Parahippocampal cortex is involved in material processing via echoes in blind echolocation experts

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For Submission to Vision Research as a RESEARCH ARTICLE
Number of words in abstract (max 250): 226
Number of words in main manuscript (excluding references): ~5590
Number of figures: 5
Number of tables: 2
Number of supplemental tables: 1

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Abstract

Some blind humans use sound to navigate by emitting mouth-clicks and listening to the echoes that reflect from silent objects and surfaces in their surroundings. These echoes contain information about the size, shape, location, and material properties of objects. Here we present results from an fMRI experiment that investigated the neural activity underlying the processing of materials through echolocation. Three blind echolocation experts (as well as three blind and three sighted non-echolocating control participants) took part in the experiment. First, we made binaural sound recordings in the ears of each echolocator while he produced clicks in the presence of one of three different materials (fleece, synthetic foliage, or whiteboard), or while he made clicks in an empty room. During fMRI scanning these recordings were played back to participants. Remarkably, all participants were able to identify each of the three materials reliably, as well as the empty room. Furthermore, a whole brain analysis, in which we isolated the processing of just the reflected echoes, revealed a material-related increase in BOLD activation in a region of left parahippocampal cortex in the echolocating participants, but not in the blind or sighted control participants. Our results, in combination with previous findings about brain areas involved in material processing, are consistent with the idea that material processing by means of echolocation relies on a multi-modal material processing area in parahippocampal cortex.

Keywords: human echolocation, material, texture, vision, audition, multisensory, neuroplasticity, blindness, fMRI

1 Introduction

Like animals such as bats and dolphins, a subset of blind humans can use echoes from self-produced signals to localize and identify silent objects and surfaces in their environment. For example, by interpreting the echoes of their mouth-clicks, these individuals can report on features such as the size, shape, location, distance, motion, and material (or texture) of objects (Arnott, Thaler, Milne, Kish, & Goodale, 2013; Hausfeld et al, 1982; Kellogg, 1962; Rice, 1967; Rice, 1969; Rice & Feinstein, 1965; Rice, Feinstein, & Schusterman, 1965; Schenkman & Nilsson, 2010; Stoffregen & Pittenger, 1995; Teng, Puri, & Whitney, 2011; Teng & Whitney, 2011; Thaler, Arnott, & Goodale, 2011; Thaler, Milne, Arnott, Kish, & Goodale, 2013; for review, see Kolarik, Cirstea, Pardhan, & Moore, 2014). Because echolocation allows blind individuals to perceive silent objects from a distance, it can be thought of as an alternative to vision; without the use of echolocation the perception of such objects would be impossible with the remaining senses.

In the first functional magnetic resonance imaging (fMRI) investigation on human echolocation, it was found that the calcarine cortices (i.e. BA17, what is typically referred to as primary visual cortex in sighted people) of two blind expert echolocators were activated when these individuals perceived objects that were identifiable only by echoes (Thaler et al., 2011). Specifically, their blood oxygenation level dependent (BOLD) activity while listening to binaural recordings of their clicks and the reflected echoes increased in not only auditory, but also calcarine cortex. Even more, when they isolated the processing of just the echoes, the BOLD activity was specific to just the calcarine cortex. Sighted control participants did not show calcarine cortical activation during the tasks.

These initial findings on the neural correlates of echo processing in general set the foundation for investigating how the blind echolocating brain parses and processes specific types of echo features. For example, we have recently shown that the processing of echoes reflected from a moving surface activated a brain area in temporal-occipital cortex that potentially corresponds to ‘visual’-motion area

MT+, and that this activation showed a contralateral preference (Thaler et al., 2014). In addition, we have shown that the processing of object shape via echoes activates areas in the ventrolateral occipital cortex, encompassing areas in the lateral occipital complex (LOC), a brain area traditionally involved in visual shape processing (Arnott et al., 2013). Taken together, these findings suggest not only that the processing of echoes may be feature-specific, but also that this processing may make use of what are normally feature-specific visual areas.

Several of the expert echolocators whom we have studied have anecdotally remarked on the saliency and utility of information about material that they routinely get from echoes, particularly in terms of navigation, orientation, and obstacle avoidance. For example, the stark difference in material (and thus the reflected echoes) between a concrete sidewalk and adjacent grass provides useful information for discerning the path ahead while walking or bike-riding. Previous behavioural investigations have shown that people can use echolocation to discriminate between reflective materials such as metal and glass and more absorptive materials such as velvet and denim (Hausfeld et al., 1982; Kellogg, 1962).

The neural basis underlying this skill is poorly understood, however. With respect to visual perception of material properties, fMRI research suggests the involvement of collateral sulcus (CoS) and the parahippocampal cortex (PHC) (Cant & Goodale, 2007, 2011; Cavina-Pratesi, Kentridge, Heywood, & Milner, 2010; Hiramatsu, Goda, & Komatsu, 2011; Jacobs, Baumgartner, & Gegenfurtner, 2014). With respect to the auditory modality, previous research suggests the involvement of right parahippocampal cortex (Arnott et al., 2008). Importantly, areas in right PHC responding to auditory materials also responded to visual surface materials, thus suggesting the existence of a visuo-auditory multimodal material processing area in PHC. Auditory materials in the context of Arnott et al. (2008) were conveyed through sounds of materials being manipulated, i.e. materials were manipulated with the hands to produce a material conveying sound, such as crumpling of paper. During echolocation, in contrast, the material is conveyed through the reverberation of a vocalization off the material, whilst the material itself remains distal and silent. Thus, one may expect a difference in terms of how the brain processes material conveyed through echoes. Accordingly, we conducted a previous study into echolocation of material, alongside echolocation of shape (Arnott et al., 2013), but the results of this study with respect to brain activation specific to material echoes were inconclusive. This could potentially be due to the design of the task in which echo-acoustic information conveying shape was not acoustically independent from echo-acoustic information conveying material properties, rendering a comparison of material echoes regardless of shape essentially impossible.

Consequently, the current study addressed the perception of material echoes per se; that is, in the absence of any other object or spatial cues. Three blind expert echolocators, three blind, and three sighted control participants took part in the experiment. Our results revealed a material-echo related increase of activation within left parahippocampal cortex in all three expert echolocators. This activation was absent in sighted and blind control participants. We did not find material echo related activations in posterior CoS, suggesting that some of the brain areas previously implicated for visual processing of materials were not involved. Our results further support the idea of feature-specific echo processing and also contribute to the possibility of a multimodal material processing area within parahippocampal cortex.

2 Materials and Methods

All testing procedures were approved by the ethics board at the University of Western Ontario, and participants gave written, informed consent prior to testing. All experimental procedures conformed to The Code of Ethics of the World Medical Association as stated in the Declaration of Helsinki (1964). The consent form was read to participants, and the location to sign was indicated through tactile and visual markers.

Software used to conduct testing was programmed using Psychophysics Toolbox 3.08 (Brainard 1997), Matlab (R2009a, The Mathworks, Natick, MA) and C/C++. fMRI data were analyzed using Brain Voyager QX version 2.8 (Brain Innovation, Maastricht, The Netherlands) and Matlab. Sound editing was performed with Adobe Audition version 1.5 software (Adobe Systems, San Jose, CA). Sound equalization was performed with filters provided by the headphone manufacturer (Sensimetrics, Malden, MA).

