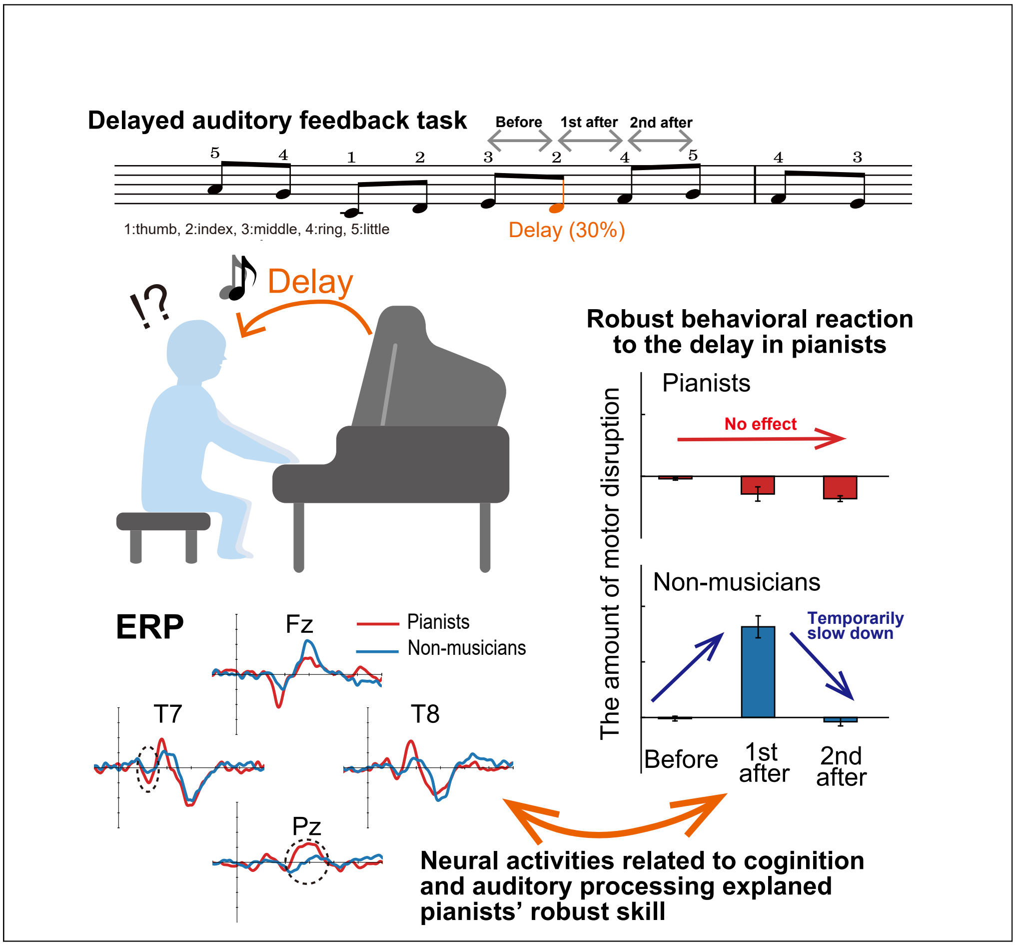
iScience

CellPress
OPEN ACCESS

Article

Robustness and adaptability of sensorimotor skills in expert piano performance



Masaki Yasuhara,
Kazumasa Uehara,
Takanori Oku,
Sachiko Shiotani,
Isao Nambu,
Shinichi Furuya

furuya@csl.sony.co.jp

Highlights

- Auditory perturbation was provided in piano playing
- Pianists adapted their performance immediately following the auditory perturbation
- Non-musicians showed transient disruption of the performance after perturbation
- Neural activities regarding cognition and auditory processing explained expertise

Yasuhara et al., iScience *27*, 110400
August 16, 2024 © 2024 Published by Elsevier Inc.
https://doi.org/10.1016/j.isci.2024.110400

iScience

CellPress
OPEN ACCESS

Article

Robustness and adaptability of sensorimotor skills in expert piano performance

Masaki Yasuhara,[1] Kazumasa Uehara,[2,3] Takanori Oku,[2,4] Sachiko Shiotani,[2,4] Isao Nambu,[5] and Shinichi Furuya[2,4,6,*]

SUMMARY

Skillful sequential action requires the delicate balance of sensorimotor control, encompassing both robustness and adaptability. However, it remains unknown whether both motor and neural responses triggered by sensory perturbation undergo plastic adaptation as a consequence of extensive sensorimotor experience. We assessed the effects of transiently delayed tone production on the subsequent motor actions and event-related potentials (ERPs) during piano performance by comparing pianists and non-musicians. Following the perturbation, the inter-keystroke interval was abnormally prolonged in non-musicians but not in pianists. By contrast, the keystroke velocity following the perturbation was increased only in the pianists. A regression model demonstrated that the change in the inter-keystroke interval covaried with the ERPs, particularly at the frontal and parietal regions. The alteration in the keystroke velocity was associated with the P300 component of the temporal region. These findings suggest that different neural mechanisms underlie robust and adaptive sensorimotor skills across proficiency level.

INTRODUCTION

Skillful behaviors are typically characterized by harmonizing both robustness and adaptability of sensorimotor control. A challenge in fast and accurate performance of sequential motor actions such as speech, typing, and musical performance is to accommodate uncertainty originating from the stochastic biological system (e.g., sensorimotor noises)[1,2] and unpredictable perturbation from the environment.[3–5] The nervous system is therefore required to optimally integrate predictive and adaptive control of movements so as to fulfill task requirements under uncertainty.[6–8] One approach to probe into this mechanism is to provide artificial sensory perturbation during motor actions.[9–14] For instance, continuously delaying the timing of tone production in speech and musical performance commonly disrupts ongoing motor actions.[15–17] However, most of previous studies have focused on motor reaction to sensory perturbation only in well-trained tasks, which limits the understanding of expertise-dependent differences in neural mechanisms subserving skillful sensorimotor control responsible for behavioral stability and adaptability.

Musical performance can be suitable for addressing this issue. Comparisons of the effects of sensory perturbation on motor actions between musicians and musically untrained individuals (i.e., non-musicians) have unveiled specialized sensorimotor skills associated with expertise.[18,19] Neural and behavioral responses to altered auditory or somatosensory feedback in musical performance differed between musicians and non-musicians.[20–23] For example, following a transient delay of timing of tone production in piano playing, non-musicians but not expert pianists, abnormally slowed down the local tempo, exhibiting movement disruption.[23] In addition, the amount of movement disruption to the perturbation was positively correlated with the age at which pianists commenced their musical training. In contrast, pianists but not non-musicians struck the key harder in response to the perturbation, which allows for elevating either somatosensory or auditory gain in motion. Yet, it has not been known what neural mechanisms mediate expertise-dependence of robust and adaptive control of fast and accurate production of sequential motor actions. One candidate neural signature is the event-related potentials (ERPs) which are electrical neural responses measured by electroencephalography (EEG) in response to cognition and sensorimotor processing.[24–27] In particular, ERPs emerging around the latency of 180 ms have been suggested to be error-related negativity (ERN), which reflects the discrepancy between the expected and actual occurrence of events.[28,29] ERPs have the potential to reflect the dynamics of internal models formed from sensory inputs and predictions about events based on prior experiences. They also reflect prediction error signals related to unexpected or deviant stimuli. Thus, assessing ERPs may provide clues to further understanding how expert musicians adjust their internal models in response to unexpected events.

---

[1]Department of Science of Technology Innovation, Nagaoka University of Technology, Nagaoka 9402137, Japan
[2]Tokyo Research, Sony Computer Science Laboratories Inc, Tokyo 1410022, Japan
[3]Department of Computer Science and Engineering, Toyohashi University of Technology, Toyohashi 4418580, Japan
[4]NeuroPiano Institute, Kyoto 6008086, Japan
[5]Graduate School of Engineering, Nagaoka University of Technology, Nagaoka 9402137, Japan
[6]Lead contact
*Correspondence: furuya@csl.sony.co.jp

https://doi.org/10.1016/j.isci.2024.110400

A more direct neuroscientific finding related to the present study is that transient alteration of the pitch in the sequential production of piano tones elicited ERN in the fronto-central region, which was more pronounced while playing the piano than listening.[28] Moreover, not only a shorter-latency component but also a longer-latency component is closely associated with metacognition including error monitoring as well as subjective error awareness.[30,31] This component is referred to as the P300 component. Based on accumulating evidence, directly comparing the N180 and the P300 components allows us to further understand what specific neural strategies skilled pianists use to cope with unexpected events and perturbations during piano playing. Here, we hypothesize that changes in ERPs elicited during a piano performance and their relation to skilled motor action may depend on musical proficiency. One reason is that skilled musicians demonstrate pronounced coupling between auditory and sensorimotor systems and their internal model is likely to involve a more complicated integration with cognitive and sensory inputs than expected. This internal model is honed by deliberate practice, enabling them to produce specific auditory sounds with highly accurate movements.

Given that the ERPs reflect certain states of internal models and metacognition, these responses can help us understand the adaptive and flexible performance abilities of expert pianists under various conditions and different environments. We infer that ERPs associated with adaptive motor response to delayed tone production let us identify whether movement flexibility in response to sensory perturbation is associated with gain modulation of unperturbed or perturbed sensory modality. However, a bottleneck for testing this is the lack of established methods to assess neurophysiological responses to sensory perturbation during fast, skillful behaviors such as piano playing.

