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OBSERVATION

Short-Term Visual Deprivation Improves the Perception of Harmonicity

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Neuroimaging studies have shown that the perception of auditory stimuli involves occipital cortical regions traditionally associated with visual processing, even in the absence of any overt visual component to the task. Analogous behavioral evidence of an interaction between visual and auditory processing during purely auditory tasks comes from studies of short-term visual deprivation on the perception of auditory cues, however, the results of such studies remain equivocal. Although some data have suggested that visual deprivation significantly increases loudness and pitch discrimination and reduces spatial localization inaccuracies, it is still unclear whether such improvement extends to the perception of spectrally complex cues, such as those involved in speech and music perception. We present data demonstrating that a 90-min period of visual deprivation causes a transient improvement in the perception of *harmonicity*: a spectrally complex cue that plays a key role in music and speech perception. The results provide clear behavioral evidence supporting a role for the visual system in the processing of complex auditory stimuli, even in the absence of any visual component to the task.

Keywords: visual deprivation, multisensory interaction, auditory perception, auditory scene analysis

There is an increasingly accepted notion in neuroscience that the primary sensory cortices are in fact multisensory in nature (e.g., Cappe & Barone, 2005; Schroeder & Foxe, 2005; Ghazanfar & Schroeder, 2006). Corticocortical connections between the primary visual cortex and auditory areas have been revealed in numerous studies of sighted subjects using retrograde tracing and neuroimaging techniques (e.g., Falchier, Clavagnier, Barone, & Kennedy, 2002; Hall & Lomber, 2008; Charbonneau, Laramée, Boucher, Bronchti, & Boire, 2012; Liang, Mouraux, Hu, & Iannetti, 2013). These findings are complemented by behavioral studies that have demonstrated that auditory processing may be enhanced by short- and long-term visual deprivation, even during tasks that are purely auditory in nature.

The impact of sensory deprivation on the function of intact sensory modalities has mainly been investigated following long-term sensory deprivation in the congenitally blind, and has primarily focused on auditory or tactile functions (e.g., Théoret, Merabet, & Pascual-Leone, 2004; Merabet & Pascual-Leone, 2010). However, the duration of sensory deprivation required to obtain enhanced perceptual abilities is still not clear. The enhancements in tactile perception observed in the congenitally blind can be reproduced in the tactile perception of sighted individuals who have undergone short-term visual deprivation ranging from 90 min (Facchini & Aglioti, 2003) to days (Kauffman, Théoret, & Pascual-Leone, 2002). To our knowledge, only two studies have investigated the effects of short-term visual deprivation on auditory processes. These investigations have suggested that visual deprivation significantly increases loudness and pitch discrimination (Gibby, Gibby, & Townsend, 1970) and reduces spatial localization inaccuracies (Lewald, 2007). Such data are unique in the exploration of auditory-visual interactions because they suggest that the visual system is implicated in the processing of auditory stimuli, even in the absence of a visual component to the task. Unfortunately, such critical explorations regarding the interaction between auditory and visual systems in the hearing have not received further investigation. In particular, it is unknown whether such improvement extends to perceptual abilities involved in the

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analysis of spectrally complex cues, such as those involved in speech and music perception.

In normal aural environments, the auditory system has to segregate multiple overlapping and concurrent Sound sources. Under everyday listening conditions, loudness, frequency, and localization represent only a fraction of the various simultaneous auditory cues available for the analysis of the acoustic scene. Many sounds that are important to humans are harmonic or quasiharmonic (Micheyl & Oxenham, 2010), thus, one of the most powerful cues used by the auditory system to segregate concurrent sounds is *harmonicity*: the harmonic relation between acoustic components (Bregman, 1990). The analysis of harmonicity, involving the processing of multiple tonal elements on the basis of periodicity, is not only recognized as a primary ability in the identification and segregation of sounds originating from different sources (e.g., Alain, McDonald, Ostroff, & Schneider, 2001, Alain, Schuler, & McDonald, 2002; Alain, 2007), but also plays a key role in both music and speech perception (e.g., Micheyl & Oxenham, 2010; Plack, 2010). The perception of harmonicity can be examined using discrimination tasks that involve the fusion of multiple tonal elements into a single sound "object" or the segregation of a mistuned element as a separate auditory object (e.g., Moore, Glasberg, & Peters, 1986; Chalikia & Bregman, 1989; Hartmann, McAdams, & Smith, 1990; Lin & Hartmann, 1998).