2.1 Participants

Three blind, male echolocation experts (EE1-EE3) participated in the study. EE1 (age 44) was enucleated in infancy due to retinoblastoma and reports to have used echolocation for as long as he can remember. EE2 (age 44) had lost sight due to retinopathy of prematurity. He reports having begun using echolocation in his early twenties, but did not practice echolocation between age 34 and 40 due to health reasons. He resumed using echolocation on a daily basis at age 40. EE3 (age 29) gradually lost sight from birth due to glaucoma, and had only bright light detection since early childhood. At the time of testing he was completely blind. EE3 reports that he has used echolocation techniques since age 12. At time of testing, each of the echolocation experts reported using click-based echolocation on a daily basis.

We also tested six control participants (three congenitally blind non-echolocators [BC1-BC3; two male, aged 36, 25, 38, respectively] and three sighted individuals [SC1-SC3; two male, aged 26, 29, 30, respectively]). Control participants reported no prior use of or training in echolocation prior to participation.

2.2 Experimental Stimuli

2.2.1 Sound stimuli: Setup and recording procedure

All auditory stimuli were recorded in a Beltone Anechoic Chamber at the National Centre for Audiology in London, Ontario, Canada, measuring 5.5 m high × 7.0 m wide × 3.7 m deep, and equipped with a 125-Hz cutoff wedge system on the walls and ceiling. The chamber floor was covered in foam baffles.

Ambient noise recordings indicated a background noise (i.e., “noise floor”) of 18.6 dBA. Recordings of the entire session's audio were acquired via in-ear binaural omni-directional microphones (Sound Professionals-TFB-2; “flat” frequency range 20–20,000 Hz) attached to a portable Edirol R-09 digital wave recorder (16-bit, stereo, 44.1-kHz sampling rate). Microphones were placed directly at the opening of the echolocators’ left and right auditory canals and held in place by a soft rubber “horn-shaped” housing that conformed to the shape of the concha. During recording, participants held their head stationary and faced straight ahead. Recordings were made separately with EE1, EE2, and EE3.

2.2.2 Echolocation Sounds

Similar to our previous studies (Arnott et al., 2013; Thaler et al., 2011, Thaler et al., 2014), echo stimuli were created by making binaural recordings of echolocation clicks and subsequent echoes as each echolocating participant was presented with sound-reflecting surfaces that were made of different materials. Thus, echolocation recordings contained both clicks and the click echoes. The advantage of using binaural microphones is that the sounds are perceived to be externalized when played back over headphones (i.e. that they are occurring ‘out in the world’ as opposed to inside of the head). The recordings were made in the presence of one of three materials: a whiteboard, synthetic foliage, and a fleece blanket covered with a fencing material[1] (Figure 1A). The objects were large (sizes varied) and were designed to encompass the entire ‘scene’ (i.e. to provide no shape or edge information). The materials were suspended from a pulley system on the ceiling and were centered at ear-level for each participant. During recording, the participant was positioned approximately 45 cm away from the material and told to click at a comfortable pace (see Figure 1B). We also made recordings of the participants’ clicks in the absence of any material (i.e. theoretically echoless) to serve as a ‘no-material’

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[1] During the planning of the experiment, we presented the echolocators with a number of different materials and had them report on the material properties they perceived (we did not provide them with any information prior to presentation). The three materials used here were chosen because the echolocators indicated that the echoes were reflected from these materials were salient and also that they sounded very differently from each other. The echolocators described the whiteboard as sounding “hard, flat, and smooth”, the synthetic foliage as sounding “like foliage”, and the fleece blanket covered in fencing material as sounding “sparse”.

condition. For all recording conditions, the participant was inside of the anechoic chamber by himself with the door closed. Examples of click-echo pairings for each condition are shown in Figure 1A.

2.2.3 Sound Editing

From each echolocator's recordings, we took individual click-echo pairings to create three unique 10-second exemplars for each condition (whiteboard, synthetic foliage, fleece blanket covered in fencing material, and the empty chamber environment). This resulted in having three different sets of sound stimuli (i.e. from each echolocator's recordings), each including 12 sounds (4 conditions x 3 exemplars). Because the echolocators were free to click at their own pace, the number of click-echo pairings per 10-second stimulus varied within and between participants, with an average of 14 pairings per sound stimulus. The average acoustic energy of the sounds (in dB root mean square [RMS]) was -48.4 (SD = 1.9) for EE1, -46.1 (SD = 1.2) for EE2, and -45.9 (SD = 2.3) for EE3.

2.3 MRI Scanning

Imaging for all participants, except EE3, was performed at the Robarts Research Institute (London, Ontario, Canada) using a 3-Tesla, whole-body MRI system (Magnetom Tim Trio; Siemens, Erlangen, Germany) with a 32-channel head coil. EE3 was scanned at Durham University Neuroimaging Centre, James Cook Hospital, Middlesbrough, using the same model scanner and head coil.

2.3.1 Setup and Scanning Parameters

Audio stimuli were delivered over MRI-compatible inset earphones (model S-14, Sensimetrics, Malden, MA). Participants adjusted the sound level to their own comfort. The earphones were encased in replaceable foam tips that provided 20- to 40-dB sound attenuation. Further sound attenuation was achieved by placing foam inserts between the head rest and the participants' ears. Due to the fact that the experiment involved listening to sound stimuli including faint echoes, the MRI's bore circulatory fan was turned off. A single-shot gradient echo-planar pulse sequence in combination with a sparse-sampling design (Hall et al., 1999) was used for functional image acquisition. Repetition time was 12 seconds (10-second silent gap + 2-second slice acquisition). The field of view was 211 mm with a 64 x 64 matrix size, which led to in-slice resolution of 3.3 x 3.3 mm. Slice thickness was 3.5mm and we acquired 38 contiguous axial slices covering the whole brain in ascending order. Echo time was 30 ms and flip angle was 78°.

2.3.2 Anatomical Image

Anatomical images of the whole brain were acquired at a resolution of 1 x 1 x 1 mm using an optimized sequence (MPRAGE).

2.3.3 Functional Paradigm

Each run contained silent baseline and experimental trials (Figure 2). Experimental trials included a 10-second sound stimulus presentation (i.e. one of the four conditions [three materials and empty anechoic chamber]). Each sound presentation was followed by a 50-ms, 1200-Hz tone, which cued the participant to provide their response via button-press (see section 2.3.4 Behavioural Paradigm below). Functional scans began 10 seconds after the run had started and lasted 2 seconds. The next trial began immediately after scanning had ended. Silent baseline trials differed from experimental trials in that the 2-second functional scan occurred after 10 seconds of silence (which was not followed by the response-cue tone and participants did not make a button-press). The echolocating participants did not listen to their own click recordings, but rather to the recordings of one of the other echolocators (see section 2.3.4 Behavioural Paradigm below). Stimulus presentation was pseudo-randomly ordered such that each run contained eight clusters, each cluster containing an exemplar of each of the four experimental conditions. The order of the four conditions was counterbalanced across clusters using a Latin square design. Each cluster of four conditions was preceded by a silent baseline trial, and each run began and ended with a silent baseline trial. Thus there were a total of 41 trials per run (9 silent + 8 x 4 experimental) and the durations of each run was 41 x 12 seconds. Each participant completed five runs.

