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A Modulatory Effect of Brief Passive Exposure to Non-linguistic Sounds on Intrinsic Functional Connectivity: Relevance to Cognitive Performance

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Abstract

A growing literature on resting-state fMRI (R-fMRI) has explored the impact of preceding sensory experience on intrinsic functional connectivity (iFC). However, it remains largely unknown how passive exposure to irrelevant auditory stimuli, which is a constant in everyday life, reconfigures iFC. Here, we directly compared pre- and post-exposure R-fMRI scans to examine: 1) modulatory effects of brief passive exposure to repeating non-linguistic sounds on subsequent iFC, and 2) associations between iFC modulations and cognitive abilities. We used an exploratory regional homogeneity (ReHo) approach that indexes local iFC, and performed a linear mixed-effects modeling analysis. A modulatory effect (increase) in ReHo was observed in the right superior parietal lobule (R.SPL) within the parietal attention network. Post hoc seed-based correlation analyses provided further evidence for increased parietal iFC (e.g., R.SPL with the right inferior parietal lobule). Notably, less iFC modulation was associated with better cognitive performance (e.g., word reading). These results suggest that: 1) the parietal attention network dynamically reconfigures its iFC in response to passive (thus irrelevant) non-linguistic sounds, but also 2) minimization of iFC modulation in the same network characterizes better cognitive performance. Our findings may open up new avenues for investigating cognitive disorders that involve impaired sensory processing.

Key words: irrelevant stimuli, modulatory effect, passive auditory oddball, resting-state fMRI, voluntary and involuntary attention

Introduction

The brain adaptively changes its functional circuitry in response to sensory experience (Pascual-Leone et al. 2005; Merzenich et al. 2013). Such experience-induced neuroplasticity in the auditory modality has been shown to be more pronounced for active, as compared to passive, exposure in both developing (Benasich et al. 2014) and mature (Jancke 2009;

Herholz and Zatorre 2012) brains. While these studies have focused on the effect of long-term auditory experience on the human brain, for example musicians versus non-musicians (Herholz and Zatorre 2012), recent animal studies have revealed a powerful modulatory effect of brief passive auditory experience (even in the timescale of minutes). For example, Yang and Vicario (2015) have demonstrated that 2 days of passive

exposure to novel sounds is sufficient to reorganize secondary auditory cortex in adult zebra finches. Similarly, 3-day passive exposure to tones can modify response strength within primary auditory cortex in mouse pups (Barkat et al. 2011). In humans, Hasson et al. (2009) have demonstrated that functional connectivity profiles during rest are differentially modulated as a function of spoken linguistic contents (e.g., more vs. less surprising stories). However, it remains largely unknown whether brief passive exposure to non-linguistic auditory stimuli (i.e., stimuli with no semantic information) will reconfigure/reorganize functional circuits in the human brain.

This gap in our knowledge as to the effect of brief passive auditory exposure on the human brain is of great interest, given that passive auditory exposure is a constant in everyday life, including exposure to a variety of irrelevant sounds (e.g., busy street noises). Crucially, the human brain is capable of filtering out irrelevant sounds that enter the auditory system (Cromwell et al. 2008). For example, in a café where background music is playing, your attention may at first be captured by the sounds, but you will then be able to effortlessly filter them out, particularly when your attention is engaged elsewhere (e.g., reading, conversing, mind wandering). This filtering mechanism, termed "sensory gating", involves an involuntary attentional shift away from irrelevant sensory input. Sensory gating is essential for efficient human information processing as it insulates the brain from an overload of irrelevant information (Cromwell et al. 2008). Dysfunction of sensory gating has been implicated in a number of disorders, including schizophrenia (Adler et al. 1982; Kiehl et al. 2005) and attention deficit hyperactivity disorder (ADHD) (Stevens et al. 2007; Aboitiz et al. 2014; Yang et al. 2015; Micoulaud-Franchi et al. 2016). In a similar vein, an impaired ability to filter out the noise (i.e., irrelevant sensory information) and extract relevant information ("noise exclusion deficits") is implicated in dyslexia (Sperling et al. 2005; Ziegler et al. 2009; Beattie et al. 2011).

Neuroplasticity induced by active sensory experience (i.e., overt responses) has increasingly been examined via resting-state fMRI (R-fMRI). This task-free method has identified experience-associated changes, over relatively brief timescales, in intrinsic functional connectivity (iFC) within the brain (Albert et al. 2009; Taubert et al. 2011; Tung et al. 2013; Guidotti et al. 2015; Sampaio-Baptista et al. 2015). For example, Albert et al. (2009) directly compared pre- and post-training R-fMRI scans, separated by 11 min of visuomotor learning, and detected an increase in post-training intrinsic functional activity as compared to pre-training, within networks that are typically involved in visuomotor learning (e.g., the fronto-parietal network). To date, there are only a few R-fMRI studies that have investigated effects of auditory experience on iFC. The most notable one is Hasson, et al. (2009), which identified differential patterns of iFC modulation as a function of the preceding language content (e.g., weaker iFC between the precuneus and precentral gyrus after passively listening to more-informative content as compared to less-informative content). However, it is important to note that in their experiment, the auditory exposure involved linguistic stimuli with semantic content, and no pre-experience R-fMRI was acquired, that is, no direct comparison was made between the baseline and post-experience iFC.

In the current study, we directly compared 2 sets of R-fMRI scans, one before, and another after 5 min of passive auditory exposure to non-linguistic sounds, to examine its modulatory effect on iFC in healthy adults. The auditory exposure consisted of tone-pairs presented in a passive oddball paradigm. Prior event-related potential (ERP) studies using a passive auditory oddball paradigm have shown that specific brain responses are elicited by an infrequently presented sound (the "oddball", also termed the "deviant" or "novel" stimulus) embedded within a repetitive sequence of "standard" sounds (Escera et al. 1998; Opitz et al. 2002; Näätänen et al. 2007; Ortiz-Mantilla et al. 2010). Several notable ERP responses often observed in this passive paradigm include the mismatch negativity or "MMN" (the deviant-minus-standard difference) and the P3 (Patel and Azzam 2005). Both responses occur involuntarily, with the MMN reflecting attentional capture and the P3 thought to represent selective attentional shifts (Polich 2007). Thus, attention can be involuntarily captured by and shifted to irrelevant but salient inputs in the environment (e.g., deviant tones during passive oddball) (Theeuwes and Godljn 2002), but once attentional capture occurs, attention can be involuntarily shifted/deallocated from the irrelevant inputs, particularly in the presence of relevant inputs (Posner and Cohen 1984; Ruz and Lupiáñez 2002).

Unlike ERP, MRI is limited in its temporal resolution, but its superior spatial resolution has successfully identified loci of significant functional activation associated with the oddball effect (e.g., "deviant-minus-standard" contrast). A recent meta-analysis (Kim 2014), in which a mix of fMRI studies using active and passive paradigms were examined, highlights the oddball effect on both dorsal and ventral fronto-parietal attention networks. Specifically, the dorsal network is more associated with attentional shifts, whereas the ventral network supports detection of salient changes. In general, passive oddball paradigms evoke focal, rather than globalized, activation in functionally specific regions for both frequent/standard and infrequent/deviant stimuli (e.g., task-evoked activation restricted to the visual cortex during a visual passive oddball) (Warbrick et al. 2013). When considering regions specifically related to passive auditory oddball paradigms, it has been shown that the superior temporal gyrus, including the auditory cortex, is robustly activated for deviant sounds (Liebenthal et al. 2003; Sabri et al. 2006; Czisch et al. 2009). In contrast, studies using active auditory oddball paradigms, in which overt attention is required (Kiehl et al. 2005; Benar et al. 2007; Stevens et al. 2010), have reported a more distributed array of regions, extending beyond auditory cortex. To our knowledge, no study to date has examined the modulatory impact of a passive auditory oddball on subsequent iFC.

