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Research paper

Musical experience shapes top-down auditory mechanisms: Evidence from masking and auditory attention performance

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ABSTRACT

A growing body of research suggests that cognitive functions, such as attention and memory, drive perception by tuning sensory mechanisms to relevant acoustic features. Long-term musical experience also modulates lower-level auditory function, although the mechanisms by which this occurs remain uncertain. In order to tease apart the mechanisms that drive perceptual enhancements in musicians, we posed the question: do well-developed cognitive abilities fine-tune auditory perception in a top-down fashion? We administered a standardized battery of perceptual and cognitive tests to adult musicians and non-musicians, including tasks either more or less susceptible to cognitive control (e.g., backward versus simultaneous masking) and more or less dependent on auditory or visual processing (e.g., auditory versus visual attention). Outcomes indicate lower perceptual thresholds in musicians specifically for auditory tasks that relate with cognitive abilities, such as backward masking and auditory attention. These enhancements were observed in the absence of group differences for the simultaneous masking and visual attention tasks. Our results suggest that long-term musical practice strengthens cognitive functions and that these functions benefit auditory skills. Musical training bolsters higher-level mechanisms that, when impaired, relate to language and literacy deficits. Thus, musical training may serve to lessen the impact of these deficits by strengthening the corticofugal system for hearing.

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1. Introduction

Deficits in auditory perception contribute to language and literacy disorders, affecting over 10% of children in developed countries (Torgeson, 1991). These deficits impact perceptual abilities that are particularly subject to cognitive control (Hartley et al., 2003; Moore et al., 2008; Wright et al., 1997). For example, temporal auditory processing can be impaired in children with language and literacy disorders (Benasich and Tallal, 2002; Gaab et al., 2007; Montgomery et al., 2005; Temple et al., 2000). This impairment manifests itself as an inability to separate brief sounds presented one after the other. Backward masking thresholds provide a metric for temporal auditory processing and are determined by measuring how loud a tone must be for it to be perceived when immediately followed by a competing signal that is longer in duration than the tone, such as broadband noise. The noise results in reduced sensitivity to the preceding tone even in unimpaired listeners, but children with temporal processing deficits show more debilitating effects of the masker on the tone (Hartley and Moore, 2002; Hartley et al., 2003; Rosen and Manganari, 2001; Tallal et al., 1993; Wright, 1998, 2001; Wright et al., 1997). In speech, deficits in backward masking may impair the perception of syllables in which vowels produce a masking effect on the preceding consonants (Johnson et al., 2007; Rosen and Manganari, 2001). Backward masking performance appears to relate to cognitive performance (Tallal et al., 1993; Wright, 1998).

Abbreviations: Mus, musicians; NonMus, non-musicians; IMAP, IHR Multicentre Battery for Auditory Processing; FD, frequency discrimination; BM, backward masking; BMgap, backward masking with a delay gap; SM, simultaneous masking; SMnotch, simultaneous masking with a notched filter; AAtt, auditory attention; VAtt, visual attention; AWM, auditory working memory; WASI, Wechsler abbreviated scale of intelligence; IQ, intelligence quotient; SNR, signal-to-noise ratio; SLI, Specific Language Impairment; APD, Auditory Processing Disorder

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A growing body of research suggests that high-level cognitive functions can drive auditory perception by tuning lower-level sensory mechanisms to increase neural signal-to-noise ratios (SNR). This interaction between cognitive and sensory mechanisms has been observed in both the visual (Ahissar and Hochstein, 2004; Dosher and Lu, 1998, 1999, 2006; Gold et al., 1999) and auditory domains (Allen et al., 2000; Kauramaki et al., 2007), with higher SNRs being associated with better perception and a more efficient system (Hartley and Moore, 2002; Hartley et al., 2003). By strengthening cognitive functions related to the task at hand (such as auditory attention for backward masking perception), deficits in sensory processing may be ameliorated (Moore, 2002).