To overcome this technical limitation, we have developed a novel system that simultaneously provides sensory perturbation and assesses behavioral and neurophysiological responses during fast piano performance with high temporal resolution. Our high-speed sensing system that measures piano key motions[32] in synchronization with the measurement of electroencephalogram (EEG) was capable of comparing the effects of transiently delayed production of a piano tone on the sequential finger movements and electrophysiological activities between expert pianists and non-musicians. By leveraging it, we characterized expertise-dependent behavioral and electrophysiological responses to sensory perturbation as well as their relationship during piano performance.

RESULTS

The novel experimental system was prepared for synchronous measurement EEG and piano key motions (Figure 1A). Fifteen pianists and 15 non-musicians performed a sequence of ten tones using their right hand (Figure 1B). Before performing the sequence, a visual cue including the metronome sound was presented to the participants (Figure 1C). The metronome sound was provided in two tempi, intermediate and fast, which were randomly assigned for each trial. Participants were instructed to perform the sequence according to the provided tempo when the Go cue was presented.

We excluded 31.4% of the trials from the analyses across all participants due to excessive noise in the preprocessed EEG signals and/or erroneous performance. Table S1 reports the excluded trials number divided by condition, group, and tempo. In addition, we computed the cumulative number of excluded trials (Figure S1). There was no significant difference in the number of excluded trials between pianists and non-musicians (t (27.538) = −0.919, $p = 0.37$).

Behavioral responses

A four-way mixed-design ANOVA with 10000 times permutation was performed to each of the inter-keystroke interval and key-descending velocity responses (Table 1). For the inter-keystroke interval, the permutation ANOVA yielded a significant four-way interaction effect. For the key descending velocity, there were significant interaction effects between group and perturbation, and between tempo, event, and perturbation. These results therefore confirmed the interaction effect of group and perturbation, which indicates a group-dependent difference in the effect of perturbation.

The mean changes in both the inter-keystroke interval and the peak key descending velocity at different events related to the delay-manipulation were computed to assess the effect of delayed auditory feedback on accuracy of the subsequent movement production (Figure 2). The value of the keystroke prior to the delay functions as a baseline of the normal unperturbed movement production.

ANOVA showed a significant three-way interaction effect for the mean inter-keystroke interval response (Table 2). Post hoc tests with correction for multiple comparisons revealed the first inter-keystroke interval after the delayed tone production differed between the pianists and non-musicians at both the intermediate tempo (F (1,28) = 70.2, $p < 0.05$) and fast tempo (F (1,28) = 32.1, $p < 0.05$). Similarly, the second inter-keystroke interval differed between the groups at both the intermediate tempo (F (1,28) = 10.6, $p < 0.05$) and fast tempo (F (1,28) = 15.7, $p < 0.05$). For both the first and second inter-keystroke intervals after the perturbation, the difference between the perturbed and unperturbed conditions was smaller for the pianists compared to non-musicians. Post hoc test also revealed that the inter-keystroke interval in the pianists differed between the two tempi at the first four successive strikes following the perturbation and that the difference between the perturbed and unperturbed conditions was smaller at slower tempo. For the non-musicians, the inter-keystroke interval differed at the first and second strikes following the perturbation between the two tempi. The one-tailed t tests revealed that the response of the inter-keystroke interval at the first strike after the perturbation was significantly greater than zero in the non-musicians ($p < 0.05$), confirming the prolongation of the local tempo in response to the disruption. For the pianists, by contrast, the response of the inter-keystroke intervals to the perturbation was significantly smaller than zero at the intermediate tempo, confirming continuous speed-up of the local tempo.

For the mean change in the key descending velocity, there were significant interaction effects between group and event, and between tempo and event (Table 2). The post hoc tests revealed the first key velocity after the tone delay significantly differed between

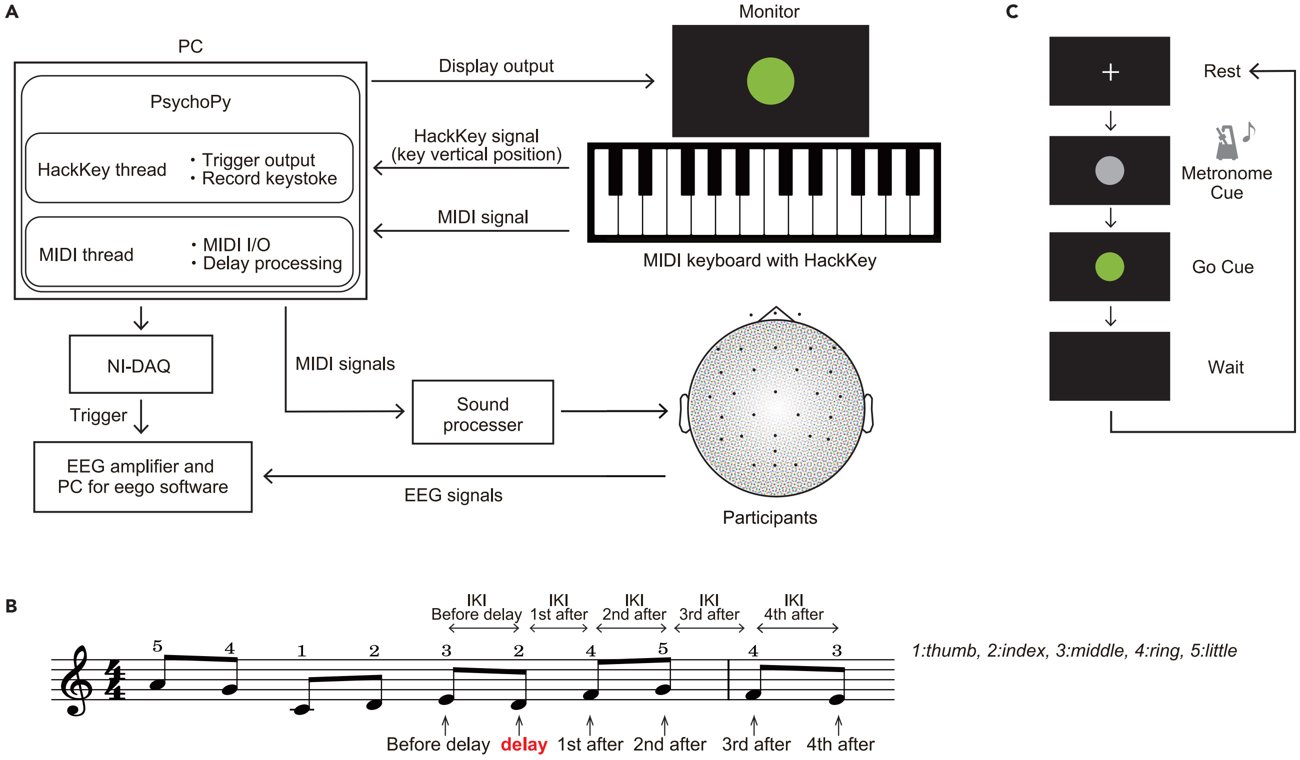


Figure 1. Experimental setup

(A) The architecture of the system for data recording and stimulus presentation. When a participant pressed the keys on the piano keyboard, the MIDI signal was transmitted into the computer (PC), and the generated sound was fed back into the participant through the binaural earphones. In parallel, the time-varying data of the key vertical position was measured by 1kHz with the HackKey system implemented in the keyboard as "HackKey signal". When the key position first moved over 5 mm, the trigger signal was sent to the EEG amplifier for the synchronous recording. The EEG signals were recorded at 1kHz from a 32-channel cap throughout a session.

(B) Musical score was presented to the participants before performing the experiment, which designated the sequence of tones and fingering. Information on the amount of timing delay of tone production was not provided. Although the musical score was not displayed on the monitor, the participants were allowed to read the score whenever necessary. The second D4 note (i.e., 6th tone) involved delayed tone production by 120 ms with a 30% probability, which was treated as the auditory perturbation in this study. EEG signals were time-locked to the onset of the 6th keystroke, which elicited the auditory perturbation, to evaluate ERP changes. IKI: the inter-keystroke interval, VEL: the key descending velocity.

(C) An experimental pipeline. Participants played the piano following the instructions displayed on the monitor. Before the Go cue was provided, a metronome sound at either 80 BPM or 160 BPM was randomly presented, and participants were instructed to play at the designated tempo.

the pianists and non-musicians, showing the larger value for the former individuals. The one-tailed t test revealed that the change in the key descending velocity was significantly smaller than zero for the non-musicians when playing at fast tempo, indicating the softer keystroke (one-tailed t test: $t(14) = -3.30$, $p = 0.003$). Conversely, in pianists, the keystroke velocity after the perturbation was larger than zero (one-tailed t test: $t(14) = 2.29$, $p = 0.038$) when playing at the intermediate tempo, indicating harder keystroke following the tone delay.

Overall, these behavioral findings indicate that the piano performance was influenced by transiently delayed auditory feedback in a distinct manner between the pianists and non-musicians. The differences between the pianists and non-musicians were evident, displaying smaller rhythmic disruption of motions and stronger strike following the perturbation in the more skilled group.

