Closing the mind's eye: deactivation of visual cortex related to auditory task difficulty

By: W. David Hairston, Donald A. Hodges, Ramon Casanova, Satoru Hayasaka, Robert Kraft,
Joseph A. Maldjian, and Jonathan H. Burdette

Hairston, D., Hodges, D., Casanova, R., Hayasaka, S., Kraft, R., Maldjian, J., & Burdette, J. (2008) Closing the mind's eye: Deactivation of visual cortex related to auditory task difficulty. *NeuroReport*, 19:2, 151-154.

Abstract:

Blood oxygen-level-dependent signal decreases relative to baseline (deactivations) can occur with stimulation of an opposing sensory modality. Here, we show the importance of the difficulty of an auditory task on the deactivation of visual cortical areas. Participants performed an auditory temporal-order judgment task in conjunction with sparse-sampling functional MRI at both moderate and high levels of difficulty (adjusted for each individual's own threshold). With moderate difficulty, small deactivations were observed not only in parietal and cingulate cortex, but occipital cortex as well. When the same task was more difficult, deactivations increased significantly to include a greater extent of functionally defined visual cortex. Together, these results suggest that cross-modal deactivations occur in compensation for task difficulty, perhaps acting as an intrinsic filter for nonrelevant information. Keywords: cross-modal; deactivation; default mode; difficulty; multisensory

Article:

Introduction

Suppressing nonrelevant information across senses is critical for daily life; dramatic behavioral drawbacks and misperceptions can arise from integrating noncongruent cross-modal signals [1–3], which may also compete for shared neural resources [4]. Thus, the suppression of nonrelevant senses is necessary to maintain maximal perceptual integrity, particularly when a task involves one sense but not others. Increases in cerebral blood flow in task-relevant sensory cortical areas are often accompanied by decreases in other task-irrelevant sensory areas (e.g. auditory cortex during visual tasks) [5–8]. The consistency, size, and factors mediating these cross-modal deactivations are, however, uncertain when comparing across paradigms [9].

Selective attention likely affects this process; during concurrent bimodal stimulation, attending to one modality leads to a decreased response in nonattended sensory cortices relative to passive stimulation [10,11]. Meanwhile, decreased activation in the opposing modality cortex is tightly coupled to the shift of attention between modalities [12]. Although not addressing cross-modal deactivation per se (activity decreases below a resting baseline state (e.g. [7])), these studies suggest that the responsiveness of unattended cortices is decreased by focusing attention on another sense (e.g. visual cortex when attending to audition).

The degree to which cross-modal deactivations within sensory cortices depend upon task difficulty is unknown. Accounting for this task-related difficulty may explain much of the variability observed in similar earlier studies [9], and has not been explored in functionally defined sensory cortices. Just as task demand can increase deactivations within general task-independent regions [13], we propose that the extent of deactivation in nonrelevant sensory cortex also depends upon task difficulty. To test this, we examined deactivations of visually responsive cortex during performance of an auditory task at varied levels of difficulty.

Methods

Participants were 18 healthy volunteers (12 men) with normal or corrected-to-normal vision and hearing from a wide variety of professional backgrounds. Procedures were approved by the WFU IRB and conformed to the 1964 Declaration of Helsinki. Before magnetic resonance scanning, we acquired each volunteer's perceptual threshold for an auditory temporal order judgment (TOJ) task. Two tones (440 and 660 Hz) were presented binaurally with a variable onset (1–150 ms SOA), but ended simultaneously (total duration 500 ms). Participants reported which occurred first. The SOA was adjusted trial-by-trial by an adaptive staircase procedure to determine the participant's threshold SOA (e.g. 46 ms) at about 70–75% accuracy.

