



Research paper

Auditory-visual integration in fields of the auditory cortex



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ABSTRACT

While multimodal interactions have been known to exist in the early sensory cortices, the response properties and spatiotemporal organization of these interactions are poorly understood. To elucidate the characteristics of multimodal sensory interactions in the cerebral cortex, neuronal responses to visual stimuli with or without auditory stimuli were investigated in core and belt fields of guinea pig auditory cortex using real-time optical imaging with a voltage-sensitive dye. On average, visual responses consisted of short excitation followed by long inhibition. Although visual responses were observed in core and belt fields, there were regional and temporal differences in responses. The most salient visual responses were observed in the caudal belt fields, especially posterior (P) and dorsocaudal belt (DCB) fields. Visual responses emerged first in fields P and DCB and then spread rostroventrally to core and ventrocaudal belt (VCB) fields. Absolute values of positive and negative peak amplitudes of visual responses were both larger in fields P and DCB than in core and VCB fields. When combined visual and auditory stimuli were applied, fields P and DCB were more inhibited than core and VCB fields beginning approximately 110 ms after stimuli. Correspondingly, differences between responses to auditory stimuli alone and combined audiovisual stimuli became larger in fields P and DCB than in core and VCB fields after approximately 110 ms after stimuli. These data indicate that visual influences are most salient in fields P and DCB, which manifest mainly as inhibition, and that they enhance differences in auditory responses among fields.

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1. Introduction

Visual modality can generally provide a beneficial influence on auditory modality (Alais et al., 2010; Driver and Noesselt, 2008; Stein and Stanford, 2008). Reaction times to combined light and sound stimuli were shorter than to sound or light stimuli alone (Hershenson, 1962). The detection of sounds was improved with combined light flashes (Lovell et al., 2003), and sounds were perceived to be greater when auditory stimuli were combined with visual stimuli (Odgaard et al., 2004). More complex sounds such as speech were also easier to comprehend in noisy environments when visual information of the speaker was available (Ross et al.,

2007; Sumby and Polack, 1954). Although the multimodal interactions underlying these behavioral benefits were thought to occur in the higher level cortices, recent studies have shown that the primary and secondary auditory cortices, considered to process a unisensory auditory modality, are also affected by a visual modality in various species including humans, monkeys, ferrets, rats, and gerbils (Bizley et al., 2007; Calvert et al., 1997; Ghazanfar et al., 2005; Giard and Peronnet, 1999; Kayser et al., 2008, 2010; Kobayashi et al., 2013; Laurienti et al., 2002; Lehmann et al., 2006; Martuzzi et al., 2007; Pekkola et al., 2005; van Atteveldt et al., 2004; Wallace et al., 2004). These findings raise the possibility that parts of the psychophysical benefits obtained from combined different sensory modalities may be related to alterations in processing caused by multimodal stimuli in the early sensory cortex fields (Kayser et al., 2010; Schroeder and Lakatos, 2009).

It was reported that inhibitory and excitatory interactions exist among sensory modalities in the cerebral cortex (Dehner et al., 2004; Iurilli et al., 2012; Nishimura and Song, 2012; Olcese et al.,

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2013). However, the combined spatial and temporal influences of other sensory modalities on various fields of particular regions of the sensory cortex are not well understood. Indeed, only a few studies have examined regional differences of visual modulation among fields of the auditory cortex (Bizley et al., 2007; Ghazanfar et al., 2005; Kayser et al., 2007; Lehmann et al., 2006). Further, it is unclear whether cross-modal interactions result in response enhancement or suppression. For example, response enhancement in the cross-modal interactions is common in studies using functional magnetic resonance imaging (fMRI) and local field potentials (LFPs) (Ghazanfar et al., 2005; Kayser et al., 2007, 2008; Lehmann et al., 2006), while response suppression is common in studies using more direct neuronal recordings such as single-unit and intracellular recordings (Bizley et al., 2007; Iurilli et al., 2012; Kayser et al., 2008).

Here we hypothesize that cross-modal influences are different spatially and temporally among fields of the auditory cortex. To test the hypothesis, we investigated the spatiotemporal organization of multimodal interactions in the guinea pig auditory cortex. To examine the spatial and temporal effects of other sensory modalities on the auditory cortex, we studied visual influences on the various fields of the auditory cortex using real-time optical imaging with a voltage-sensitive dye. Optical imaging using voltage-sensitive dyes is the method that is capable of obtaining membrane potential changes of stained membranes, depolarization and hyperpolarization of membranes, by measuring intensity changes of fluorescence of light. This method provides images of population membrane changes both at high-spatial resolution ($\sim 10 \mu\text{m}$) and high-temporal resolution (milliseconds), although there is uncertainty about cell types or membranes from which optical signals are originated. Waveforms of optical signals obtained by this method have been known to be similar to those by intracellular recordings. Indeed, waveforms of optical imaging recordings were reported to be quite similar to those of intracellular recordings from nearby pyramidal neurons in the cerebral cortex (Petersen et al., 2003). Thus we used this method to examine our hypothesis. We investigated where cross-modal influences existed in the fields of auditory cortex and how auditory responses in these fields were influenced by visual inputs.