After the values of the inter-keystroke interval and keystroke velocity were standardized across trials for each participant, Pearson's correlation coefficients were calculated to assess the relationship between the variables. The results yielded no significant correlation between these two behavioral variables ($r = -0.045$, $p = 0.28$).

ERPs responses

A four-way mixed-design ANOVA with 10000 times permutation was performed to the ERPs (Table 3). Significant three-way interaction effects were evident between group, tempo, and perturbation for both N180 and P300 (Table 3). These results confirmed the interaction effect of group and perturbation, which indicates a group-dependent difference in the effect of perturbation.

Table 1. Results of four-way permutation ANOVA on each of the behavioral variables by using Group, Tempo, Event, and Perturbation as independent variables

	p value	
	Interval	Velocity
Group	**0.0028**	**0.009**
Tempo	**0**	0.376
Event	**0**	0.422
Perturbation	**0**	**0.008**
Group x Tempo	**0**	**0.008**
Group x Event	**0.0042**	0.683
Tempo x Event	**0**	0.655
Group x Perturbation	**0.0073**	**2×10^{-4}**
Tempo x Perturbation	**5×10^{-4}**	**0.008**
Event x Perturbation	**5×10^{-4}**	0.537
Group x Tempo x Event	**0.0169**	0.281
Group x Tempo x Perturbation	**0**	0.403
Group x Event x Perturbation	**0**	0.053
Tempo x Event x Perturbation	**0.0039**	**0.019**
Group x Tempo x Event x Perturbation	**5×10^{-4}**	0.619

A bold number indicates a significant effect ($p < 0.05$).

To investigate ERPs elicited by the delayed tone production, the changes in grand-averaged ERPs were computed by subtracting the value at the unperturbed condition from one at the perturbed condition (Figure 3). The negative component N180 was elicited at around 180 ms following the keystroke, and the positive component P300 was elicited at around 300 ms in both of the groups.

For the amplitude of N180, the three-way ANOVA with group, tempo, and channel showed a significant interaction effect between group and tempo (Table 4). Post hoc tests with correction for multiple comparisons, however, revealed no significant differences between groups and between tempi.

The amplitude of P300 results showed a significant three-way interaction effect (Table 4). Post hoc tests with correction for multiple comparisons revealed significant differences between the groups at the intermediate tempo at the Pz, Oz, and Fz channels, showing a larger P300 amplitude at the Pz in the pianists. There was also a significant difference between the tempi at the T8 channel of the pianists.

To further describe the characteristics of the measured ERPs, the ERPs in both the perturbed and unperturbed conditions are depicted in Figures S2 and S3. Furthermore, the topographic distribution of the differential ERPs is shown in Figure S4. Overall, the results showed that the perturbed condition showed larger ERPs compared with the unperturbed condition (Figures S2 and S3). The topographic map showed that ERPs were elicited throughout 150 to 350 ms (Figure S4).

Multiple-regression analysis

Table 5 summarizes the results of the penalized regression analyses, which explained the changes in each of the inter-keystroke intervals and the key descending velocity when playing at the intermediate tempo according to ERPs in response to the delayed tone production. The values denoted in Table 3 indicate partial regression coefficients. Figure 4 represents the coefficients derived from the penalized regression analysis, plotted on a topographic map related to the behavioral responses to the perturbation. Coefficients of the first inter-keystroke interval following the perturbation revealed that the prolonged interval, which represents the disruption of the local tempo, was associated with the decrease of both the amplitude of N180 in the bilateral temporal, and occipital regions and the amplitude of P300 in the parietal and occipital regions. Meanwhile, the increase in the amplitude of P300 in the frontal and left temporal regions and the amplitude of N180 in the frontal region was involved in the disruption of the prolonged interval.

For the first key descending velocity after the perturbation, the coefficients revealed that the stronger strike at the first keystroke after the tone delay was related to a larger P300 elicited from the right temporal region. This result indicates an association of the right temporal region with movement adaptability to the perturbation. To further probe whether this result was associated specifically with behavioral responses at the 1st strike, a control analysis was performed with data at the 2nd strike. This analysis showed that for the second inter-keystroke interval after the perturbation, both the coefficient and R^2 were 0, indicating no relationship between this behavioral response at this event and the ERPs. For the key-descending velocity, the coefficient was not greater than 0.05 and R^2 was 0.13. These results indicate that the relationship between the behavioral and neurophysiological responses was specific to the first keystroke following the perturbation.

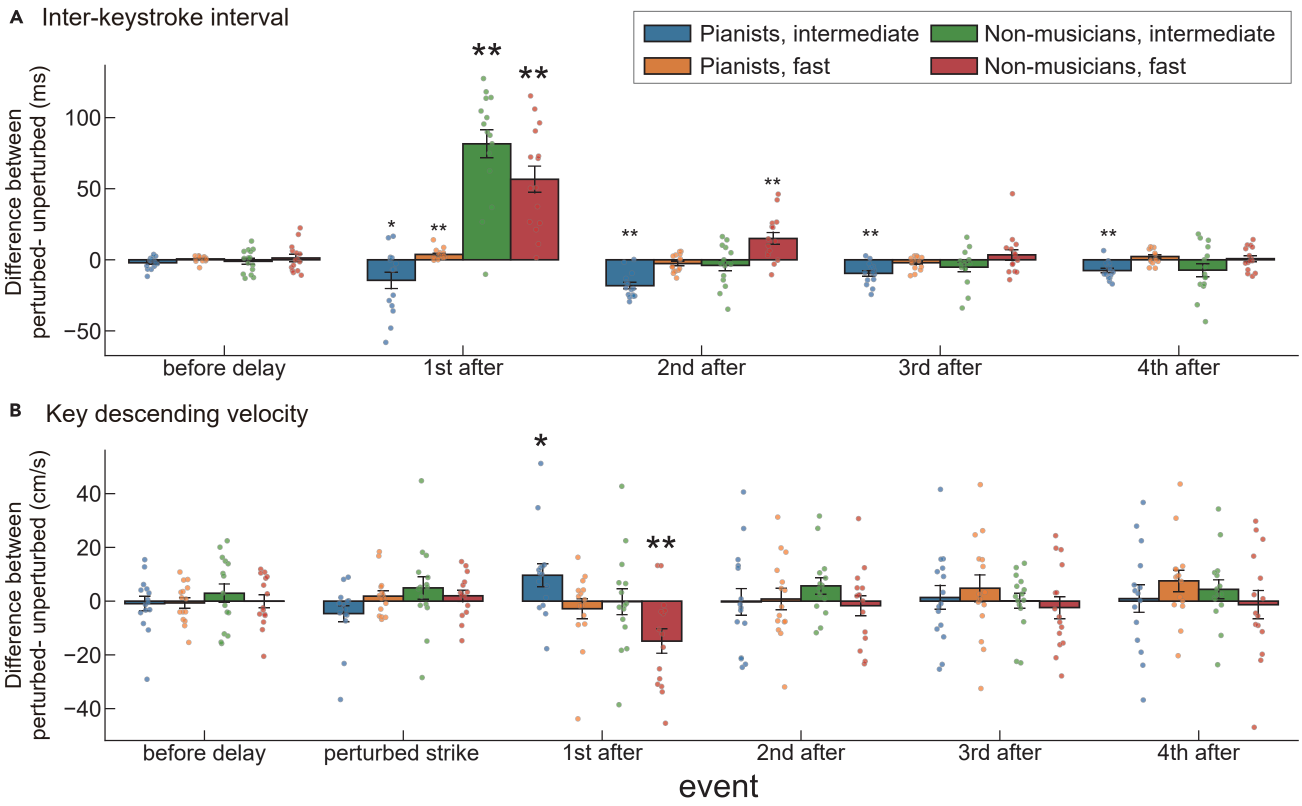


Figure 2. Effects of the transient delay of tone production on keystroke during piano playing

(A) inter-keystroke interval.

(B) peak key descending velocity.

An error bar indicates one standard error across the participants.

Blue, orange, green, and red boxes represent expert pianists at the intermediate and fast tempo, non-musicians at the intermediate and fast tempo, respectively. The value represents a difference between the conditions with and without the tone delay at each event.

The asterisk indicates the value that is significantly greater than or smaller than zero. Statistical significance: * $p < 0.05$, ** $p < 0.01$. See Figure 1B for the description of the events.

DISCUSSION

In this study, we aimed to address differences in the effects of auditory perturbation on motor and electrophysiological responses across individuals with various skill levels by leveraging the novel behavioral and neurophysiological measurement system during fast piano performance. Behaviorally, non-musicians exhibited prolonged inter-keystroke intervals after auditory perturbation. Conversely, expert pianists showed minimal changes in the inter-keystroke intervals after the perturbation, which indicates the robustness of the performance. They even appeared to compensate promptly for the tone delay by speeding up the local tempo. Furthermore, pianists were capable of increasing the key descending velocity immediately after the tone delay, probably as a way of elevating sensory gain in motion. The observation indicates that expert pianists possess a superior ability to adapt their actions online in response to auditory perturbation. Neurophysiologically, ERPs in the N180 and P300 components from the onset of the keystroke were elicited in both groups following the delayed tone production. Especially, P300 (i.e., around the parietal region) associated with aspects of cognition and efficient information processing in the brain was more sensitive to the adaptability of skillful actions. Specifically, expert musicians exhibited a significantly larger response in the Pz electrode compared to the non-musicians. The central question of the present study was to ascertain whether there exists a neural correlate explaining the high adaptability of the expert musicians to the perturbation. Our regression model revealed a close association of ERPs at both N180 and P300, specifically in the frontal and temporal regions, with the alterations in the inter-keystroke interval and key descending velocity following the perturbation, respectively. Taken together, for the first time, we provide novel evidence suggesting an association of neural activities related to cognition and auditory processing with adaptability and robustness of skillful behavior in expert musicians during fast sequential actions.