During functional MRI, the participants performed the task at two levels of difficulty. In one run (high difficulty) the SOA was centered around the participant's own threshold value (e.g. 46 ms), whereas in another run (moderate difficulty) the values were increased to be above the threshold while remaining challenging for that individual (target 80–85%, e.g. 65 ms for same individual). Typically, this was an approximately 50% change in SOA; however, the exact amount varied with a participant's performance on the previous run (e.g. if performance was poor or good, then more or less adjustment was used). ‘Difficulty’ labels were assigned on the basis of actual performance. Participants were removed from analysis if their worst score fell below 60%, had no discernable change (three cases), or demonstrated excess motion (two cases). During a separate run, participants performed a visual TOJ task in which they reported which of the two circles appeared first, above and below a central fixation cross on the screen. They responded with the right hand using a response box.

Stimuli were presented with MRI-compatible headphones and goggles (Resonance Technology, Northridge, California, USA). Sparse acquisition [14] was used to facilitate stimulus audibility during scanning. Blood oxygen-level-dependent (BOLD) images were acquired in a block design. Echo planar images were acquired on a 1.5 Tesla MRI scanner (90° flip angle, TE=40 ms, 28 axial slices, 5 mm slice thickness, no gap, 64×48 resolution and 240×180 mm FOV). During a 10-s silent period (no scanning), participants performed a cluster of three trials, then paused during 2 s of EPI acquisition. An ‘ON’ block consisted of three clusters (nine trials total), and alternated with a resting baseline OFF block with no stimuli, for a total of 10 blocks per run. During all the runs, the participants kept their eyes open and fixated on a central grey cross, verified by the eye tracker.

Preprocessing of statistical parametric maps was performed using standard methods [15]. Group-level analyses (task versus baseline) were performed in SPM5, with main effects (activations and deactivations) assessed using single-sample t-tests per condition. ‘Deactivation’ refers to significant negative deflections of the BOLD signal in task (ON) conditions relative to the resting baseline (OFF). Maps were corrected for multiple comparisons ($P<0.05$) using family-wise error rate [16]. For illustration, data are displayed with min/max T values of ±3.92 ($P<0.001$) and projected onto a normalized example participant T1-weighted image in neurologic convention. Using the Biological Parametric Mapping Toolbox (www.fmri.wfubmc.edu) [17], we accounted for the shared covariance of the moderate difficulty condition from the high difficulty condition via multiple regression. In particular, the one-sample t-test for the high difficulty condition described above was performed while accounting for participants' BOLD deactivation corresponding to moderate difficulty data entered as an image covariate. Resulting data represent the BOLD signal related solely to increased task difficulty, having accounted for areas with correlated activation/deactivation across conditions (e.g. auditory cortex, motor cortex, ‘default mode network’ [18]). Disjunction analysis was performed using a binary exclusive mask of the moderate difficulty data (at $P<0.05$) to view the high difficulty data set. Note that this fairly liberal [alpha] provides a conservative estimate on the resulting image and a qualitative description of changes in the spatial extent of deactivations exclusive to the high difficulty condition.

Mean BOLD contrast value, number, and total signal magnitude (mean×number) of significant ($P<0.001$) voxels were computed across regions defined anatomically using the WFU_PickAtlas [19] ROI tool for each participant and condition. In addition, data from the visual TOJ task were used to create an ROI of functionally defined visually responsive occipital cortex, limited to only significantly ($P<0.05$) activated voxels for the group. This ensured cluster statistics for this ROI included only low-level sensory cortical regions used for visual task performance and excluded global sensory nonspecific regions commonly deactivated during the performance of any task [18].

Results

After removing clear cases of failure of the staircase algorithm (n=3), behavioral results show that for the group, an average asynchrony of 68.5 (±11.9) ms was required to discriminate the temporal order of two distinct tones (440 and 660 Hz). When participants performed the high-difficulty TOJ task in the scanner at their own threshold SOA, making it extremely difficult, significant activations were observed bilaterally in the superior temporal gyrus, as well as the inferior and middle frontal gyri. Significant positive activity also occurred along the midline in the medial superior frontal gyrus and the anterior aspect of the right middle frontal gyrus and left precentral gyrus, consistent with performing a challenging auditory task and responding with the right hand.