2.3.4 Behavioural Paradigm

As mentioned above, the echolocating participants did not listen to their own recorded clicks and echoes. The purpose of this was to account for the fact that recordings were not made with control participants and therefore they listened to the recordings of another individual. The participants assigned to each set of recordings were as follows: EE1’s recordings: EE3, BC3, SC3; EE2’s recordings: EE1, BC1, SC1; EE3’s recordings: EE2, BC2, SC2.

Participants were asked to keep their eyes closed during the duration of the experiment. The task was a 1-interval-4-alternative forced choice paradigm. The participant listened to the echolocation sound and judged the material properties of the sound reflecting surface (whiteboard, synthetic foliage, fleece blanket with fencing, no material [empty anechoic chamber]). Participants indicated their response with a button press using a four-button magnetic resonance-compatible keypad.

2.3.5 Prior to MRI

EXPERTS: Before MRI scanning, the echolocating participants were familiarized with the sounds they would be listening to during experimentation. Feedback was provided initially to ensure that the participants were accurately identifying the echoes. A mock run was performed without feedback just prior to testing.

BLIND AND SIGHTED CONTROL PARTICIPANTS: Blind and sighted controls completed a 40-minute practice session to familiarize themselves with their respective echo stimuli. Feedback was provided for the first portion of the practice session until the participants could comfortably and reliably identify the sound stimuli. This portion of practice was followed by a mock run during which no feedback was provided. Just prior to MRI, participants were once again familiarized with the sounds and feedback was provided.

2.4 fMRI Data Analysis

2.4.1 Preprocessing and Coregistration

Each functional run began with three functional scans not saved to disk (scanner manufacturer default programming for functional sequences). Following these initial scans, functional data acquisition began. The first volume of each run was not included in the functional data analysis. Each run was subjected to slice scan time correction (tri-linear sinc), temporal high-pass filtering (cut-off at 2 sines/cosines) and three-dimensional motion correction (sinc). To align the functional to the anatomical data for each participant, we first used three-dimensional motion correction to align each volume within a run to the functional volume closest to the anatomical scan. This volume was co-registered to the anatomical scan of that same participant. The anatomical for each participant was then transformed into standard stereotactic space (Talairach and Tournoux, 1988). Spatial smoothing was not applied to the data.

2.4.2 Functional Analyses

Due to the nature of the study and the small number of participants, all analyses were performed on a single-subject level.

2.4.2.1 BOLD Activity Related to Echolocation Stimulation Compared with Silence

To compare brain activity related to the processing of echolocation sounds as compared to a silent baseline for each participant, we ran a fixed-effects general linear model (GLM) with the stick-predictor ‘All Sounds’ to the z-transformed time courses of the runs (5 runs per participant; for EE3, the first run was omitted due to head movement-related artifacts). To determine where BOLD activity during sound-stimulation trials exceeded activity during silent baseline trials, we isolated voxels where the beta value of the ‘All Sounds’ predictor was significantly larger than zero. To control for Type-I error probability, each participant’s data was subjected to a cluster threshold correction (Forman et al., 1996). Cluster threshold values were estimated in volume space using the BrainVoyager Cluster Threshold Estimator Plugin (Goebel et al., 2006). Following the cluster correction (thresholds presented in Supplemental Table S1), individual data was also subjected to a false discovery rate (FDR) correction of $p < .01$.

2.4.2.2 BOLD Activity Related to Material Echoes

The purpose of this analysis was to isolate the processing of only the echoes reflected from the materials. To obtain activity related to echo processing, we applied a fixed-effects GLM with the following contrast: (whiteboard + synthetic foliage + fleece with fence) > empty anechoic chamber. Again, each participant's data was subjected to cluster threshold correction (cluster thresholds presented in Supplemental Table S1) and FDR correction of $p < .05$. A more liberal threshold was used for this contrast because the material-related activation (contrast all materials > silence) was not as robust.

3 Results

3.1 Behaviour

The participants' behavioural task during fMRI scanning was to identify the material of the sound-reflecting surface (i.e. whiteboard, synthetic foliage, fleece blanket with fencing, or no material [empty anechoic chamber environment]). The behavioural performance (as percent correct) for all participants is shown in Table 1. Each participant completed five runs (with the exception of EE3, for whom analyses were conducted on runs 2-5), with 40 trials in each run (10 repetitions per material condition), for a grand total of 200 behavioural trials. EE3 completed four runs and thus completed 160 behavioural trials. Binomial tests were conducted on each participant's overall percentage correct performance compared to chance (25%). The results of the binomial tests revealed that all participants performed significantly better than chance ($p < .001$; Table 1). It is also evident that, even though each of our participants could perform the task, each of the echolocation experts had higher accuracy than any of the control participants. Recall that none of the participants – even the expert echolocators – listened to their own recordings. Thus, this difference in performance is due to echolocation expertise, rather than familiarity with the sounds.

3.2 BOLD Activity Related to Echolocation Stimulation Compared with Silence

Figures 3 and 4 show slice views of the expert echolocator's (Figure 3) and blind and sighted control participants' (Figure 4) BOLD activity associated with the processing of all of the sound stimuli compared to silence. The top row for each group of participants shows coronal slices (with Talairach *y*-coordinates indicated below). All participants showed highly significant activation in bilateral Heschl's gyrus, which was expected given that Heschl's gyrus contains the primary auditory cortex. The average contrast values for each of the activated regions are shown in the plot at the bottom of each figure, and the Talairach coordinates and sizes of each region are shown in Table 2 for all participants.

The bottom row in Figure 3 and in each participant section in Figure 4 shows sagittal slice views (with Talairach *x*-coordinates indicated below) for each participant. The contrast revealed activation along the right calcarine sulcus, but only in the three echolocating participants. In particular, EE1 showed activation along the entire sulcus, while EE2 and EE3 showed smaller isolated areas of activity. Previous research on the blind has shown that auditory stimulation in the blind brain can activate what are considered 'visual' brain areas in the sighted brain (for review, see Bavelier & Neville, 2002; Merabet & Pascual-Leone, 2010). Interestingly, though, the blind control participants did not exhibit significant activation in the occipital cortex in our experiment, even at more liberal thresholds (although BC1 shows a small region of activation at the parieto-occipital junction). This absence of occipital activation in the blind control participants in response to auditory stimulation is addressed in the Discussion (section 4). Sighted controls also did not show calcarine activation, even at more liberal thresholds. The average contrast values for each of the activated regions are shown in the plot at the bottom of each figure, and the Talairach coordinates and sizes of each region are shown in Table 2 for all participants.

3.3 BOLD Activity Related to Material Echoes

Figure 5 shows the BOLD activity associated with the processing of only the material echoes. As described in the methods, we isolated the echoes by subtracting the activity related to the click-only empty anechoic chamber condition from the activity related to the three click-echo material conditions.