Considerable effort has gone toward the development of language-based auditory training programs to improve auditory processing at sensory and cognitive levels (Marler et al., 2001; Merzenich et al., 1996; Moore et al., 2009). Music provides a potentially powerful alternative to traditional language-based programs because its practice requires interactive participation with complex sounds and occurs regularly, with those undergoing musical training required to spend many hours weekly with their instruments. Although other structural auditory training programs might accomplish similar feats, the frequency with which musicians must spend time manipulating and attending to complex sounds may provide a distinct advantage for engendering neural plasticity and learning. By activating the neural reward circuit, musical practice and performance promotes engagement and plasticity (Blood and Zatorre, 2001; Menon and Levitin, 2005). Furthermore, musical practice not only enhances the processing of music-related sounds but also affects processing in other domains, such as language (Marques et al., 2007; Moreno et al., 2009; Parbery-Clark et al., 2009a; Schon et al., 2004, 2008). Specifically, cognitive mechanisms pertaining to verbal abilities (Forgeard et al., 2008), working memory (Brandler and Rammsayer, 2003; Chan et al., 1998; Franklin et al., 2008; Ho et al., 2003; Jakobson et al., 2008; Ohnishi et al., 2001; Parbery-Clark et al., 2009) and auditory attention (Burns and Ward, 1978; Locke and Kellar, 1973; Siegel and Siegel, 1977) may be strengthened in musicians.

We are just now beginning to explore relationships between musicians' cognitive and perceptual enhancements and the underlying processes that drive them. It has recently been proposed that perceptual enhancements in musicians can be attributed, at least in part, to top-down modulation of cochlear (Perrot et al., 1999) and brainstem function (Kraus et al., 2009; Lee et al., 2009; Musacchia et al., 2008, 2007; Parbery–Clark et al., 2009b; Strait et al., 2009a,b; Tzounopoulos and Kraus, 2009; Wong et al., 2007). This top-down control may be mediated by the corticofugal pathway for hearing, which consists of an extensive tract of efferent fibers (Suga, 2008; Suga et al., 2000). We now ask: does sophisticated interaction with musical sound strengthen cognitive mechanisms that fine-tune auditory perception in a top-down fashion?

In order to define relationships between musicians' cognitive and perceptual enhancements, we tested adult musicians and non-musicians on a standardized battery of cognitive and perceptual tasks. We hypothesized that musicians demonstrate greater perceptual advantages for tasks that rely on cognitive abilities—especially in the auditory modality. Specifically, we anticipated a musician advantage for frequency discrimination and temporal processing, assessed by backward masking, and no advantage for simultaneous masking, which is thought to be less dependent on cognitive abilities and more dependent on physiological properties of peripheral hearing structures. We also expected musical experience to affect auditory but not visual attention. Lastly, auditory-related cognitive abilities, such as auditory attention and working memory, were only expected to correlate with performance on perceptual measures at which musicians excel, such as frequency discrimination and backward masking.

2. Methods

We collected cognitive and perceptual data using the IHR Multicentre Battery for Auditory Processing (IMAP, developed by the Medical Research Council Institute of Hearing Research, Nottingham, UK) from 33 adults between the ages of 18–40 years. Participants provided informed consent according to Northwestern University's Institutional Review Board. All participants completed an extensive questionnaire addressing family history, musical experience and educational history and demonstrated normal audiometric thresholds (<20 dB pure tone thresholds at octave frequencies from 125 to 8000 Hz) and non-verbal IQ (>40th percentile achieved on the Wechsler Abbreviated Scale of Intelligence Matrix Reasoning subtest) (Harcourt Assessment, San Antonio, TX). Musicians (Mus, $N = 18$) were self-categorized, began musical training at <9 years of age and had consistently practiced for >10 years (consistency defined as practicing at least 3 days weekly for >1 h per session). Non-musicians (NonMus, $N = 15$) were self-categorized and had <4 years of formal musical experience throughout their lifespan.

A subset of IMAP measures were administered in a sound attenuated booth using a laptop computer that was placed 60 cm from the participant. Responses were recorded using a 3-button response box. Stimuli were presented diotically through Sennheiser HD 25–1 headphones and were accompanied by animated visual stimuli. Testing sessions lasted $\sim$1.5 h, including questionnaire completion and audiometric testing.

IMAP tasks addressed auditory working memory (memory for reversed digits, AWM), auditory attention (AAtt), visual attention (VAtt), frequency discrimination (FD), frequency selectivity (simultaneous masking with and without notched filters—SM and SMnotch), temporal resolution (backward masking with and without a temporal gap between the target and masker—BM and BMgap), and non-verbal IQ (Wechsler Abbreviated Scale of Intelligence matrix reasoning subtest—WASI). All subtests except for the WASI, which was administered according to its required protocol, used an identical response paradigm, visual cues and response feedback. Perceptual subtests were initiated by a practice session of easy trials, consisting of the same stimuli used for initial trials in each subtest (a 90 dB SPL target tone for backward masking and a 50% frequency difference between the target and standard tones for frequency discrimination). Correct responses on 4 out of 5 practice trials were required to continue. All subjects achieved a minimum of 4 out of 5 correct responses for all practice sessions.