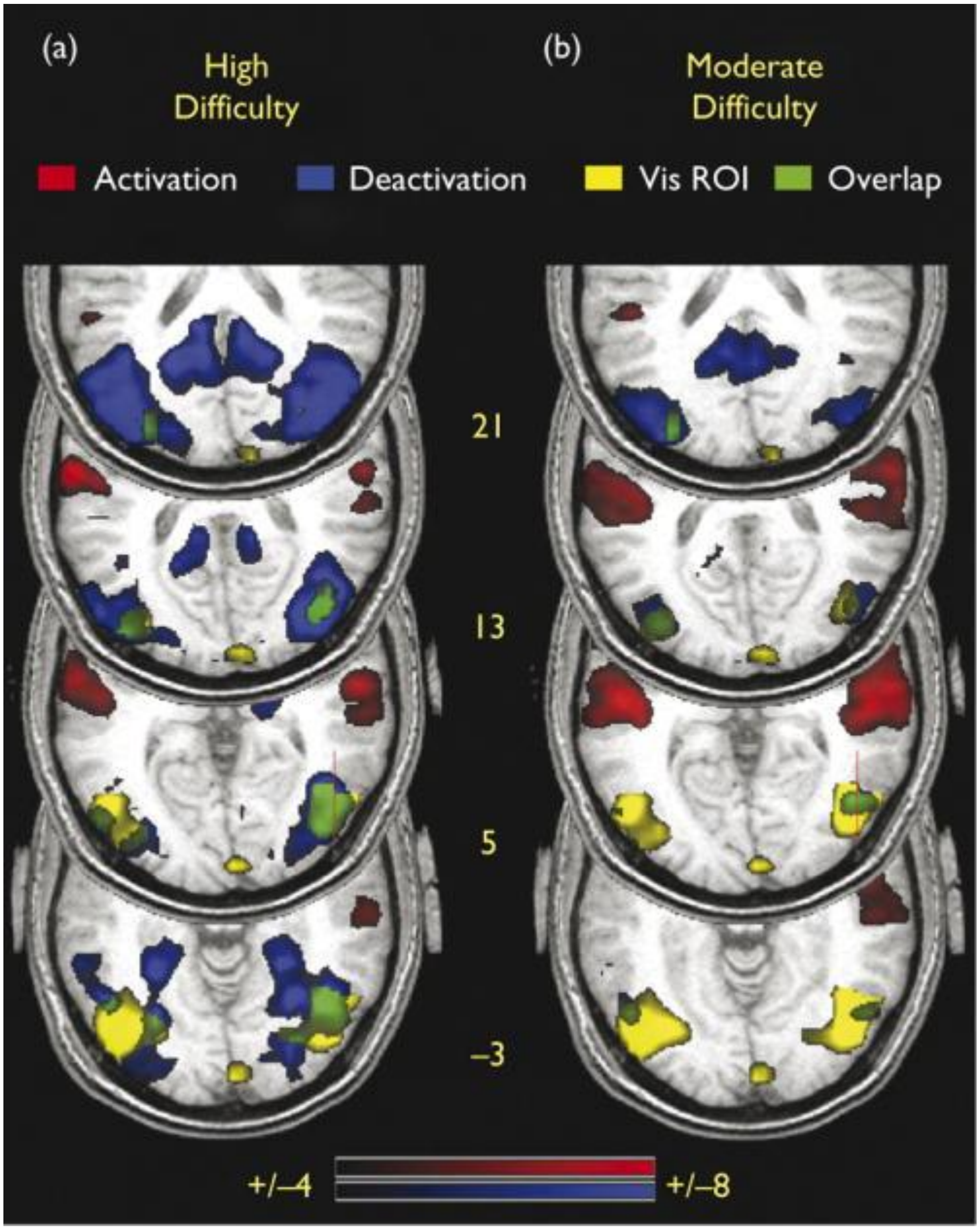
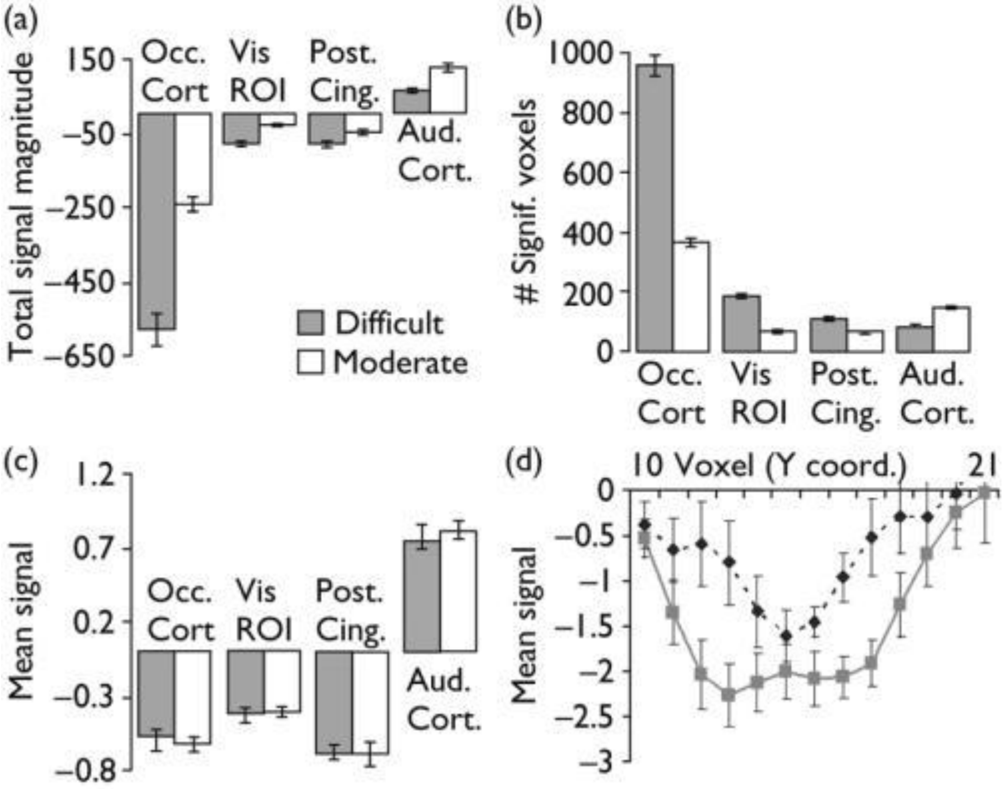


