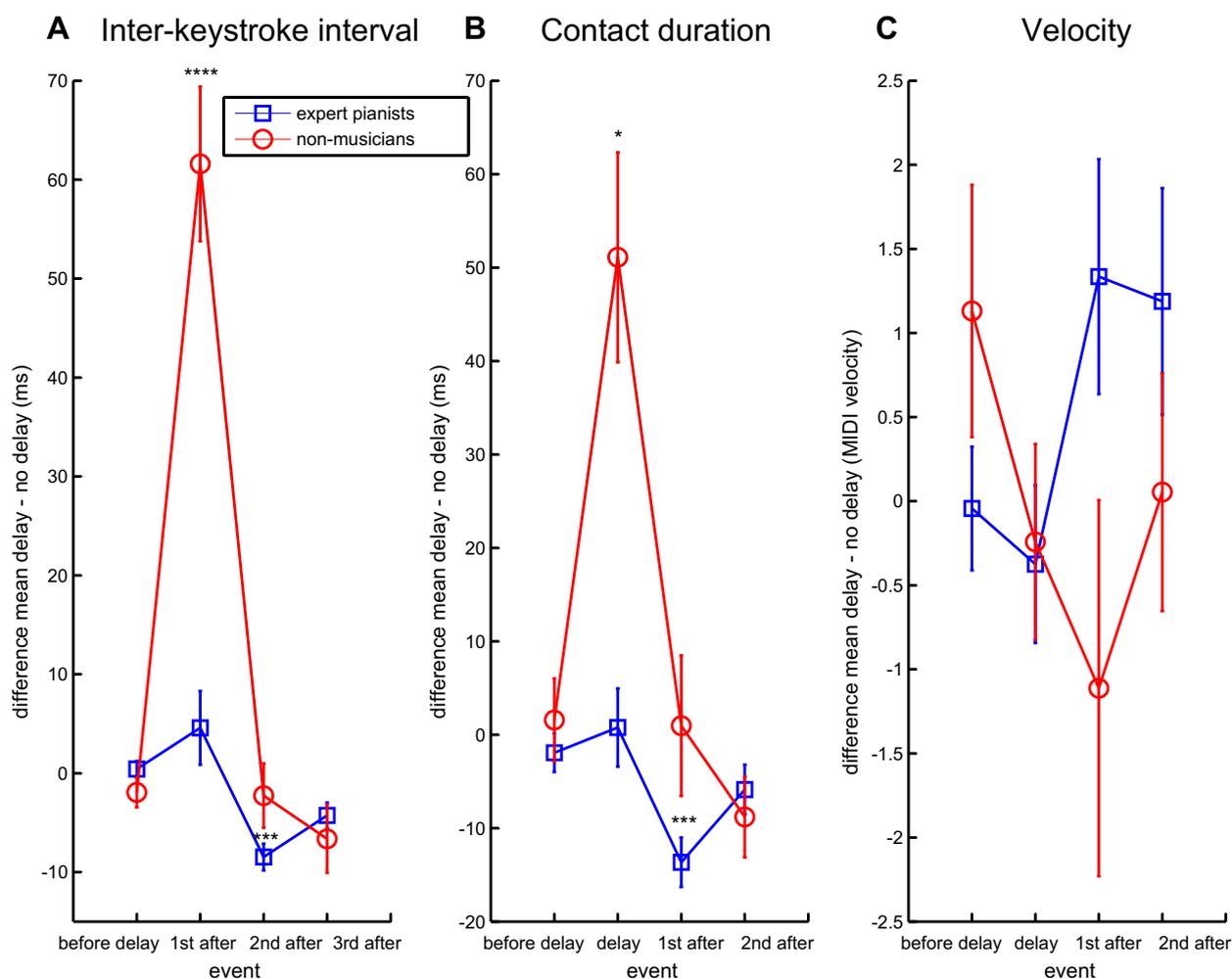


Fig. 3. Significant interaction effects of the impact of delayed auditory feedback. Error bars indicate standard error. Blue and red lines represent expert pianists and non-musicians, respectively. Group times event interaction for the change in (A) inter-keystroke interval, (B) finger-key contact duration, and (C) keystroke velocity. '*' indicates the value differed significantly from zero. Statistical significance: * $p < 0.01$, ** $p < 0.005$, *** $p = 0.001$, **** $p < 0.001$. Corrected α value was 0.0125. See Fig. 2 for the description of the events. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