This contrast revealed similar but not overlapping areas of activation within the region of the left parahippocampal cortex (an area encompassing the parahippocampal gyrus, fusiform gyrus, and anterior CoS) in all three expert echolocators. The relative location of each echolocator's region of activation is shown on an averaged brain in the magnified inset in Figure 5 (the Talairach coordinates and sizes of each region are shown in Table 2). Interestingly, Arnott et al's (2008) findings on visual and auditory material processing in sighted individuals also revealed parahippocampal cortex activation, but their participants showed activation in the right hemisphere. This difference in lateralization is addressed in the Discussion (section 4). The bottom panel of Figure 5 shows the left parahippocampal cortex of each of the blind and sighted control participants, none of whom showed any significant activation within that region, even at more liberal thresholds ($p < 0.1$). It is noteworthy that none of our participants showed activity in Heschl's gyrus, or in calcarine cortex, for this contrast.

Activation within the left parahippocampal cortex was consistent across EE1, EE2, and EE3, but activity was also seen in other areas, most notably for participant EE1. EE1 exhibited bilateral activation within the cingulate cortex and middle temporal gyrus, as well as small regions of activation within the medial parietal cortex, prefrontal cortex, and cerebellum. Because these areas of activation were present in only one echolocating participant, our discussion will focus primarily on the consistent PHC activation in all echolocators.

4 Discussion

Previous neuroimaging research in blind human echolocators has provided evidence for a functional role of calcarine cortex in processing echoes reflected from silent objects (Thaler et al., 2011). More recent research (Arnott et al., 2013; Thaler et al., 2014) has suggested that this occipital activation is likely not due to general cross-modal plasticity, but rather that the functional nature of particular visual brain areas (such as the LOC, or MT+) are preserved. In other words, the processing of echoes may show feature-specificity similar to the normal functions of such brain areas for the processing of vision. Given the evidence for feature-specific activation, the aim of the current experiment was to determine how the blind echolocating brain processes echoes reflected from surfaces of different materials. In particular, we were motivated by findings about visual (Cant & Goodale, 2007, 2010; Cavina-Pratesi et al., 2011; Hiramatsu, Goda, & Komatsu, 2011; Jacobs, Baumgartner, & Gegenfurtner, 2014) and visuo-auditory (Arnott et al., 2008) material processing that implicated CoS and PHC. Our results revealed activation in left parahippocampal cortex for all three echolocating participants.

By showing material related activity in PHC, our results suggest that material processing through echoes may recruit the same general regions of PHC that have been implicated in both visual and auditory processing of material properties (Arnott et al. 2008; Cant & Goodale, 2011; Jacobs, Baumgartner, & Gegenfurtner, 2014). We saw no activation, however, in posterior regions of CoS that have also been associated with aspects of the visual processing of material. A discrepancy between our and Arnott et al.'s (2008) findings is that Arnott et al. observed activation in the right hemisphere whereas we show activation only in the left hemisphere across all three echolocators. This difference could potentially be attributed to the fact that our stimuli were specifically designed to minimize any spatial information (i.e. the material encompassed the whole 'scene' and had no discernible edges/boundaries for the echolocators), whereas the stimuli in Arnott et al.'s study had inherent spatial properties (for example, the sound of a snack food bag could elicit spatial imagery of the object's form, or the object being spatially manipulated). The right-lateralized material-related activation found previously could then be due in part to the spatial properties of the stimuli. In fact, right occipital regions in the blind have been shown to be preferentially activated for spatial versus non-spatial stimuli in both the auditory and tactile domains (Collignon et al., 2011; Renier et al., 2010). Nevertheless, future research is needed to follow up on these differences in lateralization.

One could argue that the observation of PHC activity in only the blind echolocating participants (and not in blind or sighted controls) could be due simply to general echo expertise and not functionally specific to material perception, particularly considering that the echolocating participants showed considerably higher behavioural performance than the control participants. Sighted participant SC1, though, showed comparable performance to the expert echolocators in identifying the 'whiteboard' echoes. In a contrast isolating the processing of just the whiteboard echoes, however, we found no evidence of PHC activity in this participant, even when using liberal, uncorrected statistical thresholds. Furthermore, considering that the PHC has previously been implicated in material processing in other perceptual domains (vision and audition), we are more confident in attributing the activation found in the current study to material-echo perception. Nevertheless, future research should aim to disentangle the possibilities of expertise versus feature-specific activation in expert echolocators.

The observation of activation within the PHC invites speculation about the nature of the activity we found, particularly because of PHC's typical (though not exclusive) association with scene perception (for review, Aminoff, Kveraga, & Bar, 2013). Specifically, in our study the presence of a material could also be considered the presence of a particular material surface, or 'scene' respectively, so that one could argue that the PHC activation we found represents echo-scene related activation, rather than echo-material related activation. In previous work, however, which aimed to determine echo-scene related activation within blind echolocators (Arnott et al., 2013) we found results suggesting involvement of auditory and calcarine cortex rather than PHC. Nevertheless, it will be important for future research on material perception via echolocation to further disentangle the possible explanations for the PHC activation we found.

In sum, our results are most similar to those obtained by Arnott et al., (2008). Most importantly, the fact that we found highly consistent activation in left PHC in all three echolocating participants, in combination with those previous findings, suggests the potential involvement of visuo-auditory material processing areas in PHC for processing of material echoes in blind experts.

In addition to the main findings in parahippocampal cortex, we also observed activation along the right calcarine sulcus in all echolocating participants, but this activation was observed only for the contrast isolating activity related to echolocation stimulation compared to silence. This lateralization is consistent with previous findings on calcarine activation in human echolocators (Thaler et al., 2011) and also with general auditory stimulation in the blind (e.g. Weeks et al., 2000). Surprisingly, we did not observe calcarine activity in our blind control participants, even when applying more liberal statistical thresholds. Because we have not tested this set of blind control participants on any other auditory tasks, we cannot say whether the absence of occipital activation in this case is related to the participants themselves (i.e. they do not show occipital activation for any auditory tasks) or whether it is something related to the echolocation task. Future research should address this.

Interestingly, we did not observe calcarine activity in the echolocating participants for the contrast (all materials > empty chamber). Since this contrast isolated processing of echoes (which in our study were always material echoes), the absence of calcarine recruitment for this contrast seemingly runs counter to what we have found previously (Thaler et al., 2011). A difference between the current and our previous study, though, is that the material-echoes in the current study were designed with the goal to convey material information per-se, i.e. to minimize spatial information. Thus, again, one could argue that the material echoes in our study did not contain a spatial component, and it is possible that the calcarine activation previously associated with echo perception was particularly related to the spatial components of the echoes (Thaler et al., 2011). Based on the idea that echo-related activation in calcarine cortex is tied to the spatial component of echoes, we would expect that contrasts of various sorts of spatial echo-information should lead to differences in activation in calcarine cortex. Remarkably, this is exactly what we found when we reported modulation of echo-related activity in calcarine cortex with echo laterality (Thaler et al., 2011) and eccentricity (Arnott et al., 2013). Thus, these findings suggest the viability of the idea that echo-related activity in calcarine cortex of blind experts is tied to the spatial component of the echoes. An alternative, though not mutually exclusive, explanation for the absence of calcarine activity for the contrast (all materials > empty chamber) in our study is the idea that the recruitment of calcarine cortex in the case of material-echo perception is unnecessary due to the fact that the PHC is normally recruited for the processing of material properties within the auditory (and visual) domain. Future research should address these possibilities.