Thus, the current study has a 2-fold aim: 1) to investigate whether and how brief (5 min) passive exposure to novel but irrelevant non-linguistic sounds in a passive oddball paradigm would modulate subsequent iFC in healthy adults, and 2) to examine how the degree of iFC modulations, if present, would be associated with individual differences in cognitive abilities. Previous fMRI studies have revealed differential patterns of iFC modulation as a function of the preceding perceptual experience (Hasson et al. 2009; Stevens et al. 2010). For example, Stevens et al. (2010) have demonstrated that iFC following a 15-min visual exposure showed clear dissociations between prefrontal connections. More specifically, the right inferior frontal gyrus exhibited increased iFC within a scene-preferential region within the parahippocampal cortex after exposure to a visual scene, whereas the same prefrontal region exhibited increased iFC within a face-preference region in the right fusiform gyrus after exposure to faces. As such, it is possible that recent passive auditory experience will specifically modulate iFC in regions involved in auditory processes, as well as regions implicated in involuntary attention, given the nature of the auditory exposure (i.e., passive auditory oddball).

To address our aims, we first used regional homogeneity (ReHo) to examine differences between the pre-exposure and

post-exposure R-fMRI data. ReHo is a data-driven, whole-brain R-fMRI analytic measure, which evaluates the correlation/similarity between the time series of a given voxel and its nearest neighbors (Zang et al. 2004; Jiang and Zuo 2016). Thus, this measure is considered to index local IFC, and is deemed appropriate and sensitive for detecting iFC modulations associated with auditory exposure in a passive oddball paradigm, during which focal, rather than global, activation is typically evoked (Liebenthal et al. 2003; Warbrick et al. 2013). In addition, we performed post hoc seed-based correlation analysis (SCA) using the identified ReHo clusters, to further examine iFC associated with auditory exposure. Although we primarily employed an exploratory method (ReHo), as shown in previous fMRI studies of a passive auditory oddball paradigm (Liebenthal et al. 2003), we expected that brief passive auditory exposure to non-linguistic sounds would modulate subsequent ReHo in the auditory cortex.

Materials and Methods

Participants

Twenty-eight healthy adults participated in the current study at the Center for Molecular and Behavioral Neuroscience, Rutgers University. All participants were monolingual English speakers, right-handed, had normal hearing, and had no history of neurological or psychiatric disorders (e.g., dyslexia, ADHD). One participant was excluded due to excessive in-scanner motion, indexed by greater mean frame-wise displacement (FD) (Jenkinson et al. 2002) exceeding 0.2 mm, leaving a total of 27 participants for analysis. Participants were randomly assigned to 1 of 2 groups: 1) Auditory Group (AG: N = 17, mean age = 26 ± 8 years, 9 males/8 females), who were passively exposed to 5 min of auditory stimulation in the scanner, and 2) Control Group (CG: N = 10, mean age = 25 ± 6 years, 4 males/6 females), who did not receive the auditory exposure in the scanner. All participants were instructed to lie quietly in the scanner (i.e., no task response was required) throughout the 30-min MRI session. The study was approved by our university's Institutional Review Board. Prior to participation, written informed consent was obtained and all study participants were compensated for their time.

Behavioral Assessments

Before the MRI, all participants completed a hearing screen (using a manual audiometry procedure) and the Edinburgh Handedness Inventory (Dragovic 2004). Language and cognitive abilities were assessed by the Vocabulary and Matrix Reasoning subtests of the Wechsler Abbreviated Scale of Intelligence (WASI) (Wechsler 1999). The "Vocabulary" subtest measures expressive vocabulary, verbal knowledge, and fund of information, whereas the "Matrix Reasoning" subtest measures non-verbal fluid reasoning and general intellectual ability. To evaluate reading competence, the Word Reading subtest of the Wide Range Achievement Test (WRAT3) (Wilkinson 1993) was administered.

MRI Data Acquisition

All images were acquired via a 3T Siemens Trio at the Rutgers University Brain Imaging Center (RUBIC). Each participant completed a structural scan and 2 resting-state fMRI (R-fMRI) scans. For structural imaging, a T1-weighted magnetization-prepared rapid acquisition with gradient echo (MPRAGE) was obtained (TR = 2.5 mm; TE = 3.5 ms; voxel-size = $1 \times 1 \times 1$; slices = 192; FOV = 256 mm; flip angle: 6°; duration = 6 min). Each R-fMRI consisted of whole-brain 180 volumes (TR = 2 mm; TE = 27 ms; voxel-size = $3 \times 3 \times 3$; slices = 38; FOV = 216 mm; duration = 6 min).

Auditory Exposure

Participants in the AG were passively exposed to auditory stimuli while they were lying in the scanner. Auditory exposure was comprised of a 5-min presentation of repeating tone-pairs inserted between the first/pre-exposure (R1) and second/post-exposure (R2) R-fMRI scans (Fig. 1A). No MRI data was acquired during the auditory exposure period (Note: The sparse imaging technique, which presents auditory stimuli intermittently between each MRI slice acquisition, was not used because the current study is part of an ongoing project where the same MRI experimental design is used for infants and adults to examine differences in brain response. Sparse imaging involves significantly longer acquisition times for the same number of auditory stimuli, a distinct disadvantage when scanning infants.) We provided no specific/explicit instruction (e.g., "attend to or ignore the presented tones") to the participants in the AG. Instead, we briefly mentioned that they might hear repeating sounds in the scanner, but that no response was required. Prior research indicates that the provision of specific instruction (i.e., "attend to or ignore scanner background noise") is likely to influence participants' attentional states, increasing brain activity and functional connectivity in the default mode network (Benjamin et al. 2010).

As illustrated in Figure 1B, during the auditory exposure period, tone-pairs with an inter-stimulus interval (ISI) of 70 ms were presented in a passive oddball paradigm. Each tone was 70 ms in length and presented at 55db SPL intensity level. The standard tone-pair (800–800 Hz) and deviant tone-pair (800–1200 Hz) comprised 85% (278 trials) and 15% (49 trials) of the total pairs,
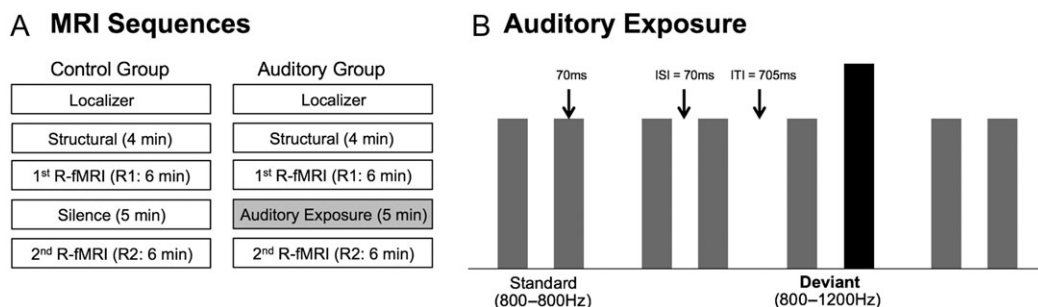

Figure 1. (A) Schematics of the MRI sequences for the Auditory and Control groups. (B) The passive auditory oddball paradigm during a 5-min exposure period. All participants were instructed to lie quietly in the scanner. For the auditory exposure period, no specific guidance was provided to those in the auditory group, but they were informed that repeating sounds might be presented, to which no responses were required. R-fMRI = resting-state fMRI, ISI = inter-stimulus interval, ITI = inter-trial interval.

respectively. No more than 2 deviant tone-pairs were presented in a row. The offset-to-onset inter-trial interval (ITI) was 705 ms. All auditory stimuli were presented via MRI-compatible in-ear headphones that also served to attenuate acoustic noise created by the MRI scanner. Before each scan session, the auditory intensity of the tones was calibrated using a sound level meter with a coupler that enabled the auditory intensity to be measured directly from the in-ear headphones. Participants in the AG were told to lie as still as possible and were informed that they might hear repeating tones during the scanning session. As previously noted, no specific or explicit instruction for the tone presentation period (e.g., "attend to or ignore the presented tones") was provided. To participants in the CG, no tones were presented during the scanning, and their instructions were only to lie as still as possible throughout the scan session.