applied delay was significantly different from zero ($t_{(9)} = 6.01, p < 0.001$), again indicating a prolongation of the local tempo as a response to the disruption. For the expert pianists the change at the second interval after the delay differed significantly from zero ($t_{(9)} = -5.21, p = 0.001$), indicating a transient acceleration of the tempo. This mean change in inter-keystroke interval (-8.46 ms) was smaller than the threshold of detectability in timing differences by experienced listeners (4% of interval) (Repp, 1999), suggesting that this change was too small to be noticeable (Fig. 3A). The standard deviation of this measure showed a significant effect of time ($F_{(2.07;37.27)} = 8.903, p = 0.001$). There was more variability for the first interval after the delay compared to the interval before and the third interval after the delay (pairwise comparison resp. $p < 0.005$ and $p < 0.001$).

For the change in mean finger-key contact duration results also showed significant main effects of group ($F_{(1,18)} = 10.92, p < 0.005$), and event ($F_{(1.56;28.10)} = 10.82, p = 0.001$). Again, pairwise comparisons as post hoc tests revealed that the difference in contact duration between the delayed and normal condition was smaller for pianists compared to non-musicians ($p < 0.001$). Contact duration was longer for the keystroke during the delay compared to the keystroke before ($p < 0.05$), the first ($p < 0.005$), and the second ($p < 0.05$) keystroke after the delay. The interaction between these two main effects ($F_{(1.56;28.10)} = 6.29, p < 0.01$) showed that this effect was most pronounced for the non-musicians (Fig. 3B). The one-tailed t -tests revealed that for the non-musicians indeed the mean change in finger-key contact duration following the delay was significantly different from zero ($t_{(9)} = 3.33, p < 0.01$), indicating a delayed occurrence of the key-release. For the expert pianists the change in contact duration during the first keystroke after the applied delay was significantly shorter than zero ($t_{(9)} = -4.53, p = 0.001$). Again this shortening was smaller (mean = -13.53 ms) than the perceptual threshold (Fig. 3B).

The interaction effect between group and event on the change in mean velocity ($F_{(3,54)} = 2.81, p < 0.05$) revealed that the expert pianists pressed harder during the two sequential keystrokes following the delay, while the non-musicians used less velocity to press the piano key during the first keystroke after the delay (Fig. 3C). For the standard deviation of this measure across trials, the main effect of event was found ($F_{(3,54)} = 3.08, p < 0.05$). This indicated that the variability of the velocity of the keystroke related to the delay was larger than the velocity of the second keystroke after the delay (pairwise comparison as post hoc test: $p < 0.05$).

Overall, these results indicate that the delayed auditory feedback mostly influences the accuracy of the measures of interest. Participants adjusted to the delayed feedback relatively quickly, since only differences related to the manipulated key-press or the first interval after the delay were found. Non-musicians were more disturbed by the delay than expert pianists as is indicated by the main effect of group and the interactions. No differences between the type of perturbation, i.e. delay on index or ring finger, were found.

Effect of exposure

To investigate whether participants adjusted their response to the delayed auditory feedback over repetitions, a difference score between the mean of the first and last five repetitions of each type of manipulation was calculated. Again, the mean and standard deviation of the inter-keystroke interval, of the finger-key contact duration, and of the velocity were used as outcome measures. Positive values indicate that the change in mean or standard deviation of the inter-keystroke interval, the finger-key contact duration, and the velocity was larger during the last five repetitions compared to the change during the first five repetitions of each type of manipulation. Negative values suggest that the difference was more pronounced in the first five repetitions compared to the last five repetitions of the manipulation.

