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How regularities in sound sequences inform action planning: Neural and behavioral evidence from silent piano performance

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1. Background

It is known that knowledge of regularities can intuitively be used to flexibly generate appropriate actions depending on the demands of the current context [1,2]. While considerable effort in perception research has focused on how the brain represents regularities extracted from sequential acoustic signals, including speech and **music**, little is known about how the brain uses this knowledge of regularities to produce sequential coherent outputs (e.g. talking or playing an instrument). Music production offers an ideal example to study how the brain achieves this.

Western tonal music is endowed with a complex system of rules which defines structurally fundamental events in a sequence (Fig. 1). For example, based on harmony, a sequence starts and ends with a reference chord to which only some chords are expected to move to, whereas others rarely do [3]. Such harmonic regularities can thus be extracted across repeated perceptual exposure throughout life span [4,5], and used to anticipate, with a certain degree of abstractness, what chord is likely to come in a musical sequence [6,7].

Crucially, musicians are exposed to musical regularities not only through sounds, but also through motor practice. This led to the hypothesis that the sensorimotor associations formed through musical training in the musicians' brain [8] may allow the generation of equivalent sensory and motor predictions about the next chord in a sequence [9].

The ability to represent anticipated musical events in both auditory and motor format may be a key step during training to detach from execution of fixed sequential movements towards flexible production of structurally coherent sequences, as in jazz improvisation or other forms of communication.

2. Approach

Based on previous behavioural and EEG studies on silent piano performance [10,11], we investigated the neural bases of motor anticipatory mechanisms based on knowledge of harmony internalised by pianists through practice ($>$10,000 hours of piano training). *Structure-based motor plans* were scrutinised in three different experiments which generally adopted the following violation paradigm: In complete absence of sound, pianists executed 5-chord sequences by imitating photos of a hand displayed on the screen (Fig. 2). Sequences ended with harmonically congruent/incongruent chords (the 'Harmony' in Fig. 2). Incongruent chords constitute a violation of the harmonic structure, and should elicit greater brain responses compared to congruent chords. This greater response should reflect more costly computations to integrate elements that mismatch the predicted chord based on the structure emerging from the context.

In study I [12], we sought to dissociate the neural networks for motor predictions from auditory information processing. Pianists were presented with harmonically congruent/incongruent 5-chord sequences as musical actions to imitate without sound. In an additional task, the same sequences were presented as sounds to listen to without imitation. In Study II [13] and III [14], we used the full motor paradigm depicted in Fig. 2, in which the last chord was additionally manipulated in terms of its harmonic predictability (it occurred after a long/short context, 5- or 2-chord sequences), and its manner of execution (correct/incorrect fingers). In study II we wanted to examine if harmony-based plans are distinguishable from motor-parameter specification of single acts, the 'manner' [15]. Harmony-based plans should be stronger in the long context because it provides more evidence to predict the final chord compared with the short context. Conversely, motor-parameter specification should occur at each single act regardless of the context. In Study III, we compared behavioural and neural responses from classical and jazz pianists (matched for amount of training hours) to test if harmony-based plans are influenced by specific focus of long-term training. Harmony is indeed highly relevant in jazz improvisation compared with classical performance in which the structure of the piece is usually already composed [16].

3. Results and discussion

Study I. The contrasts of incongruent $>$ congruent chords in motor and auditory tasks respectively yielded dissociated dorsal frontal-parietal and ventral frontal-temporal networks for harmonic processing in action and perception (Fig. 3, upper panel). In line with the predictive coding framework [17], these networks are likely to support harmonic predictions, where frontal areas keep track of structural relationships in sequential information via dynamic exchange with lower-level modality-specific systems, in the parietal or temporal lobe. Importantly, the absence of violation-related temporal

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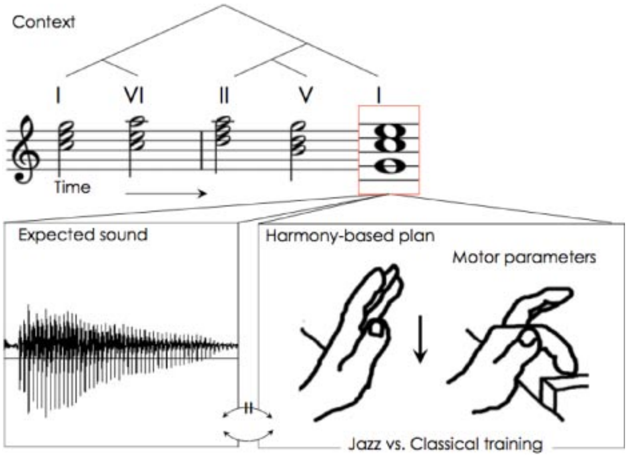

Fig. 1 Based on the context, musicians generate predictions about the next chord in a musical sequence, which can be represented as an expected sound or a motor plan necessary for playing it. This kind of 'structure-based' plan may be different from mere movement selection, and it may be influenced by specialized long-term training.