Fig. 1 Activity (T scores, deactivation in blue) related to auditory task performance at high (a) and moderate (b) levels of difficulty. Note robust deactivation and sizeable overlap at z=5 with the ROI in (a).

Significant negative deflections of the BOLD response, relative to a resting baseline (no stimuli, eyes open) were also observed. Posterior and anterior cingulate, as well as the bilateral inferior parietal lobules (IPLs) show strong deactivation, consistent with the default-mode resting-state network [18] and performing a difficult task [13]. Additionally, robust deactivations occurred within the occipital cortex. These extended through the middle occipital gyrus (MOG) and into the lateral inferior occipital gyrus, as well as superiorly through the superior occipital and into the angular gyrus (AG) and IPL (Fig. 1a). To highlight that these deactivations involve visually responsive cortex, the yellow overlay in Fig. 1 represents the functionally defined ROI (see Methods). It is clear from the green shaded regions (overlap with this ROI) that the deactivations include a substantial extent typically responsive to a fairly minimal visual stimulus.

In the moderately difficult (above threshold but challenging) condition, participants performed the same task, but with the SOA increased so as to make the task easier to perform. Note that the task still remained somewhat challenging. As would be expected, significant activations were observed in the regions listed above. The only notable change was increased bilateral activation in the superior temporal gyrus, likely because of better discrimination of the stimuli (increased interstimulus lag).

In contrast, dramatic alterations in the extent of deactivation were observed. Not only was a decrease seen in cingulate and parietal cortex, as might be expected with diminished task difficulty [13], but significant changes occurred within the visual cortex as well. Specifically, the spatial extent of deactivation decreased substantially. In this case, only small (yet significant) regions of deactivation were observed bilaterally in the AG extending into the MOG and posterior temporal gyri (Fig. 1b). Here, only a moderate overlap with the functional ROI (green areas) occurs, with deactivations including the most superior aspect of the MOG, and partially extending into the posterior temporal gyri and IPL.



