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Review

Neural sensitivity to statistical regularities as a fundamental biological process that underlies auditory learning: The role of musical practice



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ABSTRACT

There is increasing evidence that humans and other nonhuman mammals are sensitive to the statistical structure of auditory input. Indeed, neural sensitivity to statistical regularities seems to be a fundamental biological property underlying auditory learning. In the case of speech, statistical regularities play a crucial role in the acquisition of several linguistic features, from phonotactic to more complex rules such as morphosyntactic rules. Interestingly, a similar sensitivity has been shown with non-speech streams: sequences of sounds changing in frequency or timbre can be segmented on the sole basis of conditional probabilities between adjacent sounds. We recently ran a set of cross-sectional and longitudinal experiments showing that merging music and speech information in song facilitates stream segmentation and, further, that musical practice enhances sensitivity to statistical regularities in speech at both neural and behavioral levels. Based on recent findings showing the involvement of a fronto-temporal network in speech segmentation, we defend the idea that enhanced auditory learning observed in musicians originates via at least three distinct pathways: enhanced low-level auditory processing, enhanced phonoarticulatory mapping via the left Inferior Frontal Gyrus and Pre-Motor cortex and increased functional connectivity within the audio-motor network. Finally, we discuss how these data predict a beneficial use of music for optimizing speech acquisition in both normal and impaired populations.

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Accurately predicting future events is crucial for survival in an ever-changing auditory world. The detection of auditory changes in the environment and the prediction of future auditory events at different time scales are particularly interesting for the study of music and speech processing. Music and speech are two communicative activities that involve the combination of an elementary set of sounds ordered in time according to rules, allowing the perception and the production of complex and unlimited utterances or musical phrases. Both activities rely on several perceptual and cognitive processes ranging from sound identification and categorization to memory storage and retrieval. Most importantly for our present aim, because language and music evolve in time, elementary elements become part of more complex structures

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following (emerging) rules and making (emerging) predictions. The study of how the human brain builds these expectations, comprising one of the core mechanisms of language and music acquisition, informs basic principles of both auditory neuroscience and psychophysiology. Here, we present evidence showing that neural sensitivities to simple acoustic changes or more complex statistical rules in auditory sequences are one of the fundamental biological processes underlying auditory learning. We then discuss the roles of music and its practice in refining sensitivity to these statistical properties and propose testable hypotheses accounting for musicians' enhanced sensitivity to acoustic regularities.

1. Cortical correlates of change detection in animal and human models

1.1. Change detection in animals

The cerebral correlates of auditory change detection have been widely studied via neurophysiological measures both in humans

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and animals. For example, neural sensitivity to low probability auditory events has been shown within primary auditory cortex of anesthetized cats by using invasive intra-cortical single-unit recordings (Ulanovsky et al., 2003). Specifically, Ulanovsky and collaborators showed that neurons in auditory cortex responded more to rarely occurring pure tones embedded in a repetitive sequence of standard ones. This finding suggests that Stimulus Specific Adaptation (SSA), i.e., the decrease in the firing rate of neurons to repeated stimuli, might be the correlate of change detection at the level of single neurons and a simple mechanism for auditory memory. In a further study, these authors showed that SSA in primary auditory cortex occurs at different time scales ranging from a few hundred milliseconds to tens of seconds (Ulanovsky et al., 2004). More recently, Yaron et al. (2012) have revealed the presence of neurons in primary auditory cortex in anesthetized rats that are sensitive to more detailed statistical information. The authors analyzed intra- and extracellular recordings from the auditory cortex of anesthetized rats in response to two types of oddball sequences wherein the position of rare tones could be either random or periodic. They found smaller responses to oddball tones in periodic sequences than to the same tones presented randomly. Most interestingly, the activity of neurons within primary auditory cortex was modulated by the order of sound sequences at the time scale of minutes. The authors proposed that their findings reflect a neuronal correlate of statistical regularities-processing, as is necessary for extracting syntactic properties of language and music.

