

AGE-RELATED AUDIOVISUAL INTERACTIONS IN THE SUPERIOR COLLICULUS OF THE RAT

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Abstract—It is well established that multisensory integration is a functional characteristic of the superior colliculus that disambiguates external stimuli and therefore reduces the reaction times toward simple audiovisual targets in space. However, in a condition where a complex audiovisual stimulus is used, such as the optical flow in the presence of modulated audio signals, little is known about the processing of the multisensory integration in the superior colliculus. Furthermore, since visual and auditory deficits constitute hallmark signs during aging, we sought to gain some insight on whether audiovisual processes in the superior colliculus are altered with age. Extracellular single-unit recordings were conducted in the superior colliculus of anesthetized Sprague–Dawley adult (10–12 months) and aged (21–22 months) rats. Looming circular concentric sinusoidal (CCS) gratings were presented alone and in the presence of sinusoidally amplitude modulated white noise. In both groups of rats, two different audiovisual response interactions were encountered in the spatial domain: superadditive, and suppressive. In contrast, additive audiovisual interactions were found only in adult rats. Hence, superior colliculus audiovisual interactions were more numerous in adult rats (38%) than in aged rats (8%). These results suggest that intersensory interactions in the superior colliculus play an essential role in space processing toward audiovisual moving objects during self-motion. Moreover, aging has a deleterious effect on complex audiovisual interactions. © 2016 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: aging, optic flow, concentric spatial frequency, vision, auditory, audiovisual integration.

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Abbreviations: AES, anterior ectosylvian sulcus; CCS, circular concentric sinusoidal; c./deg., cycles/degree; DPOAEs, distortion product of otoacoustic emissions; GABA, γ -aminobutyric acid; imp./s, impulse/s; OHC, outer hair cells; PSTH, post-stimulus time histogram; RF, receptive field; rLS, rostral lateral suprasylvian; SAM, sinusoidal amplitude modulation; SC, superior colliculus; SPL, sound pressure level.

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INTRODUCTION

The superior colliculus (SC) has been known to be involved in integrating multisensory information in order to serve crucial functions in guiding and coordinating the orienting motor responses toward visual and auditory objects in space (Meredith and Stein, 1986a; Populin et al., 2004).

Typically, SC neurons are functionally organized to pool visual, auditory and somatosensory inputs mainly from subcortical and cortical sensory structures (Waleszczyk et al., 2004). Neurons in the superficial layers are known to be involved in the central processing of visual motion perception (Markus et al., 2009). In turn, neurons in the intermediate and deep layers of the SC are more specifically engaged in integrating audiovisual stimuli (Meredith and Stein, 1986a) as well as somatosensory signals to produce movements of the eyes, ears and head (Meredith and Stein, 1986a; Populin et al., 2004) toward novel visual and auditory stimuli in the contralateral hemispace. These movements require highly spatial congruency and temporal synchronicity (Wallace et al., 1992; Stein, 1998). The converging modality-specific inputs that endow the neurons with multisensory response properties may produce facilitatory or inhibitory interactions (King and Palmer, 1985; Meredith and Stein, 1986a) in order to enhance stimulus detection, identification and localization (Stein and Meredith, 1993). For instance, a bimodal facilitation evoked by an audiovisual stimulus may produce a summative (additive) or a multiplicative (superadditive) neuronal response. Conversely, an audiovisual stimulation can also yield an inhibitory (suppressive) interaction.

Thereby, a facilitatory neuronal response will be elicited when cross-modal stimuli are spatially congruent and gated in time. In contrast, a suppressive neuronal response will be expressed when cross-modal stimuli are spatially disparate and/or asynchronous in time (King and Palmer, 1985; Meredith and Stein, 1986a,b; Meredith et al., 1987). These SC multisensory interactions necessitate cortical descending inputs from the anterior ectosylvian sulcus (AES) and the rostral lateral suprasylvian (rLS) areas in order to develop neuronal non-linear (superadditive) functions (Wallace and Stein, 1994; Jiang et al., 2006) regarded as the inverse effectiveness rule (Meredith and Stein, 1986b).