Results showed a main effect of event ($F_{(1.94;34.84)} = 3.76, p < 0.05$) for the difference between the first and last five trials of the change in mean inter-keystroke interval (Fig. 4). This main effect of event interacted with both group ($F_{(1.94;34.84)} = 7.071, p < 0.005$) and perturbation ($F_{(2.07;37.23)} = 6.35, p < 0.005$). Furthermore, there was a significant three-way interaction between the type of perturbation, the event related to the perturbation and whether the participant was an expert pianist or non-musician ($F_{(2.07;37.23)} = 5.44, p < 0.01$). Compared to the first five trials, in the last five trials non-musicians shortened the length of the inter-keystroke interval of the index finger on the first interval after the delay, while prolonging the interval of the index finger on the second interval after the delay and the interval of the ring finger on the third interval after the delay. The expert pianists seemed to prolong the inter-keystroke interval of the ring finger during the first event after the delay (Fig. 4). The one-tailed t -tests revealed that only the shortening of the inter-keystroke interval of the index finger by the non-musicians was significantly different from zero ($t_{(9)} = -3.85, p < 0.005$) (Fig. 4).

For the difference between the first and last five trials of the change in the mean finger-key contact duration a three-way interaction between the type of perturbation, the event related to the perturbation and group was found ($F_{(2.09;37.57)} = 3.37, p < 0.05$). However, the one-tailed t -tests showed that none of the levels yielded to be significantly different from zero.

For the standard deviation of the finger-key contact duration an interaction effect between perturbation type and event was evident for the difference between the first and last five trials ($F_{(2.32;41.73)} = 3.53, p < 0.05$). Furthermore a three-way interaction between the type of perturbation, the event related to the perturbation and group was found ($F_{(2.32;41.73)} = 3.94, p < 0.05$) for the standard deviation of the finger-key contact duration. However, all the one-tailed t -tests showed no significant differences from zero.

Overall, these results indicate that non-musicians improved their behavior across repetitions of the same perturbation. The response to the delayed auditory feedback over repetitions did not differ between the

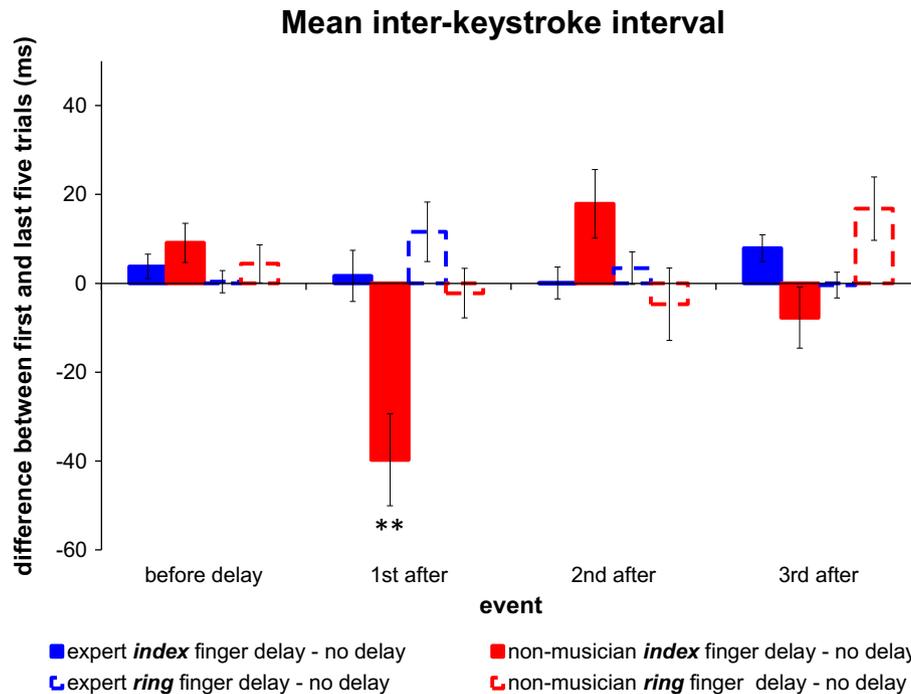


Fig. 4. Significant three-way interaction effects between group, event, and manipulation of the effect of exposure for the mean inter-keystroke interval. Expert pianists are represented in blue, non-musicians in red. Positive values indicate that the change in mean inter-keystroke interval was larger during the last five repetitions compared to the change during the first five repetitions of each type of manipulation. Negative values suggest that the difference was more pronounced in the first five repetitions compared to the last five repetitions of the manipulation. '*' indicates the value differed significantly from zero. Statistical significance: * $p < 0.01$, ** $p < 0.005$, *** $p = 0.001$, **** $p < 0.001$. Corrected α value was 0.0125. Error bars indicate standard error. See Fig. 2 for the description of the events. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

index and ring finger. For the well-trained expert pianist no meaningful effects of repetition were found.