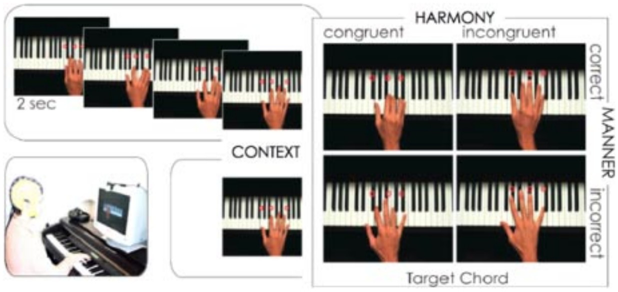

Fig. 2 Paradigm used in study II and III and partially in study I (see text). In complete absence of sound pianists executed chord sequences by imitating a model hand displayed on the screen. The last chord of the sequences was manipulated in terms of harmony (congruent/incongruent), manner (correct/incorrect), and context preceding the last chord (long/short).

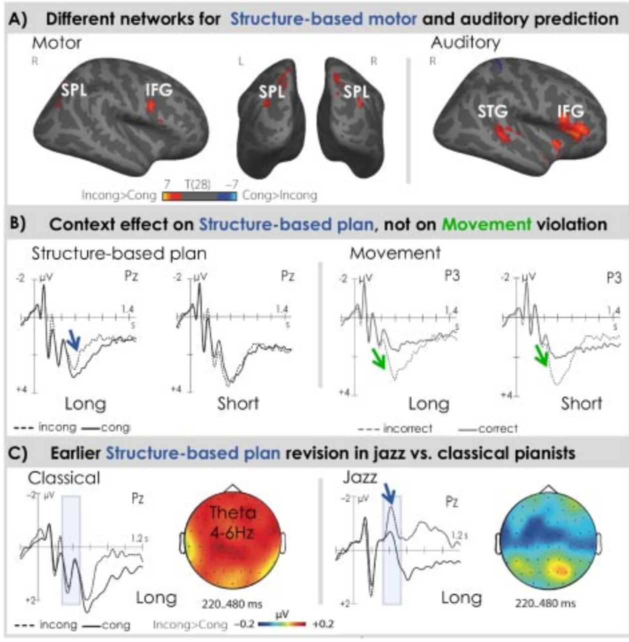

Fig. 3 Results from study I, II, and III. A) Structure-based predictions in expert musicians are supported by frontal-temporal areas during listening, and by frontal-parietal areas during action imitation (even in absence of auditory feedback). B) Structure-based motor plans evoke different neural responses ('negativity') from mere movement selection ('positivity'). C) Jazz compared with classical pianists are more flexible in response to musical structure violations (earlier negativity onset, and no increase of conflict-related theta power).

activity in the motor task indicates that predictions were not merely driven by auditory images of expected chords, but they were rather grounded in the musicians' visual-motor control system. In sum, these results suggest that, by capitalising on brain sensorimotor interactions [8], training allows models about regularities acquired through a sensory modality (auditory) to be translated into the performers' motor system.

Study II. EEG signals locked with the onset of the harmonically incongruent compared with congruent chords yielded a late negativity in event-related potentials (ERPs) in the long, but not in the short context. This effect can reflect reprogramming of an anticipated motor plan based on the preceding long context just before execution. Performance was indeed worse (increased reaction times, RTs, and decreased accuracy) for the incongruent chords embedded in the long context (data not shown, but see Bianco *et al.*, 2016a). Violation of the manner of execution yielded a different brain response (a late positivity) and was not influenced by the context (Fig. 3, middle panel), demonstrating the more abstract and context-dependent nature of harmony-based motor plan.

Study III. Both classical and jazz pianists showed the "reprogramming negativity" in response to the harmonic violation compared with the congruent chord. However, the negativity occurred earlier in jazz pianists (Fig. 3 lower panel, see the arrow in the shadowed time window between 370 and 550 ms), suggesting greater flexibility in responding to the harmonically mismatching chord. In line with this, jazz compared with classical pianists also showed less cost in terms of RTs (data not shown, but see Bianco *et al.*, 2018). Moreover, in the time-frequency domain, classical, but not jazz pianists showed increased theta power in response to the harmonic violation, possibly reflecting greater conflict and effort in resolving the unexpected chord. These results showed that although pianists performed the same exact task, they responded differently to irregularities depending on their long-term musical specialization. They thus suggest that specialised focus during long-term training not only differentially shapes auditory anticipation abilities [18,19], but also the skill to generate and revise actions conforming to the demands of the current context.

4. Conclusion

The experimental approach adopted in these studies built the basis for future research on complex sequential sensorimotor integration by taking music production as a testable example. We showed that musicians' brains generate predictions about forthcoming events with a certain degree of abstractness and flexibility not only in perception but also in action. These anticipatory mechanisms are supported by networks along the dorsal (motor) and ventral (auditory) streams. We also showed that these kinds of motor predictions are different from mere movement selection, and they are influenced by the specific focus of performers' past experience. These results suggest that models about regularities acquired through a sensory modality (auditory) can translate to the motor domain to fine tune production according to different contexts and performance demands.

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