Summary statistics show a highly significant decrease in the total signal magnitude within the region [t(12)=8.16, P<0.001], as shown in Fig. 2a (ROI, posterior cingulate and auditory cortex included for comparison). Further exploration shows this effect to be driven mostly by the striking decrease in the number of deactivated voxels [Fig. 2b, t(12)=62.1, P<0.001], as there was minimal change in the mean BOLD contrast signal of those voxels [Fig. 2c, t(12)=1.02, P>0.05].

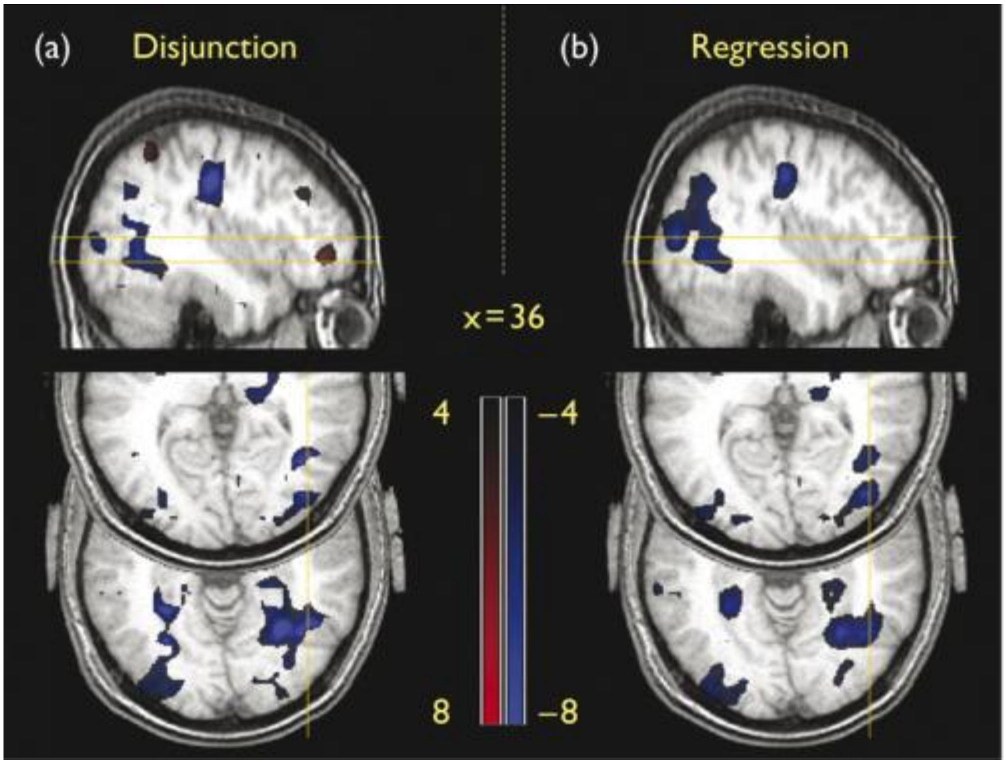


Fig. 3 SPMs resulting from disjunction between high and moderate task difficulty (a) and BPM regression of correlated activity (b).

This suggests that the change is mostly in the general spread of deactivation, and is illustrated in Fig. 2d by plotting a representative row of voxels for each condition (Fig. 1, red lines). A disjunction of the SPMs highlights portions of the superior and lateral occipital cortical regions significantly deactivated only when the task was highly difficult (Fig. 3a).

One remaining question was whether the extended deactivation seen in Fig. 3a was independent of the more moderate level of task difficulty. Figure 3b shows the results of the high difficulty condition with the moderate difficulty condition entered as a covariate using the BPM Toolbox [17]. This effectively removes correlated activity between the two conditions, emphasizing deactivation associated solely with high difficulty that is unrelated to the easier version of the task.