Because echolocation is an auditory process, it must involve auditory processing. Yet, for the contrast (all materials > empty chamber) we were unable to find significant differential activity in primary auditory cortical areas, i.e. Heschl's gyrus. The lack of any difference in activity in auditory cortex for the contrast between (all materials > empty chamber) was expected, because we had created stimuli so that the acoustic differences were minimal and the only difference was the presence or absence of very faint echoes. It is possible, therefore, that the auditory processing of the very faint echoes did not yield a significant differential BOLD signal in primary auditory areas because activity in those areas might have been dominated by the processing of the much louder and more salient clicks (which are present in both material and empty chamber sounds).

Given the possibility of a multimodal material processing area within PHC, one must also consider the perception of material properties via haptics. Research on sighted individuals has, not surprisingly, shown activation within the somatosensory cortex (such as the postcentral gyrus, parietal operculum, and insula) related to the tactile exploration of objects with different material or texture properties (Podrebarac, Goodale, & Snow, 2014; Servos, Lederman, Wilson, & Gati, 2001; Stilla & Sathian, 2008). Furthermore, haptic texture-related activation has been observed within the medial occipital cortex (MOC), with regions of activity overlapping (Stilla & Sathian, 2008) or adjacent to (Podrebarac et al., 2014) visual-texture selective areas. Interestingly, though, the visuo-haptic texture-selective areas within MOC are quite different from the visuo-auditory material area in right PHC found by Arnott et al. (2008), and from the areas within left PHC observed in the current study. In the blind, material perception has been investigated only in the tactile domain, but not in the auditory domain. With regard to tactile perception of materials no notable differences in behavioural performance have been reported to date between sighted and blind people (Grant, Thiagarajah, & Sathian, 2000; Heller, 1989), with the exception of Braille patterns which might be related to blind people's Braille proficiency (e.g., Grant, Thiagarajah, & Sathian, 2000). To the best of our knowledge, at present there is no study having investigated brain areas involved in tactile perception of materials per se in the blind (i.e. not the perception of Braille or dot position offset). In sum, it will be important for future research to address how the blind and sighted brain processes material-related information from the echolocation, pure auditory, and tactile domains.

5 Conclusions

The aim of the current study was to investigate the neural correlates of material processing through echolocation in blind human expert echolocators. The perception of material has real-world implications for blind individuals, with immediate benefits for navigation, orientation, and obstacle avoidance. Given the evidence suggesting that the blind echolocating brain may show functional specificity for echoes in a way similar to visual processing, we aimed to determine whether material processing via echoes would make use of brain areas normally associated with such functions in vision. Our results indicated that the processing of material-echoes makes use of an area within the parahippocampal cortex that has previously been implicated in both visual and auditory material processing. Future research should draw direct comparisons between material processing through echolocation, 'regular' hearing, and vision.

Acknowledgements: This work was supported by funding from the Natural Sciences and Engineering Research Council to Jennifer Milne, an operating grant to Melvyn Goodale (grant #6313), and a grant from Durham University Neuroimaging Centre to Lore Thaler. The authors declare no conflict of interest.

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Figure Captions

Figure 1. Material stimuli and setup for binaural recordings. A) Photos of the materials (and empty chamber) recording conditions, with sample waveforms for each condition (samples were extracted from EE1's recordings). B) The participant (EE1-EE3) was positioned approximately 45 cm from each material, which was suspended from the ceiling and was large enough to encompass the entire field and not provide shape or edge information. The participant wore binaural microphones (inset) and was told to click at a comfortable pace while the researchers recorded the clicks and returning echoes. For the empty anechoic chamber recordings no material was present and the participant was alone in the anechoic chamber. Recordings were made separately for EE1, EE2, and EE3.

Figure 2. Experimental design. Time is indicated by the arrow from left to right in seconds (s). An enlarged view of a single trial is shown in the inset. The presentation of the material sounds was pseudo-randomized across runs, and the labeling in the top panel for each sound is for illustrative purposes only. Each sound presentation was followed by a 'beep' which cued the participant to respond via button-press. Every fifth trial was a silent baseline which was not followed by a 'beep' and participants did not provide a response. Functional slice acquisition took place only during the 2-second period between sound presentations.

Figure 3. BOLD activation for participants EE1-EE3 related to echolocation stimulation compared with silence. The top row shows coronal slice views with activation in bilateral Heschl's gyrus for all three echolocating participants (with Talairach y-coordinates below). The bottom row shows sagittal slices views with activation in the right calcarine sulcus in all three participants (with Talairach x-coordinates below). The contrast values (with SE) for each region of activation are shown in the plot. EE1 exhibited three separate areas of activation along the calcarine sulcus, and the contrast value plotted represents the average of these three regions. Complete Talairach coordinates and sizes of all regions are shown in Table 2.

Figure 4. BOLD activation for blind (BC1-BC3) and sighted (SC1-SC3) control participants related to echolocation stimulation compared with silence. The top row for each group of participants shows coronal slice views with activation in bilateral Heschl's gyrus (with Talairach y-coordinates below). The bottom row for each group of participants shows sagittal slice views at the location of the right calcarine sulcus (which was activated in EE1-EE3; Talairach x-coordinates are below). Control participants did not exhibit any activation in this area. The contrast values (with SE) for each region of activation are shown in the plot. Complete Talairach coordinates and sizes of all regions are shown in Table 2.

Figure 5. BOLD activation for expert echolocators (EE1-EE3), blind controls (BC1-BC3), and sighted controls (SC1-SC3) related to material echoes. The top row shows coronal slice views for EE1-EE3, all exhibiting activation within the parahippocampal cortex (the location of the CoS is indicated by a dashed white line). The magnified inset shows the relative location of each participant's activation on an averaged brain (colours for each participant are indicated by the line underneath the participant label). Contrast values (with SE) are shown in the plot to the right of the inset. The bottom row shows the results from the control participants, who did not exhibit activation in this area, even at more liberal thresholds (i.e. $p < 0.1$). Complete Talairach coordinates and sizes of all regions are shown in Table 2.

Tables 1 and 2

Table 1

Summary of Participants' Behavioural Performance

Performance on Material Discrimination Task (% correct)

Participant	**Whiteboard**	**Synthetic Foliage**	**Fleece Blanket with Fence**	**Empty Anechoic Chamber**	**Overall Accuracy**	**Test Result**	**Significance**
EE1	100	100	95	72.5	91.86	21.64	p < .001
EE2	92.5	92.5	85	67.5	84.38	19.19	p < .001
EE3	97.5	95	72.5	62.5	81.88	16.53	p < .001
BC1	50	33.3	55	45	45.83	6.61	p < .001
BC2	55	45	33.3	67.5	50.2	8.08	p < .001
BC3	55	57.5	70	92.5	68.75	14.125	p < .001
SC1	92.5	45	45	45	56.88	10.21	p < .001
SC2	37.5	37.5	45	45	41.25	5.14	p < .001
SC3	55	55	45	100	63.75	12.49	p < .001

Note: Test statistics and significance values are the result of binomial tests comparing each participant's overall percentage correct performance to chance (25%).