2.1. Auditory working memory

Participants listened to a sequence of numbers presented at 70 dB SPL and were asked to repeat them in reverse order. Initial sequences were two digits in length and increased in difficulty (more digits) with subsequent correct responses, to a maximum of nine digits. All digits had to be repeated in the appropriate sequence to be considered correct. Participants were given unlimited time to respond.

2.2. Auditory and visual attention

Attention tasks were similar to the Test of Attentional Performance (Zimmerman and Fimm, 2002) and measured phasic alertness by comparing reaction times induced by the presence or absence of a cue that occurred with a variable delay (0.5–1.0 s) before a target stimulus. For both visual and auditory attention tasks, participants attended to a computer screen displaying of a single cartoon character that was standing in an open space. For the visual attention task (VAtt), participants were instructed to monitor the character for movement and press the center button on the response box with their dominant hand as soon as they saw the character raise its arms. The arm raise was considered the target stimulus. Participants were cued by a second visual stimulus (the changing of the character's shirt color) on some trials and were asked *not* to respond to that cue.

For the auditory attention task (AAtt), participants were once again instructed to watch a computer screen displaying a character that was standing in an open space. Knowing that the visual scene would not change, they were asked to listen for a "beep" (presented at 80 dB SPL) and press the center button on the response box with their dominant hand as soon as they heard it. The beep was considered the target stimulus. Participants were cued by a second auditory stimulus (a "siren," presented at 70 dB SPL) on some trials and were asked *not* to respond to that cue. Reaction times for both VAtt and AAtt tasks were measured in milliseconds.

2.3. Frequency discrimination

The frequency discrimination (FD) paradigm employed a cued three-alternative forced choice presented as an animated computer game in which each of three characters opened their mouths to "speak" a sound. The target ("odd-one-out") signal was presented with equal probability in one of the three intervals amidst a standard 1000 Hz tone that was presented twice for each trial. All tones had equal durations (200 ms) and were separated from one another by 400 ms. All stimuli incorporated 10 ms cosine ramps. The target differed in frequency from the standard, initially 50% higher in frequency but gaining in proximity to the standard with successful performance according to an adaptive staircase model (3 down, 1 up) that incorporated three diminishing step sizes (see Amitay et al., 2006 for further description). Incorrect responses resulted in a greater percent difference between the target and standard tones. Each of the cartoon characters corresponded to one of the three buttons on the response box and participants indicated which cartoon character presented the target by pressing the corresponding button. After correct responses, the character that "spoke" the target danced. Participants were given unlimited time to respond (response times were not logged). Trials continued until a total of three reversals was obtained. Threshold was determined by calculating the mean percent difference between the target and standard presented in the final two trials ($\Delta F/F_{\mathrm{standard}}$) (Amitay et al., 2006; Moore et al., 2008).

2.4. Backward and simultaneous masking

Identical visual cues, response feedback and threshold determination were employed for the frequency discrimination and four masking tasks (BM, BMgap, SM, SMnotch). For the two backward masking measures, participants were instructed to attend to the computer screen and listen to a sequence of three "noise sounds" (bandpass noise with a center frequency of 1000 Hz, a width of 800 Hz, a duration of 300 ms, and a fixed spectrum level of 30 dB). A 20 ms 1000 Hz target tone occurred immediately prior to the noise. For the BMgap task, the offset of the target and the onset of the noise occurred with a temporal gap of 50 ms, whereas in the standard BM task the target's offset and the noise's onset occurred concurrently. Initial targets were presented at 90 (BM) or 75 dB SPL (BMgap). Targets decreased in intensity on both tasks according to an adaptive staircase model (3 down, 1 up) that incorporated three diminishing step sizes (see Amitay et al. (2006) for further description). This procedure yielded a minimum detectable threshold for each task (target dB). Participants pressed the appropriate button on the response box to indicate which of three trials contained the target tone (as opposed to noise only).

Identical instructions were provided for the simultaneous masking tasks, although the relationship between the target stimulus and the masking noise differed. For SM, a 20 ms 1000 Hz target tone occurred 200 ms following the onset of a masking noise (the same masking noise used for the BM tasks). For SMnotch, the same target occurred 200 ms following the onset of a bandpass masking noise with no energy between 800–1200 Hz (a spectral notch). Initial targets were presented at 95 (SM) or 80 dB SPL (SMnotch). An identical threshold determination procedure was used for the SM tasks as for the BM tasks, yielding a minimum detectable threshold for each task (target dB). Again, participants pressed the appropriate button to indicate which trial contained the target tone. For all four masking tasks, the intensity of the target was adaptively changed according to an adaptive staircase model until threshold was established.