Expertise-dependent robustness and adaptability of skillful behavior

Expert musicians possess the capacity to dynamically and flexibly adjust their keystrokes with precision in terms of both force and tempo. This exceptional ability results not only from their finely tuned sensorimotor control but also from their cognitive capabilities, which include the

Table 2. Results of the three-way mixed-design ANOVA for the behavioral responses (i.e., local tempo and keystroke velocity) to the perturbation

		Interval	Velocity
Group	F(1,28)	34.920	0.488
	p	**2.34x 10^{-6}**	0.491
	eta^2	0.284	0.003
Tempo	F(1,28)	12.545	0.681
	p	**0.001**	0.416
	eta^2	0.046	0.008
Event	F(4,112)	57.531	0.925
	p	**1.61x 10^{-10}**	0.448
	eta^2	0.449	0.01
Group x Tempo	F(1,28)	4.672	1.248
	p	**0.039**	0.273
	eta^2	0.018	0.014
Group x Event	F(4,112)	61.183	2.916
	p	**7.19x 10^{-11}**	**0.027**
	eta^2	0.465	0.032
Tempo x Event	F(4,112)	8.206	4.616
	p	**0.000228**	**0.004**
	eta^2	0.049	0.031
Group x Tempo x Event	F(4,112)	13.388	0.539
	p	**2.23x 10^{-6}**	0.665
	eta^2	0.077	0.004

Interval: inter-keystroke interval.
Velocity: key descending velocity.
A bold number indicates a significant effect ($p < 0.05$).

capacity to discern subtle sensory perturbations. This cognitive skill enables them to execute skillful motor actions seamlessly during piano performances. However, this proves to be fairly challenging for non-musicians. It is not an exaggeration to assert that this difference in adaptability leads to variations in skillful performance specifically of expert musicians. While variations in the degree of adaptability exist, the fundamental ability to detect disruptions and errors plays a pivotal role in motor adaptation.[33–36] Through prolonged and intensive training leading to the acquisition of advanced musical skills, expert pianists may have honed their capacity for sensory-related error detection and the ability to promptly correct ongoing actions. This assumption is corroborated by our behavioral observations, which demonstrate that expert pianists exhibited minimal changes in inter-keystroke intervals immediately after auditory perturbations and employed a strategy to promptly recover from the tone delay (see Figure 2A).

Additionally, the inter-keystroke interval at the first strike after (1st after) the perturbation was explained by both ERPs, unlike the 2nd strike after it (see Figure 4). This indicates that neural activities related to error correction emerge within less than 500ms and disappear quickly. These findings corroborate with previous behavioral studies reporting that expert pianists possess a higher level of robustness against temporal perturbations[23] and the ability to compensate for the delay by advancing the subsequent keystroke after the delay to maintain the overall tempo of the musical performance.[14]

Interestingly, in response to the delay, non-musicians pressed the key more softly, whereas pianists pressed the key harder (see Figure 2B). This contrasting behavioral observation suggests that expertise allows for proactively correcting the delayed sensory consequence immediately. One plausible explanation is that pianists may elevate sensory gain to rely more on sensory-feedback control that allows for exploring the optimal action and/or maintaining online control of movements immediately after being perturbed. This is because an internal model in the nervous system, which predicts sensory consequences of actions, was disrupted by unexpected auditory feedback, which then increases reliance on sensory feedback control according to the framework of the optimal feedback control principle.[7,37] Following the auditory perturbation, pianists struck the key stronger, which may propose two putative mechanisms. They may attempt to receive stronger proprioceptive feedback from the finger. Alternatively, a stronger keystroke elicits a loud sound that can be utilized to correct ongoing actions through augmenting auditory feedback gain in motion. Consequently, we presume that pianists excel in terms of robustness against and adaptability to perturbation through undergoing intensive musical training. By contrast, the softer keystroke following the auditory perturbation at the fast tempo in the non-musicians may reflect reaction to alleviate effects of perturbing sensory feedback on performance of the demanding motor task.

Table 3. Results of four-way permutation ANOVAs for the ERP responses by using Group, Tempo, EEG Channel, and Perturbation as independent variables

	p value	
	N180	P300
Group	0.972	0.089
Tempo	**0.008**	0.748
Channel	0.510	**0.036**
Perturbation	**0.001**	**0**
Group x Tempo	0.661	0.619
Group x Channel	0.998	**0.028**
Tempo x Channel	0.771	0.904
Group x Perturbation	**0**	0.174
Tempo x Perturbation	0.141	**0.049**
Channel x Perturbation	0.820	0.977
Group x Tempo x Channel	0.924	0.173
Group x Tempo x Perturbation	**0.003**	**0**
Group x Channel x Perturbation	0.494	0.160
Tempo x Channel x Perturbation	0.696	0.478
Group x Tempo x Channel x Perturbation	0.677	0.203

A bold number indicates a significant effect ($p < 0.05$).

Functional significance of ERPs and their impact on skillful behavior

In this study, we focused on ERPs as a candidate neural signature that emerges in response to transient sensory perturbation.[28,38–40] ERPs are characterized by specific patterns of EEG activity in response to particular stimuli or events, encoding valuable neural information about the processing of cognitive, sensory, and motor functions.[19,41–43] This neural index enables us to shed light on cognitive and sensorimotor processes during musical performance. ERPs can be analyzed to identify components based on their latency from the onset of particular stimuli or events.[41,42,44] Among them, we drew attention to the observations of the N180 and P300 components. The negative potential around 180 ms has been suggested to be the ERN, which is an index of the discrepancy between expected and actual occurrence of events[28,29] as well as performance monitoring.[42] ERN often emerges from the anterior cingulate cortex (ACC) located in the frontal cortex when individuals receive an erroneous action.[45,46] A human lesion study also demonstrated the impaired ability of error monitoring due to lesions in the ACC.[47] Thus, the ACC has been a candidate brain region responsible for error detection. Recent human EEG studies have provided further evidence that ERNs code not only the awareness of errors but also the magnitude of errors in their amplitude.[42,48] As for the P300 component, this long-latency response is one of the most commonly reported components. Empirical evidence indicates that the P300 component is associated with metacognition including error monitoring and confidence.[30] In contrast to the ERN, P300 is more closely associated with subjective error awareness, i.e., the subjective judgment of response accuracy.[31] One of the important comparisons in our dataset is between-group differences, reflecting expertise-dependent proficiency. We found that pianists exhibited a significantly larger P300 response at the Pz electrode underneath the mid-central brain region compared to non-musicians, but not for the N180 response. This indicates that pianists have a superior ability to subjective error awareness in response to perturbation than non-musicians. Given that the P300 response is associated with error-related metacognition, expert musicians may be superior in terms of instantaneous decision-making to correct sensorimotor disruption.

Moreover, the specific behavioral trait observed only in pianists that should be discussed here together with our novel results of ERPs includes the sensory gain adjustment as mentioned previously. We argued that proprioceptive, auditory, or both may aid in adapting motor actions to auditory perturbation. Thus, a hierarchical structure of the multi-sensory system regarding the adaptability and robustness of sensorimotor control in response to perturbation may exist. Our regression analysis provides a clue in favor of this assumption. We found that key descending velocity co-varied positively with P300 emerging from the right temporal region (see Figure 4 right panel), but not the left somatosensory region (contralateral to the task side). If proprioceptive feedback is more involved following the perturbation, the left sensory region may also covary functionally with the descending velocity. We presume that the emphasis on the auditory feedback stemming from the increased key descending velocity plays a more dominant role in gain control than proprioceptive feedback. If this interpretation extends to the understanding of hierarchical representations of sensory-motor integration, auditory-motor integration may reside in a higher hierarchy than somatosensory-motor integration in expert pianists. To test this novel hypothesis generated through the present study, further work is needed.