1.2. Change detection in humans

There is growing evidence suggesting that several aspects of speech and music processing in humans involve similar change detection processes, from the detection of acoustic changes to the detection of changes in the statistical structure of a sequence of sounds. Thanks to excellent time resolution, Electroencephalographic (EEG) recordings offer non-invasive access to cortical activity on the order of milliseconds in response to external stimuli such as pure tones, harmonic sounds or speech sounds. Accordingly, EEG studies have provided the first evidence of sensitivity to rarely occurring auditory events in the human auditory cortex. Using tone pips, neural sensitivity to low probability auditory events was shown in human adults and newborns (Hari et al., 1984; Alho et al., 1991). The well-known Mismatch Negativity (MMN), a change-detection component of the auditory Event-Related Potentials (ERPs), is elicited by rarely occurring deviant events embedded within a repetitive sequence of standard stimuli (Näätänen et al., 2005; Grimm and Escera, 2011). The MMN is considered a measure of pre-attentive, implicit auditory processing which may reflect the formation of an echoic memory trace within auditory cortex (Näätänen et al., 2005). This ERP component is found not only in response to changes in frequency (Sams et al., 1985), intensity (Paavilainen et al., 1993), location (Paavilainen et al., 1989), duration (Schröger and Winkler, 1995) and timbre (Tervaniemi et al., 1997) but also for changes in consonant-vowel (CV) speech sounds consisting and vowels (Deguchi et al., 2010; Näätänen et al., 1978). Furthermore, the MMN can be elicited by changes in longer, more complex and/or abstract patterns of musical and speech sounds (Boh et al., 2010; Herholz et al., 2009; Wang et al., 2012). All together, these findings support the idea that detecting changes as well as detecting patterns both require that the auditory system be sensitive to statistical regularities. Furthermore, these results show that auditory change detection processes that take place within the auditory cortices can reflect the processing of formant transition variations sub-serving phoneme and timbre change detection as well as the processing of more complex structures in longer linguistic or musical contexts.

We suggest that the detection of a change, strongly linked to the predictive abilities of the auditory system, can be considered a basic biological process involved both in music and speech sequence learning.

2. Sensitivity to statistical structure of auditory input

2.1. Statistical learning of single sounds

In the context of language acquisition, it is now well accepted that sensitivity to speech sounds evolves during infancy (Kuhl, 2004). Notably, it has been shown that infants' abilities to discriminate speech sounds are sensitive to probabilistic patterns present in their language environments. During the first six months of life infants do not differentiate foreign from native phonetic units; after the age of 6 months, however, they show a drastic decrease in sensitivity to foreign phonological units while becoming attuned to phonetic units of their mother tongue (Kuhl, 2004). This property of phonetic learning has been elegantly highlighted in a behavioral experiment with 6 and 8 month-old infants (Maye et al., 2002). One group of infants was familiarized for 2 min with a [da]-[ta] continuum presenting a bimodal frequency distribution (tokens from the extremities of the continuum were the most frequent) and another group of infants was familiarized with a similar continuum but with a unimodal frequency distribution (tokens from the center of the continuum were the most frequent). Infants were subsequently tested in a phonetic discrimination test. While the group of infants exposed to the bimodal distribution discriminated tokens from the extreme points of the continuum, infants previously familiarized with a unimodal distribution did not. These results provide evidence that perceptual learning of native phonemes relies on the sensitivity to the statistical properties of the speech sounds most present in the environment (Maye et al., 2002), a process is commonly referred to as statistical learning.