Table 2.

Center-of-gravity coordinates (Talairach space) and sizes of activated regions within auditory, calcarine, and parahippocampal cortex.

All Sound Stimuli > Silence (p < .01)

		Auditory Cortex Activation			
Subject	**Hemi.**	**No. Voxels**	**x**	**y**	**Z**
EE1	Left	233	-41	-20	3
	Right	298	43	-20	9
EE2	Left	559	-35	-20	3
	Right	320	37	-26	3
EE3	Left	496	-50	-20	3
	Right	220	46	-14	0
BC1	Left	294	-41	-20	3
	Right	362	40	-20	0
BC2	Left	316	-44	-23	3
	Right	372	37	-26	6
BC3	Left	261	-38	-23	0
	Right	219	38	-22	3
SC1	Left	326	-38	-17	-3
	Right	301	37	-20	3
SC2	Left	562	-41	-20	0
	Right	215	37	-26	-1
SC3	Left	216	-38	-23	0
	Right	247	37	-23	6

All Sound Stimuli > Silence (p < .01)

		Calcarine (visual) Cortex Activation			
Subject	**Hemi.**	**No. Voxels**	**x**	**y**	**z**
EE1	Right-1	288	7	-95	3
	Right-2	432	7	-83	6
	Right-3	555	10	-77	9
EE2	Right	371	5	-77	6
EE3	Right	340	1	-92	6

All Materials > Empty Chamber (p < .05)

		Parahippocampal Cortex Activation			
Subject	**Hemi.**	**No. Voxels**	**x**	**y**	**z**
EE1	Left	25	-14	-55	-6
EE2	Left	278	-20	-53	-9
EE3	Left	56	-11	-53	-6

Figure 1

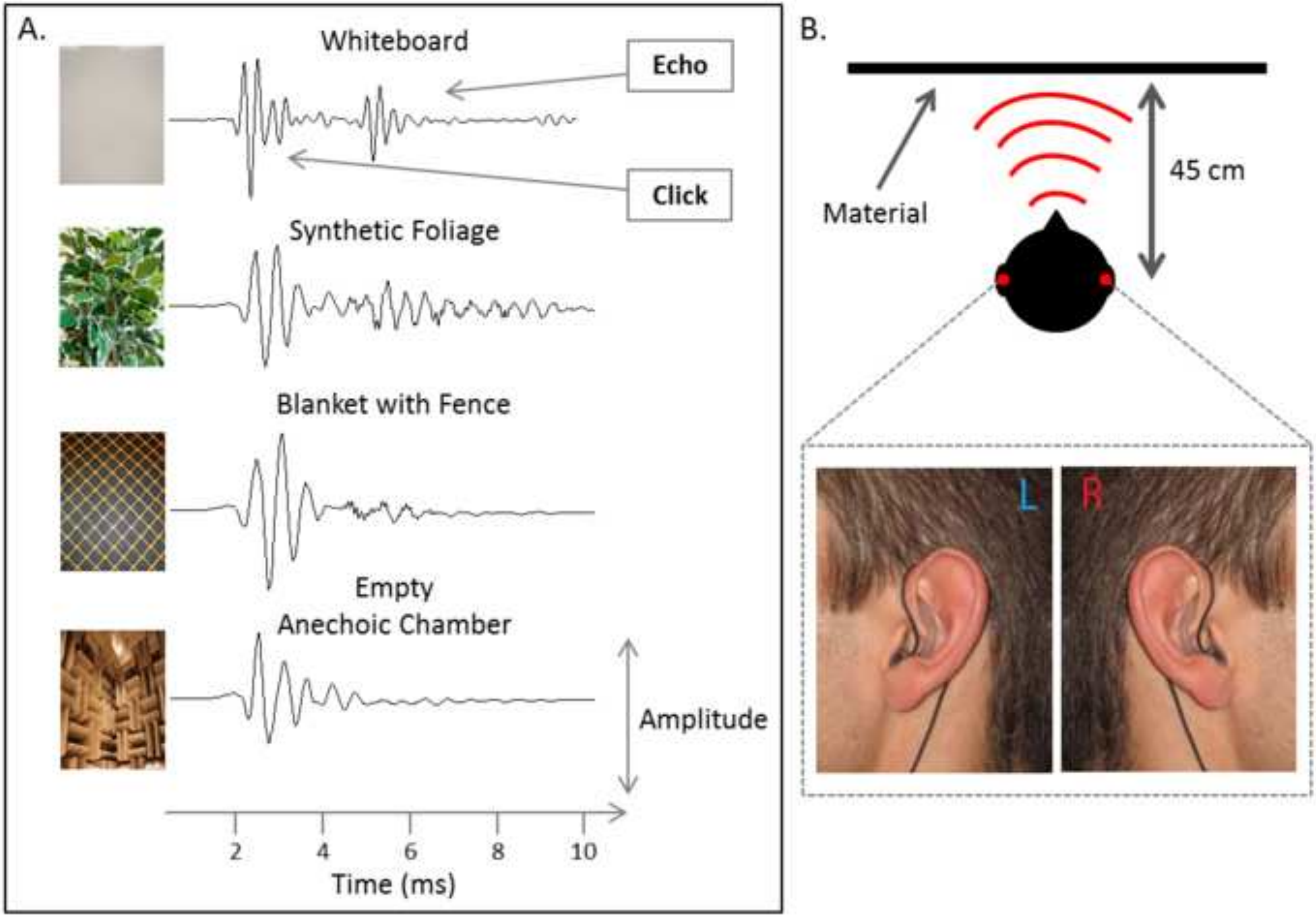
A.
Whiteboard
Echo
Click
Synthetic Foliage
Blanket with Fence
Empty
Anechoic Chamber
Amplitude
2
4
6
8
10
Time (ms)
B.
Material
45 cm
L
R