Effect of training in expert pianists

As an indicator of the effect of training, it was investigated whether the age at which expert pianists started playing the piano influenced their response to the delayed auditory feedback. Therefore, for the expert pianists Pearson's correlations between the age of onset and the mean and standard deviation of the inter-keystroke interval, of the finger-key contact duration, and of the velocity for the different events were calculated. For the perturbation on the index finger three significant correlations were found. The second interval after delay was found to be longer for pianists that started their piano training later ($r = 0.67$, $p < 0.05$). Furthermore, the length of the first and second key press after delay turned out to be longer if pianists started to play the piano at a later age (resp. $r = 0.91$, $p < 0.001$; $r = 0.63$, $p = 0.05$). Overall, these results show larger responses following the delay in pianists who commenced the training later. This indicates that the early-started pianists are more robust against the auditory perturbation compared to pianists who started their piano training at a later age.

DISCUSSION

In the present study we assessed differences in motor responses to the transient delay of auditory feedback

during musical performance between expert pianists and non-musicians. Disruptions of temporal features of finger movements following the transient delay of auditory feedback for the non-musicians were found. The movement disruption indicates the integration of rhythmic information on auditory feedback into movement production. By contrast, the expert pianists only showed marginal, not noticeable, rhythmic disruption of movements following the delayed feedback, which confirms robust motor control against external sensory perturbation. One may argue that the musical sequence played in the current experiment, due to its simple nature, required less effort from the expert pianists and was perhaps even monotonous to play. This might postulate that the expert pianists paid less attention to the task and therefore the auditory feedback. The lack of any apparent exposure effects on the keystrokes for the expert pianists contradicts this possibility, since it indicates that they performed the task well throughout the whole experiment. The distinct difference between these groups suggests the impact of extensive musical training on feedback control in sequential finger movements. Further evidence in favor of this view was provided by our correlation analysis across the pianists, which showed smaller movement disruptions in pianists who commenced musical training at an earlier age. Similar to our finding, previous studies found that perturbed pitch of vocalized sound yielded smaller motor disruption in trained singers than in untrained individuals (Jones and Keough, 2008; Zarate

and Zatorre, 2008). It is therefore likely that in both spectral and temporal domains, musical training reduces reliance on auditory feedback control and endows robust movement production against external perturbation.

Previous studies that investigated hand movements requiring a novel sensory-motor transformation, for example, in response to a prism glass or external perturbing forces, have demonstrated integration of sensory feedback both into movement execution as well as into updating the internal representation of the sensory-motor transformation at the early stage of learning (Kawato, 1999; Shadmehr and Krakauer, 2008). With practice, movement production becomes predictive with less integrating sensory feedback (Shadmehr and Mussa-Ivaldi, 1994). Dysfunctional integration of auditory feedback into the finger movements by the non-musicians in the present study can therefore be due to the lack of an accurate representation of the dynamics and acoustics of the piano. In line with this concept, a neurophysiological study has demonstrated the development of a neural network showing stronger links between auditory and motor cortices through piano practice (Bangert and Altenmüller, 2003). This specialized network could enable the expert pianists to play in a feed forward manner (Bangert and Altenmüller, 2003). In addition, our finding suggests that despite listening to the perturbed auditory feedback their special auditory-motor network did not automatically evoke motor action. This mechanism enables expert pianists to rely on internal sensory feedback elicited by internal forward model (Ruiz et al., 2009), rather than on external afferent feedback.

