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

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A R T I C L E   I N F O

Article history:
Received 1 May 2014
Received in revised form 1 July 2014
Available online xxxx

Keywords:
Texture
Vision
Audition
Multisensory
Neuroplasticity
fMRI

A B S T R A C T

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.

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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 et al., 2013; Hausfeld et al., 1982; Kellogg, 1962; Rice, 1967, 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 et al., 2014; for review, see Kolarik et al., 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, Arnott, & Goodale, 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 ventro-
lateral 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 sug-
gest 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 behavioral 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; 

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 et al., 2010; Hiramatsu, Goda, & Komatsu, 
2011; Jacobs, Baumgartner, & Gegenfurtner, 2014). With respect 
to the auditory modality, previous research suggests the involve-
ment 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 exist-
ence 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 dis-
tal and silent. Thus, one may expect a difference in terms of how 
the brain processes material conveyed through echoes. Accord-
ingly, 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 con-
voying shape was not acoustically independent from echo-acoustic 
information conveying material properties, rendering a compar-
ison 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 echolo-
cators. This activation was absent in sighted and blind control partic-
ipsants. 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 pro-
cessing 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 3.0.8 (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 retino-
blastoma 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 
clairvoyant echolocation on a daily basis.

We also tested six control participants (three congenitally blind 
non-echolocators [BC1–BC3; two male, aged 36, 25, 38, respec-
tively] 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 Chamb-
er at the National Centre for Audiology in London, Ontario, Can-
ada, 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 
celling. 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 Profes-
Sionals-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 echolocator’s 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, 
Arnott, & Goodale, 2011; Thaler et al., 2014), echo stimuli were cre-
ated by making binaural recordings of echolocation clicks and sub-
sequent echoes as each echolocating participant was presented 
with sound-reflecting surfaces that were made of different materi-
als. 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,
PVC, and a whiteboard covered in reflective material.
and a fleece blanket covered with a fencing material (Fig. 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 Fig. 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’ 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 Fig. 1A.

2.2.3. Sound editing
From each echolocator’s recordings, we took individual click-echo pairings to create three unique 10-s 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 \times 3 exemplars). Because the echolocators were free to click at their own pace, the number of click-echo pairings per 10-s 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 s (10-s silent gap + 2-s slice acquisition). The field of view was 211 mm with a 64 \times 64 matrix size, which led to in-slice resolution of 3.3 \times 3.3 mm. Slice thickness was 3.5 mm 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 \times 1 \times 1 mm using an optimized sequence (MPRAGE).

2.3.3. Functional paradigm
Each run contained silent baseline and experimental trials (Fig. 2). Experimental trials included a 10-s sound stimulus presen-
To compare brain activity related to the processing of five runs. The duration of each run was 41 s. 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-s period between sound presentations. 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 s. Each participant completed five runs.

2.3.4. Behavioral 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-min 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 & Tournoux, 1998). 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., 1995). Cluster threshold values were estimated in volume space using the BrainVoyager Cluster Threshold Estimator Plugin (Goebel, Esposito, & Formisano, 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. Behavior

The participants’ behavioral task during fMRI scanning was to identify the material of the sound-reflecting surface (i.e. whiteboard, synthetic foliage, fleece blanket with fenc...ing, or no material [empty anechoic chamber environment]). The behavioral 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 behavioral trials. EE3 completed four runs and thus completed 160 behavioral 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

Figs. 3 and 4 show slice views of the expert echolocator’s (Fig. 3) and blind and sighted control participants’ (Fig. 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 Fig. 3 and in each participant section in Fig. 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; Noppeney, 2007). 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

Fig. 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 Fig. 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 laterализation is addressed in the Discussion (Section 4). The bottom panel of Fig. 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

Table 1

<table>
<thead>
<tr>
<th>Participant</th>
<th>Performance on material discrimination task (% correct)</th>
<th>Test result</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Whiteboard</td>
<td>Synthetic foliage</td>
<td>Fleece blanket with fence</td>
</tr>
<tr>
<td>EE1</td>
<td>100</td>
<td>100</td>
<td>95</td>
</tr>
<tr>
<td>EE2</td>
<td>92.5</td>
<td>92.5</td>
<td>85</td>
</tr>
<tr>
<td>EE3</td>
<td>97.5</td>
<td>95</td>
<td>72.5</td>
</tr>
<tr>
<td>BC1</td>
<td>50</td>
<td>33.3</td>
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<tr>
<td>BC3</td>
<td>55</td>
<td>57.5</td>
<td>70</td>
</tr>
<tr>
<td>SC1</td>
<td>92.5</td>
<td>45</td>
<td>45</td>
</tr>
<tr>
<td>SC2</td>
<td>37.5</td>
<td>37.5</td>
<td>45</td>
</tr>
<tr>
<td>SC3</td>
<td>55</td>
<td>55</td>
<td>45</td>
</tr>
</tbody>
</table>

Note: Test statistics and significance values are the result of binomial tests comparing each participant’s overall percentage correct performance to chance (25%).
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, Arnott, & Goodale, 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; Cant & Goodale, 2011; Cavina-Pratesi et al., 2010; 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 func-
tionally specific to material perception, particularly considering that the echolocating participants showed considerably higher behavioral 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. Neverthe-
less, 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., 2008), and from the areas within left PHC observed in the current study. In the blind, material perception has been investigated only previously (Thaler, Arnott, & Goodale, 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, Arnott, & Goodale, 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, Arnott, & Goodale, 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 (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 et al., 2001; Stilla & Sathian, 2008). Furthermore, the texture-related activation has been observed within the medial occipital cortex (MOC), with regions of activity overlapping (Stilla & Sathian, 2008) or adjacent to (Podrebarac, Goodale, & Snow, 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 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, Arnott, & Goodale, 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, Arnott, & Goodale, 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, Arnott, & Goodale, 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.

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in the tactile domain, but not in the auditory domain. With regard to tactile perception of materials, no notable differences in behavioral 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.

Acknowledgments

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.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2014.07.004.
References