There is one interpretational caveat that may arise from data collection procedures. Because the present study explored the onset of ERPs based on the 6th keystroke, regardless of whether or not auditory perturbation was present, we acknowledge the possibility that the auditory

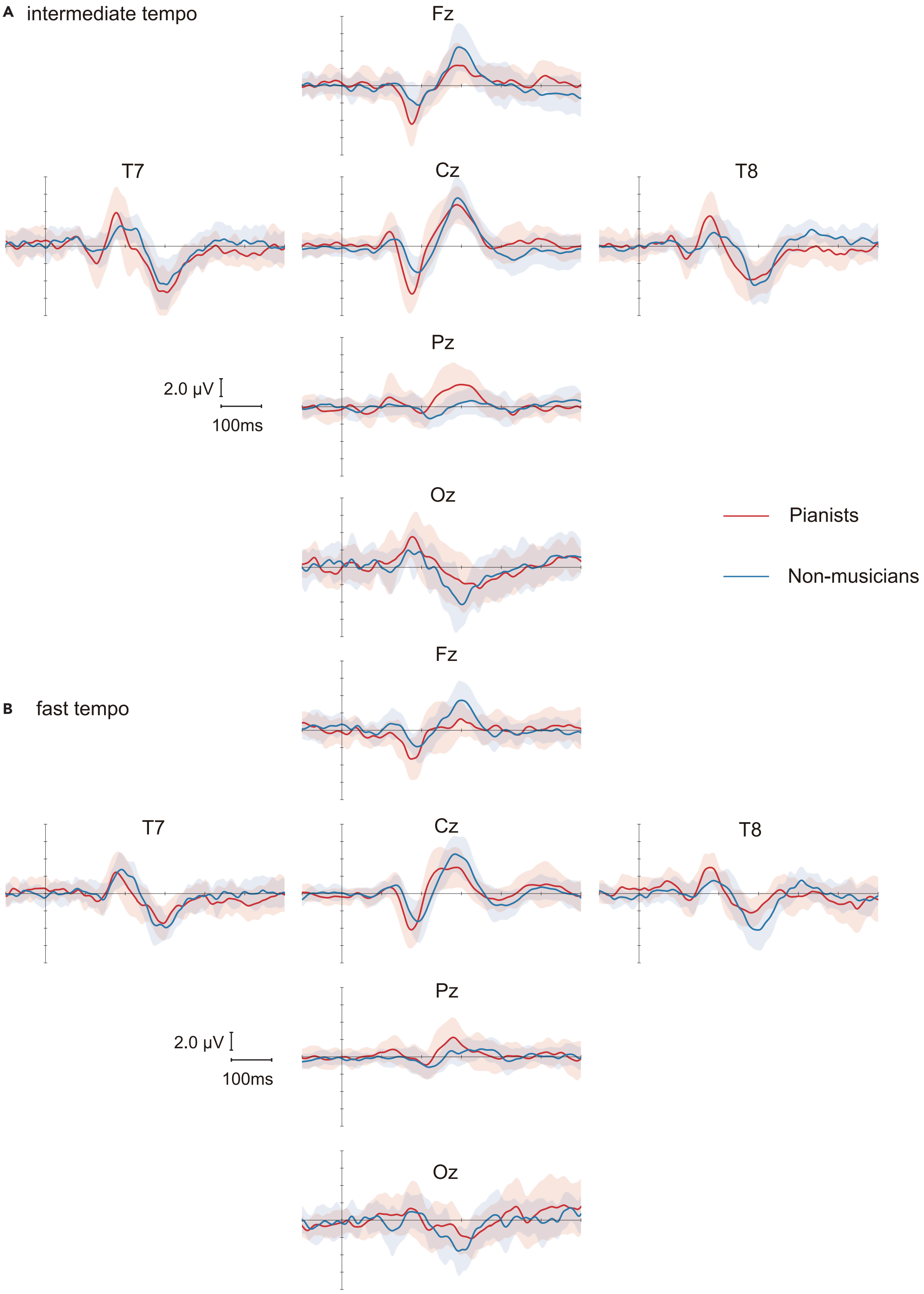

A intermediate tempo
Fz
T7
Cz
T8
Pz
2.0 µV
100ms
Oz
Pianists
Non-musicians
B fast tempo
Fz
T7
Cz
T8
Pz
2.0 µV
100ms
Oz

Figure 3. The changes in grand-averaged ERPs (perturbed - unperturbed conditions) over keystrokes after the tone production was transiently delayed
(A and B) A comparison between the pianists and non-musicians when playing at the intermediate and fast tempo, respectively.
The red and blue lines represent the pianists and non-musicians, respectively. The shaded area around the line represents one standard deviation across the participants.
Time at zero was defined as the moment when the depression of the key with delayed auditory feedback was detected. The negative component N180 was elicited at around 180 ms following the tone delay, whereas the positive component P300 was elicited at around 300 ms in both groups.
See also Figures S2–S4.

delay stemming from the perturbation merely affected the changes in ERPs. However, from a perspective of regional responses, differences in ERPs were observed between the groups in the cognitive regions specifically related to performance error monitoring and awareness of error. We therefore concluded that cognitive factors, rather than auditory effects, mainly influence changes in ERPs. Nevertheless, previous studies provide evidence for higher sensitivity to auditory evoked potential in musicians compared to non-musicians. For example, prolonged musical training leads to the enhancement of auditory discrimination and the ability of auditory perception.[28,49] Given this evidence, there is a possibility that the superior auditory function possessed by expert pianists may contribute somewhat to the adaptability of auditory perturbation.

Limitations of the study

We show here, for the first time, that high-speed behavioral and neurophysiological measurement systems allowed for successfully capturing the unique neural phenomenon. However, the present study has some limitations. We designed our experiment to reveal the neural correlates of expertise-dependent robustness and adaptability of skillful behavior. Therefore, it is still debatable whether a causal relationship exists between neural activities and behavioral characteristics. This limitation must be considered when interpreting our correlational results. Our next step should be to design a causal approach, such as triggering a virtual lesion with non-invasive brain stimulation or EEG-based neurofeedback. However, given that the adaptation of skillful performance occurs instantaneously, it is very challenging to manipulate target brain activities during high-speed actions. In addition, the present study is not designed to elucidate whether

Table 4. Summary of the three-way repeated mixed-design ANOVA with factors of Group, Tempo, and EEG channels

		Amplitude	
		N180	P300
Group	F(1,28)	1.273	0.281
	p	0.269	0.600
	eta^2	0.003	0.000
Tempo	F(1,28)	0.712	0.017
	p	0.406	0.896
	eta^2	0.001	1.55×10^{-5}
Channel	F(5,140)	22.750	44.859
	p	**1.16×10^{-16}**	**1.87×10^{-27}**
	eta^2	0.350	0.541
Group x Tempo	F(5,140)	7.113	1.404
	p	**0.013**	0.246
	eta^2	0.006	0.001
Group x Channel	F(5,140)	2.025	2.600
	p	0.079	**0.003**
	eta^2	0.046	0.064
Tempo x Channel	F(5,140)	3.364	1.424
	p	**0.007**	0.219
	eta^2	0.029	0.010
Group x Tempo x Channel	F(5,140)	1.373	2.381
	p	0.238	**0.042**
	eta^2	0.012	0.016

A bold number indicates a significant effect ($p < 0.05$).

Table 5. Summary of the Ridge regression analyses between the individual behavioral features of the keystrokes and ERPs at the intermediate tempo

		Interval		Velocity	
		1st after	2ND after	1st after	2ND after
N180	Fz	0.064	0.001	−0.053	0.039
	Cz	−0.008	−0.001	−0.104	0.011
	Oz	−0.039	0.000	0.109	−0.013
	T7	−0.056	−0.001	−0.037	0.024
	T8	−0.040	0.000	−0.054	−0.042
	Pz	0.020	0.001	0.010	−0.014
P300	Fz	0.073	0.001	−0.024	−0.005
	Cz	0.027	0.001	−0.053	−0.050
	Oz	−0.051	−0.001	−0.115	−0.040
	T7	0.084	0.000	−0.068	0.029
	T8	0.012	0.000	0.341	0.053
	Pz	−0.052	−0.001	0.102	−0.011
R^2		0.209	0.003	0.385	0.131

Interval: inter-keystroke interval.
Velocity: key descending velocity.
A sign indicates whether each dependent variable covaried positively or negatively with the independent variable.

the expertise-dependent differences in behavioral and neurophysiological responses are mediated by sensorimotor or cognitive processes. To clarify this may require a novel experimental design controlling attention in the performance or analyses of functional connectivity between sensory, cognitive, and motor regions. Also, the task difficulty can affect cognitive process, which may motivate to investigate motor reaction to sensory perturbation when playing technically demanding, naturalistic piano tasks, in order to cognitive effects on the reaction process. In our previous study,[14] however, motor reactions to transient auditory perturbation in playing naturalistic musical pieces was similar to the present observation, which may imply that the task should be one that was not learned previously. Another important issue is potential effects of the style of piano training on the sensorimotor flexibility, which has been reported to differ between classical and jazz pianists.[50] Because the present pianists are all classical pianists, pianists with different backgrounds of education and training may behave differently in response to the present auditory perturbation. Last but not least, the present observation is based solely on the

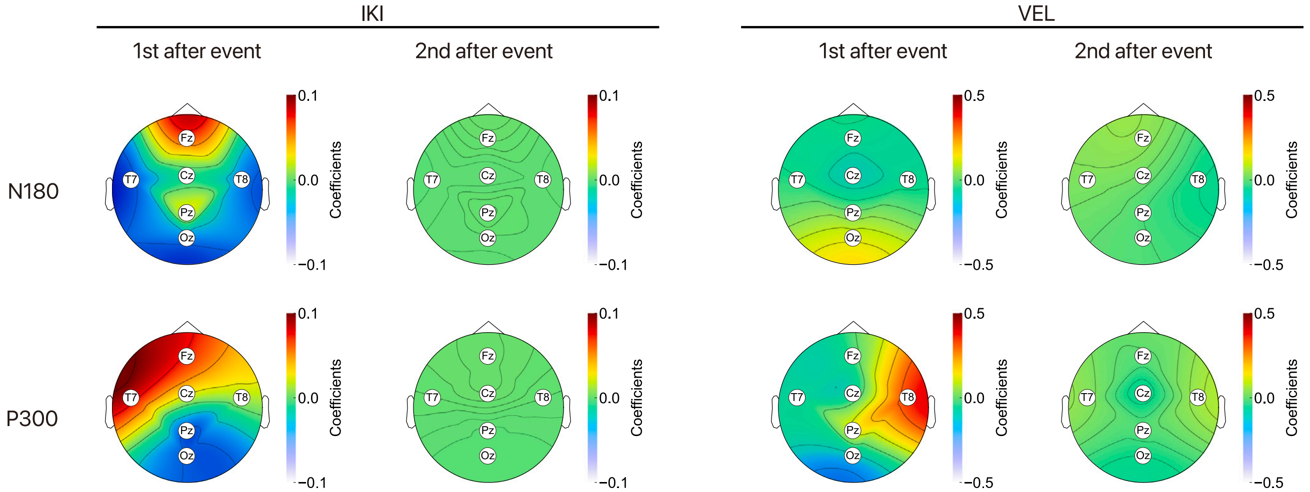


Figure 4. Topographic distribution map representing the coefficients derived from the regression analysis