MRI Data Preprocessing

MRI data were preprocessed by Configurable Pipeline for the Analysis of Connectomes (CPAC 0.3.9.1 http://fcp-indi.github.io). Preprocessing included the following steps: slice timing correction, realignment to the mean echo-planar imaging image to correct for motion, grand mean-based intensity normalization (all volumes scaled by a factor of 10 000), nuisance regression, spatial normalization, temporal band-pass filtering (0.01–0.1 Hz), and spatial smoothing. Nuisance regression was performed to control for the effects of head motion and to reduce the influence of signals of no interest (e.g., those from white matter). The regression model included linear and quadratic trends, the Friston-24 motion parameters (6 head motion, their values from one time point before, and the 12 corresponding squared items) (Friston et al. 1996), and signals of 5 principal components derived from noise regions of interest (e.g., white matter, cerebral spinal fluid) using the component-based noise correction methods (CompCor) (Behzadi et al. 2007).

Spatial normalization included the following steps: 1) anatomical-to-standard registration using Advanced Normalization Tools (http://www.picsl.upenn.edu/ANTS) (Avants et al. 2011), 2) functional-to-anatomical registration using FMRIB's Linear Image Registration Tool (FLIRT) with a 6-degrees of freedom linear transformation (Note: This co-registration was further refined using Boundary-based Registration implemented in the FMRIB Software Library (FSL) (Greve and Fischl 2009)), and 3) functional-to-standard registration by applying transformation matrix obtained from steps (1) and (2) using ANTs. Spatial smoothing was performed using a Gaussian kernel (FWHM = 6 mm).

Regional Homogeneity

At the individual level, a data-driven ReHo method was applied to each participant's R-fMRI data. ReHo assesses local iFC, being defined as the Kendall's coefficient of concordance for the time series of a given voxel with those of its 26 nearest neighboring voxels (Zang et al. 2004). ReHo is considered to reflect the hierarchical organization of the brain: higher ReHo indicates greater functional specificity (Jiang and Zuo 2016). For example, within the visual ventral pathway, there is an anterior-posterior gradient, with the highest ReHo value being observed in the primary visual cortex. The ReHo approach is appropriate for detecting iFC modulation associated with auditory exposure in a passive oddball paradigm, during which focal activation is dominant (Liebenthal et al. 2003; Warbrick et al. 2013). For each participant, ReHo was computed in the native space, registered in the MNI space, and then smoothed. Individual ReHo maps

were standardized into ReHo Z scores by subtracting the mean ReHo obtained from the whole-brain mask, and then dividing by the standard deviation (SD).

At the group level analysis, we used AFNI's 3dLME to perform a whole-brain linear mixed-effects (LME) model, with "Group" (AG vs. CG) as a between-subjects factor and "Scan" (R1 vs. R2) as a within-subjects factor. We specifically focused on the interaction effect of "Group × Scan", which would allow an unbiased identification of the modulatory effect of the passive auditory exposure that was presented between R1 and R2 in the AG. Clusters that show significant R1–R2 differences specifically in the AG (but not in the CG) can be defined as the loci that exhibit the modulatory effect of the auditory exposure. We used a study-specific mask to include voxels (in MNI space) present in at least 90% of participants. The LME model included mean FD as a covariate to adjust for the effect of in-scanner head motions. Correction for multiple comparisons was applied at the cluster level following Monte Carlo simulations performed in AFNI 3dClustSim (the minimum numbers of voxels necessary to achieve a height $P < 0.001$ and a cluster extent $P < 0.05 \geq 98$). To illustrate the interactions, we plotted ReHo values extracted from each of the identified clusters.

ReHo Gradients

We expected that the most prominent effect of auditory exposure would be observed immediately after the auditory exposure. To test this hypothesis, we split the time series of each R-fMRI dataset into 2 halves (total of 4 sub-datasets: R1–1, R1–2, R2–1, and R2–2), applied the same preprocessing steps to each sub-dataset, computed separate ReHo maps for each sub-dataset, and then made direct comparisons of ReHo values extracted from clusters identified as the loci showing a modulatory effect of the auditory exposure.

Seed-Based Correlation Analysis

Using ReHo-based clusters identified as the loci of the modulatory effect as "regions of interest" (ROIs), post hoc SCA was performed to examine their iFC profiles associated with the auditory exposure. At the individual level, the average time series across the voxels within each ROI was extracted and correlated with all voxels within the group-specific mask, using Pearson's correlation. Correlation values were transformed to Fisher Z scores to provide a whole-brain iFC map. For the group level analysis, we used a paired t-test (AFNI 3dttest++) to examine group-specific differences in iFC of a given ROI between R1 and R2. The model included mean FD as a covariate to adjust for the effect of in-scanner head motions. The resultant iFC maps were corrected for multiple comparisons using the permutation approach embedded in 3dttest++.

Connectivity-Behavior Relationships

To examine connectivity-behavior relationships, we plotted R1–R2 differences as a function of cognitive performance. ReHo Z scores for both R1 and R2 were extracted from clusters showing the interaction effect, whereas Fisher Z scores (i.e., SCA) were extracted from clusters showing significant paired t-test results in each group. To make quantitative comparisons, we used "relative" differences using the following equation:

$$\frac{(\text{R2 iFC} - \text{R1 iFC})}{\text{R1 iFC} * \text{SIGN(R1 iFC)}}$$

Results

Behavioral Results

The 2 groups did not significantly differ in age, gender, mean FD, verbal IQ, performance IQ, or WRAT Word Reading (Table 1). This ensures that the interaction effect, if present, is more likely to arise from the auditory exposure. In each group, there was 1 participant whose word reading score was below a standard score of 85 (–1 SD). For the verbal IQ, 3 AG participants and 1 CG participant scored below the average range (t-score < 40, –1 SD). Similarly, for the performance IQ, 2 AG participants and 1 CG participant scored below the average range (t-score < 40, –1 SD).

Imaging Results

ReHo Results Using the LME Model

The LME analysis revealed a significant "Group × Scan" interaction in the right inferior frontal gyrus (R.IFG: $F = 16.98$, $k = 283$, $xyz = 40\ 8\ 22$, Fig. 2A) and the right superior parietal lobule (R.SPL: $F = 11.06$, $k = 124$, $xyz = 34\ -56\ 46$, Fig. 3A). To examine the nature of the interactions (Figs 2B and 3B), we plotted ReHo Z scores extracted from these clusters: For the R.IFG cluster, all participants in the CG showed a decrease (R1 > R2), but this pattern was absent in the AG (Fig. 2C). In contrast, for the R.SPL cluster, all participants in the AG showed an increase (R1 < R2), but this pattern was absent in the CG (Fig. 3C).

As expected, a paired t-test using the extracted ReHo Z scores confirmed a significant difference in R.IFG between R1 and R2 in the CG ($t = 5.49$, $P < 0.01$) but not in the AG (Fig. 2D). For the R.SPL ReHo Z scores, a significant difference was also present between R1 and R2 in the AG ($t = 5.14$, $P < 0.01$) but not in the CG (Fig. 3D). Additionally, we performed independent t-tests, showing no significant group difference in the pre-exposure, baseline ReHo (R1) for either cluster (Fig. 3D). For the post-exposure ReHo (R2), a significant group difference was observed for both clusters (R.SPL, $t = 2.15$, $P < 0.05$; R.IFG, $t = 2.15$, $P < 0.05$).

ReHo results for gradients. Our main interest was the comparison between R2–1 and R2–2 for R.SPL ReHo: In contrast to our expectations, no significant difference was observed between R2–1 and R2–2 ($t = 1.27$, $P = 0.22$) (Fig. 4). The pre-exposure ReHo (i.e., R1–2) was also compared with each of the post-exposure ReHo datasets (i.e., R2–1 and R2–2), showing that R1–2 for R.SPL ReHo was significantly lower than both R2–1 ($t = 5.07$, $P < 0.001$) and R2–2 ($t = 3.23$, $P < 0.01$). These results indicate that the modulatory effect of passive auditory exposure on R.SPL remained relatively constant throughout the entire post-exposure R-fMRI (i.e., no fade-out effect on the subsequent iFC).

ReHo-Behavior Results for R1–R2 Differences

First, to identify potential outliers that could influence our least-squares results, we performed robust nonlinear regression with the Marquardt method (Motulsky and Brown 2006) to fit a curve based on the assumption of a Lorentzian (rather than Gaussian) distribution of residuals. The residuals of the robust fit were then analyzed to identify any outliers. After thresholding (the q value was set to 1%), no outlier was detected, and thus we subsequently performed a standard least-squares fit on our dataset including all participants.