2.5. Data analysis

To determine the effects of musical experience, response times (attention tasks) and thresholds (frequency discrimination and masking tasks) for both groups (Mus/NonMus) were subjected to a multivariate analysis of variance (MANOVA). All results reported herein reflect two-tailed values. Normality for all data was confirmed by the Kolmogorov–Smirnov test for equality. Relationships between length of musical experience and task performance as well as among individual tasks were explored with correlation analyses. In interpreting the results, the α level for correlations was corrected for multiple comparisons. All statistical analyses were performed using SPSS (SPSS Inc., Chicago, IL).

3. Results

Overall, musicians performed with greater proficiency than non-musicians on a subset of IMAP tasks. Enhanced musician performance was observed for frequency discrimination, auditory attention and both backward masking measures. Musicians demonstrated lower thresholds than non-musicians for the frequency discrimination and backward masking measures (Fig. 1; FD $F(1, 32) = 10.16$, $P < 0.005$; BM: $F(1, 32) = 6.08$, $P < 0.02$; BMgap: $F(1, 32) = 5.64$, $P < 0.03$) and faster reaction times to targets in the auditory attention paradigm (Fig. 1; $F(1, 32) = 4.67$, $P < 0.04$). None of the other measures differed between groups, including SM, SMnotch, AWM, VAtt and non-verbal IQ (Table 1).

Furthermore, we observed correlations between performance on standard backward masking and auditory attention tasks with years of musical practice among all subjects with musical practice histories, regardless of group status (Fig. 2). Performance on both tasks correlated with the number of years individuals had spent practicing their instruments, with more years of practice relating to lower BM thresholds and faster AAtt reaction times (BM: $r = -0.409$, $P < 0.03$; AAtt: $r = -0.486$, $P < 0.01$). These correlations also held with the inclusion of subjects with zero years of musical practice (BM: $r = -0.401$, $P < 0.02$; AAtt: $r = -0.375$, $P < 0.04$).

Within the musician group only, temporal perception related with performance on auditory-related cognitive abilities as measured through auditory working memory and auditory attention. For musicians, BM performance correlated with AWM (Fig. 3; Mus: $r = -0.479$, $P < 0.05$; NonMus: $r = -0.117$, $P < 0.70$), whereas BMgap performance correlated with AAtt (Fig. 3; Mus: $r = 0.478$, $P < 0.05$; NonMus: $r = -0.506$, $P < 0.06$). Lower backward masking thresholds in musicians related to the ability to remember more digits in reverse sequence and faster auditory attention reaction times.

Frequency discrimination thresholds also correlated with cognitive performance, as measured by non-verbal IQ. Although this