Herein, we sought to study the effect of short-term visual deprivation on performance in a harmonicity discrimination task. Because short-term temporary visual deprivation has been shown to enhance other auditory abilities (Gibby et al., 1970; Lewald, 2007), we hypothesized that a 90-min period of visual deprivation would also significantly improve the perception of harmonicity (i.e., decrease harmonicity discrimination thresholds). The results support the hypothesis, suggesting that a perceptual auditory enhancement of spectrally complex sounds can be triggered following a short period of visual deprivation. Moreover, our results highlight the transiency of such an enhancement in temporarily blindfolded participants.

Method

Participants

Seventy-four healthy volunteers (36 men, 38 women; age range: 18–32 years) participated in this study. Pure-tone detection thresholds were within normative limits at octave frequencies ranging from 125−8000 Hz for all participants. All participants reported normal or corrected-to-normal vision. The Research Ethics Board of the Université de Montréal approved the study, and all the participants provided written informed consent.

Procedure, Stimuli, and Design

All participants completed a harmonicity discrimination task and were naïve about the objectives of the research and to their group assignment (experimental vs. control). The auditory stimuli consisted of a fundamental frequency (220 Hz) and five additional harmonically related tonal elements (i.e., integer multiples of the fundamental frequency; see Zendel & Alain, 2009). Each component (220, 440, 660, 880, 1100, and 1320 Hz) was a 150-ms pure tone sine wave with a 10-ms rise and fall time. The third frequency component of the series was either tuned (precisely 660 Hz) or mistuned in steps of 1 Hz. Participants were asked to report verbally whether each stimulus presented was perceived as "tuned" (the percept resulting from all components being in tune with the others) or "mistuned" (the percept resulting from one component tone not being in tune with the others). Before running the experiment, participants had the chance to hear the tuned and mistuned sound.

The minimum frequency step needed by subjects to detect a change in harmonicity (tuned vs. mistuned) was determined using a three-down and one-up adaptive staircase procedure (see Levitt, 1971; Amitay, Irwin, Hawkey, Cowan, & Moore, 2006, for further description). The initial amount of mistuning was set well above the expected threshold (50 Hz), corresponding to a stimulus clearly identified by subjects as "mistuned." The third frequency component was then reduced in 3-Hz increments until the stimuli were perceived as "tuned," at which point the direction of stimulus change was reversed (increased in 1-Hz increments). Following the subsequent judgment of the stimulus as "mistuned," the direction was again reversed and the process repeated. The run was terminated after six reversals. The threshold was calculated as the average of the last four reversals. The stimuli were generated using Logic Pro 8 (Apple, Cupertino, CA) and were presented binaurally at a comfortable level (sound pressure level = 55–60 dB) through headphones (10S-DC; David Clark, Worcester, MA). The output of the acoustic system was calibrated using a sound level meter (Model 2230; Brüel and Kjaër Sound & Vibration Measurement, Nærum, Denmark) and artificial ear (6 cm^3 coupler, Model 4153; Sound & Vibration Measurement).

The discrimination task was administered twice to two groups of participants who were matched for age and gender. Each evaluation lasted approximately 5 min. All participants, including those in the control group, were blindfolded at the time of the evaluation (Mindfold Relaxation Mask; Mindfold Inc., Tucson, AZ). After the first test of discrimination (pretest), participants waited 90 min during which one group of participants ($n = 32$) remained visually deprived, while the other group ($n = 32$) had their blindfolds removed. During this interval, participants were asked to view or listen to a movie. Participants were kept alert by the examiner who remained in the room. Participants' thresholds were measured again immediately after this 90-min interval (posttest).[1] No feedback about the correctness of the responses was given to participants at any time.