Figure 2

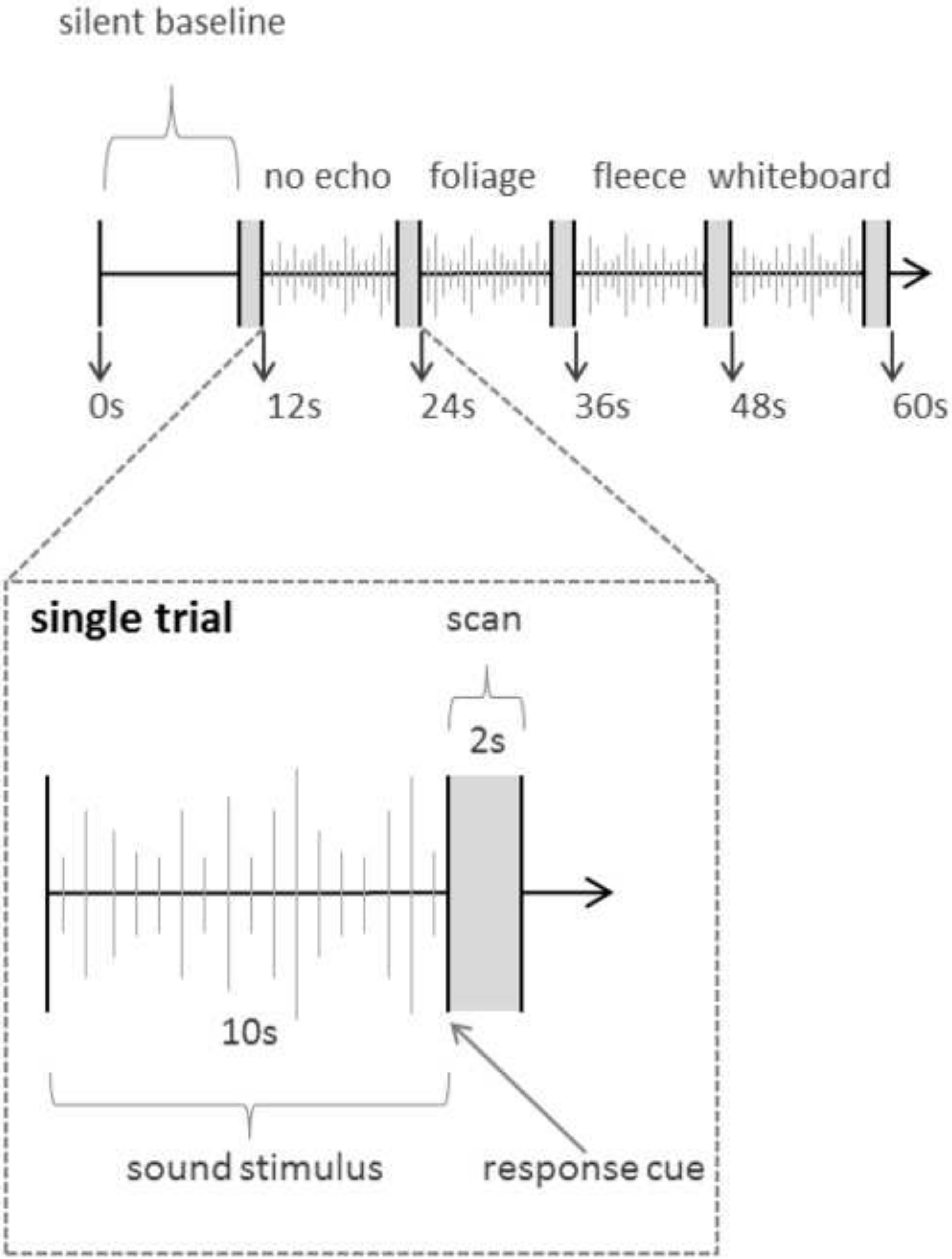
silent baseline
no echo
foliage
fleece
whiteboard
0s
12s
24s
36s
48s
60s
single trial
scan
2s
10s
sound stimulus
response cue