For the R.IFG cluster, the relative R1–R2 differences did not significantly correlate with any measures of cognitive performance in either group (Fig. 5A). In contrast, for the R.SPL cluster, the relative R1–R2 differences showed significant negative correlations with WRAT ($R^2 = 0.58$, $P < 0.01$), verbal IQ scores ($R^2 = 0.52$, $P < 0.01$), and performance IQ ($R^2 = 0.48$, $P = 0.01$) in the AG (Fig. 5B). That is, AG individuals with lower word reading competence and those with lower IQ tended to exhibit greater ReHo increase in R.SPL. Additionally, we examined relationships between the baseline ReHo (R1) in the R.SPL and each of the 3 cognitive measures. The baseline ReHo Z scores in either R.SPL or R.IFG were not correlated with cognitive performance for any of these measures in either group (Supplementary Fig. 1). This indicates that the ReHo-behavior relationship (i.e., word reading, IQ) is specific to the modulation in ReHo within R.SPL.

SCA Results Using R.SPL

To further examine iFC changes associated with the auditory exposure, we performed post hoc SCA, with a specific focus on the R.SPL cluster that showed a significant increase in the AG. As shown in Figure 6, paired t-tests in the AG revealed that the AG exhibited a significant difference (i.e., increase: R1 < R2) in iFC between the R.SPL seed and each of 2 adjacent regions within the parietal cortex: 1) the right inferior parietal lobule in Figure 6A (R.IPL: $Z = 5.70$, $k = 1159$, $xyz = 46\ -44\ 42$), located immediately ventral to the R.SPL seed, and 2) the dorsal part of the posterior cingulate cortex in Figure 6B (PCC: $Z = 4.64$, $k = 695$, $xyz = 8\ -44\ 56$), which was spatially more extended into the right hemisphere. We also examined the 2 identified connections (R.SPL with R.IPL and PCC) in the CG, finding no significant R1–R2 differences in either connection.

Connectivity-behavior relationships, shown in Figure 6C, were largely similar to those observed in the ReHo results. In the AG, the difference/increase in R.SPL's connections (with R.IPL and PCC) negatively correlated with WRAT performance ($R^2 = 0.25$, $P < 0.05$ for R.IPL; $R^2 = 0.42$, $P < 0.01$ for PCC). The

Table 1 Demographic and cognitive descriptions of the auditory and control groups

	Auditory group Mean (SD)	Control group Mean (SD)	Differences Significance level
Age (years)	26 (7.9)	25 (5.7)	N.S. ($P = 0.74$)
Gender	9 M/8 F	4 M/6 F	N.S. ($P = 0.52$)
R1 Mean FD	0.06 (0.04)	0.05 (0.02)	N.S. ($P = 0.70$)
R2 Mean FD	0.07 (0.04)	0.06 (0.02)	N.S. ($P = 0.57$)
Verbal IQ (t)	53.9 (13.0)	53.9 (8.5)	N.S. ($P = 0.99$)
Performance IQ (t)	52.9 (10.4)	50.5 (11.4)	N.S. ($P = 0.58$)
WRAT Word (ss)	105.2 (13.6)	103.4 (8.7)	N.S. ($P = 0.16$)

SD = Standard Deviation, N.S. = Not Significant, M = Male, F = Female, R1 = the pre-exposure resting-state fMRI scan, R2 = the post-exposure resting-state fMRI scan, FD = Frame-wise Displacement, t = t-score, ss = standard score.
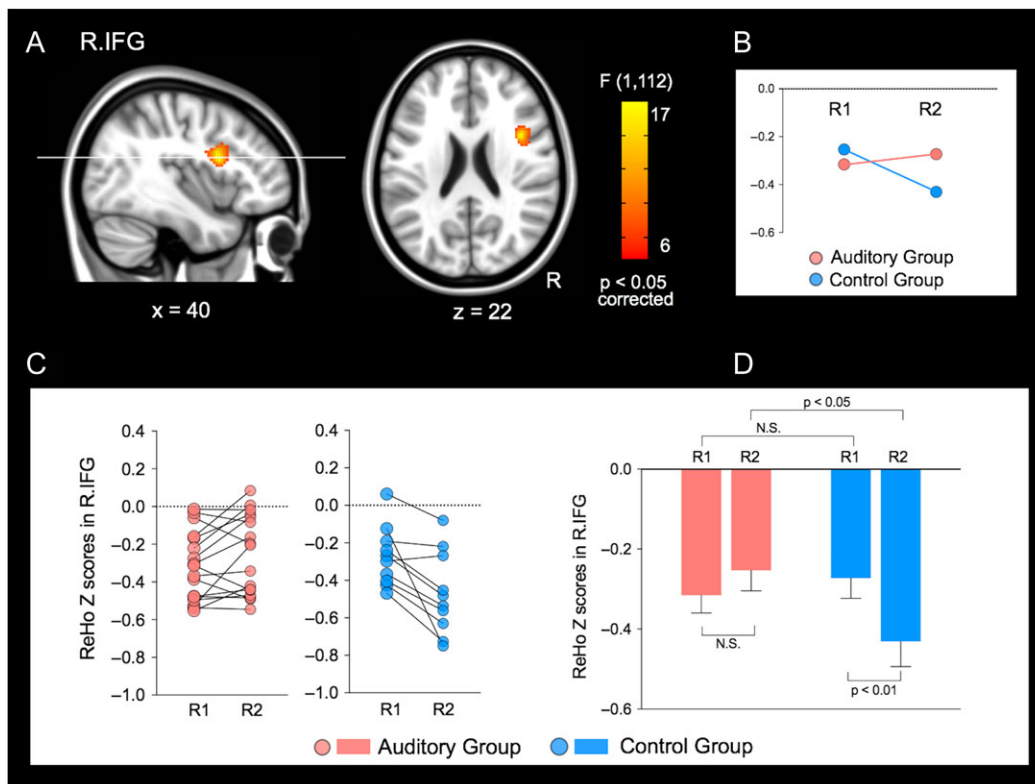
Figure 2. (A) The right inferior frontal gyrus (R.IFG) as a locus of the Group × Scan interaction effect on ReHo. (B) The interaction effects on R.IFG. Participants in the control group showed a significant decrease (R1 > R2) relative to the auditory group that exhibited no significant modulation between R1 and R2. (C) The difference between the pre-exposure (R1) and post-exposure (R2) ReHo Z scores in R.IFC for each individual in each group. All participants in the control group showed a decrease, whereas such a consistent pattern was absent in the auditory group. (D) Within-group and between-group comparisons for the pre-exposure (R1) and post-exposure (R2) ReHo Z scores in R.IFG. A significant R1–R2 difference was observed only in the control group. No significant group difference was observed in R1, whereas R2 was significantly lower in the control group than the auditory group. R1 = the first (pre-exposure) R-fMRI scan, R2 = the second (post-exposure) R-fMRI scan, N.S. = Not Significant

same connections were not significantly associated with any behavioral outcomes in the CG. Significant negative connectivity-behavior relationships in the AG were also observed for verbal IQ ($R^2 = 0.26$, $P < 0.05$ for R.IPL; $R^2 = 0.41$, $P < 0.01$ for PCC), but not for performance IQ ($R^2 = 0.09$, $P = 0.24$ for R.IPL; $R^2 = 0.16$, $P = 0.11$ for PCC).