For display purposes, the results outlined in Table 5 are visualized on topographic maps to facilitate a spatial understanding of their distribution. The distribution is displayed from the top, looking down at the head. Each open circle containing a label of EEG channels overlaid on each topoplot indicates channels of interest in the multiple regression analyses.

piano performance that involves a succession of discrete events. Unlike piano playing, playing the other instruments such as string and brass, as well as singing are characterized by performing continuous events, which may require different approaches from the present one.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact
  - Materials availability
  - Data and code availability
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
  - Participants
- METHOD DETAILS
  - Experimental setup
  - Experimental design
  - EEG recording
  - Data analysis
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Behavioral responses
  - Event-related potentials
  - Multiple regression analysis

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.110400.

ACKNOWLEDGMENTS

This work was supported by JST, Moonshot R&D grant number JPMJMS2012.

AUTHOR CONTRIBUTIONS

Conceptualization: S.F. and K.U.; methodology: S.F., K.U., and M.Y.; software: M.Y. and T.O.; formal analysis: M.Y., S.F., and K.U.; investigation: S.S. and M.Y.; resources: S.F., T.O., and I.N.; writing – original draft: M.Y., S.F., and K.U.; writing – review & editing: S.F., K.U., M.Y., I.N., T.O., and S.S.; project administration: S.F.

DECLARATION OF INTERESTS

All authors have no conflicts of financial and/or non-financial interest to declare.

Received: November 25, 2023
Revised: March 31, 2024
Accepted: June 25, 2024
Published: June 27, 2024

REFERENCES

1. Osborne, L.C., Lisberger, S.G., and Bialek, W. (2005). A sensory source for motor variation. Nature *437*, 412–416. https://doi.org/10.1038/nature03961.
2. Faisal, A.A., Selen, L.P.J., and Wolpert, D.M. (2008). Noise in the nervous system. Nat. Rev. Neurosci. *9*, 292–303. https://doi.org/10.1038/nrn2258.
3. Leonardo, A., and Konishi, M. (1999). Decrystallization of adult birdsong by perturbation of auditory feedback. Nature *399*, 466–470. https://doi.org/10.1038/20933.
4. Tremblay, S., Shiller, D.M., and Ostry, D.J. (2003). Somatosensory basis of speech production. Nature *423*, 866–869. https://doi.org/10.1038/nature01710.
5. Sober, S.J., and Brainard, M.S. (2009). Adult birdsong is actively maintained by error correction. Nat. Neurosci. *12*, 927–931. https://doi.org/10.1038/nn.2336.
6. Diedrichsen, J., Shadmehr, R., and Ivry, R.B. (2010). The coordination of movement: optimal feedback control and beyond. Trends Cognit. Sci. *14*, 31–39. https://doi.org/10.1016/j.tics.2009.11.004.
7. Scott, S.H. (2016). A Functional Taxonomy of Bottom-Up Sensory Feedback Processing for Motor Actions. Trends Neurosci. *39*, 512–526. https://doi.org/10.1016/j.tins.2016.06.001.
8. Uehara, K., Yasuhara, M., Koguchi, J., Oku, T., Shiotani, S., Morise, M., and Furuya, S. (2023). Brain network flexibility as a predictor of skilled musical performance. Cerebr. Cortex *33*, 10492–10503. https://doi.org/10.1093/cercor/bhad298.
9. Howell, P., and Archer, A. (1984). Susceptibility to the effects of delayed auditory feedback. Percept. Psychophys. *36*, 296–302. https://doi.org/10.3758/BF03206371.
10. Desmurget, M., Epstein, C.M., Turner, R.S., Prablanc, C., Alexander, G.E., and Grafton, S.T. (1999). Role of the posterior parietal cortex in updating reaching movements to a

visual target. Nat. Neurosci. *2*, 563–567. https://doi.org/10.1038/9219.