Auditory-related activations are virtually eliminated, as would be expected with high correlations between conditions. In contrast, smaller (yet significant) deactivations remain bilaterally in the IPL and cingulate cortex. Importantly, robust deactivations also remain in visual cortex, extending along the AG, MOG, and lateral inferior occipital gyrus and into the MTG, suggesting that the effect in these areas is unique to the difficult version of this task. Note that these are the same clusters observed in Fig. 3a, highlighting the fact that they are functionally dependent only on the higher level of task difficulty.

Discussion

Performing a highly difficult auditory task leads to selective activity decreases in a substantial portion of visually responsive occipital cortex. More importantly, when the task is easier, the degree of deactivation diminishes to include only a small portion of this cortex. As the physical properties of the stimuli used in each case were only subtly different (same two tones in both cases) and elicited only minor changes in the BOLD response in task-related cortices, we propose that the observed attenuation must be related to the difficulty of the task.

The neurophysiology of this apparent cross-modal inhibition remains unclear. One prospect is a direct modulation of activity from other sensory regions. Recent primate anatomical studies have shown projections between core visual and auditory core and associative areas [20,21]. A direct circuit in itself, however, would not explain the effects, as sensory stimulation was nearly identical in both cases. In fact, the greatest deactivation observed (the high difficulty condition) was associated with less auditory cortical activity. Rather, the visual modulation is more likely to involve top-down mediation; for example, the prefrontal gyrus is involved in inhibiting the processing of irrelevant information in posterior sensory areas [11,22,23], and dealing with competing cross-modal resources [4].

The modulation shown here involves mediation of fairly low-level visual circuitry, as suggested in other cross-modal paradigms [2,24]. Although the deactivated regions might not represent primary visual cortex (e.g. calcarine fissure) per se, they do clearly involve at least secondary and tertiary visual areas commonly involved in visual stimulation. Here, they are involved in the performance of a visual TOJ task. By restricting the focus to occipital regions with significant visual response, this likely represents a genuine cross-modal deactivation of the visual cortex. Our result of decreased visual activity during auditory discrimination is in agreement with other studies [7,10–12]; however, the use of a no-task baseline and varied difficulty allows the interpretation to be taken further. As the BOLD contrast is against a resting baseline (no stimulation) with eyes open, the decreased signal represents a general suppression of baseline neural activity [25] within otherwise inactive visual cortex.

Use of regression [17] techniques enhances this conclusion. By removing the correlated voxel-wise common variance between the two tasks, the residual image (Fig. 3b) represents the effect of task difficulty alone, with any specific stimulus-related relationship that is common across tasks already removed. It allows us to ascertain the primary deactivation effect with less concern for specific stimulus details, which often contaminate comparisons of differing levels of task load, and conclude that the remaining regions of deactivation (also highlighted in the disjunction) are independent of the same task performed at a less difficult level.

Conclusion

Performing a severely difficult auditory task leads to a suppression of visual cortex, akin to further closing ‘the mind's eye’. Decreasing the difficulty of the task greatly alters the level of cross-modal deactivation. As this affects the task-related, visually responsive cortex, we propose that this is a direct interaction between sensory systems. The task-dependent nature of this effect likely represents a dynamic neural filter of irrelevant information within other senses, stemming from a top-down mediation by higher-level cognitive control.

Acknowledgements

Research support was provided by grant numbers NS044149 and EB004673 and the Human Brain Project. The authors thank Kathy Pearson for computer programming support.

References

1. Wallace MT, Roberson GE, Hairston WD, Stein BE, Vaughan JW, Schirillo JA. Unifying multisensory signals across time and space. Exp Brain Res 2004; 158:252–258.

2. Watkins S, Shams L, Tanaka S, Haynes JD, Rees G. Sound alters activity in human V1 in association with illusory visual perception. Neuroimage 2006; 31:1247–1256.

3. Calvert GA, Spence C, Stein B, editors. The handbook of multisensory processes. Cambridge, Massachusetts: MIT Press; 2004.