SCA Results Using the Primary Auditory Cortex
Although we expected that the primary auditory cortex would show the modulatory effect following auditory exposure, our primary LME analysis with ReHo did not yield any significant result in this region. Hence, as a complementary analysis, we performed SCA for both left and right Heschle Gyrus (HG) seeds, using the same LME model. Both L.HG and R.HG seeds were defined by the Harvard-Oxford Atlases. The minimum numbers of voxels necessary to achieve a height $P < 0.001$ and a cluster extent $P < 0.05$ was 55, calculated by 3dClustSim. As shown in Figure 7, a significant "Group × Scan" interaction was observed for 3 L.HG connections with: 1) the left precentral gyrus (L.PCG: $F = 12.03$, $k = 120$, $xyz = -34$ 0 42), 2) L.SPL ($F = 6.51$, $k = 92$, $xyz = -26$ −58 42), and 3) R.SPL ($F = 8.58$, $k = 68$, $xyz = 46$ −52 50), as well as for 3 R.HG connections with: 1) L.PCG ($F = 13.74$, $k = 164$, $xyz = -28$ −16 52), 2) R. PCG ($F = 12.86$, $k = 193$, $xyz = 44$ −16 50), and 3) R.SPL ($F = 12.86$, $k = 90$, $xyz = 54$ −36 54). Note that the identified 2 R.SPL clusters from these SCA (Fig. 7C and F) and the R.SPL cluster from the LME analysis with ReHo (Fig. 3A) are adjacent to each other, but there was no overlap among these 3 R.SPL clusters.

To examine the nature of the interactions, we plotted Fisher Z scores extracted from these connections (Fig. 7A–F). Notably, HG connections with SPL (i.e., L.HG with L.SPL and R.SPL, as well as R.HG with R.SPL) significantly increased in the AG, whereas the same connections either remained largely unchanged or decreased in the CG. The opposite pattern was observed for HG connections with PCG: L.HG with L.PCG, as well as R.HG with L.PCG and R.PCG, significantly increased in the CG, whereas the same connections remained largely unchanged in the AG.

Discussion

Building on the growing literature exploring the impact of a preceding sensory experience on iFC, we directly compared pre- and post-exposure R-fMRI scans to examine modulatory effects of brief passive auditory experience on the subsequent iFC. Collectively, our findings support the hypothesis that a preceding auditory exposure to non-linguistic sounds, even when it is brief and passive (and thus irrelevant), is capable of modulating the subsequent iFC, especially within the posterior parietal cortex that supports human attention processing (Critchley 1953; Corbetta and Shulman 2002; Huang et al. 2012; Shomstein 2012). In addition, the degree of such iFC modulations characterizes individual differences in cognitive abilities—word reading, verbal IQ, and performance IQ.
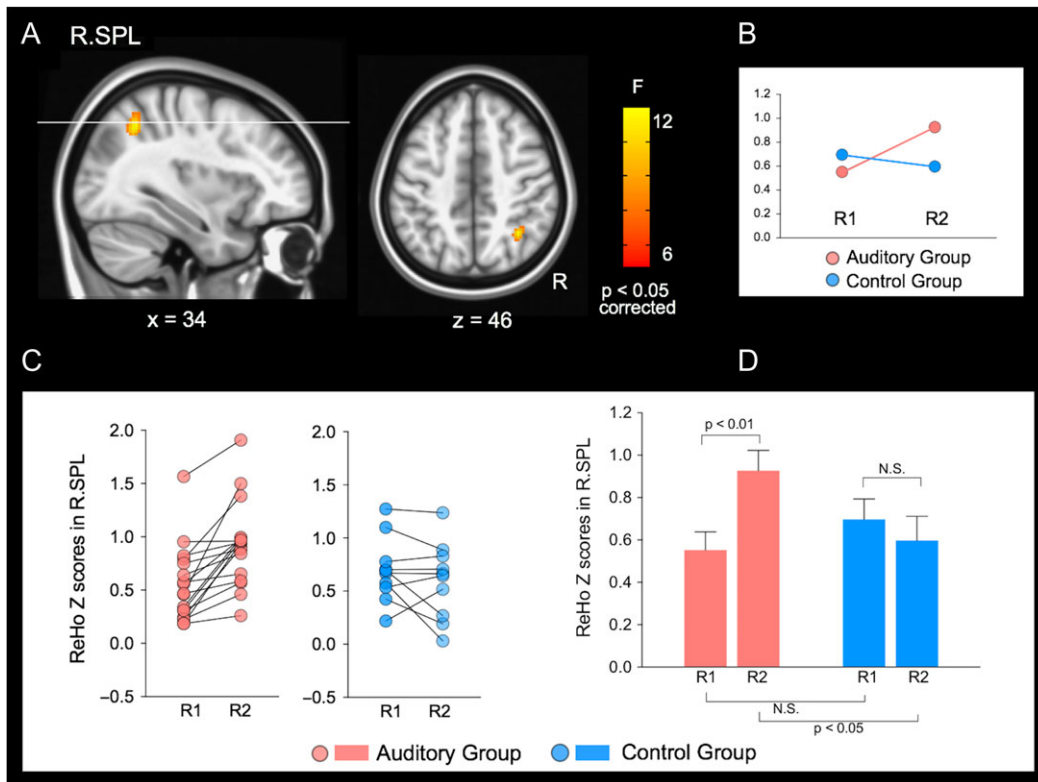
Figure 3. (A) The right superior parietal lobule (R.SPL) as a locus of the Group × Scan interaction effect on ReHo. (B) The interaction effects on R.SPL. Participants in the auditory group showed a significant increase (R1 < R2) relative to the control group that exhibited no significant modulation between R1 and R2. (C) The difference between the pre-exposure (R1) and post-exposure (R2) ReHo Z scores in R.SPL for each individual in each group. All participants in the auditory group showed an increase, whereas such a consistent pattern was absent in the control group. (D) Within-group and between-group comparisons for the pre-exposure (R1) and post-exposure (R2) ReHo Z scores in R.SPL. A significant R1–R2 difference was observed only in the auditory group. No significant group difference was observed in R1, whereas R2 was significantly higher in the auditory group than the control group. Error bars represent standard error of the mean, R1 = the first (pre-exposure) R-fMRI scan, R2 = the second (post-exposure) R-fMRI scan, N.S. = Not Significant

The Modulatory Effect of the Auditory Exposure on the Posterior Parietal Cortex

A significant difference between pre- and post-exposure ReHo in R.SPL was observed, but only in the AG, not in the CG. Notably, the ReHo modulation (increase; R1 < R2) in R.SPL seen in the AG remained stable throughout the post-exposure R-fMRI scan. Similarly, intrinsic connections of R.SPL with its adjacent parietal regions (R.IPL and PCC) were increased only in the AG group, following the auditory exposure period. These results indicate that a brief (5 min) passive auditory exposure to non-linguistic information is sufficient to significantly modulate the subsequent iFC "locally" within the parietal attention network (Corbetta and Shulman 2002; Shomstein 2012; Vossel et al. 2014), independent of potential impacts of the MRI noise present for both groups. Supplementary Figure 2 illustrates that the R.SPL cluster is a part of the attention network, in reference to the iFC map showing the dorsal and ventral networks (Fox et al. 2006) and reverse interference maps associated with "attention" and "dorsal attention" via NeuroSynth (Yarkoni et al. 2011).

Although posterior parietal regions can be functionally heterogeneous, all these regions, SPL, IPL, and PCC, are involved in attentional control (Husain and Nachev 2007; Yantis 2008; Leech et al. 2012; Shomstein 2012). Note that although PCC is a core hub of the default network, the dorsal part of PCC, which spatially coincides with our PCC finding, is highly connected with the fronto-parietal network involved in attentional control (Leech et al. 2012). Specific to auditory attention, Huang et al.
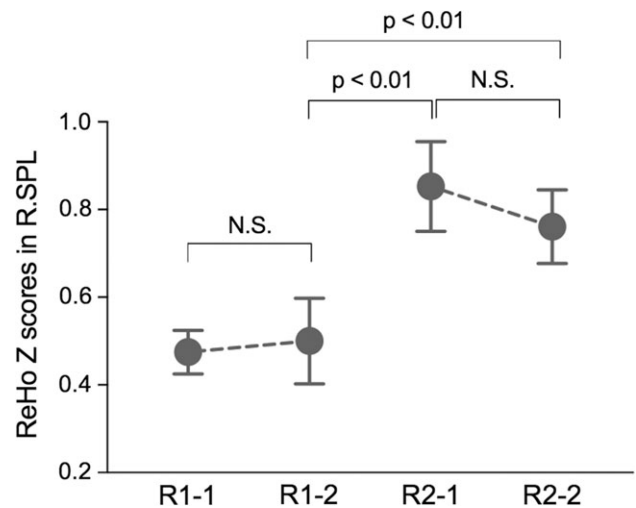

