Auditory click stimuli evoke event-related potentials in the visual cortex
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The objective of this study was to determine whether unimodal auditory stimuli evoke event-related potentials (ERPs) in brain areas normally designated as the visual cortex (VC). The topographical distribution of ERPs evoked by auditory click stimuli was measured from (a) electroencephalographic electrodes on the scalp of six neurologically normal adult human participants and (b) intracranial electrodes implanted on the cortex of one epileptic adult human participant. In all participants, unimodal click stimuli evoked ERPs over both the auditory cortex (AC) and the VC. Relative amplitudes of ERPs at different scalp electrodes did not support the idea that the ERPs over VC were volume-conducted versions of those over AC, and intracranial records confirmed the origin of some click-evoked ERPs in both V1 and other regions of VC. We conclude that unimodal auditory stimuli can evoke ERPs in VC. This finding adds to the earlier evidence for the effect of visual stimuli on AC by providing new evidence for bidirectional functional connectivity in the audio-visual network of the human brain. The implication is that not only do visual stimuli affect hearing; auditory stimuli also affect visual perception. \textit{NeuroReport} 24:837–840 @ 2013 Wolters Kluwer Health | Lippincott Williams & Wilkins.

Introduction
Perception of the natural world involves the integration of acoustic and visual information into a unitary consciousness. Until relatively recently, it was assumed that auditory cortex (AC) dealt exclusively with the auditory stimuli, visual cortex (VC) dealt exclusively with the visual stimuli, and any integration of the two stimulus modalities took place in an ill-defined region labelled ‘association’ cortex. Over the last decade, however, this has increasingly been recognized not to be the case. Areas of sensory cortex that were traditionally associated exclusively with one or the other stimulus modality actually respond to both [1,2].

Anatomical studies in animals [3,4] have shown long-distance connections from AC to primary and secondary VC. However, most physiological studies on humans have so far concerned the effects of visual or audio-visual stimuli on auditory processing [5–7]. Hitherto there has been no direct evidence that auditory stimuli have physiological effects in primary VC. In this study we ask whether unimodal auditory stimuli evoke event-related potentials (ERPs) in human VC.

Materials and methods
Participants
Scalp electroencephalographic (EEG) recordings were made from sixty-four 10–20 scalp electrodes on six normal-hearing adult participants (two women). All gave informed consent to participate in experiments approved by the Human Ethics Committee of the University of Auckland. These participants ranged in age from 23 to 54 years (mean age 35.8, SD 13.9).

Electrocorticographic (ECoG) recordings were made from one normal-hearing female patient aged 51 years in whom intracranial electrodes had been implanted for the purpose of localizing the focus of medically refractory epilepsy. The placement of ECoG electrodes in this case was dictated solely by clinical considerations but the patient also gave informed consent to participate in research studies approved by and conducted under the auspices of the University of Washington Human Subjects Review Committee.

Electrophysiology
Data were sampled at 1 kHz in the scalp EEG experiments and 1.2 kHz in the ECoG experiment. In scalp EEG experiments, electrode-scalp impedances were kept below 5 kΩ. In all cases, auditory click stimuli (100 μs duration, ~60 dB SL) were presented bilaterally through insert earphones, with an interstimulus interval randomized between 1 s and 7 s. ERPs were computed offline in Matlab (Mathworks, Natick, Massachusetts, USA). For the scalp EEG experiments, ~40 click stimuli were presented once with the participants’ eyes open and focussed on a fixation cross on a computer screen in front of their comfortable chair, and again with the participants’ eyes closed. The patient fitted with...
intracranial electrodes only participated in the eyes-open part of the experiment.

**Results**

Figure 1 shows that with eyes open, auditory click stimuli evoked scalp ERPs of similar shape and amplitude over AC and most of VC. This result was obtained in all six of the scalp EEG participants. The one participant who repeated the experiment in a second session conducted 2 months after the first produced much smaller ERPs over VC in the second session, suggesting that novelty may increase activation of the putative audio-visual network.

That the activity over VC was not caused by any form of visual stimulus is shown by the fact that similar ERPs were seen over VC when the participants’ eyes were closed throughout the experiment. The major difference between eyes-open and eyes-closed conditions was that with eyes closed, significant α activity appeared throughout what looked like an audio-visual network similar to that described in the study of Stephen et al. [8]. In the participant whose results are shown in Fig. 1, this activity appeared only over the right hemisphere, but in some participants it was bilateral.

Figure 2 shows that in the intracranial experiment, click stimuli evoked ERPs at electrodes implanted on both AC [Fig. 2 (J to S)] and parts of VC [Fig. 2 (A to H)].

**Discussion**

EEG is a composite of local field potentials (LFPs) generated by the synchronous activity of chemical...
synapses on many anatomically aligned cortical pyramidal cells. Such LFPs always come in dipole pairs (for pictorial explanation see Figs 1 and 2 of [9]). At distances greater than the interpole length of a dipole – in this case maximally the depth of the cerebral cortex, 2–3 mm – the electric field of that dipole falls off with distance according to an inverse cube law [10]. Volume conduction is generally taken to imply current flow through the extracellular fluid, which is at least heavily influenced by local electric field values, so the effects of volume conduction also fall off as more or less the cube of distance from a source. This means that if the ERPs over early VC in Fig. 1 were trivially due to volume conduction from sources in AC, they should be very much smaller than the ERPs over AC. In fact they are approximately of the same size, which already militates against the possibility that scalp ERPs evoked by click stimuli over VC are due to volume conduction from sources in AC.

This possibility is then conclusively disproved by the data in Fig. 2. That volume conduction makes at best a minor contribution to the ERPs in Fig. 2 is shown by the facts that (a) there can be big differences between ERPs at adjacent electrodes [e.g. Fig. 2 (I) vs. Fig. 2 (J)], and (b) numerous electrodes showing no ERPs at all [Fig. 2 (B to G)] are spatially interposed between the major ERP over visual area V1 [Fig. 2 (A)] and those over the peri-Sylvian AC [Fig. 2 (J to T)].

The difference between the smooth progression of scalp ERPs over the whole of what Stephen et al. [8] identified as the audio-visual network (Fig. 1) and the patchy distribution of intracranial ERPs over the same region (Fig. 2) is easily explained by the spatial blurring effect of the greatly increased distance between source and recording sites in scalp records as compared with ECoG records. Even if one ignores the extra blurring effect of low skull conductivity, mathematical modelling shows that two radial dipoles in a cortical gyrus have to be at least 18 mm apart before they can be resolved in records taken from the closest section of scalp [11].

Conclusion

Purely auditory stimuli can evoke ERPs that are generated in various regions of VC. This provides further evidence for the existence of a bidirectional audio-visual network in the human brain.

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**Conflicts of interest**
There are no conflicts of interest.

**References**