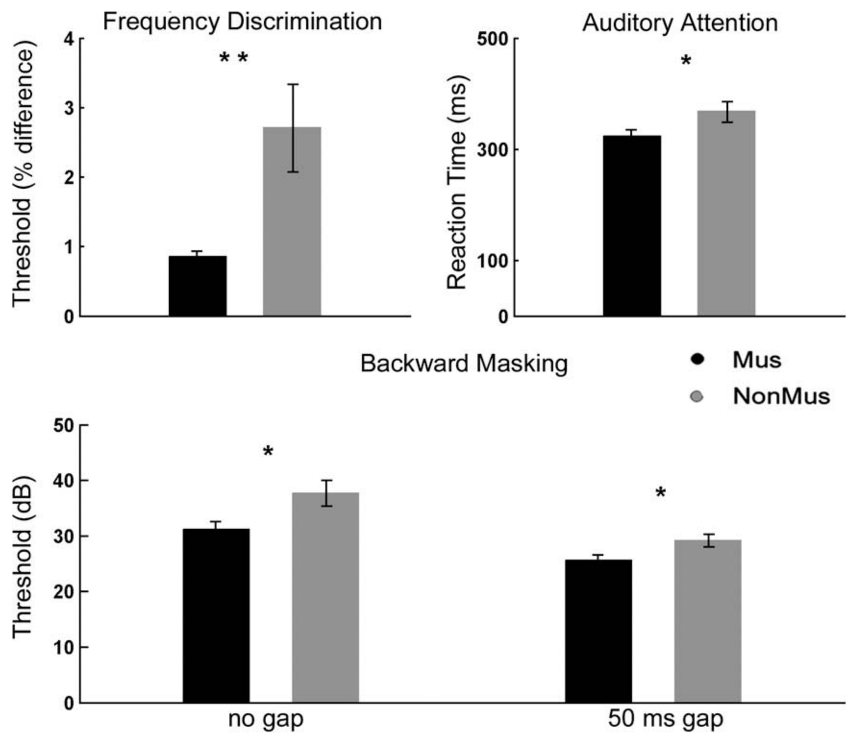

Fig. 1. Performance for musicians (black) and non-musicians (grey) on IMAP subtests. Musicians demonstrated lower thresholds for frequency discrimination, auditory attention, backward masking and backward masking with a 50 ms delay between the target and the masking noise. Error bars represent one standard error. * $P < 0.05$ ** $P < 0.01$.

Table 1
Task performance means (standard deviations) for musicians and non-musicians.

	Mus	Non-mus
Frequency discrimination (%)[a]	0.85 (0.37)	3.12 (3.38)
Backward masking (dB)[a]	31.15 (8.93)	37.67 (6.21)
Backward masking 50 ms gap (dB)[a]	25.60 (4.10)	29.14 (4.44)
Simultaneous masking (dB)	65.33 (6.06)	65.44 (4.20)
Simultaneous masking notch (dB)	41.98 (2.47)	43.17 (3.69)
Auditory attention: reaction time (ms)[a]	322.96 (47.38)	368.29 (72.49)
Visual attention: reaction time (ms)	267.87 (27.96)	271.17 (33.03)
Non-verbal IQ	64.06 (4.21)	61.60 (8.31)
Auditory working memory	9.61 (1.94)	10.13 (2.36)

[a] Measures for which group means differed statistically at $P < 0.05$.

relationship was observed in both groups, the correlation was stronger for musicians than for non-musicians (Fig. 3; Mus: $r = -0.600$, $P < 0.01$; NonMus: $r = -0.318$, $P < 0.06$).

4. Discussion

We observed enhanced perception in musicians for backward masking, which is understood to interact with cognitive mechanisms due to the cognitive resources required for separating rapidly-presented sounds (Hartley and Moore, 2002; Hartley et al., 2003; Tallal et al., 1993; Wright, 2001; Wright et al., 1997). A musician enhancement for frequency discrimination has been previously documented (Micheyl et al., 2006; Parbery-Clark et al., 2009a) and will not be discussed here in detail. Still, it has been proposed that frequency discrimination abilities relate with enhanced short-term memory traces (Kishon-Rabin et al., 2001; Tervaniemi et al., 2001, 2005) and auditory attention (Moore et al., 2008), although the present study only confirms a correlation between frequency discrimination and non-verbal IQ. We did not observe musician enhancements for tasks largely dependent on

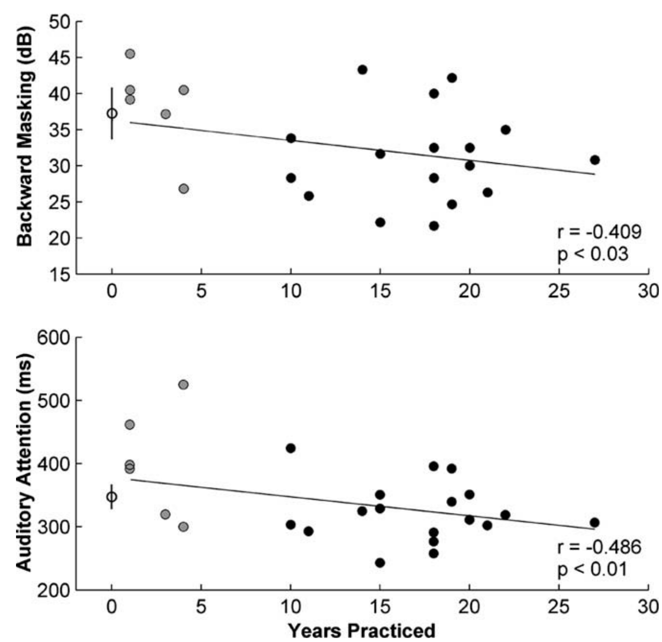

Fig. 2. Correlations between IMAP subtests and years of consistent musical practice. The more years individuals had spent consistently practicing their instruments, the lower their backward masking thresholds and the faster their auditory attention reaction times. All subjects with musical experience are represented, regardless of group status. For comparison, the mean thresholds of individuals with zero years of musical practice are also provided (white circle), ±1 standard error.