Figure 4. ReHo gradients in the right superior parietal lobule (R.SPL) across R-fMRI sub-datasets. For the post-exposure R-MRI dataset (R2), the group mean of ReHo in R.SPL was not significantly different between in the first half (R2–1) and the second half (R2–2). Error bars represent standard error of the mean. R1–1 = the first half of the pre-exposure R-fMRI dataset, R1–2 = the second half of the pre-exposure R-fMRI dataset, N.S. = Not Significant

(2012) have demonstrated that top-down voluntary attentional shifting (cue-driven) activates bilateral SPL, whereas bottom-up involuntary shifting (novelty-driven) activates bilateral IPL and
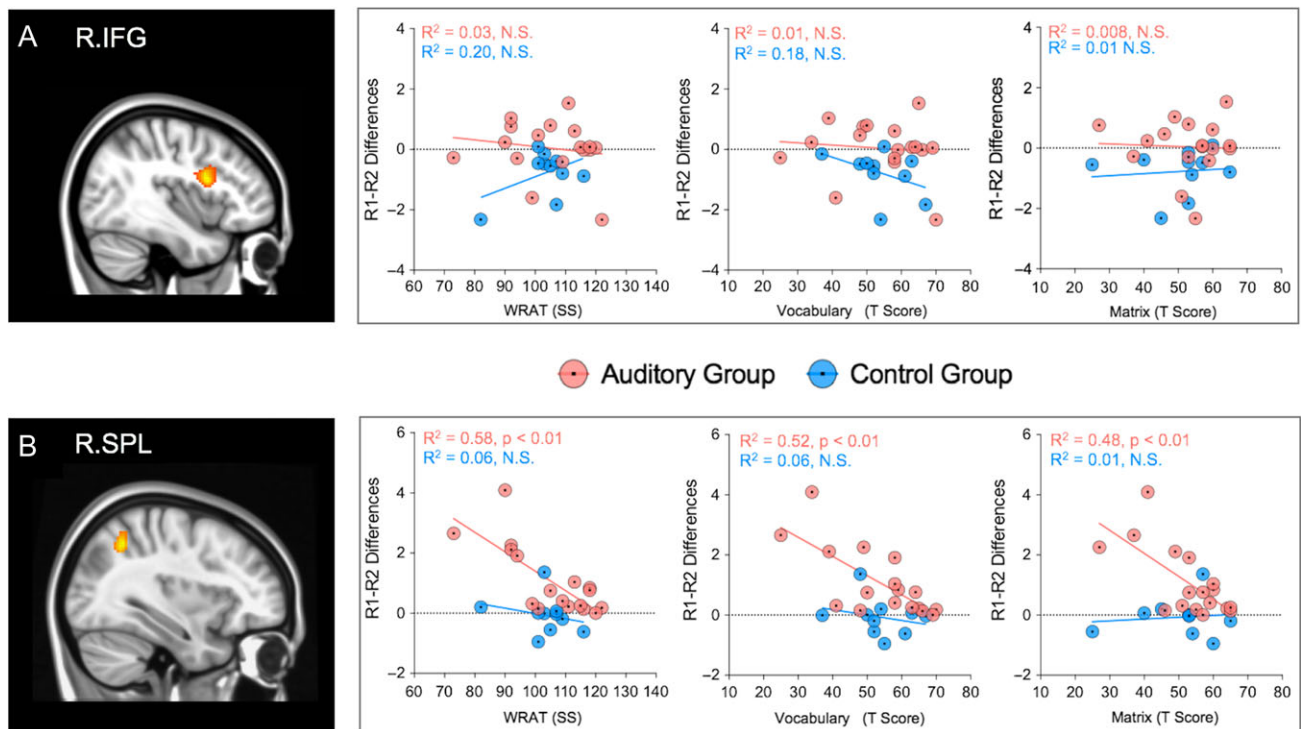
Figure 5. Scatter plots of ReHo modulations in (*A*) the right inferior frontal gyrus and (*B*) the right superior parietal lobule (R.SPL) as a function of cognitive performance. The modulations in R.IFG ReHo showed no significant relationships with any measure of cognitive performance in either group, whereas the modulations in R.SPL ReHo showed significant negative relationships with all measures—word reading (WRAT), verbal IQ (Vocabulary), and performance IQ (Matrix)—only in the auditory group. WRAT = Wide Range Achievement Test Word Reading, Vocabulary = The Wechsler Abbreviated Scale of Intelligence Vocabulary subtest, Matrix = The Wechsler Abbreviated Scale of Intelligence Matrix Reasoning subtest, SS = Standard Scores, N.S. = Not Significant. To make quantitative comparisons, "relative" R1–R2 differences in ReHo Z scores were calculated for each participant.

precuneus/PCC. This is consistent with a recent review focusing on roles of dorsal and ventral regions within the posterior parietal cortex in attention (Shomstein 2012). From the activation/connectivity patterns of these parietal regions reported in the fMRI literature, we infer that our iFC results in the AG may well reflect the involvement of not only involuntary attention, which we hypothesized, but also voluntary attention, during the preceding brief passive auditory exposure.

It would not be surprising if AG participants engaged both voluntary and involuntary attention networks during the passive auditory exposure period in this study. Although we designed the passive auditory exposure to be as irrelevant to the participants as possible, we provided minimal information that they would hear repeated tones in the scanner. This knowledge, albeit aiming to minimize attentional shift to the tones, may have served as a top-down cue (i.e., anticipating the upcoming sounds). This could have elicited voluntary allocation of attention and thus have potentially activated R.SPL, a region associated with voluntary attentional shift (Huang et al. 2012; Shomstein 2012), leading to modulation of the subsequent ReHo within the same region.

In addition to this potential involvement of voluntary attention, the irrelevant but novel, and perhaps salient, deviant tone-pairs could have activated regions associated with involuntary attentional capture, as is shown in ERP studies (Escera et al. 1998; Näätänen et al. 2007). Such activation, assumed to have occurred during the preceding event, could also have contributed to the observed increase in iFC between R.SPL and each of R.IPL and PCC—posterior parietal regions associated with bottom-up involuntary attention (Huang et al. 2012). Of

note, our iFC results were restricted to right hemisphere SPL and IPL, consistent with previous auditory oddball fMRI results (Stevens et al. 2005), as well as the well-demonstrated right hemisphere dominance for tonal stimuli and music (Tervaniemi and Hugdahl 2003; Hyde et al. 2008).

In contrast to our hypothesis, there was no modulatory effect of the auditory exposure on ReHo in the auditory cortex, a region known to be activated during passive auditory oddball paradigms (Liebenthal et al. 2003; Sabri et al. 2006). However, post hoc SCAs using the primary auditory cortex seeds (L.HG and R.HG) reveal a significant increase (R1 < R2) in their connections with R.SPL in the AG only. These results indicate that the increased auditory-attentional iFC may have contributed to the increased ReHo within the parietal attention network. Considering that sustained modulation in the auditory cortex is manifested as an increased response only to trained/learned auditory stimuli (van Wassenhove and Nagarajan 2007), ReHo modulation within this region could be observed if our oddball paradigm involved active learning, rather than passive exposure. Because we acquired no fMRI data during auditory exposure, a direct link between task-/stimuli-evoked activation in the auditory cortex and the subsequent iFC awaits further investigation.