2.2. Statistical learning of sequences of sounds

In addition to identifying the phonemic building blocks of speech, language acquisition involves the ability to extract words from fluent speech. In typical adult-directed speech there are no systematic acoustic cues to signal word segmentation such as silences or stresses at words boundaries. By contrast, infant-directed speech presents exaggerated pitch contour changes and slower speech rates that contribute to solving the speech segmentation problem (Fernald, 1992; Thiessen et al., 2005). Nonetheless, it has been shown that speech can be segmented in an implicit manner based on only one source of information: the statistical structure of the language (Saffran et al., 1996a). Saffran writes, "syllables that are part of the same word tend to follow one another predictably, whereas syllables that span word boundaries do not" (Saffran et al., 2001).

The role of transitional probabilities in speech segmentation (i.e., the probability of syllable Y given syllable X: p(Y|X) = frequency of XY/ frequency of X) has been elegantly shown by Saffran and collaborators in both infants and adults (Saffran et al., 1996a,b; Aslin et al., 1998) and studies using EEG and Near Infrared Spectroscopy have extended this phenomenon to neonates (Gervain et al., 2008; Teinonen et al., 2009). The employed paradigm generally consists of a familiarization (learning) phase followed by a behavioral test. During the familiarization phase, participants are exposed to several minutes (depending on the complexity of the stream and on the population of interest) of a statistically structured, continuous flow of artificial syllables lacking any acoustic cues at words boundaries. The test phase for adult

participants is typically a two-alternative forced choice (AFC) procedure during which participants have to choose, in each trial, between a familiar pseudo-word that was part of the language and a pseudo-word built with similar syllables but that was not part of the language (see Fig. 1 for an illustration of the experimental procedure used in François and Schön, 2011). Above chance performance is interpreted as participants' ability to segment the speech stream on the basis of statistical properties of the input. The extraction of units using statistical properties of sound input has also been shown for non-linguistic stimuli such as sounds with different pitches (Saffran et al., 1999) and timbres (Tillmann and McAdams, 2004), as well as with environmental sounds (Sanders et al., 2009). These results suggest that statistical learning is a domain general learning process. Additionally, this statistical sensitivity has been revealed in the cotton top tamarin and in rats (Hauser et al., 2000, 2002; Ramus et al., 2000; Toro and Trobalón, 2005), suggesting that sensitivity to acoustic regularities is a fundamental auditory process that undergirds normal auditory processing, survival in a complex acoustic environment and even, in many cases, successful expressive and receptive vocal communication.

In the domain of music, statistical learning has been shown to be at play for the acquisition of new musical scales and for learning 12-tone serial musical sequences (Loui et al., 2010; Dienes and Longuet-Higgins, 2004). Loui and collaborators familiarized adult participants with melodies originating from a finite-state musical grammar over a 30 min period. The results provided evidence of learning as revealed by recognition, generalization and preference for repeated melodies from the grammar. The authors suggested that sensitivity to statistical regularities is a basic principle accounting for music acquisition and preference. To summarize, these studies provide converging evidence suggesting that sensitivity to statistical regularities is one of the fundamental perceptual—cognitive processes underlying auditory learning and that it serves as a basis for several aspects of language and music acquisition.

2.3. Brain correlates of auditory statistical learning

A growing number of studies have been conducted in human adults and children to unravel the cortical network involved during statistical learning of speech and tone sequences. Using fMRI, it has been shown that compared to a random stream (thus containing no predictable patterns of syllables), listening to a statistically structured stream of syllables activates more of the fronto-temporal dorsal pathway including the Superior Temporal Gyrus, the Middle Temporal Gyrus, the Pre-Motor Cortex and the Inferior Frontal Gyrus (Hickok and Poeppel, 2007; Cunillera et al., 2009; Rodríguez-Fornells et al., 2009; McNealy et al., 2006, 2010). Using EEG, other studies have shown larger learning-related modulations of the N100 and N400 components for structured compared to random