11. Sainburg, R.L., Ghez, C., and Kalakanis, D. (1999). Intersegmental dynamics are controlled by sequential anticipatory, error correction, and postural mechanisms. J. Neurophysiol. *81*, 1045–1056. https://doi.org/10.1152/jn.1999.81.3.1045.
12. Tian, X., and Poeppel, D. (2015). Dynamics of self-monitoring and error detection in speech production: evidence from mental imagery and MEG. J. Cognit. Neurosci. *27*, 352–364. https://doi.org/10.1162/jocn_a_00692.
13. Popp, N.J., Hernandez-Castillo, C.R., Gribble, P.L., and Diedrichsen, J. (2022). The role of feedback in the production of skilled finger sequences. J. Neurophysiol. *127*, 829–839. https://doi.org/10.1152/jn.00319.2021.
14. Furuya, S., and Soechting, J.F. (2010). Role of auditory feedback in the control of successive keystrokes during piano playing. Exp. Brain Res. *204*, 223–237. https://doi.org/10.1007/s00221-010-2307-2.
15. Pfordresher, P.Q., and Palmer, C. (2002). Effects of delayed auditory feedback on timing of music performance. Psychol. Res. *66*, 71–79. https://doi.org/10.1007/s004260100075.
16. Hashimoto, Y., and Sakai, K.L. (2003). Brain activations during conscious self-monitoring of speech production with delayed auditory feedback: an fMRI study. Hum. Brain Mapp. *20*, 22–28. https://doi.org/10.1002/hbm.10119.
17. Ozker, M., Doyle, W., Devinsky, O., and Flinker, A. (2022). A cortical network processes auditory error signals during human speech production to maintain fluency. PLoS Biol. *20*, e3001493. https://doi.org/10.1371/journal.pbio.3001493.
18. Zatorre, R.J., Chen, J.L., and Penhune, V.B. (2007). When the brain plays music : auditory – motor interactions in music perception and production. Nat. Rev. Neurosci. *8*, 547–558. https://doi.org/10.1038/nrn2152.
19. Hirano, M., Kimoto, Y., and Furuya, S. (2020). Specialized Somatosensory-Motor Integration Functions in Musicians. Cerebr. Cortex *30*, 1148–1158. https://doi.org/10.1093/cercor/bhz154.
20. Jones, J.A., and Keough, D. (2008). Auditory-motor mapping for pitch control in singers and nonsingers. Exp. Brain Res. *190*, 279–287. https://doi.org/10.1007/s00221-008-1473-y.
21. Zarate, J.M., and Zatorre, R.J. (2008). Experience-dependent neural substrates involved in vocal pitch regulation during singing. Neuroimage *40*, 1871–1887. https://doi.org/10.1016/j.neuroimage.2008.01.026.
22. Kleber, B., Zeitouni, A.G., Friberg, A., and Zatorre, R.J. (2013). Experience-dependent modulation of feedback integration during singing: role of the right anterior insula. J. Neurosci. *33*, 6070–6080. https://doi.org/10.1523/JNEUROSCI.4418-12.2013.
23. van der Steen, M.C.M., Molendijk, E.B.D., Altenmüller, E., and Furuya, S. (2014). Expert pianists do not listen: the expertise-dependent influence of temporal perturbation on the production of sequential movements. Neuroscience *269*, 290–298. https://doi.org/10.1016/j.neuroscience.2014.03.058.
24. Falkenstein, M., Hoormann, J., Christ, S., and Hohnsbein, J. (2000). ERP components on reaction errors and their functional significance: a tutorial. Biol. Psychol. *51*, 87–107. https://doi.org/10.1016/S0301-0511(99)00031-9.
25. van Schie, H.T., Mars, R.B., Coles, M.G.H., and Bekkering, H. (2004). Modulation of activity in medial frontal and motor cortices during error observation. Nat. Neurosci. *7*, 549–554. https://doi.org/10.1038/nn1239.
26. Luck, S.J., Woodman, G.F., and Vogel, E.K. (2000). Event-related potential studies of attention. Trends Cognit. Sci. *4*, 432–440. https://doi.org/10.1016/S1364-6613(00)01545-X.
27. Gehring, W.J., Goss, B., Coles, M.G.H., Meyer, D.E., and Donchin, E. (1993). A Neural System for Error Detection and Compensation. Psychol. Sci. *4*, 385–390. https://doi.org/10.1111/j.1467-9280.1993.tb00586.x.
28. Maidhof, C., Vavatzanidis, N., Prinz, W., Rieger, M., and Koelsch, S. (2010). Processing expectancy violations during music performance and perception: an ERP study. J. Cognit. Neurosci. *22*, 2401–2413. https://doi.org/10.1162/jocn.2009.21332.
29. Proverbio, A.M., Cozzi, M., Orlandi, A., and Carminati, M. (2017). Error-related negativity in the skilled brain of pianists reveals motor simulation. Neuroscience *346*, 309–319. https://doi.org/10.1016/j.neuroscience.2017.01.030.
30. Boldt, A., and Yeung, N. (2015). Shared neural markers of decision confidence and error detection. J. Neurosci. *35*, 3478–3484. https://doi.org/10.1523/JNEUROSCI.0797-14.2015.
31. Steinhauser, M., and Yeung, N. (2010). Decision processes in human performance monitoring. J. Neurosci. *30*, 15643–15653. https://doi.org/10.1523/JNEUROSCI.1899-10.2010.
32. Oku, T., and Furuya, S. (2022). Noncontact and High-Precision Sensing System for Piano Keys Identified Fingerprints of Virtuosity. Sensors *22*, 4891. https://doi.org/10.3390/s22134891.
33. Tan, H., Jenkinson, N., and Brown, P. (2014). Dynamic neural correlates of motor error monitoring and adaptation during trial-to-trial learning. J. Neurosci. *34*, 5678–5688. https://doi.org/10.1523/JNEUROSCI.4739-13.2014.
34. Seidler, R.D., Mulavara, A.P., Bloomberg, J.J., and Peters, B.T. (2015). Individual predictors of sensorimotor adaptability. Front. Syst. Neurosci. *9*, 100. https://doi.org/10.3389/fnsys.2015.00100.
35. Uehara, S., Mawase, F., and Celnik, P. (2018). Learning Similar Actions by Reinforcement or Sensory-Prediction Errors Rely on Distinct Physiological Mechanisms. Cerebr. Cortex *28*, 3478–3490. https://doi.org/10.1093/cercor/bhx214.
36. Uehara, S., Mawase, F., Therrien, A.S., Cherry-Allen, K.M., and Celnik, P. (2019). Interactions between motor exploration and reinforcement learning. J. Neurophysiol. *122*, 797–808. https://doi.org/10.1152/jn.00390.2018.
37. Todorov, E. (2004). Optimality principles in sensorimotor control. Nat. Neurosci. *7*, 907–915. https://doi.org/10.1038/nn1309.
38. Strübing, F., Herrojo Ruiz, M., Jabusch, H.C., and Altenmüller, E. (2012). Error monitoring is altered in musician's dystonia: evidence from ERP-based studies. Ann. N. Y. Acad. Sci. *1252*, 192–199. https://doi.org/10.1111/j.1749-6632.2011.06417.x.
39. Sammler, D., Novembre, G., Koelsch, S., and Keller, P.E. (2013). Syntax in a pianist's hand: ERP signatures of "embodied" syntax processing in music. Cortex *49*, 1325–1339. https://doi.org/10.1016/j.cortex.2012.06.007.
40. Bianco, R., Novembre, G., Keller, P.E., Scharf, F., Friederici, A.D., Villringer, A., and Sammler, D. (2016). Syntax in Action Has Priority over Movement Selection in Piano Playing: An ERP Study. J. Cognit. Neurosci. *28*, 41–54. https://doi.org/10.1162/jocn_a_00873.
41. van Dinteren, R., Arns, M., Jongsma, M.L.A., and Kessels, R.P.C. (2014). Combined frontal and parietal P300 amplitudes indicate compensated cognitive processing across the lifespan. Front. Aging Neurosci. *6*, 294. https://doi.org/10.3389/fnagi.2014.00294.
42. Iwane, F., Sobolewski, A., Chavarriaga, R., and Millán, J.D.R. (2023). EEG error-related potentials encode magnitude of errors and individual perceptual thresholds. iScience *26*, 107524. https://doi.org/10.1016/j.isci.2023.107524.
43. Polich, J. (2007). Updating P300: an integrative theory of P3a and P3b. Clin. Neurophysiol. *118*, 2128–2148. https://doi.org/10.1016/j.clinph.2007.04.019.
44. Squires, N.K., Squires, K.C., and Hillyard, S.A. (1975). Two varieties of long-latency positive waves evoked by unpredictable auditory stimuli in man. Clin. Neurophysiol. *38*, 387–401. https://doi.org/10.1016/0013-4694(75)90263-1.
45. Ullsperger, M., and von Cramon, D.Y. (2001). Subprocesses of performance monitoring: a dissociation of error processing and response competition revealed by event-related fMRI and ERPs. Neuroimage *14*, 1387–1401. https://doi.org/10.1006/nimg.2001.0935.
46. Brázdil, M., Roman, R., Falkenstein, M., Daniel, P., Jurák, P., and Rektor, I. (2002). Error processing–evidence from intracerebral ERP recordings. Exp. Brain Res. *146*, 460–466. https://doi.org/10.1007/s00221-002-1201-y.
47. Maier, M.E., Di Gregorio, F., Muricchio, T., and Di Pellegrino, G. (2015). Impaired rapid error monitoring but intact error signaling following rostral anterior cingulate cortex lesions in humans. Front. Hum. Neurosci. *9*, 339. https://doi.org/10.3389/fnhum.2015.00339.
48. Spinelli, G., Tieri, G., Pavone, E.F., and Aglioti, S.M. (2018). Wronger than wrong: Graded mapping of the errors of an avatar in the performance monitoring system of the onlooker. Neuroimage *167*, 1–10. https://doi.org/10.1016/j.neuroimage.2017.11.019.
49. Sanju, H.K., and Kumar, P. (2016). Enhanced auditory evoked potentials in musicians: A review of recent findings. J. Otolaryngol. *11*, 63–72. https://doi.org/10.1016/j.joto.2016.04.002.

50. Bianco, R., Novembre, G., Keller, P.E., Villringer, A., and Sammler, D. (2018). Musical genre-dependent behavioural and EEG signatures of action planning. A comparison between classical and jazz pianists. Neuroimage *169*, 383–394. https://doi.org/10.1016/j.neuroimage.2017.12.058.
51. Peirce, J., Gray, J.R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., Kastman, E., and Lindeløv, J.K. (2019). PsychoPy2: Experiments in behavior made easy. Behav. Res. Methods *51*, 195–203. https://doi.org/10.3758/s13428-018-01193-y.
52. Gramfort, A., Luessi, M., Larson, E., Engemann, D.A., Strohmeier, D., Brodbeck, C., Goj, R., Jas, M., Brooks, T., Parkkonen, L., and Hämäläinen, M. (2013). MEG and EEG data analysis with MNE-Python. Front. Neurosci. *7*, 267. https://doi.org/10.3389/fnins.2013.00267.
53. Li, A., Feitelberg, J., Saini, A.P., Höchenberger, R., and Scheltienne, M. (2022). MNE-ICALabel: Automatically annotating ICA components with ICLabel in Python. J. Open Source Softw. *7*, 4484. https://doi.org/10.21105/joss.04484.
54. Groppe, D.M., Urbach, T.P., and Kutas, M. (2011). Mass univariate analysis of event-related brain potentials/fields I: a critical tutorial review. Psychophysiology *48*, 1711–1725. https://doi.org/10.1111/j.1469-8986.2011.01273.x.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
Psychopy	Peirce et al.[51]	https://www.psychopy.org/
MNE-Python	Gramfort et al.[52]	https://mne.tools/stable/index.html
R Version 4.4.3	R Foundation	http://www.r-project.org/
The custom-made codes	This paper	https://doi.org/10.5281/zenodo.11178751
Other		
VPC1	KAWAI, Hamamatsu, Japan	https://www.kawai.jp/product/vpc1/
HackKey	Oku and Furuya[32]	https://doi.org/10.3390/s22134891
eego sports	ANT Neuro, Enschede, The Netherlands	https://www.ant-neuro.com/products/eego_sports

RESOURCE AVAILABILITY

Lead contact

Questions and requests for information and data/code should be directed to the lead contact, Shinichi Furuya (furuya@csl.sony.co.jp).

Materials availability

This study did not generate new materials.

Data and code availability

- EEG and behavioral data are available on Zenodo: https://doi.org/10.5281/zenodo.11178751.
- The custom-made codes have been deposited at Zenodo and are publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Participants

Fifteen expert pianists (mean ± standard deviation of age was 25.5 ± 7.2 years, 10 females) and 15 non-musicians (mean ± standard deviation of age was 25.6 ± 4.8 years, 10 females) participated in the study. All pianists are classical pianists and started to play the piano at 4.6 ± 1.2 years old (mean ± SD across participants), and had specialized piano education at music conservatories, which were our inclusion criteria when recruiting pianists online. The non-musicians had no piano training or less than three years of piano training, which was our inclusion criteria when recruiting non-musicians online. The local ethics committee of Sony Corporate approved this study in accordance with the guidelines established in the Declaration of Helsinki. Before starting the data collection, we obtained written informed consent from all participants.

