Musical genre-dependent behavioural and EEG signatures of action planning. A comparison between classical and jazz planists

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Abstract

It is well established that musical training induces sensorimotor plasticity. However, there are remarkable differences in how musicians train for proficient stage performance. The present EEG study outlines for the first time clear-cut neurobiological differences between classical and jazz musicians at high and low levels of action planning, revealing genre-specific cognitive strategies adopted in production. Pianists imitated chord progressions without sound that were manipulated in terms of harmony and context length to assess high-level planning of sequence-structure, and in terms of the manner of playing to assess low-level parameter specification of single acts. Jazz pianists revised incongruent harmonies faster as revealed by an earlier reprogramming negativity and beta power decrease, hence neutralising response costs, albeit at the expense of a higher number of manner errors. Classical pianists in turn experienced more conflict during incongruent harmony, as shown by theta power increase, but were more ready to implement the required manner of playing, as indicated by higher accuracy and beta power decrease. These findings demonstrate that specific demands and action focus of training lead to differential weighting of hierarchical action planning. This suggests different enduring markers impressed in the brain when a musician practices one or the other style.

Keywords: plasticity, action planning, specialised-musical training, event-related potentials, oscillations

INTRODUCTION

Human skilled behaviours require optimal adaptation of brain structure and function to proficiently meet environmental demands. Music production is emblematic for how extensive training can foster precision and fluency in performance accompanied by remarkable anatomical and functional changes in sensorimotor brain areas (Herholz and Zatorre, 2012; Münte et al., 2002). Importantly, research in the auditory domain not only points to general effects of musical training but suggests nuanced neurocognitive adaptations depending on specialised training or even stylistic enculturation (Stewart, 2008; Tervaniemi, 2009). In fact, not only are low-level auditory perception (Munte et al., 2003; Schneider et al., 2005; Shahin et al., 2008) or basic motor functions (Rüber et al., 2013) differentially shaped by the type of practiced instrument; even higher levels of music anticipation based on structural properties of the music are differentially shaped by practiced genre such as classical, rock or jazz (Eerola et al., 2009; Hansen et al., 2016; Loui et al., 2014; Vuust et al., 2012). However, concerning this last point, virtually all research to date remains confined to the auditory domain, leaving potentially similar impact of genre on production unexplored. Here, we ask whether and how training in different musical styles—classical or jazz—affects musical action planning, with the goal to unveil the neurobiological grounds for specialised cognitive-motor strategies adopted in skilled motor behaviours. We show behavioural and neural differences between musicians from the two genres reflecting differential calibration of hierarchical planning processes depending on classical or jazz training.

It is widely established that skilled behaviours are generated by the interaction of hierarchical representational levels, ranging from movement goals (selection level) down to the specification of the actual muscle commands (execution level) (Diedrichsen and Kornysheva, 2015; Rosenbaum et al., 2007; Verwey et al., 2015). For example, sequential finger movements or simple actions require planning of the whole movement sequence which binds the appropriate single acts ('what' should be done in which order at the sequence level), and to specify motor implementation details of each act ('how' to do at the single act level) (Grafton and Hamilton, 2007; Koechlin and Summerfield, 2007; Lashley, 1951; Rosenbaum et al., 2007; Schmidt, 1975; Uithol et al., 2012; Verwey et al., 2015; Wohlschläger et al., 2003). Such hierarchical representations of actions are formed through motor training and allow generalization and flexible generation of novel behaviours (Diedrichsen and Kornysheva, 2015; Waters-Metenier et al., 2014). Skilled musicians, for instance pianists, not only accurately specify the fingers used to implement each single act on the keyboard; to enhance fluency, they also plan in advance what to play next based on the preceding musical sequence (Bianco et al., 2016a; Novembre and Keller, 2011; Sammler et al., 2013). However, practice in different genres may predominantly engage one or another hierarchical level of action representation (see below), hence action planning processes may become subject to habits. In this study, we investigate whether experience-dependent biases, as specialized musical training, are manifest at different hierarchical representational levels during music production.

Recent event-related potential (ERP) studies identified neural markers of distinct representational levels of musical action planning in piano performance. Specifically, these reports dissociated planning at sequence and single act level, contrasting high-level music-structural goals, the 'what', and low-level setting of appropriate movement parameters, the 'how'. Classically trained pianists imitated unrehearsed chord sequences in which final chords were violated either in their musicstructural fit with the preceding harmonic context, i.e., the sequence-level harmonic goal according to the rules of western tonal music, or in their manner of execution, i.e., the fingering of the single chord. Context-dependent behavioural (response costs) and neural responses (a late "reprogramming" negativity) to the unexpected structure violations indicated that musicians use the context and their knowledge of musical structure to (i) generate motor predictions at the level of the action sequence and anticipate the identity of the next chord to play (Novembre and Keller, 2011; Sammler et al., 2013). At the same time, a distinct neural response to violations in the manner of execution (a late positivity) disclosed (ii) the lower-level representation of *single act* movement parameters, that is usually optimally set for achieving the desired action goal (Bianco et al., 2016a). In addition, other research on prediction and motor control in music production documented an increase of frontal theta power during performance errors at sequence-level (i.e., execution of a wrong note) (Ruiz et al., 2011), in line with multiple reports of frontal theta modulations during conflict-detection (Botvinick et al., 2004; Cavanagh and Frank, 2014; Luu et al., 2004; Trujillo and Allen, 2007) and inhibition of anticipated congruent responses (Harmony et al., 2009; Kirmizi-Alsan et al., 2006). Altogether, these studies provide measurable neural evidence that expert musicians plan their actions at different hierarchical representational levels and that they implement motor-predictive/control mechanisms in order to plan performance efficiently and to react to unexpected events/performance errors.

However, these neural mechanisms have been investigated only in one type of musician, namely, performers specialising in the classical genre. To the best of our knowledge, no study has tested if these effects depict a rigid, common cognitive organization of motor-predictive strategies developed after extensive general training or whether they can be differentially modulated by specific demands and action focus of the training. For example, improvising jazz or playing a classical concerto requires focus on different levels of performance and may—in the long run—shape action tendencies and cognitive-motor strategies of musicians. Jazz musicians can be said to adopt a *structure-generative focus* when playing (more than classical musicians): they focus particularly on building musical *sequences* in real-time and in a way that plays with the audience's expectations (Beaty, 2015; Pressing, 1984). These skills not only require perfect mastery of musical conventions and (harmonic) rules in order to creatively deviate from them (Johnson-Laird, 2002); they also imply increased familiarity with non-canonical structural alternatives¹ that the musician actively embraces or revokes more or less on the fly (Pressing, 1987). In contrast, classical musicians (more than jazz musicians)

¹ Note that both classical and jazz music traditions are similarly rooted in Western tonal harmony (Goldman, 2012; Johnson-Laird, 2002), which defines the arrangement of chords into well-structured musical sequences (Swain, 1995).

adopt a *structure-interpretative focus* when playing: they specifically focus on the range of possible expressive features to be applied to the musical structure, which is usually fixed by the composer (Shaffer, 1984). These features include, amongst others (see Keller 2012), the choice of particular fingerings for each *single act* (e.g., the thumb being stronger and better suited for accentuation; Parncutt, 2014), which is usually a crucial component in the preparation of classical performance and requires intensive practice of fingering technique (Gellrich and Parncutt, 1998). This experience not only entails the ability to select the optimal fingering on the spot, even when the music is unrehearsed as in sight-reading (Clarke, 2001); it also implies a rapid and straightforward inference of the most likely forthcoming structural element, to immediately proceed to expressive stages of action planning (Chaffin et al., 2007; Clarke, 2001). In the present study, we tested the hypothesis that, despite equal amounts of training, differences in focus of daily practice may induce genre-specific cognitive-motor strategies, as reflected in neural and behavioural markers of musicians specialising in jazz improvisation versus classical performance, even when playing the same music. These differences in strategies may most likely be reflected in different calibration of the hierarchical levels of action planning (see Figure 1).



Figure 1. Multiple layers of action planning and hypothesized influence of action focus. High-level structure-based plans of action sequences are formed based on structural (e.g., harmonic) knowledge and the unfolding musical context. These plans determine the appropriate ordering ('Order') and consequently the identity ('What') of single acts in a sequence. Lower-level parameters (e.g., fingering) are specified at later stages of action planning. These parameters determine the optimal motoric implementation ('How') of the single act. This multilayer organization of actions may be tuned by (i) a structure-generative (jazz) or (ii) a structure-interpretative (classical) action focus: (i) requires active (re)arrangement of structural alternatives at the level of the action sequence (as indicated by double arrows), while (ii) requires straightforward planning of the most probable order of the action sequence (single arrow) for rapid assignment of relevant motor parameters of the single act (bold arrow).

To study genre-specific differences at high and low levels of action planning, we adopted the same real-time music production task as in Bianco et al. (2016) while measuring EEG in jazz and classical planists. In complete absence of sound, planists were required to watch and imitate unrehearsed chord sequences played by a performing planist's hand presented in series of photos on a computer screen.

Although unusual, absence of sound was essential, as in previous studies, to focus on the cognitivemotor aspects of the task and to eliminate exogenously driven auditory predictive processes. Similarly, the decision to display musical sequences by virtue of a model hand instead of for instance scores aimed to minimise intermediate translation processes of abstract symbolic stimuli into action, and to level out potential inter-individual or between-group differences in score-reading abilities.