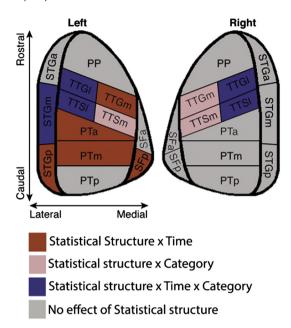


Fig. 2. From Tremblay et al. (2013), the figure illustrates the patterns of activity to sound category, statistical structure, exposure time and their interactions within the bilateral supratemporal areas of healthy adult participants. The anteroposterior gradient is visible from the color-coded patterns of responses with sensitivity to the statistical structure independently of sound category in posterior areas and the absence of sensitivity in anterior areas. Regions' legend: PP = planumpolare; TTG = transverse temporal gyrus (m = medial, l = lateral); TTS = transverse temporal sulcus (m = medial, l = lateral); PT = planum temporale (a = anterior, m = middle, p = posterior); <math>STG = transverse temporal gyrus (a = anterior, m = middle, p = posterior).

syllable sequences (Cunillera et al., 2009; De Diego Balaguer et al., 2007). Moreover, in a study using sequences of tones, Abla and colleagues reported similar modulations of the N100 and N400 components during the exposure phase, suggesting that similar processes might be at play for speech and tone segmentation (Abla et al., 2008). A recent study provides a precise description on the organization of the STG with respect to statistical sensitivity for speech and non-speech sounds (Tremblay et al., 2012). In this study, participants were presented with random and highly structured sequences of speech and bird songs while performing a visual task. The results revealed several important findings. While some subregions of the STG showed a relative preference to speech (i.e., significant activation for both speech and bird songs), others showed an absolute preference for speech. Some sub-regions in the Posterior SupraTemporal plane including the medial Transverse Temporal Gyrus were sensitive to the statistical structure of the input independent of the sound category. The authors proposed that the supratemporal plane is functionally organized according to



Fig. 1. Illustration of the experimental design used in François and Schön (2011). Participants were presented with a statistically structured stream of sung syllables (exposure phase) and then tested with a 2AFC for recognition of both linguistic and musical structures. Stimuli were presented through loudspeakers.

an anteroposterior gradient (Fig. 2). More anterior regions might be operating specifically for speech at the level of single phonemes while more posterior regions might be involved in processing statistically structured sequences of both speech and non-speech sounds. This study is particularly informative because it supports the idea that processing of different categories of structured sequences (speech and non speech sounds) may rely on shared neural processes in the posterior STG. Moreover, it supports Patel's OPERA hypothesis (Patel, 2011), which is presented in a expanded version in this same issue of Hearing Research (Patel, 2013).

2.4. Sensitivity to statistical structure as a domain general skill

The body of literature presented above suggests that sequencing abilities in music and speech partly rely on shared learning mechanisms and that these abilities may be sustained by shared and overlapping cortical resources (see also Patel, 2003; Kraus and Chandrasekaran, 2010). However, studies investigating statistical learning have focused on one dimension or the other but not on both concurrently, complicating the comparison of results issued from different tasks, participants, and analyses. The use of song is particularly well suited to the study of the relationship of statistical learning of language and music because both linguistic and musical information are merged into a single acoustic signal containing two salient dimensions, thus allowing for a direct comparison in the same experiment. We recently ran a set of behavioral experiments using sung languages presented according to different statistical structures during the exposure phase. In the first experiment, we compared segmentation performance of a spoken language versus segmentation performance of a sung language (Schön et al., 2008). Two groups of participants were familiarized with an artificial language that was either spoken or sung (each syllable sung on a specific pitch). While 7 min of familiarization were not enough to segment a spoken language, they were sufficient to learn the sung language, suggesting that the learning process is facilitated when the statistical structure of the musical and linguistic dimensions match. Because one may claim that song is simply more arousing than speech, we ran a further experiment using another sung language wherein the statistics of linguistic and musical structures were mismatched. The participants' performance was exactly in between the spoken and the matching sung versions obtained in the previous experiment, thus confirming a beneficial effect of both distributional and motivational properties of music in language acquisition (Thiessen et al., 2005; Schön et al., 2008).