2. Material and methods

All experiments were conducted in accordance with the NIH Guide for the Care and Use of Laboratory Animals, and with approval of the animal care committee of Toyohashi University of Technology.

2.1. Surgical procedures

Surgical procedures were performed as previously described (Horikawa et al., 1996, 2001; Kubota et al., 2008). Briefly, fourteen male guinea pigs (Hartley, 6–10 weeks old) were used. Animals were anaesthetized with ketamine (40 mg/kg) and xylazine (12.5 mg/kg). The trachea was cannulated, and the head was clamped using a head holder (Narishige, Tokyo, Japan). The dura mater was removed and the exposed cortex was stained with a voltage-sensitive dye RH795 (Thermo Fisher Scientific, Waltham, MA, USA) for 90 min. Anesthesia was maintained with supplemental doses of ketamine (12.5 mg/kg/h) and xylazine (5 mg/kg/h). To maintain the state of anesthesia, the heart rate, pupil reflex, and electroencephalography were monitored during the experiments. The experiments were conducted in a sound-proof room with the guinea pigs artificially ventilated after intraperitoneal injection of a muscle relaxant (pancuronium bromide; Organon, Netherlands, 1 mg/kg/h).

2.2. Optical imaging

Optical imaging using a voltage-sensitive dye RH795 was performed as previously described (Horikawa et al., 1996, 2001; Kubota et al., 2008). Briefly, the cortical surface was illuminated with light between 480 and 580 nm generated by a 150-W halogen lamp. The optical signals were long-pass filtered at 620 nm and recorded with a 100×100 channel CMOS camera (MiCAM Ultima; BrainVision, Tokyo, Japan) at a rate of 2 ms/frame. Noise due to pulsation was reduced by synchronizing the recording with the heartbeat, and subtracting the activity when no stimulus was presented from that during stimulus presentation (Horikawa et al., 1996). The optical signals were averaged over the four trials in which a particular stimulus was presented. The optical responses were expressed as $\Delta F/F$, where ΔF is the change in intensity due to neural responses and F is the light intensity at rest.

The recording area of the CMOS camera was 5×5 mm of the auditory cortex and each channel detected a signal from a $50 \times 50 \mu\text{m}$ region of the cortex. To record from cortical areas larger than 5×5 mm, recordings from different locations of the auditory cortex were conducted, and composite response maps were later produced from several recordings by blending overlapping areas. Composite response maps were produced by simply averaging overlapping regions. The amplitudes of the responses were color-coded and superimposed on an image of the cortical surface. Response latencies were determined as the time at crossing thresholds of three standard deviations (SDs) of baseline responses. The core and belt fields of auditory cortex were determined by differences in tonotopic organization and response time courses, as previously described (Horikawa et al., 2001). The imaging camera was focused $200 \mu\text{m}$ below the cortical surface. Since no optical responses were obtained when the camera was focused $200 \mu\text{m}$ above the cortical surface, it is likely that most of the responses were from layers 2/3 of the auditory cortex (Horikawa et al., 1996).

2.3. Sound stimuli

Sound stimuli were delivered from a loudspeaker (MSP3; Yamaha, Hamamatsu, Japan) placed 10 cm from the ear contralateral to the recording cortex. The sound level was measured with a 1/4-inch condenser microphone (4125; Brüel and Kjaer, Nærum, Denmark) placed near the entrance of the external auditory meatus. The sound used was a wide-band noise (WN; 0.1–18 kHz). The sound level was 65 dB SPL and the duration was 100 ms with 5-ms cosine ramps at start and end of sound.

2.4. Light stimuli

Light stimuli (duration of 100 ms) were delivered from a blue LED placed 2 cm in front of the eye contralateral to the recording cortex. Absence of sound from the LED was confirmed with the 1/4-inch condenser microphone.

2.5. Statistical methods

For statistical multiple comparisons non-parametric multiple comparisons were performed by Friedman test followed by pairwise comparisons using Nemenyi post-hoc test. For pairwise comparisons Wilcoxon signed-rank test was performed.

3. Results

3.1. Responses to auditory stimuli

We examined the caudal belt fields as well as the core fields. The

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