

THE CORTICAL DISTRIBUTION OF MULTISENSORY NEURONS WAS MODULATED BY MULTISENSORY EXPERIENCE

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Abstract—Previous studies have indicated a sparse distribution of multisensory neurons in the transition zones between cortical areas associated with specific sensory modalities. However, little is known about the distribution and functional properties of such neurons. The bimodal visual–auditory neurons in the transition area between visual and auditory cortices in rats were examined to determine whether these neurons are modulated by simultaneous input from visual and auditory modalities. Visual–auditory neurons were found to have a non-uniform distribution within this region, instead gathering together and forming a small zone. Electrophysiological recordings revealed that visual–auditory neurons possess integrative characteristics similar to neurons of the superior colliculus, a midbrain structure in the visual pathway. Exposing adult animals to combined visual and auditory stimuli resulted in an expansion of bimodal neuron distribution in the visual–auditory transition area. These effects were more pronounced in young animals; in this case, the distribution of visual–auditory neurons extended past the limits of the transition area and invaded the flanking modality-specific cortical areas. These results provide a direct demonstration of the role of sensory experience in shaping cortical structure, which can have implications for neuronal integration and cognitive function. © 2014 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: audition, vision, cortices, multisensory experience, plasticity.

INTRODUCTION

To understand outside events or stimuli well, the brain must integrate information obtained through various sensory modalities. In the past three decades, a host of studies were conducted to explore the neural

mechanisms underlying the multisensory integration (Stein, 2012). General principles governing sensory integration, including spatial and temporal encoding of neuronal input and the principle of inverse effectiveness (Stein and Stanford, 2008), have emerged from these works, and have been found to apply to many brain areas (King et al., 1996; Alais et al., 2004; Baier et al., 2006; Keniston et al., 2009; Fetsch et al., 2013). Human and animal studies showed that combined cues from different senses were of important value in enhancing the detection, localization and identification of external events or objects (Romanski, 2007; Rowland et al., 2007; Helbig et al., 2012).

The relay of neural inputs is hierarchical; in the cortex, multisensory integration properties were formerly attributed to the higher level association and premotor cortices (Jones and Powell, 1971; Stein and Meredith, 1993; Macaluso and Driver, 2005; Sugihara et al., 2006; Porter et al., 2007; Angelaki et al., 2009; Zahar et al., 2009). However, it is now known that integration occurs even in lower level sensory regions, including the primary cortices (Ghazanfar and Schroeder, 2006; King and Walker, 2012). Electrophysiological recordings in rats showed that epicortical distribution of evoked potentials extended beyond the anatomically defined primary sensory areas (PSA) (Fu et al., 2003; Ghazanfar et al., 2005; Kayser et al., 2005; Lakatos et al., 2007; Musacchia and Schroeder, 2009), where possible associative or multisensory information processing functions were discovered (Di et al., 1994; Brett-Green et al., 2003). On this basis, the classic view of sensory cortical parcellation was redefined, with the stipulation that zones interposing two sensory cortical areas are predominantly multimodal and can therefore perform integrative functions in rodent animals (Wallace et al., 2004).

Sensory cortical areas are highly plastic, and can be modified based on sensory experience. Many studies have shown that the ablation of one modality results in the compensatory anatomical and functional reorganization of other modalities (Sadato et al., 1996; Finney et al., 2001; Sanchez-Vives et al., 2006; Meredith and Lomber, 2011). In congenitally deaf mice, all of what would normally be the auditory cortex is taken over by the visual and somatosensory system (Hunt et al., 2006). Multisensory experience has also been shown to affect the integrative properties and responses of multisensory neurons (Wallace and Stein, 2007; Stein and Rowland, 2011; Yu et al., 2013a). For instance, exposure to cross-modal sensory stimuli triggered the development

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Abbreviations: LED, light emitting diode; MSI, multisensory integrative index; MZ, multisensory zone; PSA, primary sensory areas; SC, superior colliculus; SPL, sound pressure level; SRMZ, the surrounding region of the multisensory zone.

of multisensory enhancement in the superior colliculus (SC) of dark-reared cats (Yu et al., 2010; Xu et al., 2012). An investigation of hemianopic subjects showed that concurrent aural and visual stimulation could induce a long-lasting amelioration of visual field disorders (Bolognini et al., 2005).

The present study mapped the cortical distribution of visual–auditory neurons in the transition area between visual and auditory cortices and characterized their electrophysiological properties in normal adult animals, and then examined the influence of multisensory experience on them in two groups of animals. One group was subjected to the spatiotemporally congruent visual–auditory exposure at the early age (the juvenile-exposed group) and the other group got this exposure in adult (the adult-exposed group). The results revealed that multisensory experience increased the number of bimodal neurons within the visual–auditory transition region, and caused the expansion of their distribution into the adjacent visual and auditory cortices.