[1] The period of 90 min of visual deprivation was based on the results of a preliminary study from our laboratory conducted with 60 individuals. In this study, as in the main study described above, the discrimination task was administered twice. For one group ($n = 30$), the tasks were separated by an interval of 60 min, while for the other group ($n = 30$) the tasks were separated by 90 min. In each group, 15 participants were blindfolded and 15 had normal or corrected-to-normal vision. The interaction between factors was significant, $F(1, 28) = 10.538$, $p = .003$, $\eta_p^2 = .273$. Specifically, the shorter period of visual deprivation (60 min) was found to be insufficient to elicit a significant change in auditory perception compared to controls, $t(28) = 0.560$, $p = .580$. In contrast, a period of 90 min induced a significant change in auditory perception between control and visually deprived groups, $t(28) = -6.607$, $p < .001$. This pilot study confirmed a previous estimation of the period required to elicit a change in perception established by Facchini and Aglioti (2003), and concomitantly lessened the implication of a change in response strategy to explain any improvement in performance (see Durgin et al., 2009).

Complementary data was collected for 34 of the 74 participants to assess the transiency of the effect. Additional measures of the harmonicity discrimination threshold were carried out after 15, 30, and 60 min of visual restoration in 17 nondeprived and 17 visually deprived individuals. These successive testing sessions were conducted to evaluate the transiency of effect and to better control for some of the cognitive factors that could account for a change in measured harmonicity discrimination threshold, such as habituation or learning. Changes in performance were computed as the difference between the first evaluation and those conducted after visual deprivation.

Results

Overall, the performance of nonvisually deprived participants remained relatively constant between the pretest and posttest, whereas the visually deprived participants exhibited an improvement in performance during their second discrimination test (see Figure 1). More specifically, 31 of the 32 visually deprived participants showed an improvement (i.e., decrease) in their discrimination threshold, ranging from 7−85% (M = 28.7%) relative to their initial discrimination score. A 2 × 2 analysis of variance (ANOVA) with group (Group 1: control; Group 2: visually deprived) as the between-subjects factor and condition (Condition 1: before visual deprivation; Condition 2: after visual deprivation) as a within-subjects factor was conducted. The interaction between factors was significant, $F(1, 62) = 41.298$, $p < .001$, $\eta_p^2 = .400$, reflecting group-specific changes from pretest to posttest. Post hoc tests with Bonferroni correction ($\alpha = 0.025$) revealed no significant difference in the ability to discriminate auditory stimuli prior to visual deprivation between the two groups, $t(62) = -0.026$, $p = .979$. Results from the subsequent testing session revealed a significant improvement for the visually deprived individuals' discrimination ability compared to the nonvisually deprived group, $t(62) = 3.786$, $p < .001$.