physiological properties of sensory structures, such as critical bandwidths along the basilar membrane, and less susceptible to cognitive modulation (e.g., simultaneous masking and hearing thresholds) (Oxenham and Shera, 2003). This selective effect of musical experience on backward versus simultaneous masking

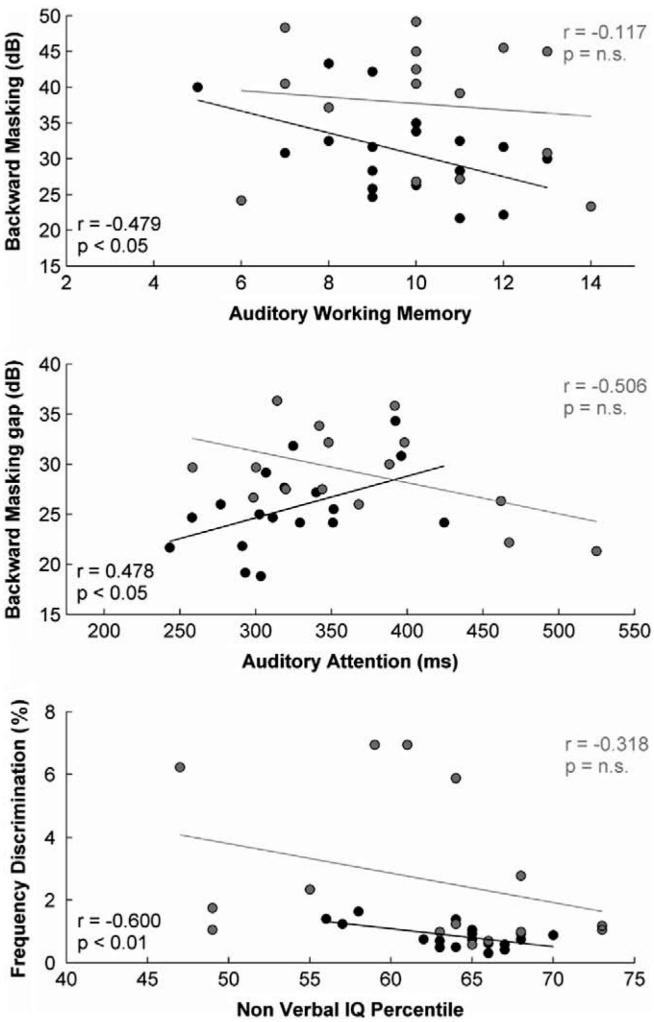

Fig. 3. Correlations between cognitive and perceptual task performance for musicians (black) and non-musicians (grey). For musicians, backward masking thresholds correlated with auditory working memory (memory for reversed digits), with lower thresholds relating to better auditory working memory. Backward masking with a 50 ms delay between the target and the masking noise correlated with auditory attention abilities, with lower delay gap backward masking thresholds relating to faster auditory attention reaction times. No correlations were observed within the entire subject pool, nor within non-musicians. Frequency discrimination thresholds also correlated with cognitive performance as measured by non-verbal IQ. Although observed in both groups, the correlation was stronger for musicians than for non-musicians.

performance and frequency discrimination thresholds lends credence to the argument that musicians' sensory enhancements result from strengthened cognitive modulation of auditory processing. This argument is strengthened by the fact that relationships between auditory-specific cognitive functions and sensory perception were only observed in musicians. That these enhancements were specific to auditory-related cognitive performance (e.g., auditory, not visual, attention) emphasizes the importance of auditory-specific training in shaping attention networks implicated in language processing (Moore et al., 2005). Overall, our findings provide insight into mechanisms underlying auditory perceptual advantages in musicians.

4.1. Perceptual enhancement in musicians driven by cognitive processes

Our data indicate that long-term musical practice bolsters auditory-specific cognitive mechanisms (auditory attention, in the absence of effects for visual attention), which lend advantages to auditory perception. These enhancements are not surprising given that music learning and performance invoke high-level cognitive engagement, required for mapping sound patterns to meaning and on-line manipulation of musical output. Still, the present experiment cannot wholly disambiguate innate from training-related factors; as such, we do not claim a lack of influence by innate factors that might lead an individual to sustain musical training. Nevertheless, it is unlikely that either innate qualities or early predispositions alone can account for our results. This is because these factors alone cannot predict professional development as a musician, which is largely driven by socio-cultural influences (Burland and Davidson, 2002; Davidson et al., 1998; Moore et al., 2003), nor the correlations we observed between auditory abilities and extent of musical experience.