To address (i) planning at high action sequence level, we manipulated the predictability and harmonic fit of the final chord by placing it at the end of 5- or 2-chord sequences (long/short Context) and by rendering it harmonically (in)congruent with the preceding musical context (congruent/incongruent Harmony). Given that long compared to short sequences provide more information for harmonic structure building, context-dependent behavioural costs and a late negativity (Sammler et al., 2013; Bianco et al., 2016a) associated with the harmonic violation were taken as relevant indices of highlevel structure-plan building/reassessment. To address (ii) the lower level of single act *implementation*, the final chord was manipulated not only in terms of Harmony (i.e. 'what' to play) but also in terms of fingering used for execution (conventional/unconventional Manner; i.e. 'how' to play). Because movement parameters are related to single acts and are specified at late stages of action planning, context-independent response time costs and a late positivity (Bianco et al., 2016a) associated with the manner violation were taken as indices of low-level movement parameter setting of single acts. Beyond these behavioural and ERP signatures, we further explored neural oscillatory activity in the theta band as an established marker of action monitoring in specialized musicians (Ruiz et al., 2011) and the beta band as a correlate of general motor processes (Kilner et al., 1999) and error detection during action observation, planning and execution (Koelewijn et al., 2008; Ruiz et al., 2011; Tzagarakis et al., 2010).

We hypothesised different weightings and dynamics within different hierarchical levels of action planning depending on classical and jazz training: (i) If a *structure-generative focus* fosters active (re)arrangement of structural alternatives at the level of the *action sequence*, then jazz compared to classical pianists should show behavioural and neural signals of less conflict and greater flexibility in the processing and revision of their motor plans when responding to harmonically unexpected final chords, particularly in the long context; (ii) if a *structure-interpretative focus* leads pianists to rely on the most likely structure-plan to rapidly proceed to setting the manner of execution at the level of the *single act*, then classical compared to jazz pianists should show behavioural and neural signals of greater conflict in response to harmonic novelties, yet greater accuracy in setting appropriate fingering parameters.



Figure 2. Experimental design. In absence of sound, pianists executed unrehearsed chord progressions by imitating a performing hand presented in series of photos. The sequences were manipulated in their last chord in terms of Harmony (congruent/incongruent) and Manner (correct/incorrect). Furthermore, the length of the Context (long/short) manipulated the overall structure-based predictability of the last chord.

MATERIAL AND METHODS

Participants

Fifteen classical pianists (classical group, CG, 11 females) and 15 jazz pianists (jazz group, JG, 1 female)² gave informed consent to participate in the study. All pianists had received formal training at music academies with focus on the classical or jazz genre, e.g., the Hochschule für Musik und Theater "Felix Mendelssohn-Bartholdy" in Leipzig. Classical pianists were a subset of the original dataset of 26 individuals (from Bianco et al., 2016) chosen to match the jazz pianists in the following criteria: The two groups were comparable in age (mean age \pm *SEM* of CG: 25.5 \pm 1 years; JG: 25.7 \pm 1.3 years; t(28) = 0.123, p > .903), total accumulated hours of piano training across their life (CG: 11886 \pm 1621 hours; JG: 11485 \pm 1387 hours; t(28) = -0.188, p > .852), and onset of piano playing (age of onset, CG: 6.7 \pm 0.7 years; JG: 9.0 \pm 1.0 years; t(28) = 1.88, p > .071). All pianists had at least 6 years of musical training. At the time of testing, all participants were similarly musically active in terms of current piano practice, as revealed by the comparison of average practice hours per week over the past year (CG: 8.9 hours; JG: 13.3 hours; t(28) = 1.19, p > .245). The criteria to qualify as a classical pianist was to have no jazz or improvisation experience, while a minimum of 2 years of jazz piano training was required to be assigned to the jazz group. The JG had in fact more accumulated training

 $^{^{2}}$ Studies on sex-difference in fine-motor skills have so far shown no effects of sex at expert stages of motor performance (Dorfberger et al., 2009), and no relationship between sex and jazz improvisation ability, skills or knowledge (Madura, 1996). However, it is possible that the gender imbalance we encountered in recruiting the jazz group may have social-psychological grounds, e.g., confidence and attitude, that influence female participation in instrumental jazz improvisation (Wehr-Flowers, 2006).

hours in jazz than in classical piano (in JG: 7202 ± 954 jazz training hours and 4684 ± 621 classical training hours; t(28) = 2.78, p < .014). On a scale from 1 to 9, the JG reported to practice music more often without reading from scores than the CG (CG: 4.8 ± 0.6 ; JG: 6.5 ± 0.5 ; t(28) = 2.22, p < .035), although both groups reported comparable abilities to read scores (CG: 5.73 ± 0.7 ; JG: 4.26 ± 0.6 ; t(28) = -1.72, p > .100). All participants were naïve with regard to the purpose of the study and received monetary compensation for participation. The local ethics committee of the University of Leipzig approved the study (016-15-260-12015).

Stimuli

Stimuli were the same as those used in Bianco et al. (2016a), i.e., photos showing a male pianist's right hand playing sequences of chords on the piano (Yamaha Clavinova CLP150). All participants were presented with 72 sequences that were composed according to the rules of classical harmony in four tonalities with either two or four sharps or flats, i.e., D, E, Bb, and Ab major. Sequences consisted of chords of three keystrokes each and differed in melodic contour. The last chord of each sequence was manipulated according to a 2 x 2 factorial design, in terms of Harmony (H) to target structurebased planning (congruent Tonic chord vs. an incongruent Neapolitan chord) and/or in terms of Manner (M) to target parameter specification (conventional fingering – i.e., 124, 125, 135, vs. unconventional fingering – i.e., 123, 235, 245, where 1 represents the thumb, 2 the index and 3, 4 and 5 the middle, the ring and the little finger, respectively; for a more detailed description of the stimuli, see Bianco et al., 2016a and Figure 2). Thirty-six sequences were conventional in terms of both Harmony and Manner (H congruent/M correct: H_cM_c), 12 contained violations in terms of Harmony but not Manner (H incongruent/M correct: H_iM_e), 12 in terms of Manner but not Harmony (H congruent/M incorrect: H_cM_i), and 12 were violated in terms of both factors (H incongruent/M incorrect: H_iM_i). The harmonic predictability of the last chord was manipulated by placing it either at the end of five-chord sequences (long context for high predictability), or two-chord sequences (short context for low predictability). The two-chord sequences were identical with the last two chords of the five-chord sequences. Hence, comparing the 4 conditions across the two contexts allowed us both to measure context-dependent structure-based planning of the last chord while controlling for motoric differences, i.e., longer movement trajectories from penultimate to incongruent / unconventional chords than in the congruent / conventional conditions. The total duration of the long and short sequences was 12 and 6 sec, respectively, including a 2 sec preparatory photo showing a hand about to press the first chord, followed by photos of the 5- or 2-chord sequences presented at a rate of 2 sec per photo. Each trial started with a visual fixation cross of 0.5 sec and ended with a black screen of 1.5 sec after the final photo of the stimulus sequence. To facilitate recognition of the relevant keys and fingers, red circles were superimposed on top of each pressed key for the whole duration of the photo.

Procedure

We adopted the same experimental procedure as Bianco et al. (2016a). Pianists were asked to watch the photo series of the model hand on a computer monitor (100 Hz refresh rate) and simultaneously to execute the chords with their right hand on a MIDI (musical instrument digital interface) piano (Yamaha Clavinova CLP150, Yamaha Music Europe GmbH, Rellingen, Germany) (see Figure 2). Note that the piano was muted and no sound was presented with the photos. Pianists were instructed to execute the chords one by one, as quickly and accurately as possible, both in terms of the keys pressed (Harmony) and in terms of fingering (Manner). The experiment consisted of 6 experimental blocks. Each block contained 24 non-violated trials (H_cM_c) intermixed with 24 trials of one of the violation conditions (H_iM_c , H_cM_i , or H_iM_i), separately for long and short sequences. Block order was counterbalanced across participants and alternated between blocks with long and short sequences. To increase the number of trials, each pianist participated in two sessions on separate days with the same stimuli and the same block order. In order to acquaint participants with the task, the first session started with 6 short blocks of 24 practice trials each (12 H_cM_c and 12 H_iM_c, H_cM_i, or H_iM_i in long or short context) in tonalities that were not used in the main experiment (G, F, Db, and B major). Stimulus presentation and response registration were controlled by Presentation software (Version 14.9, Neurobehavioural System, Inc.). MIDI piano key values were converted into a serial signal compatible with Presentation software through a custom-built MIDI interface. Participants' right hands were filmed with a video camera placed above the keyboard for (off-line) analysis of their fingering accuracy.