METHOD DETAILS

Experimental setup

A custom-made experimental system was developed in order to synchronously record EEG and piano keystrokes data (Figure 1A). A digital piano (VPC1; KAWAI, Hamamatsu, Japan) that implemented position sensors under all piano keys (hereinafter referred to as "HackKey")[32] enabled to measure the time-varying vertical position of piano keys. The core experimental program was operated by Psychopy[51] (Figure 1A). The program provided instructions to participants using a display connected to the PC. The HackKey thread was responsible for monitoring and recording key vertical position over time at a sampling rate of 1kHz, and once detecting a key press that amounts 5 mm, a trigger signal was sent to the EEG recording device via an NI-DAQ (National Instruments Corporation, Texas, US). In parallel, the time-varying key position data were stored for each session. The MIDI thread either passed through the input MIDI signals or artificially delayed the timing of issuing the output signal by 120 ms (i.e., delayed auditory feedback). A Rubix22 (Roland, Hamamatsu, Japan) was used for inputting and outputting the MIDI signals. The MIDI signals processed by the MIDI thread were converted to piano sounds by a Sound Processor

(PIANO BOX PRO; MIDITECH, Cologne, Germany). Participants were provided with auditory feedback through earphones (MDREX155; SONY, Tokyo, Japan) connected to the PIANO BOX PRO.

Experimental design

Participants were asked to play a sequence of ten tones requiring the use of all five digits of the right hand (Figure 1B). Before initiating the data collection, participants underwent the familiarization session, in which they played the designated sequence at two tempi without looking at the musical score. The training period was not more than 20 min, which enabled participants to practice until they felt confident with their ability to accurately execute the sequence without seeing the hand/keyboard. Pianists typically spent about 1 min on practice, while non-musicians generally required around 15 min, and in some non-musicians, practice time extended up to 20 min. As a result of the familiarization session, the number of erroneous performances by non-musicians did not change during the experiment, indicating no learning effect following the familiarization (Figure S1). The system delayed the timing of tone production by 120 ms with a 30% probability on the second strike of the D4 key. Before the performance, a visual cue was presented to the participants via a display placed in front of them, and a metronome provided tones prior to the GO cue, indicating the tempo to be played with (Figure 1C). Metronome tones at two tempi were randomly provided, either 80 beats per minute (BPM) or 160 BPM, and participants were instructed to perform according to the played tempo when the Go cue was presented. The target inter-keystroke interval was 375 ms for 80 BPM (= intermediate tempo) and 187.5 ms for 160 BPM (=fast tempo), respectively. The experiment consisted of two sessions, each with 100 trials, which included 30 trials with the provision of delayed auditory feedback (DAF) for each of the two tempi. The participants were instructed to play as accurately as possible at the target tempo with legato touch. The participants were also asked to keep watching the display put in front of them without seeing their hands and piano keys.

EEG recording

Continuous EEG data were recorded using EEG equipment (eego sports, ANT Neuro, Enschede, The Netherlands) with a 32-channel electrode cap (WaveGuard EEG cap, Advanced Neuro Technology, Netherlands) in accordance with the international 10-10 layout at a sampling rate of 1kHz. The ground and system reference electrodes were placed at AFz and CPz, respectively. Skin/electrode impedance was kept at below 5 kΩ throughout data collection. The EEG signal was interpolated with the surrounding electrodes throughout offline analysis using the ”Raw_interpolate_bads” function in the MNE-Python when a high-impedance electrode was detected.

Data analysis

Behavioral responses

During the session, the time-varying key position data were recorded. Using this data, the inter-keystroke interval (from one key depression to the subsequent key depression) and the peak key descending velocity were computed. The key depression was defined as an event when a key moved down by 5 mm from the neutral position. The changes in the keystroke timing and loudness in response to the transient tone delay were defined as the difference in the average values of each measure between the perturbed and unperturbed conditions. The trials of the unperturbed condition were therefore used as a baseline.

Event-related potentials

MNE-python[52] was used for the EEG data analysis. The EEG data were first re-referenced to the common averaged reference. A high-pass filter with a cutoff frequency of 1 Hz was applied to remove linear trends and a notch filter targeting 50 Hz (49.75–50.25 Hz) was used to eliminate power line noise. Artifacts arising from eye blinks and muscle contractions were excluded using independent component analysis (ICA) with the InfoMax algorithm. The excluded components were selected based on ICLabel (Pion-Tonachini et al., 2019) which was implemented in Python-based software.[53] ICA-processed EEG data were epoched ranging from −100 to 600 ms with respect to the onset of the 6th keystroke, which was defined as the time of 0 ms. This indicates that ERPs were temporally synchronized with the 6th keystroke regardless of whether there was a delay or not (Figure 1B). Epochs including residual artifacts, were detected using an EEG amplitude criterion (above 100 μV) and were then excluded from the reported results. In addition, the erroneous performances were also detected and excluded according to the recorded trigger signal produced upon each key press. The erroneous performance was defined as a trial where the measured performance did not match perfectly with the target tone sequence (Figure 1B). To quantify the amplitudes of ERPs, we selected a first component of 80 ms in length (140–220 ms) for N180, and a second component of 140 ms in length (230–370 ms) for P300. These windows were selected based on previous ERP studies.[41,42,44] Grand averages were then calculated for each condition (presence or absence of delayed events, tempi), and event-related potentials (ERPs) were obtained from each individual. To quantify concrete data related to the auditory perturbation effects, the changes in grand-averaged ERPs in response to the tone delay were determined as the difference in the average values for each measure between the perturbed and unperturbed conditions. The trials in the unperturbed condition were treated as a baseline.

QUANTIFICATION AND STATISTICAL ANALYSIS

The whole statistical analyses for the behavioral and EEG responses were performed using R (version 4.4.3), ez package (version 4.4.0), and glmnet package (version 4.1.7). For both the behavioral responses and event-related potentials, a four-way mixed-design analysis of variance

(ANOVA) with 10000 times permutation were performed. Once the permutation ANOVA confirmed the interaction effect between group and condition (i.e., group-dependent effects of a difference between the perturbed and unperturbed conditions), we then performed the ANOVA by using a differential value between the conditions as a dependent variable, which was each of the behavioral responses (i.e., the inter-keystroke interval and key-descending velocity) and ERPs (i.e., N180 and P300). Post hoc tests with the Benjamini-Hochberg correction for multiple comparisons were performed in the case of significance. A statistical significance level was defined as $p = 0.05$.

Behavioral responses

To test the effects of the perturbation on the subsequent movements, a three-way mixed-design ANOVA with a group (pianists and non-musicians) as a between-subject variable, and tempo (80 BPM and 160 BPM), and event (strikes or intervals before, during and after the delayed tone production, see Figure 2) as within-subject variables were carried out. If the assumption of sphericity was violated, the Greenhouse-Geisser correction was performed. Post-hoc tests were performed to test differences between groups and tempi. In addition, one-tailed t-tests with correction for multiple comparisons using the Benjamini-Hochberg method were performed to test whether the value was greater or smaller than zero (=baseline).

Event-related potentials

To test the effects of delayed auditory feedback on ERPs, a three-way mixed-design ANOVA was performed with group (expert pianists and non-musicians), tempo (80 BPM and 160 BPM), and EEG channel (six representative channels; Fz, Cz, Pz, Oz, T7, T8) as independent variables. To avoid massive multiple comparison problems associated with post-hoc testing after ANOVA,[54] we opted for 6 representative EEG channels of each brain region (frontal, bilateral temporal, central, parietal, occipital) from 32 channels. If the assumption of sphericity was violated, the Greenhouse-Geisser correction was applied. Post-hoc tests were performed to further test differences between groups and tempo factors.

Multiple regression analysis

The primary goal of this study was to identify neural correlates of the robustness and adaptability to the transient auditory perturbation. To infer how brain activities are associated with behavioral responses, we performed a penalized multiple regression analysis with L2 norm regularization, so called Ridge regression, including all pianists and non-musicians in the model. Ridge regression was used to avoid the problem of multicollinearity. The λ parameter that determines the overall intensity of regularization was optimized through the leave-one-subject-out cross-validation to resolve over-fitting problems. The goodness of the fitting model was expressed by the R squared value (R^2). Based on the findings from our previous study[23] and from the results of behavioral responses (see Figure 2), we used four behavioral responses as dependent variables, which are the first and second inter-keystroke intervals after the perturbation and the first and second key descending velocity after the perturbation. Here, we included the behavioral responses at the second strike following the perturbation for the control analysis. The amplitudes of N180 and P300 at the six representative channels (Fz, Cz, Pz, Oz, T7, T8) were treated as independent variables of the model. All variables used were the differential value between the perturbed and unperturbed conditions in each participant. The inter-keystroke interval following the delayed tone production indicates whether or not the performance temporarily slowed down, representing the robustness of tempo control to the perturbation. The first key descending velocity after the perturbation indicates whether the keystroke becomes stronger, which is considered to be a reaction to adapt to the perturbation.[14,23] We performed the regression analyses by pooling both pianists and non-musicians as an entity, because one-sample Kolmogorov-Smirnov tests confirmed Gaussian distributions of each of all independent and dependent variables, except only for the N180 at the Pz channel ($p > 0.05$). However, we considered that N180 at the Pz channel is also one key neural signature to identify the neural correlations with musical performance. We therefore did not exclude it from the group of independent variables. In this regression analysis, we focused on the intermediate tempo condition data, because both the shorter interval and stronger keystroke following the delay in the pianists, which may reflect robustness and adaptation of movements to the perturbation, were evident only at this tempo condition.