Neurophysiologic data provide evidence for the influence of musical practice on brain structure, brain function and cognitive ability. Data consistently reveal correlations between the extent of neural enhancement in musicians and years of musical practice or age of practice onset (Gaser and Schlaug, 2003; Hutchinson et al., 2003; Musacchia et al., 2007; Strait et al., 2009a; Wong et al., 2007). Specifically, lower-level sound processing can be shaped by musical training, extending to the levels of the brainstem (Kraus et al., 2009; Musacchia et al., 2008, 2007; Parbery–Clark et al., 2009b; Strait et al., 2009a,b; Wong et al., 2007) and cochlea (Perrot et al., 1999). Precisely *how* this shaping of lower-level sensory mechanisms occurs is not known. What is known is that the human descending auditory system is vast, consisting of an extensive corticofugal circuitry of efferent fibers that synapse at a wealth of points along the auditory pathway (Suga et al., 2000). The strength of the efferent auditory pathway, the effects of musical experience on subcortical sound processing and this study's outcomes bolster the view that well-developed cognitive mechanisms, honed by years of musical practice, interact with earlier sensory processing to fine-tune auditory perception.

Ahissar and Hochstein's Reverse Hierarchy Theory provides a model for such top-down learning, originally with reference to visual processing (Ahissar and Hochstein, 2004) and more recently applied to the auditory domain (Ahissar et al., 2009; Kral and Eggermont, 2007; Nahum et al., 2008). They suggest that perceptual learning results from a task-dependent top-down search for higher neural signal-to-noise ratios (SNRs). This search begins in the association cortices and descends toward earlier input levels that provide better SNRs, thus implicating cognitive functions in the refinement of neural encoding at earlier structures in the processing stream and resulting in better perceptual performance. Ahissar and Hochstein argue that such learning is characteristic of highly trained populations, applied here to musicians. Conversely, this learning fails to occur in clinical disorders where auditory processing is impaired (e.g., dyslexia, auditory deprivation) (Kral and Eggermont, 2007). In theory, more efficient top-down processing requires less computational work to achieve high SNRs. Hartley and Moore similarly argue that more efficient auditory systems have higher internal SNRs, which contribute to better auditory perception, evidenced here by musicians' backward masking (Hartley and Moore, 2002; Hartley et al., 2003) and frequency discrimination thresholds.

4.2. Relationships between cognitive and perceptual abilities

Musicians in the present study demonstrated ties between auditory-related cognitive abilities and auditory perception, such as backward masking and frequency discrimination. That non-musicians showed weaker or no correlations between cognitive and perceptual abilities suggests that musicians make more efficient use of cognitive abilities for auditory processing than non-musicians. Such interactions may relate to musicians' recruitment of more efficient neural pathways for processing auditory input. Previous work shows that, even when matched for perceptual skill and hemispheric asymmetry, musicians and non-musicians recruit different neural networks for auditory-related perceptual and cognitive processing (Gaab and Schlaug, 2003a,b; Gaab et al., 2005; Schlaug et al., 2005). For example, while musicians recruit short-term auditory storage centers to solve pitch memory tasks (e.g., the supramarginal gyrus), non-musicians rely on earlier perceptual regions, such as those within the superior temporal lobe (Gaab and Schlaug, 2003a,b). The recruitment of more efficient neural networks may contribute to enhanced auditory processing in musicians (Gaab et al., 2005) and account for musical training benefitting language processing (Forgeard et al., 2008; Overy, 2003; Schlaug et al., 2005) and the advantages reported here.

4.3. Implications for language-based learning and auditory processing disorders

By demonstrating musical training's impact on temporal processing (i.e., backward masking perception), our results may shed light on the role temporal processing abilities play in language-based learning and auditory processing disorders. While there is considerable debate regarding the role of temporal processing in these disorders (Rosen et al., 2009), it appears that a temporal processing deficit affects a subset of children with specific language impairment (SLI) (Hartley and Moore, 2002; Hartley et al., 2003; Rosen and Manganari, 2001; Tallal et al., 1993; Wright, 1998, 2001; Wright et al., 1997), dyslexia (Conlon et al., 2004; Hari and Kiesilä, 1996; Walker et al., 2006) and auditory processing disorder (APD) (Chermak, 2002; Chermak and Musiek, 1997; Moore, 2007). Within this subset, the impairments that children experience for identifying speech syllables may relate to the effect of backward masking produced by the vowel on the preceding consonant (Johnson et al., 2007; Rosen and Manganari, 2001).