EEG data acquisition

EEG recordings were acquired from 61 Ag/AgCl electrodes (Fpz, Fp1, Fp2, AFz, AF3, AF4, AF7, AF8, Fz, F3, F4, F5, F6, F7, F8, F1, FC2, FCz, FC3, FC4, FC5, FC6, FT7, FT8, FC1, F2, Cz, C1, C2, C3, C4, C5, C6, T7, T8, CPz, CP3, CP4, CP5, CP6, TP7, TP8, P1, P2, Pz, P3, P4, P5, P6, P7, P8, CP1, CP2, POz, PO3, PO4, PO7, PO8, O1, O2, Oz) placed according to the international 10-20 system (Sharbrough et al., 1991). The left mastoid (M1) served as reference. Three additional electrodes were placed on the sternum as common ground, on the right mastoid bone (M2), and on the tip of the nose for off-line re-referencing. Vertical and horizontal EOG was recorded from two bipolar montages, one with electrodes located above and below the left eye, the other with two electrodes placed on the outer canthus of each eye. Signals were amplified using a 24-bit Brainvision QuickAmp 72 amplifier (Brain Products GmbH, Gilching, Germany) with input impedances below 5 k Ω and digitised at a 500 Hz sampling rate.

Behavioural data analysis

Response times (RTs) and execution errors of the last chord of valid trials were analysed as in previous studies (Novembre and Keller, 2011; Sammler et al., 2013; Bianco et al., 2016). Trials were considered valid when (1) no key and fingering mistakes occurred in the last and the second last

chords, (2) the keystrokes within a chord were synchronous (i.e., no more than 150 msec elapsed between the first and the last of the 3 keystrokes) and (3) RTs were below 3000 msec (Drost et al., 2005). RTs were averaged across the three keystrokes and were time-locked to the onset of the photo showing the last chord. Fingering of the participants was analysed through off-line inspection of the video recordings of their hands. Statistical evaluation of the RT data was done using four-way of (ANOVAs) with the repeated-measures analyses variance factors Harmony (congruent/incongruent), Context (long/short), Manner (correct/incorrect), and the between-subjects factor Group (classical/jazz). Errors were analysed with two analogous ANOVAs, separately for key and fingering errors.

EEG data analysis

Pre-processing. EEG data were pre-processed using EEGLAB 9 (Delorme and Makeig, 2004) implemented in MATLAB 7.4. Data were first re-referenced to the algebraic mean of the mastoids and filtered with a 0.3-Hz high-pass filter (FIR 5854 points, Blackman window). Then, electrode drifts, strong muscle and technical artefacts were manually rejected and data were entered into an Independent Component Analysis (ICA) to parcel out the contribution of artefacts such as eye movements, continuous tension of muscles, slow drifts and technical noise. After 45-Hz low pass filtering (fir, 810 points, Blackman window), epochs were extracted from behaviourally correct trials between -900 and 2200 msec relative to the onset of the last (target) chord. Only trials with signal voltages within \pm 80 µV at all electrodes were included in further analyses and averaged separately for each condition. 21% and 38% of the total number of trials were discarded in the classical (CG) and jazz group (JG), respectively. To ensure that group differences cannot be attributed to trial count or signal-to-noise ratio, we randomly eliminated further trials in CG to equate them with the trial numbers of the JG in each condition.

Event-related potentials. For each participant and each condition, event-related potentials (ERPs) were computed from -200 to 1200 ms relative to the onset of the target photo and baseline correction was performed (baseline: -200 to 0 ms). For statistical analysis, mean amplitudes were extracted separately for each condition from 9 regions of interest (ROIs) in specific time-windows (see below). The ROIs comprised: (i) left anterior (F3, F5, F7, FC3, FC5, FT7, AF3), (ii) left central (C3, C5, T7, CP3, CP5, TP7), (iii) left posterior (P3, P5, P7, PO3, PO7), (iv) middle anterior (F1, FZ, F2, FC1, FCZ, FC2, AFZ), (v) middle central (C1, CZ, C2, CP1, CPZ, CP2), (vi) middle posterior (P1, PZ, P2, POZ), (vii) right anterior (F4, F6, F8, FC4, FC6, FT8, AF4), (viii) right central (C4, C6, T8, CP4, CP6, TP8), (ix) right posterior (P4, P6, P8, PO4, PO8). Time windows were defined for analyses of the Harmony and the Manner effects according to the relative effects found in previous research (Bianco et al., 2016a; Sammler et al., 2013) and adjusted to the new data-set according with objective criteria as following: assuming that different map topographies and polarities directly indicate different underlying generators (Michel et al., 2004), borders of the time windows were placed at the average time point (across electrodes) at which changes in polarity and/or topography were found in

one or the other group. This procedure yielded time windows (i) from 370 to 550 ms and (ii) from 550 to 1200 ms for Harmony effects; (i) from 180 to 420 ms and (ii) from 420 to 800 ms for Manner effects. Non-parametric cluster-based permutation tests applied to the data with standard parameters in FieldTrip (<u>http://www.fieldtriptoolbox.org</u>) led to qualitatively similar results as those obtained with the above defined time windows, hence validating the choice of the borders. Statistical analyses of mean amplitude values were carried out by means of six-way ANOVAs with the repeated measures factors Harmony (congruent/incongruent) x Context (long/short) x Manner (correct/incorrect) x Laterality (left/middle/right) x AntPost (anterior/central/posterior) and the between-subjects factor Group (classical/jazz), separately for each time window and in line with our previous work (Bianco et al., 2016a; Sammler et al., 2013). Greenhouse-Geisser correction for non-sphericity was applied where appropriate (Keselman and Rogan, 1980).

Time-frequency analysis. Time-frequency (TF) analysis was carried out in FieldTrip (http://www.fieldtriptoolbox.org, downloaded on 2012-12-05) (Oostenveld et al., 2011). To define frequency bands and time windows that were generally associated with visual-motor processing of chords regardless of experimental manipulation, we first analysed TF responses consistently evoked by all (not only the final) chords. Therefore, the preprocessed EEG data were cut into epochs from -900 to 2200 ms for each chord of long and short sequences. Epochs with voltages exceeding a \pm $80 \,\mu V$ rejection criterion at one or more electrodes were rejected. Then, TF information was extracted from each clean trial in 1-Hz bins within a 1-45 Hz frequency range using a Hanning-tapered window with 5 cycles and steps of 20 ms (using the 'ft frequalysis' function with 'mtmconvol' method as implemented in FieldTrip) and collapsed across all conditions and groups. Trials were baselinecorrected (-400 to ms with respect to the onset of the target photo) and further divided by the baseline band power to centre values on zero (Figure 3). To reduce the set of statistical inferences, we adopted a rigorous data-driven approach: time-points and frequency bins in which average power (across all electrodes) differed significantly from zero (Bonferroni-corrected) were used to define time-frequency borders/regions for statistics. These were: 4-6 Hz (theta band) (i) from 220 to 480 ms and (ii) from 1080 to1200 ms, and 22-26 Hz (beta band) (i) from 360 to 520 ms.



Figure 3. Raw spectral power change averaged across all electrodes during imitation of all chords across all conditions and groups. Time zero corresponds to chord onset on screen.

For statistical comparison of the TF data of the final chords, mean power values were then extracted in the three time-frequency regions identified above, in the same 9 ROIs as used for the ERP analysis. Six-way ANOVAs with the repeated measures factors Harmony (congruent/incongruent) x Context (long/short) x Manner (correct/incorrect) x Laterality (left/middle/right) x AntPost (anterior/central/posterior) and the between-subjects factor Group (classical/jazz) were calculated separately for theta and beta frequency band. Greenhouse-Geisser correction for non-sphericity was applied where appropriate. Non-parametric cluster-based permutation tests (cf. Maris and Oostenveld 2007) with specific contrasts of interest (effects of Harmony and Manner for each context and each group) corroborated the main effects yielded by the ANOVAs.

RESULTS

The present study compared musical action planning between classical (CG) and jazz pianists (JG) at (i) action sequence and (ii) single act levels. Behavioural and electrophysiological signatures (ERPs and spectral power) of (i) sequence-level structure-based planning should be context-*dependent*, i.e. statistically stronger in long than short sequences, reflected in interactions of Harmony x Context, while markers of (ii) single-act parameter specification should be context-*independent*, i.e. reflected in main effects of Manner (without Manner x Context interaction). Genre-specific differences in these planning processes should surface as Group x Harmony x Context and Group x Manner interactions, respectively.

Behavioural data

Response times. Statistical values of the four-way mixed-measures ANOVA with factors Harmony (congruent/incongruent), Context (long/short), Manner (correct/incorrect), and Group (classical/jazz) are reported in Table 1 and Figure 4A-B. Overall, both groups performed similarly fast (no main effect of Group; p > .594), and imitated harmonically congruent chords faster than incongruent chords (main effect of Harmony; p < .001; no interaction of Group x Harmony; p > .660). However, differences were revealed in the way classical and jazz pianists reacted to harmonic manipulations in the two contexts: A significant interaction of Group x Harmony x Context (p < .046) indicated a stronger effect of context on the execution of harmonically congruent vs. incongruent chords in the classical (CG) compared to the jazz group (JG). Follow-up ANOVAs with factors Harmony and Context testing CG and JG separately confirmed an interaction of Harmony x Context only in the CG [F(1,14) = 17.51, p < .001, $\eta_p^2 = .56$], not in the JG [F(1,14) = 1.37, p > .261, $\eta_p^2 = .09$]. This suggests differences in structure-based planning between the two groups, with CG being potentially inclined to build narrower plans than JG to rapidly proceed to planning expressive features, and/or JG being potentially better able than CG to flexibly adapt their plans to unexpected external musical events, as practiced during structure-generative training.