3. Musical practice facilitates the extraction of statistical regularities

In two recently published studies we assessed effects of musical expertise (in adults) and active musical training (in children) on speech segmentation abilities (François and Schön, 2011; François et al., 2012a, see also Shook et al., 2013 for additional behavioral evidence of enhanced statistical learning in musicians). The underlying prediction was that if some auditory processes involved in both linguistic and musical learning are shared, musical training may enhance these common processes, with beneficial effects for language processing. We used both behavioral and electrophysiological measures to assess speech segmentation skills in participants exposed to several minutes of a sung speech stream. While in adults we tested both the recall of linguistic and musical dimensions contained in the sung language, we tested only the recall of the linguistic dimension in children.

In adults, we showed that musicians marginally outperformed nonmusicians behaviorally and both groups performed above chance level in the linguistic test while staying at chance in the musical test. Interestingly, ERP data were more sensitive and showed a main effect of expertise on the N1 component with larger amplitude for musicians than for nonmusicians in both dimensions. Additionally, the amplitude of a later N400-like fronto-central negative component was more sensitive to the transitional probabilities in musicians compared to nonmusicians, again in both dimensions. These findings suggest that musicians may have more robust representations of musical and linguistic structures brought about during the exposure phase than nonmusicians. Interestingly, in the musical test we found a similar interaction of expertise and sensitivity to statistical structure on two early ERP components. Musicians showed both a larger P2 and MMN to low transitional probability melodies than to high transitional probability melodies while nonmusicians did not show these effects. The transitional probability effect on the P2 and MMN components suggested that musicians learned the musical structure (both tonal and interval structures) better than nonmusicians.

In children, we compared a group of children enrolled in a musictraining program over the course of two school years to a matched control group of children enrolled in an equally motivating painting training program. Results were impressive in that while no pretraining between-group behavioral or electrophysiological differences were observed, only musically trained children showed a significant increase in speech segmentation abilities after one and two years of training. After 2 years this behavioral benefit was accompanied by greater sensitivity of a fronto-central N400-like component to transitional probabilities in musically trained children than in painting trained children, as observed in adult musicians. These findings provide causal evidence that music training enhances sensitivity to statistical regularities in speech, a fundamental biological process that underlies language learning. Additionally, this result argues in favor of music's ability to augment children's language development by facilitating speech segmentation, a building block of language acquisition. In the following sections we suggest three non-exclusive explanations that may account for the observed benefit of musicians over nonmusicians in speech segmentation.

4. Why musical practice may facilitate speech segmentation

4.1. Enhanced low-level processing of speech and musical sounds in musicians

The study of professional musicians is of great interest because it reveals how the long-term coupling of auditory and motor systems fine-tunes the brain. Studying professional musicians elucidates functional and structural modifications fostered by musical practice, although definitive conclusions could only be drawn using longitudinal designs. Indeed, the musician's brain is considered a model of neuroplasticity both at the structural and functional levels (Münte et al., 2002; see also Strait and Kraus, 2013, this issue). Compared to non-musicians, musicians show enhanced cortical attentive and pre-attentive processing of linguistic (for example see Chobert et al., 2011 for Voice Onset Time, frequency and duration deviances) and musical features (for example see Vuust et al., 2011). This enhancement is reflected by larger amplitudes and/or shorter latencies of many ERP components such as the N1, P2, MMN and P300 (Pantev et al., 1998; Koelsch et al., 1999; Shahin et al., 2003; Van Zuijen et al., 2005). For instance, adult musicians show larger MMNs than nonmusicians to deviants in contour and interval structure inserted in 5-note melodies (Fujioka et al., 2004). Even sub-cortically, adult, child and preschool musicians show more robust encoding of linguistic and musical features as reflected by earlier and larger brainstem responses compared to non-musicians (Kraus and Chandrasekaran, 2010; Musacchia et al., 2007; Strait et al., 2012, 2013; Parbery-Clark et al., 2011; Strait and Kraus, 2013).