Figure 3

Click here to download high resolution image

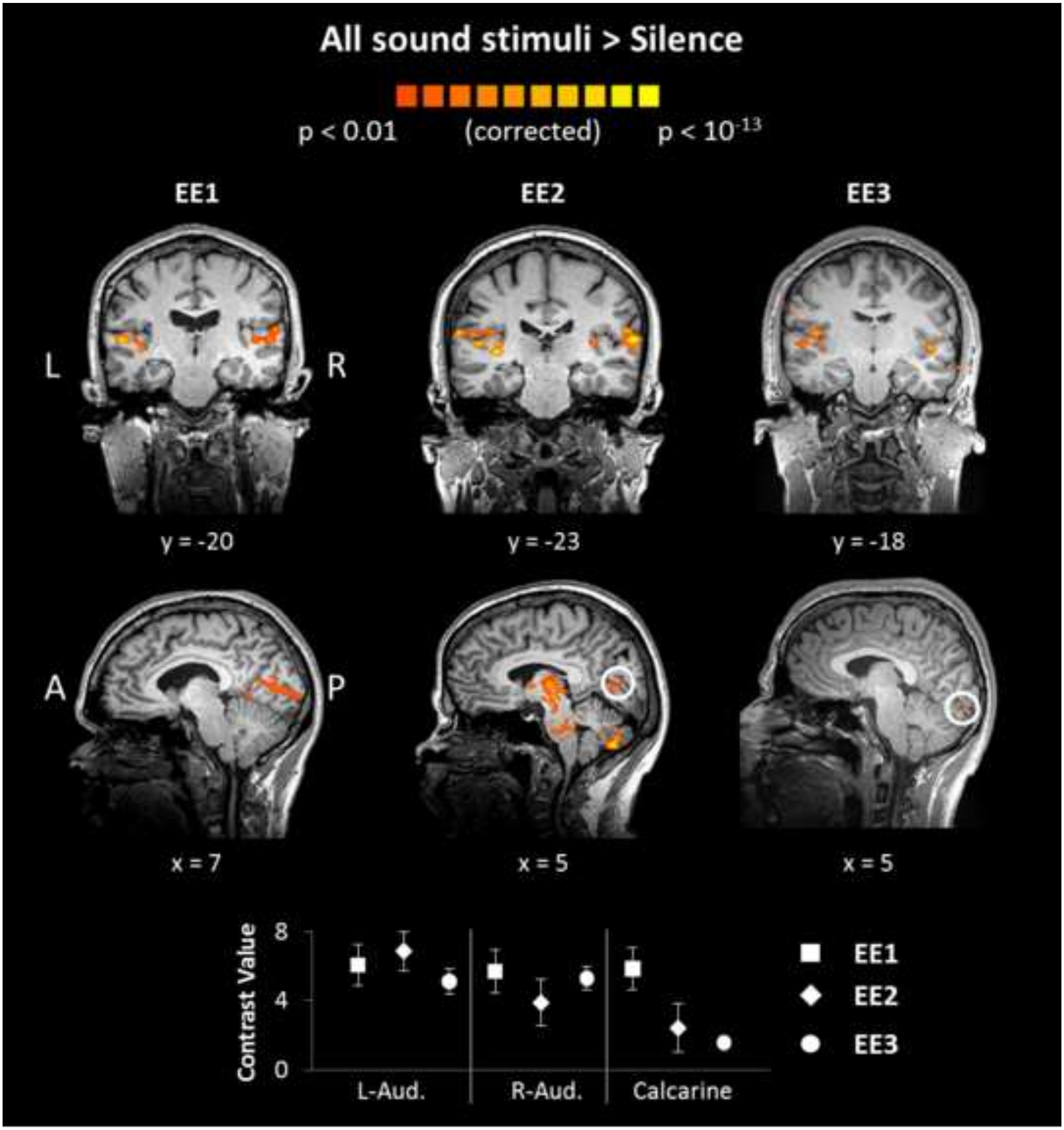

Figure 4

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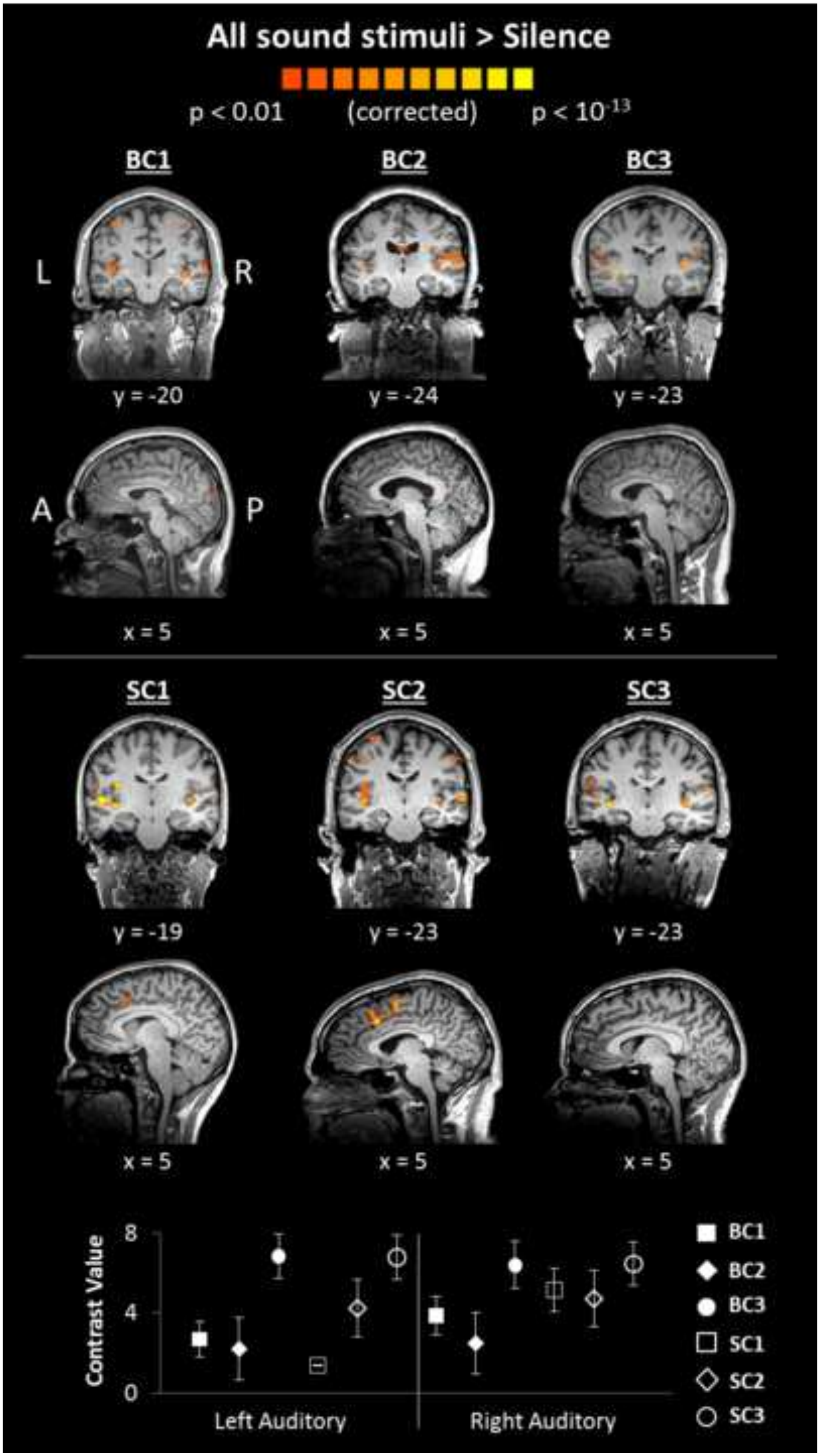

Figure 5

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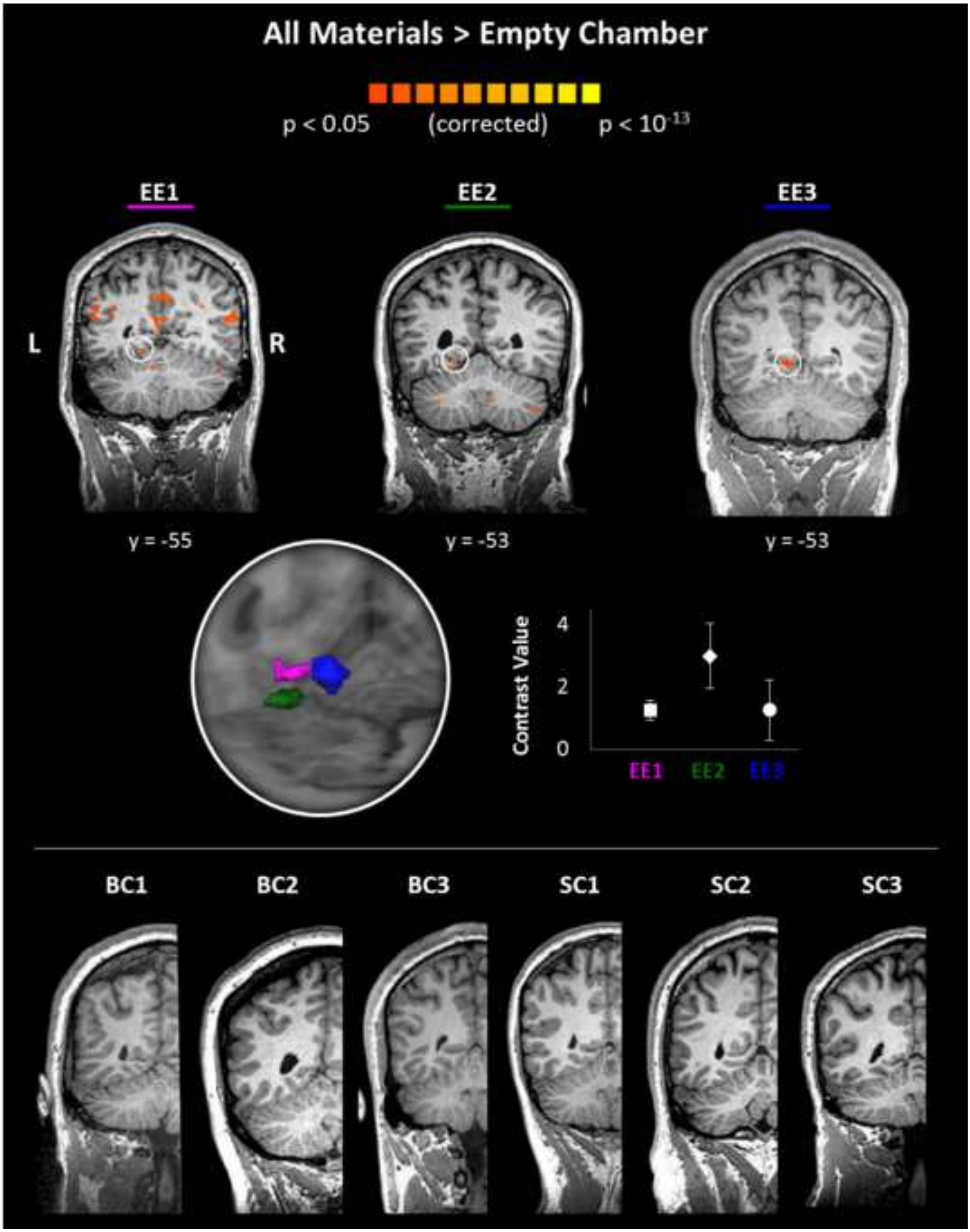

Supplementary Table