Both groups were overall faster in executing conventional compared to unconventional fingerings, as expected (main effect of Manner; p < .001; no interaction of Group x Manner; p > .146). Neither CG

nor JG showed significant Manner x Context interactions (no Manner x Context interaction; p > .149; no Group x Manner x Context interaction; p > .745) indicating that movement parameters are specified at the level of single acts (not of the action sequence) regardless of training specialization.

Error analysis. Key and fingering errors were analysed separately (for statistical details, see Table 1) because they are assumed to be associated with structure-based planning (i.e., Harmony) or parameter specification, respectively (i.e., Manner; see Bianco et al., 2016a; Novembre & Keller, 2011). Overall, pianists committed very few errors (mean \pm *SEM* of key errors: 2.0 \pm 0.2%; fingering errors: 9.0 \pm 0.8%). With regard to key errors, classical and jazz pianists performed similarly well (CG: 3.0 \pm 1.0%; JG: 2.0 \pm 1.0%; no main effect of Group; p > .166) and produced less key errors during execution of harmonically congruent than incongruent chords (main effect of Harmony; p < .001; no interaction of Group x Harmony x Context; p > .980).

Importantly, classical pianists were overall more accurate than jazz pianists in imitating the fingering (error rate in CG: $4.0 \pm 1.0\%$; JG: $14.0 \pm 4.0\%$; main effect of Group; p < .001), most likely due to stronger focus on hand posture in classical than jazz education (see also below). Accordingly, both groups committed more errors when imitating unconventional compared to conventional fingerings (main effect of Manner; p < .001), however, particularly the JG (interaction of Group x Manner, p < .001) .011) (see Figure 4C). Moreover, more fingering mistakes in the harmonically incongruent than congruent chords (main effect of Harmony; p < .049) in jazz compared to classical pianists (a trend in the interaction of Group x Harmony; p > .079) suggest that the JG allocated more resources to the keys to be pressed when harmonic violations occurred, to the detriment of the manner of execution. Finally, an interaction of Group x Manner x Context x Harmony (F(1, 28) = 7.056, p < .012, $\eta^2 = 0.201$) indicated that only the CG (Manner x Context x Harmony in CG: F(1, 28) = 7.94, p < .014, $\eta_p^2 = .36$; in JG: F(1, 28) = 2.35, p > .148, $\eta_p^2 = .14$) committed more fingering errors when the manner was violated on top of harmonically congruent chords in the long context (Manner x Context interaction in harmonically congruent chords: F(1,14) = 10.34, p < .006, $\eta_p^2 = .42$; in harmonically incongruent chords F(1,14) = 0.50, p > .490, $\eta_p^2 = .03$). This indicates that the CG, more than the JG, tended to associate conventional fingering with congruent harmony, suggesting that structure-interpretative focus strengthens the link between structure-based plan and optimal parameter specification.

ERP data

Harmony ERPs. In both groups, harmonically incongruent (compared to congruent) chords evoked a late posterior negativity between 550 and 1200 ms, which was stronger in the long than the short context (see also Table 2 for statistical details). This indicates that both CG and JG adopted predictive strategies at the sequence-level based on the context and had to reprogram their pre-planned action in response to the harmonic violations. Most importantly, this negativity started significantly earlier in jazz pianists, already between 370 to 550 ms, than in classical pianists (only after 550 ms) (Figure

5A). This earlier onset might reflect prompt revision of the pre-planned motor act in JG, enabling them to compensate potential behavioural costs during execution. Effects are displayed in Figure 5A and will be statistically assessed below.

In the 1^{st} time window (370 to 550 ms), only the JG showed an early posterior negativity that was stronger in the long than in the short context (interaction of Harmony x AntPost: p < .017, interaction of Group x Harmony x Context x AntPost x Laterality: p < .029).

In the $2n^d$ time window (550 to 1200 ms), both groups displayed a similar late negativity that was stronger in the long than in the short context (interactions of Harmony x Context x Laterality: p < .023; Harmony x Context x AntPost: p < .048; no interactions involving Group x Harmony x Context: ps > .143).

Manner ERPs. In both CG and JG, manner incorrect compared to correct chords evoked similar neural signatures comprising an early left anterior positivity (180 to 420 ms), followed by a late posterior positivity (420 to 800 ms). None of these potentials was stronger in the long than the short context, similarly in both groups, indicating that both CG and JG planned low-level movement parameters (i.e., fingering) at the level of the single act (not the musical sequence). Effects are displayed in Figure 5B and will be statistically assessed below (see also Table 3 for statistical details). In the 1^{st} time window (180 to 420 ms), a left-anterior positivity was elicited by manner incorrect compared to manner correct chords in both groups (interaction of Manner x AntPost x Laterality: p < .004), with CG showing a more broadly distributed positivity than JG (interaction of Group x Manner x AntPost x Laterality; p < .008). In the 2^{nd} time window (420 to 800 ms), the positivity attained a predominantly central-posterior distribution in both groups as confirmed by a Manner x AntPost x Laterality interaction (p < .026), and no interaction involving the factor Group (ps > .054).



Figure 4. Mean RTs and Manner errors for classical (left panels) and jazz pianists (right panels). (A) RTs during imitation of harmonically incongruent (dashed line) and congruent chords (solid line), (B) RTs during imitation of manner incorrect (dashed line) and correct chords (solid line), and (C) fingering errors during imitation of manner incorrect (dashed line) and correct chords (solid line) in the long and short context. Error bars indicate ± 1 *SEM*. Asterisks indicate significance of the Harmony x Context and Manner x Context interactions: ***p < .001, ns: p > .05.

Effect	<i>F</i> (1,28)	<i>p</i> -value	${\Pi_p}^2$
Response times			
G	< 1	.594	< .01
Н	124.85	<.001	.82
М	190.65	<.001	.87
HxC	14.13	<.001	.34
M x C	2.20	.149	.07
G x H	0.20	.660	.01
G x M	2.24	.146	.07
G x H x C	4.34	.046	.13
G x M x C	< 1	.745	< .01
Key errors			
G	2.02	.166	.07
Н	33.59	<.001	.55
М	2.66	.114	.09
H x C	6.40	.017	.19
M x C	< 1	.799	< .01
G x H	2.64	.116	.09
G x M	< 1	.964	< .01
G x H x C	< 1	.980	< .01
G x M x C	1.10	.302	.04
Fingering errors			
G	17.36	<.001	.38
Н	4.23	.049	.13
М	34.70	<.001	.55
H x C	< 1	.790	< .01
M x C	6.51	.016	.19
G x H	3.33	.079	.11
G x M	7.36	.011	.21
G x H x C	2.40	.133	.08
G x M x C	1.75	.197	.06

Table 1. Results of the ANOVAs with factors Group xHarmony x Manner x Context on the behavioural data.

Bold values indicate significant results (p < .05). Partial eta squared $\eta_P^2 > 0.5 =$ large effect size, $\eta_P^2 > 0.3 =$ medium effect size, $\eta_P^2 > 0.1 =$ small effect size (Bortz and Döring, 2003). G = Group, H = Harmony, M = Manner, C = Context.

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Figure 5. ERP effects of Harmony and Manner. (A) ERPs evoked by harmonically incongruent (red line) compared to congruent chords (blue line) in the long (top) and short context (bottom) in CG (left panel) and JG (right panel). **(B)** ERPs evoked by manner incorrect (red line) compared to correct chords (blue line) averaged across long and short contexts in CG (left panel) and JG (right panel). Time windows are shaded in grey. Topography maps for each statistical time window depict the difference potentials of harmonically incongruent / manner incorrect minus congruent / correct chords. Positions of the respective electrodes are indicated as "o" in the head-plots.

		1st tw: 370550 ms			2 nd tw: 5501200 ms			
Effect	df	F	р	η_P^2	F	р	η_P^2	
G	1,28	3.92	.058	0.12	3.00	.094	0.10	
Н	1,28	4.97	.034	0.15	8.32	.007	0.23	
Н х АР	2,56	9.09	.004	0.25	1.93	.173	0.06	
H x L	2,56	1.51	.230	0.05	5.56	.013	0.17	
H x AP x L	4,112	1.00	.398	0.03	2.83	.043	0.09	
H x C	1,28	8.34	.007	0.23	3.88	.059	0.12	
H x C x AP	2,56	2.05	.160	0.07	4.00	.048	0.13	
H x C x L	2,56	3.98	.024	0.12	4.46	.023	0.14	
H x C x AP x L	4,111	1.03	.377	0.04	1.43	.241	0.05	
G x H	1,28	3.77	.062	0.12	0.28	.601	0.01	
G x H x AP	2,56	1.79	.191	0.06	3.92	.051	0.12	
G x H x L	2,56	0.30	.742	0.01	0.07	.878	0.01	
G x H x AP x L	4,112	0.37	.778	0.01	1.17	.326	0.04	
G x H x C	1,28	0.00	.984	0.01	0.34	.562	0.01	
G x H x C x AP	2,56	1.54	.227	0.05	0.09	.808	0.01	
G x H x C x L	2,56	0.57	.567	0.02	0.44	.607	0.02	
G x H x C x AP x L	4.112	3.38	.029	0.11	1.77	.163	0.06	

 Table 2. Harmony ERPs – Results of the ANOVAs on ERP amplitude values with factors Group x Harmony x Context x AntPost x Laterality in two time windows.