The transient delay of auditory feedback yielded an increase in the inter-keystroke interval for the non-musicians. This finding is in agreement with previous observations of the slowing down of movements by providing delayed auditory feedback during speech (Black, 1951) and musical performance (Pfordresher, 2003; Pfordresher and Benitez, 2007). The slow-down supports the benefit that can be elicited by sensory feedback control with longer latencies. By contrast, the experts did not display any noticeable changes in the local tempo of movements following the perturbation. Instead, they transiently increased the key-striking velocity. The lack of such an increase in the non-musicians indicates that this motor response is specific to trained individuals. It is possible that the stronger keystroke following a perturbation reflects the role of somatosensory feedback in the control of rhythmic movements. A previous study found a positive correlation between the peak finger acceleration at the moment of finger-key contact and the temporal accuracy of the subsequent inter-keystroke interval during piano performance (Goebel and Palmer, 2008). This suggested that a stronger keystroke facilitates the timing accuracy of the subsequent keystrokes due to facilitated somatosensory feedback. A stronger keystroke following the delayed feedback could reflect a compensatory strategy of ensuring rhythmic stability of movements. Indeed, salient roles of somatosensory feedback in fine motor control have been demonstrated during speech (Nasir and Ostry, 2006, 2008; Ito and Ostry, 2010; Lametti et al., 2012) and singing (Kleber et al., 2013).

Furthermore, especially for non-musicians the finger-key contact duration becomes longer in response to the delayed auditory feedback. As if, the non-musician waited for the auditory feedback before they let go of the piano key. This result suggests that the initiation of the finger lift of the key is triggered by the auditory feedback. A study examining the mechanisms underlying the control of intersegmental dynamics during reaching movements also showed that feedback mediated changes decreased the accuracy of movement reversal when errors in perception occurred (Sainburg et al., 1999).

For the expert pianists both the mean inter-keystroke interval as well as the finger-key contact duration became shorter in response to the perturbation. However, these responses were below the perceptual threshold (Repp, 1999), suggesting that they were not noticeable for the expert pianists. This might reflect an implicit compensation for the delay in order to maintain the global tempo of the motor action (Furuya and Soechting, 2010). It is also possible that as a response to the perturbation, the expert pianists struck a key slightly earlier in order to highlight the tone (Goebel, 2001), which may well shorten the inter-keystroke interval.

Over trials, the non-musicians displayed a shorter inter-keystroke interval following the delayed auditory feedback during strokes with the index finger. This finding indicates short-term learning, since repetition of the perturbed keystrokes gives rise to less disruption of movements. A previous study showed development of a neural linkage between the auditory and motor cortices after 20 min of piano practice (Bangert and Altenmüller, 2003). A formation of an internal representation of auditory-motor transformation might thus aid in decreasing reliance on auditory feedback for musical performance.

A previous study found that pianists displayed equal independence of movement control across fingers (Furuya et al., 2011), possibly due to extensive musical training. By contrast, for musically-untrained individuals a difference in independent control of movements across fingers was substantial (Häger-Ross and Schieber, 2000; Zatsiorsky et al., 2000). These studies reported less independent movement control for the middle and ring fingers compared to the index and little fingers. Based on these findings, a larger reliance on sensory feedback during a keystroke with the ring finger compared to a keystroke with the index finger might be expected for the non-musicians, but not for the expert pianists. Overall, for the results on the effect of auditory perturbation, there were no differences in the disruption between the index and ring fingers for both groups (Fig. 3). However, the improvement for the non-musicians over trials appeared for the index finger, but not the ring finger (Fig. 4). This suggests superior controllability of the index finger for the non-musicians. These findings propose finger-dependent reliance on auditory feedback in the finger movements for non-musicians, but not for expert pianists.

Overall, the findings of the present study represent that expert pianists have a higher level of robustness against perturbations of auditory delayed feedback and that they depend less on auditory feedback during the

performance of sequential movements compared to non-musicians.