In addition to the increased auditory-attention iFC in the AG, both L.HG and R.HG connections with the precentral gyrus, the site of the premotor cortex, were increased in the CG only. Given that this auditory-motor circuitry is strong during rest and speech perception (Skipper and Hasson 2017), individuals in the CG may have been more greatly involved in inner speech (Bastian et al. 2017) or spontaneous thoughts (Chou et al. 2017)
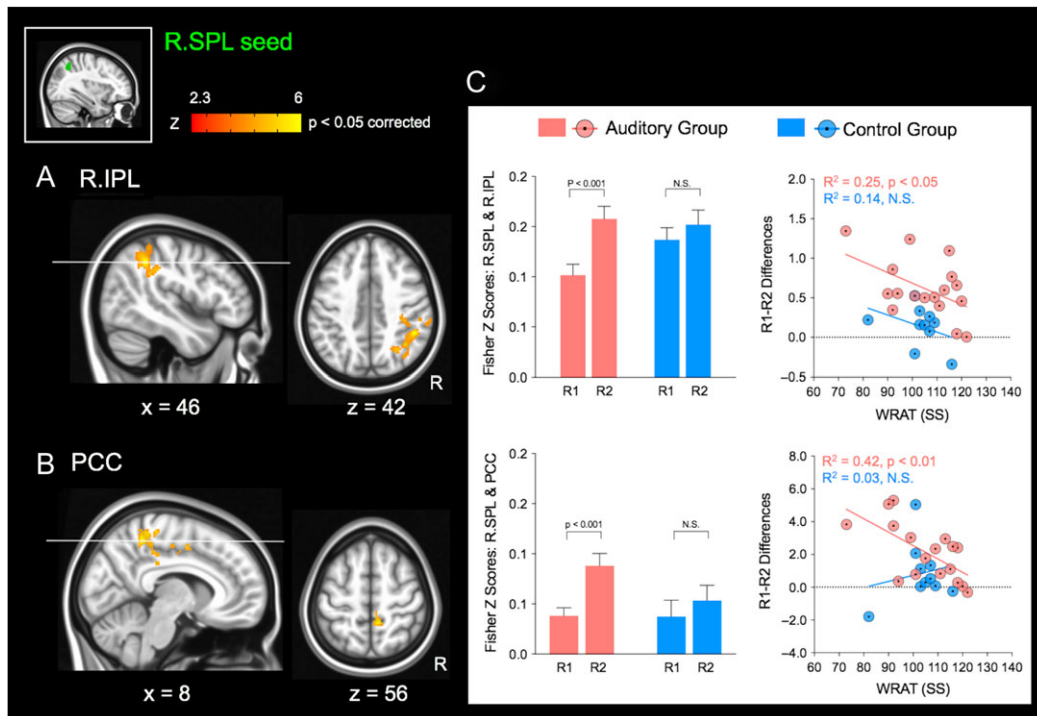
Figure 6. Seed-based correlation analysis (SCA) of the right superior parietal lobule (R.SPL) with (A) the right inferior parietal lobule (R.IPL) and (B) the posterior cingulate cortex (PCC). Paired *t*-test revealed a significant increase in R.SPL connections with 2 adjacent parietal regions, R.IPL and PCC, only in the auditory group. (C) Within-group and between-group comparisons for the pre-exposure (R1) and post-exposure (R2) ReHo Z scores, as well as connectivity-behavior relationships for R. IPL and PCC. R.SPL connections with R.IPL and PCC exhibited significant negative relationships with word reading (WRAT) in the auditory group only. WRAT = Wide Range Achievement Test Word Reading, SS = Standard Scores, N.S. = Not Significant.

while "mind-wandering" at rest, relative to those in the AG whose mind wandering was potentially disrupted during or at the beginning of the auditory exposure. This assumption needs to be tested by linking iFC to resting-state cognition (e.g., the presence/frequency of mind wandering), assessed by post-MRI questionnaires (Delamillieure et al. 2010; Diaz et al. 2013).

Modulation in the Right Prefrontal Cortex

In addition to R.SPL, R.IFG is highlighted as another locus of the Group × Scan interaction effect. However, the modulation (i.e., decrease, R1 > R2) in this prefrontal region was specific to the CG, and thus cannot be attributed to the effect of either the auditory exposure (i.e., only in the AG) or MRI noise that both groups experienced. A possible explanation for this observation is that individuals in the CG may have been more greatly involved in spontaneous thoughts throughout the scanning session, relative to those in the AG who were presented with repeating sounds for 5 min between the 2 R-fMRI scans. This assumption, which we suggest may also apply to the results of the HG iFC, is in line with a recent R-fMRI study that provides a framework for characterizing mind wandering during rest (Chou et al. 2017): individuals who report spending more time in spontaneous thoughts during R-fMRI scan tend to show more decrease in iFC profiles, including frontal regions, relative to those who report spending less time in spontaneous thoughts. However, our interpretation remains speculative given a lack of questionnaire-based information that allows the assessment of mind wandering and spontaneous thoughts during R-fMRI scans (Delamillieure et al. 2010; Diaz et al. 2013). Combining iFC profiles with quantified resting-state cognition

could have aided us in determining a potential explanation of the decreased R.IFG ReHo in the CG.

No Decrease After the Auditory Exposure

Another unexpected finding in the current study is the absence of any decrease (R1 > R2) after auditory exposure in either ReHo or R.SPL's iFC. In general, when stimuli are repeated, a reduction in neural activity at the cellular level is expected. This phenomenon is known as adaptation and can be readily captured using fMRI techniques (Grill-Spector and Malach 2001; Krekelberg et al. 2006; Perrachione et al. 2016). During the 5-min auditory exposure in this study, the repeating standard tones were frequently interrupted by novel/deviant tones, which may have remained more salient, thus continuing to activate the parietal attention network during the exposure period. This ongoing activation could have prevented or attenuated the adaptation process, resulting in no significant decrease on the subsequent iFC. Indeed, prior fMRI studies using oddball paradigms have reported increased activation for deviant as compared to standard stimuli (Kim 2014), indicating that the observed increase in parietal iFC may reflect the effect of potential activation driven by deviant sounds during the preceding auditory exposure. Alternatively, as noted in a review by Krekelberg et al. (2006), even when single cells show reduced response after adaptation, fMRI activation may not necessarily show reduced activation patterns. Further discussion about a link between cellular activation and fMRI activation is beyond the scope of the current R-fMRI study, but constitutes a crucial step towards a deeper understanding of adaptation in the human brain.
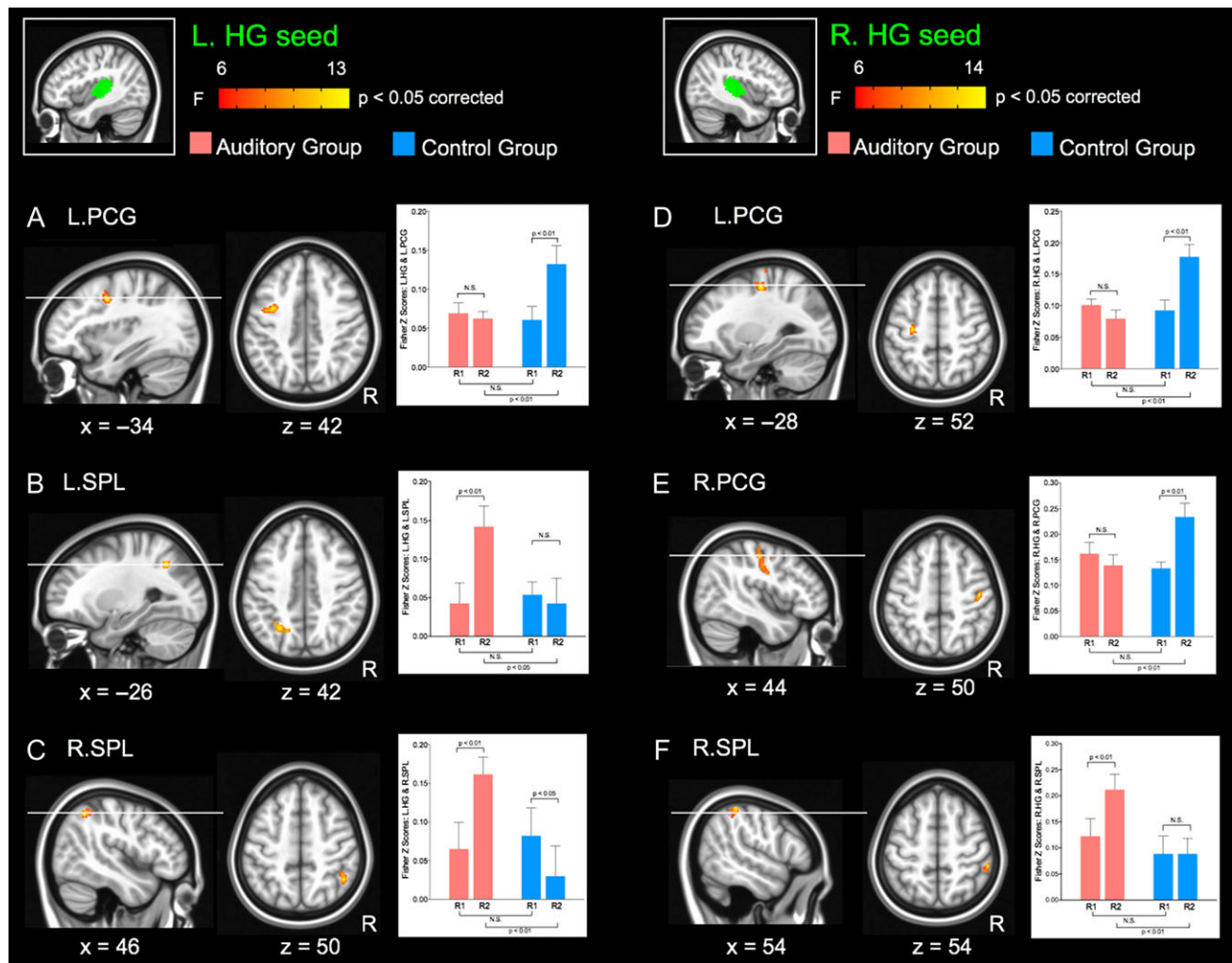
Figure 7. SCA of the primary auditory cortex. The left Heschl's Gyrus (L.HG) seed with (A) the left precentral gyrus (L.PCG), (B) the left superior parietal lobule (L.SPL), and (C) the right SPL (R.SPL). The right Heschl's Gyurs (R.HG) seed with (D) L.PCG, (E) R.PCG, and (F) R.SPL. In general, HG connections with R.SPL (C and F) were increased in the auditory group only, whereas HG connections with PCG (A, D, and E) were increased in the control group only.