Bold values indicate significant results (p < .05). Partial eta squared $\eta_P^2 > 0.5 =$ large effect size, $\eta_P^2 > 0.3 =$ medium effect size, > 0.1 = small effect size (Bortz & Döring, 2003). G = Group, H = Harmony, C = Context, AP = AntPost, L = Laterality. Degrees of freedom were corrected after Huynh-Feldt if necessary.

		1^{st} tw:	· 180420 m	\$	2^{nd} tw: 420800 ms			
Effect	df	F	р	η_P^2	F	р	η_P^2	
G	1,28	2.92	.099	0.09	3.51	.071	0.11	
М	1,28	0.35	.557	0.01	10.12	.004	0.27	
M x AP	2,56	4.99	.028	0.15	4.81	.030	0.15	
M x L	2,56	9.78	.001	0.26	8.35	.001	0.23	
M x AP x L	4,112	4.95	.004	0.15	3.47	.026	0.11	
C x M	1,28	0.22	.640	0.01	0.31	.579	0.01	
C x M x AP	2,56	2.65	.112	0.09	2.16	.148	0.07	
C x M x L	2,56	1.48	.239	0.05	1.31	.277	0.04	
C x M x AP x L	4,111	2.49	.047	0.08	2.03	.117	0.07	
G x M	1,28	1.06	.311	0.04	1.72	.200	0.06	
G x M x AP	2,56	0.07	.827	0.01	0.04	.875	0.01	
G x M x L	2,56	0.09	.913	0.01	0.63	.538	0.02	
G x M x AP x L	4,112	4.42	.008	0.14	2.79	.054	0.09	
G x C x M	1,28	0.00	.981	0.01	0.01	.940	0.01	
G x C x M x AP	2,56	0.87	.366	0.03	0.03	.899	0.01	
G x C x M x L	2,56	0.30	.699	0.01	2.77	.071	0.09	
G x C x M x AP x L	4,112	1.10	.358	0.04	1.98	.123	0.07	

 Table 3. Manner ERPs – Results of the ANOVAs on ERP amplitude values with factors Group x Manner x Context x AntPost x Laterality in two time windows.

Bold values indicate significant results (p < .05). Partial eta squared $\eta_P^2 > 0.5 =$ large effect size, $\eta_P^2 > 0.3 =$ medium effect size, > 0.1 = small effect size (Bortz & Döring, 2003). G = Group, H = Harmony, C = Context, AP = AntPost, L = Laterality. Degrees of freedom were corrected after Huynh-Feldt if necessary.

Time frequency data

Harmony theta. Only CG, not JG, showed a strong increase of early theta power during harmonically incongruent compared to congruent chords, particularly in the long sequences, disclosing that this effect was associated with sequence-level structure-based planning (see Table 4 and Figure 6A). In fact, in the 1^{st} time window (220 to 480 ms), a Group x Harmony x Context x AntPost x Laterality interaction (p < .042) indicated a broad increase in theta power after the violation only in CG and only in long sequences (interaction of Harmony x Context in CG: p < .013; but not in JG: p > .633). No relevant effects were found in the 2^{nd} time window (1080 to 1200 ms).

Harmony beta. An interaction of Group x Harmony x Laterality and of Group x Harmony x AntPost (ps < .035, see Table 4) indicated that beta power associated with the violation decreased more strongly in JG than in CG, but similarly in both contexts (interaction of Group x Harmony x Context: ps > .071).

Manner theta. No significant group differences were found; therefore manner-related effects in theta will not be discussed.

Manner beta. Beta power decreased in manner-incorrect compared to correct conditions in both contexts (interaction of Manner x Antpost: p < .039, interaction of Manner x Context: ps > .220) (see Table 4). However, this effect appeared to be mainly driven by a stronger decrease of beta power in CG than in JG, as can be seen in Figure 6B. Although a Group x Manner x AntPost interaction fell short of statistical significance (p > .082), exploratory ANOVAs for each group separately lent some support for a CG-driven beta de-synchronisation (interaction of Manner x AntPost in the CG: p < .015; JG: p > .230).



Figure 6. Spectral power effects of Harmony and Manner. (A) Topography of normalised power change in the harmonically incongruent minus congruent chords for CG (left panel) and JG (right panel) in the theta band (I^{st} time window) separately for the long and the short context, and in the beta band averaged across long and short contexts. (B) Topography of normalised power change in the manner incorrect minus correct condition for CG (left panel) and JG (right panel) in the beta band averaged across long and short contexts.

		Harmony theta tw: 220480 ms		Har	Harmony beta			Manner beta			
				tw: 360520 ms			tw: 360520 ms				
Effect	df	F	р	η_P^2	F	р	η_P^2	F	р	η_P^2	
G	1,28	8.72	.006	0.24	2.99	.095	0.1	2.99	.095	0.10	
V	1,28	1.79	.192	0.06	5.56	.026	0.17	0.16	.692	0.01	
V x AP	1,28	0.42	.571	0.01	2.47	.115	0.08	4.18	.039	0.13	
V x L	1,28	1.96	.150	0.07	3.40	.041	0.11	0.02	.985	0.01	
V x AP x L	2,56	1.14	.334	0.04	0.18	.893	0.01	0.18	.883	0.01	
V x C	2,56	1.70	.202	0.06	1.44	.241	0.05	0.00	.969	0.01	
V x C x AP	1,28	0.27	.719	0.01	0.10	.817	0.01	0.44	.602	0.02	
V x C x L	2,56	4.08	.032	0.13	0.28	.701	0.01	1.25	.295	0.04	
V x C x AP x L	2,56	0.35	.759	0.01	0.39	.818	0.01	1.49	.220	0.05	
G x V	2,56	0.70	.409	0.02	0.10	.757	0.01	0.70	.410	0.02	
G x V x AP	2,56	1.15	.305	0.04	4.24	.035	0.13	3.01	.082	0.10	
G x V x L	4,112	1.46	.241	0.05	6.58	.003	0.19	0.09	.842	0.01	
G x V x AP x L	2,56	0.35	.759	0.01	2.51	.071	0.08	0.49	.661	0.02	
G x V x C	2,56	0.33	.568	0.01	0.19	.669	0.01	0.24	.630	0.01	
G x V x C x AP	4,112	0.97	.373	0.03	2.61	.106	0.09	0.16	.805	0.01	
G x V x C x L	4,112	0.02	.952	0.01	3.02	.071	0.1	0.94	.395	0.03	
G x V x C x AP x L	4,112	3.02	.042	0.10	0.73	.571	0.03	1.11	.352	0.04	

Table 4. Time frequency analysis – Results of the ANOVAs on spectral power values with factors Group x Violation x Context x AntPost x Laterality.

Bold values indicate significant results (p < .05). Partial eta squared $\eta_P^2 > 0.5 =$ large effect size, $\eta_P^2 > 0.3 =$ medium effect size, > 0.1 = small effect size (Bortz & Döring, 2003). G = Group, V = Violation (i.e., Harmony or Manner), C = Context, AP = AntPost, L = Laterality. Degrees of freedom were corrected after Huynh-Feldt if necessary. No effects involving H were found for Manner theta.

Post-experiment ratings. In the debriefing questionnaires after the experiment, both groups reported similar active prediction of the next chord during execution of the chord progressions (mean \pm *SEM* on a scale from 1 to 9; CG: 5.64 \pm 0.37; JG: 4.26 \pm 0.67; t(28) = -1.79, p > .080), indicating that both groups were adopting predictive strategies about the what to play. Moreover, none of the pianist groups reported explicit reliance on auditory imagery to predict the next chord (CG: 4.68 \pm 0.68; JG: 4.06 \pm 0.52; t(28) = -0.21, p > .83). However, prediction strategies differed significantly between groups, with JG preferring to internally name the harmonic chord functions (CG: 3.78 \pm 0.62; JG: 6.40 \pm 0.43; t(28) = 3.46, p < .002), and CG paying more attention to the hand as a whole (CG: 5.57 \pm 0.32; JG: 3.67 \pm 0.57; t(28) = -2.92, p < .007). These preferences are compatible with the key and fingering error results described above and may reflect more explicit harmony and manner processing in jazz and classical pianists, respectively.

DISCUSSION

The present data show clear-cut neural differences between jazz and classical pianists resulting in different behavioural outcome under same task-demands. Within an overall similar hierarchical core structure of action control, pianists differently weigh high-level structure-based planning of the action sequence and low-level parameter specification of single acts during execution of unrehearsed musical

sequences without sound. Classical pianists rapidly narrow down sequence-level structural interpretations to optimally set movement parameters at single-act level, while jazz pianists remain aware of structural alternatives for longer, allowing them to flexibly revise structure-based action plans when faced with harmonic incongruities. These results argue for training-style influence on core high- and low-level processes of action planning, upgrading the notion of sensorimotor plasticity (Herholz and Zatorre, 2012; Münte et al., 2002) to high-level motor cognition.