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REFERENCES

- Bangert M, Altenmüller EO (2003) Mapping perception to action in piano practice: a longitudinal DC-EEG study. *BMC Neurosci* 4:26.
- Bangert M, Peschel T, Schlaug G, Rotte M, Drescher D, Hinrichs H, Heinze HJ, 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 (2005) A network for sensory-motor integration: what happens in the auditory cortex during piano playing without acoustic feedback? *Ann N Y Acad Sci* 1060:186–188.
- Baumann S, Koeneke S, Schmidt CF, Meyer M, Lutz K, Jäncke L (2007) A network for audio-motor coordination in skilled pianists and non-musicians. *Brain Res* 1161:65–78.
- Bhatara A, Tirovolas AK, Duan LM, Levy B, Levitin DJ (2011) Perception of emotional expression in musical performance. *J Exp Psychol Hum Percept Perform* 37:921–934.
- Black JW (1951) The effect of delayed side-tone upon vocal rate and intensity. *J Speech Disord* 16:56–60.
- D'Ausilio A, Altenmüller E, Olivetti Belardinelli M, Lotze M (2006) Cross-modal plasticity of the motor cortex while listening to a rehearsed musical piece. *Eur J Neurosci* 24:955–958.
- Engel A, Bangert M, Horbank D, Hijmans BS, Wilkens K, Keller PE, Keyzers C (2012) Learning piano melodies in visuo-motor or audio-motor training conditions and the neural correlates of their cross-modal transfer. *Neuroimage* 63:966–978.
- Engel A, Hijmans BS, Cerliani L, Bangert M, Nanetti L, Keller PE, Keyzers C (2013) Inter-individual differences in audio-motor learning of piano melodies and white matter fiber tract architecture. *Hum Brain Mapp.* <http://dx.doi.org/10.1002/hbm.22343>.
- Furuya S, Altenmüller E (2013) Flexibility of movement organization in piano performance. *Front Hum Neurosci* 7:173.
- Furuya S, Soechting JF (2010) Role of auditory feedback in the control of successive keystrokes during piano playing. *Exp Brain Res* 204:223–237.
- Furuya S, Soechting JF (2012) Speed invariance of independent control of finger movements in pianists. *J Neurophysiol* 108:2060–2068.
- Furuya S, Flanders M, Soechting JF (2011) Hand kinematics of piano playing. *J Neurophysiol* 106:2849–2864.
- Gates A, Bradshaw JL, Nettleton NC (1974) Effect of different delayed auditory feedback intervals on a music performance task. *Percept Psychophys* 15:21–25.
- Goebel W (2001) Melody lead in piano performance: expressive device or artifact? *J Acoust Soc Am* 110:563–572.
- Goebel W, Palmer C (2008) Tactile feedback and timing accuracy in piano performance. *Exp Brain Res* 186:471–479.
- Häger-Ross C, Schieber MH (2000) Quantifying the independence of human finger movements: comparisons of digits, hands, and movement frequencies. *J Neurosci* 20:8542–8550.
- Hashimoto Y, Sakai KL (2003) Brain activations during conscious self-monitoring of speech production with delayed auditory feedback: an fMRI study. *Hum Brain Mapp* 20:22–28.
- Houde JF, Jordan MI (1998) Sensorimotor adaptation in speech production. *Science* 279:1213–1216.
- Howell P, Archer A (1984) Susceptibility to the effects of delayed auditory feedback. *Percept Psychophys* 36:296–302.
- Howell P, Sackin S (2002) Timing interference to speech in altered listening conditions. *J Acoust Soc Am* 111:2842–2852.
- Ito T, Ostry DJ (2010) Somatosensory contribution to motor learning due to facial skin deformation. *J Neurophysiol* 104:1230–1238.
- Jones JA, Keough D (2008) Auditory-motor mapping for pitch control in singers and nonsingers. *Exp Brain Res* 190:279–287.
- Katahira K, Abba D, Masuda S, Okanoya K (2008) Feedback-based error monitoring processes during musical performance: an ERP study. *Neurosci Res* 61:120–128.
- Kawato M (1999) Internal models for motor control and trajectory planning. *Curr Opin Neurobiol* 9:718–727.
- Keough D, Jones JA (2009) The sensitivity of auditory-motor representations to subtle changes in auditory feedback while singing. *J Acoust Soc Am* 126:837–846.