Parietal iFC Modulations Associated with Cognitive Performance

We find that the degree of iFC modulation within the posterior parietal cortex (i.e., ReHo in R.SPL, R.SPL iFC with R.IPL and PCC) negatively correlates with measures of word reading, verbal IQ, and performance IQ (only ReHo in RSL) in AG participants. That is, individuals who exhibit a lesser (i.e., minimized or close-to-zero) iFC modulation following the auditory exposure tend to have higher cognitive abilities, particularly in language-related domains. While we demonstrate a robust modulatory effect of the auditory exposure on parietal iFC, the connectivity-behavior results suggest that the brain's resilience to the modulatory effect characterizes individual differences in cognitive abilities. In other words, although it has been reported that the brain adaptively reconfigures its iFC to cope with the ongoing environment and task (Cole et al. 2013; Di and Biswal 2015), when the incoming information is irrelevant, its capacity to optimally minimize undesirable changes/perturbations caused by sensory experience (e.g., the lowest or no change reflects the highest resilience) is associated with better cognitive performance.

Our connectivity-behavior results are consistent with reported deficits in perceptual noise exclusion in individuals

with lower reading performance (i.e., dyslexia) (Sperling et al. 2005; Ziegler et al. 2009). These studies indicate that individuals who are less capable of automatically excluding/filtering noise tend to be poorer readers. In our findings, those participants who were less capable of minimizing the modulatory effect of exposure to irrelevant sounds tended to have lower reading scores. Further evidence to support this interpretation comes from recent studies of sensory gating, which is a neurological mechanism used to filter out redundant/repeated or unnecessary sensory stimuli in the brain (Cromwell et al. 2008). For example, Jones et al. (2016) have examined cognitive correlates of auditory sensory gating, showing that successful sensory gating (defined as attenuated P50 responses) is related to higher intelligence. Another study that examined ADHD individuals, who have diminished attentional capacity, reported abnormalities in sensory gating (Micoulaud-Franchi et al. 2016).

Since there was no task (and no specific instructions) for the auditory exposure, we assume that the AG participants were able to gradually gate out the sounds during the exposure period. Accordingly, we propose that the resilience of the iFC modulation in the presence of intervening irrelevant auditory stimuli might be key to successful cognitive performance. The

flip side of this proposal is that a greater degree of iFC modulation to incoming sensory inputs can be beneficial when the inputs are relevant and goal-oriented (Stevens et al. 2010; Schlaffke et al. 2016). It would be of interest to contrast modulatory effects of the 2 auditory exposure conditions, one involving active/relevant information processing and another with passive/irrelevant information processing (like our current experimental design), and then to link the iFC modulations to behavioral performance. From a clinical perspective, iFC modulations following a passive sensory exposure, which places less cognitive demands on clinical and/or pediatric populations during scanning, could provide metrics that would enable identification and characterization of impaired sensory gating or noise exclusion, which is proposed to play a role in dyslexia (Beattie et al. 2011) and ADHD (Micoulaud-Franchi et al. 2016).

Limitations

Limitations exist in the current study that should be taken into account when interpreting the present outcomes as well as for planning the next set of experiments. First, we used the same dataset for ReHo and SCA analyses. An important point is that our SCA findings obtained in the same dataset used for the ReHo analysis should not be interpreted as independent verification (Kriegeskorte et al. 2009), but rather as post hoc results that can provide complementary perspectives of the ReHo findings (e.g., specific sets of connections associated with ReHo findings), and also impart valuable insights into generating hypotheses for replication in future work. In the current study, the R.SPL cluster found by ReHo analysis, which restricts its computation to local connectivity between a given voxel time series and those of its nearest 26 neighboring voxels, further showed its strong connectivity with adjacent/local regions (e.g., R.IPL) even when SCA interrogated a given voxel time series for all other voxels in the brain. Thus, our SCA findings are complementary to our ReHo finding, emphasizing the effect of auditory exposure on local connectivity in the posterior parietal cortex.

Second, the current study lacked either task-evoked fMRI data or simultaneous fMRI-ERP data collection during the 5-min passive auditory exposure period. The information provided by task-evoked activation could potentially verify a direct link between activation/functional connectivity in the preceding event and the subsequent iFC. As mentioned previously, we chose not to acquire fMRI data during the auditory exposure period, mainly because a sparse imaging sequence, which is frequently employed for auditory fMRI experiments, is very time-consuming for the number of trials we collected. The length of data acquisition was an important consideration in the current study, because these data are a subset of an ongoing infant-adult comparative study that uses the same MRI sequences to collect data in naturally sleeping infants. However, acquiring task-evoked fMRI during the passive auditory exposure, followed by R-fMRI acquisition (as was done in the current study), is an important next step that should be explored.

Finally, we collected neither behavioral measures that can assess attentional abilities, nor post-scan questionnaires to explore participants' spontaneous thoughts and mind wandering during R-fMRI scan. Such information could provide further insights as to what type of attention might correlate with the observed modulation effect of auditory exposure in the AG (i.e., R.SPL), as well as elucidating the behavioral relevance of the variations in the observed modulation specific to the CG (i.e., R.IFG).

Conclusion

Taken together, the results of the current study provide further evidence for the impact of a preceding sensory experience on the brain, demonstrating the modulatory effect of passive auditory exposure to irrelevant, non-linguistic information on the subsequent iFC. Increased iFC (R1 < R2) within the parietal attention network may reflect the involvement of both voluntary and involuntary attentional processes during the auditory exposure. Voluntary attention is likely to be driven by the minimal information provided to the AG participants, which may serve as a top-down cue (e.g., anticipation of incoming sounds) and thus modulate local iFC within R.SPL—a region implicated in voluntary attention. In addition, given that the sounds were presented in a passive oddball paradigm, involuntary attention (i.e., capture by and shift from deviant sounds) might well play a significant role in modulating R.SPL's connections with regions in the ventral attention network (R.IPL and PCC). Notably, negative associations between parietal iFC modulations and cognitive performance (e.g., word reading, verbal IQ) suggest that a lesser degree of iFC modulation, potentially reflecting higher cerebral resilience to undesirable change caused by exposure to irrelevant sounds, characterizes better cognitive abilities. These findings provide a framework for future investigation of impaired sensory gating or noise exclusion in clinical populations with language-related deficits, such as dyslexia (Ziegler et al. 2009; Beattie et al. 2011), as well as those disorders characterized by deficits in attentional control, such as ADHD (Micoulaud-Franchi et al. 2016).

Supplementary Material

Supplementary data are available at *Cerebral Cortex* online.

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Notes

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