Hierarchical action planning regardless of genre-specific training

Before turning to genre-specific group differences, it is worth pointing out that jazz pianists showed a similar multi-level core structure of action planning as previously identified in classical planists (Bianco et al., 2016a), and in line with hierarchical action theories (Rosenbaum et al., 2007; Vallacher and Wegner, 1987; Wohlschläger et al., 2003; see Figure 1). At sequence-level, both groups, regardless of training specialization, used long-term knowledge of structure and accumulating harmonic contextual evidence to narrow down the possibilities of likely forthcoming chords ('what' to play). This was indicated by faster and more accurate imitation of harmonically congruent compared to incongruent chords, particularly in the long context, and by the context-dependent negativity (Figure 6A) associated with the reprogramming of a prepotent motor response when expectancies are violated (Leuthold and Jentzsch, 2002; Sammler et al., 2013). Similarly, at the single-act level, the manner of execution was specified at late stages of action planning³ regardless of training specialization. This was indicated by slower imitation of unconventional manner along with more fingering errors, irrespective of context length, and a context-independent positivity (Figure 6B) associated with visual-spatial detection of fingering mistakes in action observation (Panasiti et al., 2016). Altogether, combined data from differently specialised musicians indicate that previously identified multilayer planning processes (i.e., concerning the sequence and the single acts levels) constitute core levels of the hierarchical representation of skilled behaviours. Future studies should test to what extent this core structure is generalizable to action planning in other instrument players or in non-musical production contexts.

Greater structural flexibility in jazz pianists

Within this hierarchical core structure of action planning, the present data highlight a variable tuning of the action control hierarchy depending on action tendencies developed through classical or jazz training as will be discussed in the following. At the *sequence level*, classical pianists showed the tendency to build narrower structural plans than jazz pianists, while jazz pianists showed greater readiness and flexibility to revise their structure plans in case of harmonically unexpected chords. Classical pianists displayed a context-dependent slowing of response times, an increase of early

³ Note that particularly in classical performance, fingering is usually worked out by pianists during training and can thus be planned ahead in *rehearsed* pieces. The present task comprised *unrehearsed* music material only, hence, reducing anticipatory planning of fingering.

conflict-related theta when asked to imitate harmonic violations (Harmony x Context interaction), while jazz pianists showed none of these effects (Harmony x Context x Group interaction; Figures 4A and 6A). Instead, they reacted to harmonic violations with an earlier onset of the context-dependent "reprogramming" negativity (Figure 5A, 1st *time window*: 370 to 550 ms), a stronger desynchronisation of beta power (between 360 and 520 ms), and lower fingering accuracy.

Improvisation in jazz practice focuses on the active and flexible re-arrangement of structure-based plans often in non-canonical ways (Clarke, 2001; Pressing, 1987). The present neurobehavioural data reflect this structure-generative focus and readiness for novelties and argue for an easier access to several simultaneously pre-activated harmonic options, the most likely of which has right of way but can be rapidly reprogrammed into one of the other alternatives (Cisek, 2006). Although it remains to be clarified whether the earlier onset of the negativity in the jazz group reflects an earlier action "reprogramming", or faster visual detection of the harmonically unexpected chord in the displayed hand actions (Panasiti et al., 2016; Stefanics et al., 2011), it speaks for quicker reassessment of structure-based action plans after jazz training, which may in fact prevent response time costs (no context-dependent slowing). This jazz-specific optimization of structure-based planning indicates a stronger propensity for *online* extraction of harmonic relationships that may even be proceduralized (Hansen et al., 2016), lending greater flexibility in handling harmonic violations. This account was further supported by high self-reported attention to harmony, the absence of early conflict-related effects in the theta band, observed instead in classical pianists (see below), and a stronger decrease in beta power after harmonic violations than in classical pianists. Beta de-synchronization typically accompanies movement preparation (Pfurtscheller and Lopes, 1999) and is enhanced during observation of incorrect actions (Koelewijn et al., 2008). This fits with the latency of the present beta effect between target onset and action execution, and may suggest that jazz pianists were motorically more prepared to encode harmonic content of the displayed action, allowing faster error detection and more flexible execution. On the other hand, greater focus on harmony in jazz pianists, which binds more resources to high-level sequence planning, might have come at the expense of low-level action plans, especially under time pressure. Indeed, jazz compared to classical planists had higher rates of fingering errors suggesting a speed-accuracy trade-off (Berlyne, 1957) observed across two levels of action planning.

Classical pianists, in turn, experienced more cognitive conflict and effort than jazz pianists when a structural revision was required in the long context, as shown by the early context-sensitive increase of theta power after the harmonic violation (220 to 480 ms). Increased theta power constitutes a conflict signal of frontal control functions (Botvinick et al., 2004; Cavanagh et al., 2009; Miller and Cohen, 2001) and is enhanced during inhibition of prepotent actions and initiation of goal-relevant responses (Aron et al., 2014; Harmony et al., 2009; Kirmizi-Alsan et al., 2006; Munakata et al., 2011; Ruiz et al., 2011). Note that classical pianists still showed increased theta power (220 to 480 ms) when jazz pianists already displayed the "reprogramming" negativity (onset at 370 ms). This suggests that

classical pianists experienced higher cognitive effort to resolve conflict in response to the unexpected chord, which may have delayed reprogramming and induced context-sensitive response time costs. In other words, classical pianists' structure-*interpretative* focus, which aims for fast narrowing of harmonic possibilities to rapidly proceed to expressive stages of action planning (the 'how', see below) (Clarke, 2001; Shaffer, 1984), may have necessitated greater cognitive effort to initiate other alternatives in case of structural-harmonic deception. On the other hand, pre-activation of only the most likely harmonic option may serve to optimize lower-level single act planning to meet the high expressive demands in classical training as will be discussed below.

Finally, it should be stressed that classical and jazz pianists did not differ in their reported auditory imagery scores during mute production in our task. Hence, between-group differences in structure-based planning more likely derive from motor-specific than auditory tendencies developed through long-term practice of the one or the other style. This interpretation also finds support in recent neuroimaging evidence that silent imitation of harmonic violations did not elicit auditory brain activation in expert pianists (Bianco et al., 2016b). Future studies should test how between-group differences in auditory perception influence action planning.

Greater focus on movement parameters in classical pianists

At *single act level*, classical compared to jazz pianists revealed a higher propensity to encode and accurately set movement parameters (as reflected by Group x Manner interactions): Classical pianists were overall more accurate in the imitation of the fingering (Figure 4C) that was partly determined by pianists' higher-level structural-harmonic predictions (Manner x Harmony x Context interaction in CG, not JG). Moreover, they showed a broader early positivity (180 to 420 ms; Figure 5B) and a stronger decrease of beta power (360 to 520 ms) upon detection of the fingering violation (Figure 6B).

These manner-related data indicate that classical compared with jazz pianists were more focused on the way musical acts are motorically rendered. Structure-interpretative abilities imply that pianists rapidly plan expressive features on top of the musical structure by relying on strong associations between fingering and frequent musical patterns (Gellrich and Parncutt, 1998). Greater fingering accuracy, stronger self-reported focus on hand posture, a more broadly distributed early positivity (Bianco et al., 2016a; Polich, 2007) and a stronger decrease in beta power in CG than JG reflect classical pianists' enhanced focus on the fingering. In line with our account that classical pianists rapidly project over-trained movement parameters to the structure-based plan as soon as it has emerged from the context, classical pianists' imitation of unconventional fingering was in fact least accurate on top of structurally *congruent* chords (Manner x Harmony x Context interaction only in CG). This suggests that they anticipated fingerings that matched with their structure-based plans. Crucially, the stronger decrease in beta power indicates that classical pianists were overall motorically more prepared to encode the fingering of the displayed action (Candidi et al., 2014; Fagioli et al., 2007; Hommel, 2010), potentially facilitating error detection in the photos (Koelewijn et al., 2008)

and supporting own execution (Ruiz et al., 2011; Tzagarakis et al., 2010). Interestingly, the similar beta power decrease found in jazz pianists, but for harmonic violations (as discussed above), may express the differential habitual action focus after specialized training. These findings suggest that beta oscillations are not only modulated when the observed action is erroneous (Caetano et al., 2007; Koelewijn et al., 2008; van Schie et al., 2004), but that the modulation increases for specific types of action errors ('what' and 'how') that are in the focus of the performer.

Altogether, these findings show that classical and jazz pianists give different weights to the hierarchical levels of action planning, intuitively and despite identical instruction and material: On the one hand, habitual action focus on structure generation and revision in jazz may inadvertently bind resources to high levels of planning, even in a task that did not require creative improvisation. On the other hand, the building of solid associations between finger configurations and frequent structural figures (e.g., scales, intervals, cadences) in classical training (Clarke et al., 1997; Gellrich and Parncutt, 1998; Parncutt, 2014) may shift focus from high to low levels to ease the structure-based selection of fine-grained expressive features that colour interpretative performance (Clarke, 2001). Therefore, these findings demonstrate that generative jazz training coincides with a higher flexibility to deal with harmonic possibilities, whereas interpretative classical training enhances the preparedness to accurately set fine movement parameters. Whether the different prevalence of maladaptive plastic changes such as focal dystonia in classical and jazz pianists (Altenmüller and Jabusch, 2009; Elbert et al., 1998) is tied to differential action focus is a interesting topic for future research. In sum, this genre-specific weighting of the motor control hierarchy suggests that, beyond general musical longterm knowledge and contextual evidence, habitual focus plays an important role in the optimization of not only auditory (Eerola et al., 2009; Hansen et al., 2016; Vuust et al., 2012) but also motor predictive processes.