- Kleber B, Zeitouni AG, Friberg A, Zatorre RJ (2013) Experience-dependent modulation of feedback integration during singing: role of the right anterior insula. *J Neurosci* 33:6070–6080.
- Lahav A, Saltzman E, Schlaug G (2007) Action representation of sound: audiomotor recognition network while listening to newly acquired actions. *J Neurosci* 27:308–314.
- Lametti DR, Nasir SM, Ostry DJ (2012) Sensory preference in speech production revealed by simultaneous alteration of auditory and somatosensory feedback. *J Neurosci* 32:9351–9358.
- MacDonald EN, Johnson EK, Forsythe J, Plante P, Munhall KG (2012) Children's development of self-regulation in speech production. *Curr Biol* 22:113–117.
- Maidhof C, Vavatzanidis N, Prinz W, Rieger M, Koelsch S (2010) Processing expectancy violations during music performance and perception: an ERP study. *J Cogn Neurosci* 22:2401–2413.
- Munhall KG, MacDonald EN, Byrne SK, Johnsrude I (2009) Talkers alter vowel production in response to real-time formant perturbation even when instructed not to compensate. *J Acoust Soc Am* 125:384–390.
- Münste TF, Altenmüller E, Jäncke L (2002) The musician's brain as a model of neuroplasticity. *Nat Rev Neurosci* 3:473–478.
- Nasir SM, Ostry DJ (2006) Somatosensory precision in speech production. *Curr Biol* 16:1918–1923.
- Nasir SM, Ostry DJ (2008) Speech motor learning in profoundly deaf adults. *Nat Neurosci* 11:1217–1222.
- Pfordresher PQ (2003) Auditory feedback in music performance: evidence for a dissociation of sequencing and timing. *J Exp Psychol Hum Percept Perform* 29:949–964.
- Pfordresher PQ (2005) Auditory feedback in music performance: the role of melodic structure and musical skill. *J Exp Psychol Hum Percept Perform* 31:1331–1345.
- Pfordresher PQ (2012) Musical training and the role of auditory feedback during performance. *Ann N Y Acad Sci* 1252:171–178.
- Pfordresher PQ (2014) "Deafness" effects in detecting alterations to auditory feedback during sequence production. *Psychol Res* 78:96–112.
- Pfordresher PQ, Benitez B (2007) Temporal coordination between actions and sound during sequence production. *Hum Mov Sci* 26:742–756.
- Pfordresher PQ, Dalla Bella S (2011) Delayed auditory feedback and movement. *J Exp Psychol Hum Percept Perform* 37:566–579.
- Pfordresher PQ, Palmer C (2002) Effects of delayed auditory feedback on timing of music performance. *Psychol Res* 66:71–79.
- Purcell DW, Munhall KG (2006) Compensation following real-time manipulation of formants in isolated vowels. *J Acoust Soc Am* 119:2288–2297.
- Repp BH (1999) Detecting deviations from metronomic timing in music: effects of perceptual structure on the mental timekeeper. *Percept Psychophys* 61:529–548.
- Ruiz MH, Jabusch HC, Altenmüller E (2009) Detecting wrong notes in advance: neuronal correlates of error monitoring in pianists. *Cereb Cortex* 19:2625–2639.
- Sainburg RL, Ghez C, Kalakanis D (1999) Intersegmental dynamics are controlled by sequential anticipatory, error correction, and postural mechanisms. *J Neurophysiol* 81:1045–1056.

- Seidler RD, Noll DC, Thiers G (2004) Feedforward and feedback processes in motor control. *Neuroimage* 22:1775–1783.
- Shadmehr R, Krakauer JW (2008) A computational neuroanatomy for motor control. *Exp Brain Res* 185:359–381.
- Shadmehr R, Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14:3208–3224.
- Tumer EC, Brainard MS (2007) Performance variability enables adaptive plasticity of 'crystallized' adult birdsong. *Nature* 450:1240–1244.
- Yates AJ (1963) Delayed auditory feedback. *Psychol Bull* 60:213–232.
- Zarate JM, Zatorre RJ (2008) Experience-dependent neural substrates involved in vocal pitch regulation during singing. *Neuroimage* 40:1871–1887.
- Zatorre RJ, Chen JL, Penhune VB (2007) When the brain plays music: auditory-motor interactions in music perception and production. *Nat Rev Neurosci* 8:547–558.
- Zatsiorsky VM, Li ZM, Latash ML (2000) Enslaving effects in multi-finger force production. *Exp Brain Res* 131:187–195.

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