EXPERIMENTAL PROCEDURES

All experimental procedures were performed in compliance with the Guide for the Care and Use of Laboratory Animals of East China Normal University. Adult and juvenile Sprague–Dawley rats (17 male and 12 female; 250–300 g) were used.

Sensory stimulation

Two groups of animals (juveniles, $n = 7$; adults, $n = 6$) were subjected to a 2-month period of exposure to visual–auditory stimuli, beginning at postnatal day 21 (P21) for juveniles, and postnatal weeks 9–10 for adults. The protocol was as follows. Unrestrained animals ($n = 3$ or 4) enclosed in a stainless steel wire cage ($40 \times 30 \times 25$ cm) placed inside a larger wooden box ($100 \times 80 \times 55$ cm) were exposed to a combination of visual and auditory stimuli originating from the same location with the same time of onset (Fig. 1). The box was well-ventilated, and the inner faces were covered with anisotropic foam to reduce sound deflection and environmental noise. The stimuli were presented every 2 s for 12 h daily (7 days/week). For the other 12 h, animals were housed in a normal controlled environment. The visual stimulus consisted of a flash of white light (intensity: 12.5 cd/m^2 vs. 0.15 cd/m^2 for ambient light; duration: 50 ms) generated by a fixed light emitting diode (LED) inside the wooden box. The auditory stimulus was generated by a speaker fixed directly above the LED, and consisted of a short burst of white noise (duration: 50 ms; on/off time: 5 ms; intensity: 70-dB sound pressure level (SPL) vs. 41-dB SPL background noise). The delivery of both types of stimuli was controlled by a computer. Juvenile animals remained with their mother during the exposure period until P35, at which time the juveniles were able to eat solid food and were weaned. The weight of each animal was continuously monitored to ensure that they were comparable to that of age-matched controls.

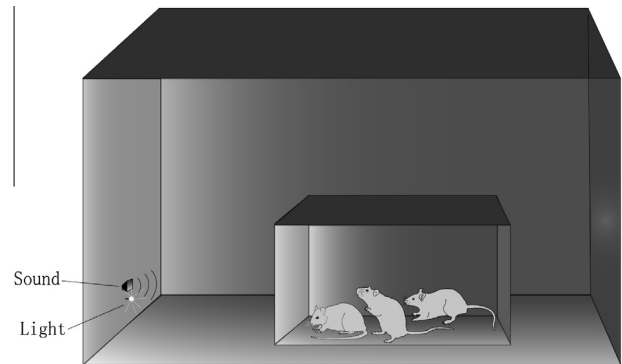


Fig. 1. Experimental paradigm for delivery of cross-modal stimuli. Animals ($n = 3$ or 4) were enclosed in a wire cage placed in a wooden box. Visual and auditory stimuli were presented from one side of the box every 2 s. Animals were exposed to the stimuli for 12 h daily, 7 days/week, over 2 months. The auditory stimulus delivered from the speaker was a 50-ms burst of white noise at an intensity of 70-dB SPL over a background level of 41-dB SPL. The visual stimulus was a 50-ms flash of white light from an LED on the wall at an intensity of 12.5 cd/m^2 against the background intensity of 0.15 cd/m^2 . For the other 12 h of each day, animals were housed with age-matched controls under standard conditions in a controlled environment.

Animal surgery

Rats received subcutaneous injections of atropine sulfate (0.01 mg/kg) prior to the surgery to reduce bronchial secretions. Animals were anesthetized with intraperitoneal (i.p.) injections of sodium pentobarbital (40–50 mg/kg). Following tracheal cannulation, a unilateral craniotomy was performed to expose a wide region of the left hemisphere encompassing the temporal, occipital, and parietal lobes (Fig. 2A, B), from 4.5 mm caudal to the bregma to lambda, and from 5 mm lateral to the mid-sagittal suture, past the lateral limit of the temporal bone. The dura was carefully removed to expose the cortical tissue, which was regularly doused with warm saline to prevent drying.

Following surgery, animals were moved to a double-walled, shielded room for electrophysiological recordings, in which inner walls and ceiling were coated with convoluted polyurethane foam to reduce echoes and environmental noise. The head was fixed on a stereotaxis using a 2-cm nail stick, which was attached to the skull with dental cement and 502 Super Glue. During the recording session, a stable body temperature was maintained for the animal using an aluminum foil-coated electrical heating pad (37°C), and depth of anesthesia was ensured by administering periodic i.p. injections of sodium pentobarbital, and gauging eye blink and the pedal withdrawal reflexes. The pupils were dilated with 1% atropine sulfate and eyes were kept moist with artificial tears. At the end of the experiment, animals were sacrificed by administering an overdose of sodium pentobarbital (150 mg/kg, i.p.).

Sensory stimulation

The visual search stimuli consisted of flashes of white light (duration: 50 ms; intensity: $3\text{--}15 \text{ cd/m}^2$) emitted by

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