Additional data were collected to examine the transiency of the effect (see Figure 2). A 2 × 5 ANOVA with group (control, visually deprived) as the between-subjects factor and condition (Condition 1: prior to visual deprivation; Condition 2: after visual deprivation; Condition 3: 15 min of visual restoration; Condition 4: 30 min of visual restoration; Condition 5: 60 min of visual restoration) as a within-subjects factor was conducted. The interaction between factors was significant, $F(1, 32) = 6.338$, $p < .001$, $\eta_p^2 = .165$, reflecting group-specific changes from pretest to posttests. Specifically, t tests with Bonferroni correction ($\alpha = 0.01$) showed no significant difference in the ability to discriminate auditory stimuli prior to visual deprivation between the two groups, Condition 1: $t(32) = 0.252$, $p = .803$. A significant enhancement in performance for the sensory deprived group (relative to control) was observed after 90 min of visual deprivation, Condition 2: $t(32) = 3.018$, $p = .005$; however, no significant differences were observed in the subsequent conditions, Condition 3: $t(32) = 2.288$, $p = .029$; Condition 4: $t(32) = 1.681$, $p = .103$; Condition 5: $t(32) = 0.454$, $p = .653$. Within-group analyses comparing performance among the different time points revealed a similar pattern. As expected, there were no significant differences across time points (relative to baseline) for the control group, Condition 2: $t(16) = -0.841$, $p = .413$; Condition 3: $t(16) = -1.737$, $p = .102$; Condition 4: $t(16) = -0.895$, $p = .384$; Condition 5: $t(16) = 0.517$, $p = .612$. In accordance with the previous results (see Figure 1), the data showed a significant enhancement in performance (relative to baseline) after 90 min of visual deprivation, Condition 2: $t(16) = 5.548$, $p < .001$. The enhancement in performance was still significant after 15 min of visual recovery, Condition 3: $t(16) = 3.266$, $p = .005$, and progressively returned to normal at 30 and 60 min of recovery time, Condition 4: $t(16) = 2.519$, $p = .023$; Condition 5: $t(16) = 1.701$, $p = .108$.

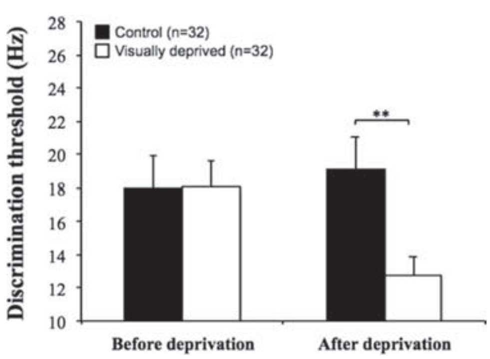

Figure 1. Individual performance of the control group and the visually deprived group before and after an interval of 90 min. Error bars are standard error of the mean. ** $p < .001$.

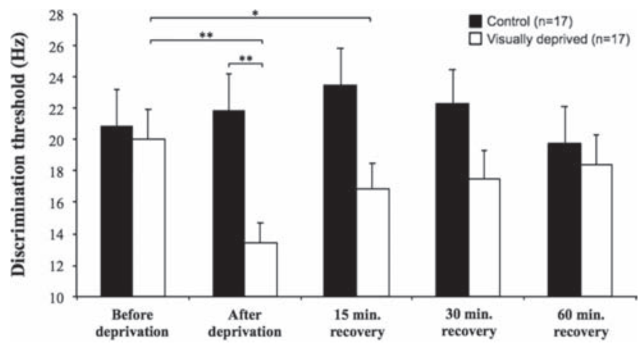

Figure 2. Results of the harmonicity discrimination task before visual deprivation, immediately after 90 min of visual deprivation, and then 15, 30, and 60 min after the recovery of visual input. Error bars are standard error of the mean. * $p < .01$. ** $p < .001$.

Discussion

The present study aimed to investigate the effect of short-term visual deprivation on the perception of a primary auditory scene analysis cue. Using a harmonicity discrimination task, we demonstrated that 90 min of visual deprivation results in an enhancement of auditory acuity. These results are consistent with recent findings suggesting short-term changes in auditory perception in blindfolded-sighted individuals in a variety of tasks, including spatial localization and the discrimination of frequency and loudness (Gibby et al., 1970; Lewald, 2007). It should be noted, however, that not all auditory perceptual tasks previously investigated have revealed such changes (e.g., a frequency modulation discrimination task; Lazzouni, Voss, & Lepore, 2012). Our results

also revealed the transiency of the effect, demonstrating a washout of the enhancement effect 30 min after the removal of the blindfold.