Most of the studies above used cross-sectional approaches and causation can only be inferred in the case of well-controlled longitudinal studies with pseudo-random assignment of the participants; very few studies of this kind exist. Lappe et al. (2008), however, compared MMNs elicited by deviant 3 piano tones sequences embedded in standard sequences before and after 2 weeks of musical training in one group with sensory-motor training and in another with auditory training only. The results showed a greater enhancement of MMN amplitude in the sensory-motor trained group compared to the auditory training group. More recently, Chobert and collaborators revealed that 6 and 12 months of active musical training in 8–10 year old children were sufficient to induce an enhanced MMN in response to changes in VOT and duration of CV syllables (Chobert et al., 2012). At the level of sound sequence processing, Hyde et al. (2009) showed that 15 months of musical training in 6-year-old children enhanced auditory discrimination performance in melodic and rhythmic tasks as well as in a finger motor sequencing task. Moreno et al. (2009) trained 8-year-old nonmusician children with music or painting for 6 months and revealed better pitch discrimination abilities for both melodies and sentence prosody in the musically trained group only. These last studies demonstrate that active musical training positively impacts multiple functional aspects of the brain. Most importantly, these studies show that music training facilitates both pre-attentive and attentive processing of acoustic deviance in linguistic and musical inputs, one the basic biological process involved both in music and speech sequence learning.

Recently, Paraskevopoulos et al. (2011) used MEG recordings in a MMN paradigm to study the effect of musical practice on the neural and behavioral sensitivity to statistical structure of tone sequences. The stimuli consisted of repetitive three tone sequences as standard sequences, which were interleaved with deviant sequences in which the final tone was changed compared to standard ones. Musical experts and nonmusicians showed similar level of performance and similar MMN amplitude to deviance. Nonetheless, compared to nonmusicians musical experts showed a larger difference between standards and deviants on an early ERP component, the P50. These results suggested that enhanced P50 to deviant tones might index a better encoding of transitional probabilities in musicians than in nonmusicians (Paraskevopoulos et al., 2011). Similarly, Skoe and colleagues conducted an experiment demonstrating sensitivity to statistical in evoked responses understood to be generated by the auditory midbrain/brainstem (Skoe et al., in press). They used brainstem recordings during the presentation of random and statistically structured sequences of doublets of tones while participants watched a silent photo-slideshow. Results showed that the best learners were participants having the most enhanced response to structured sequences.

Interestingly, there is evidence showing that brain structural distinctions in musicians may underlie their functional enhancements: musicians have larger planum temporale than non-musicians (Keenan et al., 2001; Luders et al., 2004) and white matter integrity in the right hemisphere, including the planum temporale, predicts success in a pitch-related grammar-learning task (Loui et al., 2011). Additionally, trans-magnetic brain stimulation applied to Heschl's gyrus modulates the level of performance in a pitch discrimination task (Mathys et al., 2011). Taken together, these results show that an enhanced neural sensitivity to statistical properties in auditory input within the cortex and brainstem in musicians may contribute to enhanced auditory learning skills.

4.2. Enhanced IFG/PMC functioning

In addition to the involvement of the auditory cortex, prefrontal cortices (left IFG and PMC) are clearly activated during exposure to

an artificial language learning task (Cunillera et al., 2009; McNealy et al., 2006, 2010). IFG/PMC regions have been shown to be involved in language perception and production and in music processing as well (Vigneau et al., 2006; Koelsch et al., 2005; Brown et al., 2006). Grey matter density in the IFG has been found to correlate with the level of language proficiency (Stein et al., 2012) and in the number of years of phonetic training in expert phoneticians (Golestani et al., 2011). Interestingly, there is evidence that white matter integrity in the left-IFG predicts the level of performance in an artificial grammar learning task (Flöel et al., 2009) and that musicians show increased gray matter density and volume in this same region (Sluming et al., 2002). Thus, a greater recruitment of associative frontal areas in musicians compared to nonmusicians could contribute to enhanced neural sensitivity by acting as a top-down modulator onto low-level auditory cortices or as phonoarticulatory matching process (Rodríguez-Fornells et al., 2009).