Previous research has shown that musicians exhibit enhanced auditory temporal processing (Kraus et al., 2009; Musacchia et al., 2007; Parbery-Clark et al., 2009b; Rammsayer and Altenmuller, 2006; Strait et al., 2009a; Yee et al., 1994), placing them at the opposite end of the temporal processing spectrum than children with SLI (Gaab et al., 2005; Wright, 1998) and APD (Chermak, 2002; Chermak and Musiek, 1997; Moore, 2007). This could account for why musicians demonstrate enhanced abilities for distinguishing phonemes (Anvari et al., 2002; Munzer et al., 2002). Musicians' perceptual acuity may relate to experience-dependent neural plasticity; in fact, the very neural measures of auditory encoding that are deficient in children with language-based learning problems (Banai et al., 2009; Hornickel et al., 2009) are enhanced in musicians (Kraus et al., 2009; Parbery-Clark et al., 2009b; Tzounopoulos and Kraus, 2009). Such neural enhancements relate with musical experience histories (e.g., years of musical practice) (Kraus et al., 2009; Musacchia et al., 2008, 2007; Strait et al., 2009a,b; Wong et al., 2007). Likewise, results from the present study demonstrate relationships between musician perceptual enhancements and years of consistent practice, indicating that musician advantages are driven, at least in part, by experience rather than innate abilities. A recent study indicated this same dependent relationship between musical training and musician abilities by assessing neural, cognitive and musical abilities in a group of untrained children, half of whom were about to initiate musical training. Initially, the two groups showed no measurable differences but, after just 18 months of lessons, musician children demonstrated neural, cognitive and musical ability enhancements (Norton et al., 2005). These results suggest that experience with music contributes to the changes seen in musicians over and above genetic factors. Because of its effects on temporal processing musical training may provide remedial benefits for individuals with temporal processing-related deficits (Overy, 2003), such as SLI (Tallal and Gaab, 2006; Wright, 1998), dyslexia (Chandrasekaran and Kraus, in press; Conlon et al., 2004; Hari and Kiesilä, 1996; Walker et al., 2006), APD (Chermak, 2002; Chermak and Musiek, 1997; Moore, 2007) and other conditions in which auditory processing is impaired (e.g., hearing loss, older adults) (Fitzgibbons and Gordon-Salant, 1994; Phillips et al., 1994; Strouse et al., 1998).

Musical training's impact on auditory attention further supports the therapeutic use of music in clinical populations, such as children with language-based learning and auditory processing disorders. Other structural auditory training programs might boost auditory attention in a similar fashion, but the frequency with which musical trainees must practice their instruments and music's activation of the neural reward circuit provide advantages for engendering learning. As we demonstrated, auditory but not visual attention is enhanced in musicians. Furthermore, backward masking advantages in musicians relate with auditory and not visual attention performance. Similar observations have been made in children, with elevated auditory perceptual thresholds linked to poor auditory attention (Moore et al., 2005, 2008). Auditory-specific attention deficits may be largely responsible for language-based learning and auditory processing disorders (e.g., SLI, dyslexia, APD), with auditory training's success in such children due to the strengthening of auditory, rather than general, attention networks.

5. Conclusions

Overall, our data support the view that musicians' perceptual enhancements are driven by cognitive processes and that relationships between cognitive and perceptual abilities are strengthened in musicians, compared to non-musicians. Such enhancements could be the result of more efficient neural mechanisms for performing auditory tasks, such as backward masking and frequency discrimination. This fine-tuning occurs over the course of long-term musical training and appears to be specific to the auditory domain, as musicians did not show similar enhancements for visual processing. This auditory-specific effect of long-term musical training likely relates to the language processing benefits associated with musicians (Brandler and Rammsayer, 2003; Chan et al., 1998; Franklin et al., 2008; Ho et al., 2003; Jakobson et al., 2008; Marques et al., 2007; Moreno et al., 2009; Ohnishi et al., 2001; Parbery-Clark et al., 2009a; Schon et al., 2004, 2008).

Most importantly, results from the present study join others (Forgeard et al., 2008; Kraus et al., 2009; Overy, 2003; Overy et al., 2003) to promote musical training as a potential remediation strategy for children with language-based learning and auditory processing disorders. Still to be determined is how the perceptual benefits we document relate to language and literacy measures and their developmental trajectories during childhood, when learning and neural malleability are at their peak. Investigations into musical training's effects on auditory processing, language and literacy abilities in children at different developmental stages could help to resolve remaining uncertainties.

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