It has long been suggested that blind individuals have enhanced auditory sensory abilities, though demonstrations of such enhancements have been limited to a relatively small set of auditory skills (e.g., Lessard, Paré, Lepore, & Lassonde, 1998; Röder et al., 1999; Gougoux et al., 2004; Lewald, 2013). To date, the effect of short-term visual deprivation on auditory skills in sighted individuals has also remained underexplored. The results of the present study confirm that short-term visual deprivation can significantly enhance auditory perception. To our knowledge, this is the first demonstration of such an auditory perceptual enhancement involving the analysis of a spectrally complex cue, such as those involved in speech and music perception.

These results highlight the extent and relative swiftness of neural changes in response to sensory deprivation. Considering that the enhanced auditory capability reported here can be triggered after only 90 min of visual deprivation and begins to return to a normal level soon after the visual input is restored, it is of interest to consider the mechanisms that might be responsible for such changes. One possibility is that existing auditory neural pathways are rapidly "unmasked" following the loss of visual input. Merabet and Pascual-Leone (2010) have suggested that, unlike cortical plasticity after long-term visual deprivation, changes following short-term visual deprivation may not be related to a compensatory process. Rather, such changes are consistent with a *metamodal* model of cortical function in which cortical regions, including primary sensory areas, receive multiple sensory inputs and are organized on the basis of task requirements rather than unique sensory modalities (Pascual-Leone & Hamilton, 2001). According to the metamodal model, visual sensory dominance in the striate cortex occurs because the assigned computation of the area is more efficiently used for retinal information. Therefore, in case of the removal of visual input, nonvisual inputs (i.e., auditory and tactile) in visual cortex may be rapidly unsuppressed. This model has been used to explain the rapid neural plasticity observed in the tactile domain in temporarily blindfolded participants (Kauffman et al., 2002; Facchini & Aglioti, 2003), and may be applicable to other neural systems as well (Merabet et al., 2008). The model is also consistent with the increasingly accepted notion that primary sensory cortices receive input from other sensory modalities, and are thus not limited to unimodal processing of sensory information (e.g., Cappe & Barone, 2005; Schroeder & Foxe, 2005; Ghazanfar & Schroeder, 2006: Liang et al., 2013). Unfortunately, the functional implications of such intermodal projections remain unclear. Given that different auditory processes have been associated with distinct cortical pathways (e.g., Romanski et al., 1999; Alain, Arnott, Hevenor, Graham, & Grady, 2001; Maeder et al., 2001), it would be interesting to further explore the characteristics of neural activity in response to sound in the primary visual cortex in sighted individuals in relation to short-term sensory deprivation, possibly using neuroimaging techniques. Such future work is necessary to explain why some types of auditory processing, such as the perception of harmonicity, exhibit improvement after short-term visual deprivation, while other auditory processes exhibit changes only in the case of congenital or prolonged blindness.

In the present study, an adaptive staircase procedure was used to measure auditory discrimination thresholds. Several aspects of our results indicate that the changes in measured thresholds after 90 min of visual deprivation reflect a true change in perceptual sensitivity, and not simply a response bias (toward a greater proportion of "tuned" responses) somehow introduced by the visual manipulation. First, it should be noted that all participants (including controls) were perceptually tested while blindfolded, hence any immediate influence of visual deprivation on responses was balanced between the groups. Further, the influence of visual deprivation on harmonicity discrimination was found to be highly time-sensitive: no improvement in discrimination was observed in participants who were visually deprived for 60 min, and the perceptual enhancement in participants who were visually deprived for 90 min was found to dissipate 30–60 min following the restoration of visual input. Such specificity in the observed auditory−perceptual change after visual deprivation cannot readily be explained as a change in response strategy.

Although the mechanisms underlying the reported enhancement in harmonicity perception remain unknown, the results of the present study suggest that the potential for change in auditory scene analysis in sighted individuals is much greater than previously assumed. Future psychophysical and neuroimaging studies exploring other acoustic cues related to auditory scene analysis are necessary to further our understanding of the effect of temporary visual deprivation on auditory capacities.

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