4.3. Enhanced connectivity from pSTG to IFG/PMC

Finally, we must consider feedforward and feedback neuronal projections within the speech segmentation network. The neuronal fibers forming the Arcuate Fasciculus or Superior Longitudinal Fasciculus (AF/SLF) directly connect the posterior STG to the IFG/ PMC. Lesions of the AF/SLF induce impairment not only of phonological and word repetition but also in verbal short-term memory tasks (Benson et al., 1973; Damasio and Damasio, 1980; Anderson et al., 1999). Moreover, studies have found that the AF/SLF is notably decisive in mapping speech sound sequences to articulatory sequences of gestures (Catani et al., 2005; Schmahmann et al., 2007) and in word learning (Lopez-Barroso et al., 2013). Interestingly, both adult musicians and in 8-year old children who followed 2 years of musical training show more developed AF/SLF than nonmusicians (Oechslin et al., 2010; Wan and Schlaug, 2010; Halwani et al., 2011). Taken together, these results suggest that an increased connectivity between auditory regions within the temporal lobe and motor regions within the frontal lobe might underlie enhanced segmentation skills in musicians compared to nonmusicians.

5. Conclusion

Further research is needed to decipher the relative contributions of the three non-exclusive possibilities suggested above to account for musicians' enhanced sensitivity to regularities in ongoing speech and musical sound streams, which will surely benefit from the use of innovative data processing techniques involving both structural and functional measures (François et al., 2012b). For instance, the analysis of ERPs during exposure to new speech- or music-based "languages" are of great interest because implicit electrophysiological measures (EEG/MEG) reveal subtle differences between groups in language acquisition that might be underestimated by behavioral estimates (e.g., McLaughlin et al., 2004; Abla et al., 2008; Cunillera et al., 2009; De Diego Balaguer et al., 2007). Additionally, implicit electrophysiological measures may be informative when studying less accessible populations such as very young infants (Teinonen et al., 2009; Kudo et al., 2011), who are unable to deliver an overt behavioral response while being at the same time the most promising naive population for disentangling the contribution of nature vs. nurture in the acquisition of language and music. The use of implicit measures could also be useful in the case of patients with communication disorders such aphasia, autism or motor disorders such as in Parkinson's disease.

It is important to keep in mind that the present article focused exclusively on first-order statistical regularities. Natural languages also make use of higher order statistics, for instance in hierarchical syntactical structures. Interestingly, recent work by Brod and Opitz (2013) brings evidence of enhanced sensitivity to long distance dependencies in musicians' learning of an artificial language compared to nonmusicians. This suggests that musical practice benefits the learning of more complex syntactical rules in more natural language. Together, effects of singing on speech segmentation and effects of musical practice on brain functions to strengthen auditory sequencing skills promote the use of music as a tool for optimizing speech acquisition trajectories both in normal and impaired populations.

Here, we have presented evidence for enhanced sensitivity to statistical regularities in musicians compared to nonmusicians. We have interpreted this benefit to stem from training-related plasticity and propose that it relies on a complex interaction between enhanced low-level auditory processing in both cortical and subcortical regions, enhanced functioning of associative frontal areas, and enhanced connectivity between those areas. One possible mechanism bringing about musicians' enhanced sensitivity to statistical regularities may involve corticofugal projections that shape low-level auditory regions in a top-down manner (Skoe et al., in press). Future research, however, is needed to clearly define the respective roles of bottom-up and top-down mechanisms for engendering neural sensitivity to acoustic regularities and how they are strengthened in musicians.

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