4. Hein G, Alink A, Kleinschmidt A, Muller NG. Competing neural responses for auditory and visual decisions. PLoS ONE 2007; 2:e320.

5. Haxby JV, Horwitz B, Ungerleider LG, Maisog JM, Pietrini P, Grady CL. The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. J Neurosci 1994; 14 (11 Pt 1):6336–6353.

6. Kawashima R, O'Sullivan BT, Roland PE. Positron-emission tomography studies of cross-modality inhibition in selective attentional tasks: closing the 'mind's eye'. Proc Natl Acad Sci U S A 1995; 92:5969–5972.

7. Laurienti PJ, Burdette JH, Wallace MT, Yen YF, Field AS, Stein BE. Deactivation of sensory-specific cortex by cross-modal stimuli. J Cogn Neurosci 2002; 14:420–429.

8. Lewis JW, Beauchamp MS, DeYoe EA. A comparison of visual and auditory motion processing in human cerebral cortex. Cereb Cortex 2000; 10:873–888.

9. Shulman G, Corbetta M, Buckner R, Raichle ME, Fiez JA, Miezin FM, et al. Top-down modulation of early sensory cortex. Cereb Cortex 1997; 7:193–206.

10. Johnson JA, Zatorre RJ. Attention to simultaneous unrelated auditory and visual events: behavioral and neural correlates. Cereb Cortex 2005; 15:1609–1620.

11. Johnson JA, Zatorre RJ. Neural substrates for dividing and focusing attention between simultaneous auditory and visual events. Neuroimage 2006; 31:1673–1681.

12. Shomstein S, Yantis S. Control of Attention Shifts between Vision and Audition in Human Cortex. J Neurosci 2004; 24:10702–10706.

13. McKiernan KA, Kaufman JN, Kucera-Thompson J, Binder JR. A parametric manipulation of factors affecting task-induced deactivation in functional neuroimaging. J Cogn Neurosci 2003; 15:394–408.

14. Hall DA, Haggard MP, Akeroyd MA, et al. 'Sparse' temporal sampling in auditory fMRI. Hum Brain Mapp 1999; 7:213–223.

15. Laurienti PJ, Burdette JH, Maldjian JA. Separating neural processes using mixed event-related and epoch-based fMRI paradigms. J Neurosci Methods 2003; 131:41–50.

16. Nichols T, Hayasaka S. Controlling the familywise error rate in functional neuroimaging: a comparative review. Stat Methods Med Res 2003; 12:419–446.

17. Casanova R, Srikanth R, Baer A, et al. Biological parametric mapping: a statistical toolbox for multimodality brain image analysis. Neuroimage 2007; 34:137–143.

18. Gusnard DA, Raichle ME. Searching for a baseline: functional imaging and the resting human brain. Nat Rev Neurosci 2001; 2:685–694.

19. Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. Neuroimage 2003; 19:1233–1239.

20. Cappe C, Barone P. Heteromodal connections supporting multisensory integration at low levels of cortical processing in the monkey. Eur J Neurosci 2005; 22:2886–2902.

21. Clavagnier S, Falchier A, Kennedy H. Long-distance feedback projections to area V1: implications for multisensory integration, spatial awareness, and visual consciousness. Cogn Affect Behav Neurosci 2004; 4:117–126.

22. Chao LL, Knight RT. Contribution of human prefrontal cortex to delay performance. J Cogn Neurosci 1998; 10:167–177.

23. Miller EK, Cohen JD. An integrative theory of prefrontal cortex function. Annu Rev Neurosci 2001; 24:167–202.

24. Molholm S, Ritter W, Murray MM, Javitt DC, Schroeder CE, Foxe JJ. Multisensory auditory–visual interactions during early sensory processing in humans: a high-density electrical mapping study. Brain Res Cogn Brain Res 2002; 14:115–128.

25. Pasley BN, Inglis BA, Freeman RD. Analysis of oxygen metabolism implies a neural origin for the negative BOLD response in human visual cortex. Neuroimage 2007; 36:269–276.