CONCLUSION

The findings of the current study demonstrate that complex actions are not rigid entities but can reflect specialised cognitive-motor strategies depending on previous experience and habitual action focus. We show that (i) structure-based planning at the level of the action sequence and (ii) movement parameter specification at the level of single acts are plastic processes in action control: they are calibrated differently – despite equal instruction and task – depending on the stylistic specialization of musicians. Remarkably, long-term adaptive plasticity in the action control hierarchy was behaviourally reflected in structure flexibility in jazz planists and fine movement accuracy in classical planists during the execution of the same task. Hence, the specific demands and focus of previous experience may result in dramatic and enduring changes in performers' motor control system, providing neurobiological accounts for the great divide between musicians of the "swing" and the "legit" style.

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References

- Altenmüller, E., Jabusch, H.-C., 2009. Focal hand dystonia in musicians : phenomenology , etiology , and psychological trigger factors. J. Hand Ther. 22, 144–155. doi:10.1016/j.jht.2008.11.007
- Aron, A.R., Robbins, T.W., Poldrack, R., 2014. Inhibition and the right inferior frontal cortex: one decade on. Trends Cogn. Sci. 18, 177–185. doi:10.1016/j.tics.2013.12.003
- Beaty, R.E., 2015. The neuroscience of musical improvisation. Neurosci. Biobehav. Rev. 51, 108–117. doi:10.1016/j.neubiorev.2015.01.004
- Berlyne, D.E., 1957. Uncertainty and conflict: a point of contact between information-theory and behavior-theory concepts. Psychol. Rev. 64, 329–339. doi:10.1037/h0041135
- Bianco, R., Novembre, G., Keller, P.E., Scharf, F., Friederici, A.D., Villringer, A., Sammler, D., 2016a. Syntax in action has priority over movement selection in piano playing: an ERP study. J. Cogn. Neurosci. 28, 41–54. doi:10.1162/jocn
- Bianco, R., Novembre, G., Keller, P.E., Seung-Goo, K., Scharf, F., Friederici, A.D., Villringer, A., Sammler, D., 2016b. Neural networks for harmonic structure in music perception and action. Neuroimage 142, 454–464. doi:10.1016/j.neuroimage.2016.08.025
- Botvinick, M.M., Cohen, J.D., Carter, C.S., 2004. Conflict monitoring and anterior cingulate cortex: an update. Trends Cogn. Sci. 8, 539–46. doi:10.1016/j.tics.2004.10.003
- Caetano, G., Jousmäki, V., Hari, R., 2007. Actor's and observer's primary motor cortices stabilize similarly after seen or heard motor actions. Proc. Natl. Acad. Sci. U. S. A. 104, 9058–62. doi:10.1073/pnas.0702453104
- Candidi, M., Maria Sacheli, L., Mega, I., Aglioti, S.M., 2014. Somatotopic mapping of piano fingering errors in sensorimotor experts: TMS studies in pianists and visually trained musically naives. Cereb. Cortex 24, 435–443. doi:10.1093/cercor/bhs325
- Cavanagh, J.F., Cohen, M.X., Allen, J.J.B., 2009. Prelude to and resolution of an error: EEG phase synchrony reveals cognitive control dynamics during action monitoring. J. Neurosci. 29, 98–105. doi:10.1523/JNEUROSCI.4137-08.2009
- Cavanagh, J.F., Frank, M.J., 2014. Frontal theta as a mechanism for cognitive control. Trends Cogn. Sci. 18, 414–421. doi:10.1016/j.tics.2014.04.012
- Chaffin, R., Lemieux, A.F., Colleen, C., 2007. It is different each time I play: variability in highly prepared musical performance. Music Percept. 24, 455–472.
- Cisek, P., 2006. Integrated neural processes for defining potential actions and deciding between them: a computational model. J. Neurosci. 26, 9761–70. doi:10.1523/JNEUROSCI.5605-05.2006
- Clarke, E., 2001. Generative principles in music performance, in: Generative Processes in Music: The Psychology of Performance, Improvisation, and Composition. Oxford University Press, New York, pp. 1–26. doi:10.1093/acprof
- Clarke, E., Parncutt, R., Raekallio, M., Sloboda, J., 1997. Talking fingers: an interview study of pianists' views on fingering. Music. Sci. 1, 87–107. doi:10.1177/102986499700100106
- Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Methods 134, 9–21. doi:10.1016/j.jneumeth.2003.10.009
- Diedrichsen, J., Kornysheva, K., 2015. Motor skill learning between selection and execution. Trends Cogn. Sci. 19, 227–233. doi:10.1016/j.tics.2015.02.003
- Dorfberger, S., Adi-Japha, E., Karni, A., 2009. Sex differences in motor performance and motor learning in children and adolescents: An increasing male advantage in motor learning and consolidation phase gains. Behav. Brain Res. 198, 165–171. doi:10.1016/j.bbr.2008.10.033
- Drost, U.C., Rieger, M., Brass, M., Gunter, T.C., Prinz, W., 2005. Action-effect coupling in pianists. Psychol. Res. 69, 233–41. doi:10.1007/s00426-004-0175-8

- Eerola, T., Louhivuori, J., Lebaka, E., 2009. Expectancy in Sami Yoiks revisited: The role of datadriven and schema-driven knowledge in the formation of melodic expectations. Music. Sci. 13, 231–72.
- Elbert, T., Candia, C.A.V., Altenmüller, E., Rau, H., Sterr, A., Rockstroh, B., Pantev, C., Taub, E., 1998. Alteration of digital representations in somatosensory cortex in focal hand dystonia 9, 3571–3575.
- Fagioli, S., Ferlazzo, F., Hommel, B., 2007. Controlling attention through action: observing actions primes action-related stimulus dimensions. Neuropsychologia 45, 3351–3355. doi:10.1016/j.neuropsychologia.2007.06.012
- Gellrich, M., Parncutt, R., 1998. Piano technique and fingering in the eighteenth and nineteenth centuries: bringing a forgotten method back to life. Br. J. Music Educ. 15, 5–23. doi:10.1017/S0265051700003739
- Goldman, A., 2012. What Does One Know When One Knows How to Improvise?, in: Proceedings of the 12th International Conference on Music Perception and Cognition. pp. 360–368.
- Grafton, S.T., Hamilton, A.F.D.C., 2007. Evidence for a distributed hierarchy of action representation in the brain. Hum. Mov. Sci. 26, 590–616. doi:10.1016/j.humov.2007.05.009
- Hansen, N.C., Vuust, P., Pearce, M., 2016. "If you have to ask, you'll never know": Effects of specialised stylistic expertise on predictive processing of music. PLoS One 11, 1–20. doi:10.1371/journal.pone.0163584
- Harmony, T., Alba, A., Marroquín, J.L., González-Frankenberger, B., 2009. Time-frequencytopographic analysis of induced power and synchrony of EEG signals during a Go/No-Go task. Int. J. Psychophysiol. 71, 9–16. doi:10.1016/j.ijpsycho.2008.07.020
- Herholz, S.C., Zatorre, R.J., 2012. Musical training as a framework for brain plasticity: behavior, function, and structure. Neuron 76, 486–502. doi:10.1016/j.neuron.2012.10.011
- Hommel, B., 2010. Grounding attention in action control: The intentional control of selection, in: B. J. Bruya (Ed.), Effortless Attention: A New Perspective in the Cognitive Science of Attention and Action. MA: MIT Press, Cambridge, pp. 121–140.
- Johnson-Laird, P.N., 2002. How jazz musicians improvise. Music Percept. An Interdiscip. J. 19, 415–442.
- Keller, P.E., 2012. What movement force reveals about cognitive processes in music performance., in: Art in Motion II. Peter Lang, Frankfurt, pp. 115–153.
- Keselman, H.J., Rogan, J.C., 1980. Repeated measures F tests and psychophysiological research: controlling the number of false positives. Psychophysiology 17, 499–503.
- Kilner, J.M., Baker, S.N., Salenius, S., Jousmäki, V., Hari, R., Lemon, R.N., 1999. Task-dependent modulation of 15-30 Hz coherence between rectified EMGs from human hand and forearm muscles. J. Physiol. 516, 559–570. doi:10.1111/j.1469-7793.1999.0559v.x
- Kirmizi-Alsan, E., Bayraktaroglu, Z., Gurvit, H., Keskin, Y.H., Emre, M., Demiralp, T., 2006. Comparative analysis of event-related potentials during Go/NoGo and CPT: Decomposition of electrophysiological markers of response inhibition and sustained attention. Brain Res. 1104, 114–128. doi:10.1016/j.brainres.2006.03.010
- Koechlin, E., Summerfield, C., 2007. An information theoretical approach to prefrontal executive function. Trends Cogn. Sci. 11, 229–235. doi:10.1016/j.tics.2007.04.005
- Koelewijn, T., van Schie, H.T., Bekkering, H., Oostenveld, R., Jensen, O., 2008. Motor-cortical beta oscillations are modulated by correctness of observed action. Neuroimage 40, 767–775. doi:10.1016/j.neuroimage.2007.12.018
- Lashley, K., 1951. The problem of serial order in behavior, in: Jeffress, L.A. (Ed.), Cerebral Mechanisms in Behavior. New York: Wiley, pp. 112–131.
- Leuthold, H., Jentzsch, I., 2002. Spatiotemporal source localisation reveals involvement of medial premotor areas in movement reprogramming. Exp. Brain Res. 144, 178–88. doi:10.1007/s00221-002-1043-7
- Loui, P., Przysinda, E., Aklaff, P., Maves, K., Arkin, C., Zeng, T., 2014. Jazz Improvisation as a Model of the Creative Process : Heightened Perceptual Awareness and Sensitivity.
- Luu, P., Tucker, D.M., Makeig, S., 2004. Frontal midline theta and the error-related negativity: Neurophysiological mechanisms of action regulation. Clin. Neurophysiol. 115, 1821–1835. doi:10.1016/j.clinph.2004.03.031
- Madura, P.D., 1996. Relationships among Vocal Jazz Improvisation Achievement, Jazz Theory Knowledge, Imitative Ability, Musical Experience, Creativity, and Gender. J. Res. Music Educ.

44, 252–267. doi:10.2307/3345598

- Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. J. Neurosci. Methods 164, 177–190. doi:10.1016/j.jneumeth.2007.03.024
- Michel, C.M., Murray, M.M., Lantz, G., Gonzalez, S., Spinelli, L., Grave de Peralta, R., 2004. EEG source imaging. Clin. Neurophysiol. 115, 2195–222. doi:10.1016/j.clinph.2004.06.001
- Miller, E.K., Cohen, J.D., 2001. An integrative theory of preforntal cortex function. Annu. Rev. Neurosci. 24, 167–202.
- Munakata, Y., Herd, S. a, Chatham, C.H., Depue, B.E., Banich, M.T., O'Reilly, R.C., 2011. A unified framework for inhibitory control. Trends Cogn. Sci. 15, 453–9. doi:10.1016/j.tics.2011.07.011
- Münte, T.F., Altenmüller, E., Jäncke, L., 2002. The musician's brain as a model of neuroplasticity. Nat. Rev. Neurosci. 3, 473–8. doi:10.1038/nrn843
- Münte, T.F., Nager, W., Beiss, T., Schroeder, C., Altenmüller, E., 2003. Specialization of the Specialized: Electrophysiological Investigations in Professional Musicians. Ann. N. Y. Acad. Sci. 999, 131–139. doi:10.1196/annals.1284.014
- Novembre, G., Keller, P.E., 2011. A grammar of action generates predictions in skilled musicians. Conscious. Cogn. 20, 1232–43. doi:10.1016/j.concog.2011.03.009
- Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.M., 2011. FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Comput. Intell. Neurosci. 2011. doi:10.1155/2011/156869
- Panasiti, M.S., Pavone, E.F., Aglioti, S.M., 2016. Electrocortical signatures of detecting errors in the actions of others: An EEG study in pianists, non-pianist musicians and musically naïve people. Neuroscience 318, 104–113. doi:10.1016/j.neuroscience.2016.01.023
- Parncutt, R., 2014. Fingering, in: Music in the Social and Behavioral Sciences: An Encyclopedia. Los Angeles: Sage, pp. 481–484.
- Pfurtscheller, G., Lopes, F.H., 1999. Event-related EEG / MEG synchronization and desynchronization : basic principles. Clin. Neurophysiol. 110, 1842–1857. doi:10.1016/S1388-2457(99)00141-8
- Polich, J., 2007. Updating P300: an integrative theory of P3a and P3b. Clin. Neurophysiol. 118, 2128–48. doi:10.1016/j.clinph.2007.04.019
- Pressing, J., 1987. Improvisations: methods and models, in: Generative Processes in Music. Oxford University Press, pp. 129–178.
- Pressing, J., 1984. The history of classical improvisation. Baroque music and beyond. Keyboard.
- Rosenbaum, D. a, Cohen, R.G., Jax, S. a, Weiss, D.J., van der Wel, R., 2007. The problem of serial order in behavior: Lashley's legacy. Hum. Mov. Sci. 26, 525–54. doi:10.1016/j.humov.2007.04.001
- Rüber, T., Lindenberg, R., Schlaug, G., 2013. Differential Adaptation of Descending Motor Tracts in Musicians. Cereb. Cortex 10. doi:10.1093/cercor/bht331
- Ruiz, M.H., Strübing, F., Jabusch, H.-C., Altenmüller, E., 2011. EEG oscillatory patterns are associated with error prediction during music performance and are altered in musician's dystonia. Neuroimage 55, 1791–803. doi:10.1016/j.neuroimage.2010.12.050
- Sammler, D., Novembre, G., Koelsch, S., Keller, P.E., 2013. Syntax in a pianist's hand: ERP signatures of "embodied" syntax processing in music. Cortex 49, 1325–1339. doi:10.1016/j.cortex.2012.06.007
- Schmidt, R. a. R., 1975. A schema theory of discrete motor skill learning. Psychol. Rev. 82, 225–260. doi:10.1037/h0076770
- Schneider, P., Sluming, V., Roberts, N., Scherg, M., Goebel, R., Specht, H.J., Dosch, H.G., Bleeck, S., Stippich, C., Rupp, A., 2005. Structural and functional asymmetry of lateral Heschl's gyrus reflects pitch perception preference. Nat. Neurosci. 8, 1241–1247. doi:10.1038/nn1530
- Shaffer, L.H., 1984. Timing in solo and duet piano performances. Q. J. Exp. Psychol. 36, 577–595. doi:10.1080/14640748408402180
- Shahin, A.J., Roberts, L.E., Chau, W., Trainor, L.J., Miller, L.M., 2008. Music training leads to the development of timbre-specific gamma band activity. Neuroimage 41, 113–122. doi:10.1016/j.neuroimage.2008.01.067
- Sharbrough, F., Chatrian, G.E., Lesser, R.P., Luders, H., Nuwer, M., Picton, T.W., 1991. American Electroencephalographic Society guidelines for standard electrode position nomenclature. J. Clin. Neurophysiol. 200–202.
- Stefanics, G., Kimura, M., Czigler, I., 2011. Visual mismatch negativity reveals automatic detection of

sequential regularity violation. Front. Hum. Neurosci. 5, 46. doi:10.3389/fnhum.2011.00046

Stewart, L., 2008. Do musicians have different brains? Clin. Med. J. R. Coll. Physicians London 8, 304–308. doi:10.7861/clinmedicine.8-3-304

- Swain, J.P., 1995. The concept of musical syntax. Music. Q. 79, 281-308. doi:10.1093/mq/79.2.281
- Tervaniemi, M., 2009. Musicians-Same or Different? Ann. N. Y. Acad. Sci. 1169, 151–156. doi:10.1111/j.1749-6632.2009.04591.x
- Trujillo, L.T., Allen, J.J.B., 2007. Theta EEG dynamics of the error-related negativity. Clin. Neurophysiol. 118, 645–668. doi:10.1016/j.clinph.2006.11.009
- Tzagarakis, C., Ince, N.F., Leuthold, A.C., Pellizzer, G., 2010. Beta-Band Activity during Motor Planning Reflects Response Uncertainty. J. Neurosci. 30, 11270–11277. doi:10.1523/JNEUROSCI.6026-09.2010
- Uithol, S., van Rooij, I., Bekkering, H., Haselager, P., 2012. Hierarchies in action and motor control. J. Cogn. Neurosci. 24, 1077–86. doi:10.1162/jocn a 00204
- Vallacher, R.R., Wegner, D.M., 1987. Action identification and human behavior. Psychol. Rev. 94, 3– 15. doi:10.1037/0033-295X.94.1.3
- van Schie, H.T., Mars, R.B., Coles, M.G.H., Bekkering, H., 2004. Modulation of activity in medial frontal and motor cortices during error observation. Nat. Neurosci. 7, 549–54. doi:10.1038/nn1239
- Verwey, W.B., Shea, C.H., Wright, D.L., 2015. A cognitive framework for explaining serial processing and sequence execution strategies. Psychol. Bull. 22, 54–77. doi:10.3758/s13423-014-0773-4
- Vuust, P., Brattico, E., Seppänen, M., Näätänen, R., Tervaniemi, M., 2012. Practiced musical style shapes auditory skills. Ann. N. Y. Acad. Sci. 1252, 139–146. doi:10.1111/j.1749-6632.2011.06409.x
- Waters-Metenier, S., Husain, M., Wiestler, T., Diedrichsen, J., 2014. Bihemispheric Transcranial Direct Current Stimulation Enhances Effector-Independent Representations of Motor Synergy and Sequence Learning. J. Neurosci. 34, 1037–1050. doi:10.1523/JNEUROSCI.2282-13.2014
- Wehr-Flowers, E., 2006. Differences between Male and Female Students' Confidence, Anxiety, and Attitude toward Learning Jazz Improvisation. J. Res. Music Educ. 54, 337–349.
- Wohlschläger, A., Gattis, M., Bekkering, H., 2003. Action generation and action perception in imitation: an instance of the ideomotor principle. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 358, 501–15. doi:10.1098/rstb.2002.1257