Throughout the course of aging, audiovisual perceptual abilities diminish due to significant changes in the peripheral sensory organs as well as in the central visual and auditory structures (Mendelson and Wells, 2002; Langrová et al., 2006; Wang et al., 2006;

Caspary et al., 2008). More specifically, in elderly individuals, many studies reported central visual deficits in the spatio-temporal domain such as visual acuity (Weale, 1975), directional motion discrimination (Owsley et al., 1981; Tran et al., 1998) and contrast sensitivity (Owsley et al., 1981). Mendelson and Wells (2002) also reported that visual cortical neurons of aged rats were significantly less sensitive to speed of moving bars and that they had lower temporal frequency cut-offs. Analogously, Schmolesky et al. (2000) as well as Hua et al. (2006) demonstrated respectively that both orientation and direction selectivity of the primary visual cortex neurons in aged monkeys and cats were decreased significantly.

In the auditory modality, the most prevalent age-related deficit is presbycusis due to peripheral and/or central perturbations (Willott, 1991). Central presbycusis is characterized by alterations in the processing of spatial, spectral and temporal complex auditory stimuli (Humans: Corso, 1984; Mazelová et al., 2003; animals: Barsz et al., 2002; Turner et al., 2005). In the auditory cortex A1 of aged rats, Turner et al. (2005) showed that the auditory spectral receptive fields (RFs) were significantly less tuned. In addition, Ingham et al. (1998b) highlighted that the topographic directional auditory spatial map in the SC was severely disrupted in aged guinea pigs.

The above studies show that aging is responsible for unisensory deficits in the central auditory and visual systems. Thereby, this issue raises the question of whether age-related deficits will also affect audiovisual integration. To this end, the present study aims more specifically to examine if SC audiovisual neurons are sensitive to radial movement of looming circular concentric sinusoidal (CCS) gratings in the presence of sinusoidal amplitude modulated (SAM) white noise. Secondly, since visual and auditory age-related decrements affect central unisensory neurons, we also address the question of whether audiovisual neurons in the SC are affected during aging.

EXPERIMENTAL PROCEDURES

Animals

Seventeen Sprague–Dawley rats of either sex (eight adults: 10–12 months; nine aged: 21–22 months) were examined in the present study. Adult rats were obtained from Charles River (Saint-Constant, QC, Canada) and the aged rats were supplied by Harlan Laboratories Inc. (Indianapolis, IN, US). They were housed at the animal facility of the Université de Montréal, a light–dark cycle of 14/10 h was maintained. Experimental procedures were performed in accordance with approved protocols by the Université de Montréal Animal Care Committee which was in compliance with the guidelines of the Canadian Animal Care Committee. All efforts were made to diminish the number of animals used and to alleviate any discomfort due to surgical or experimental procedures.

Functional integrity of the cochlea

Prior to the evaluation of distortion product otoacoustic emissions (DPOAEs) and unit recordings in the SC, we

ensured that all animals were in good health and had no apparent pathologies, ear obstruction or eye diseases. Behaviorally, every animal elicited a robust orienting response toward auditory and visual stimuli.

Since age-related changes in hearing function are commonly associated with peripheral cochlear pathologies, all rats underwent DPOAE testing (Intelligent Hearing Systems 4630, Miami, FL, US; SmartDPOAE version 4.60) in order to evaluate the integrity of the outer hair cells (OHCs). First, atropine sulfate (0.5 mg/kg, Atro-sol; Ormond Veterinary Supply Ltd, Ancaster, ON, Canada) was i.m. injected to reduce bronchial secretions. Then sedation was induced with an i.m. injection of ketamine (50 mg/kg, Ketaset, Ayerst Veterinary Laboratories, Guelph, ON, Canada) and xylazine (5 mg/kg, Rompun, Bayer, Toronto, ON, Canada). In mammals, the amplitude of the distortion product at the frequency defined by $2f_1 - f_2$ is the most robust and reliable indicator of the OHCs function (Lonsbury-Martin and Martin, 1990). Thus, cubic difference tone ($2f_1 - f_2$) DPOAEs were acquired (4.5 frequencies/octave; sampling rate: 128 kHz, 32-bit A/D) using two calibrated primary tones, f_1 and f_2 (ratio $f_2/f_1 = 1.22$), set to the same sound level (65 dB SPL). Since the rat's auditory sensitivity is at its highest between 4 and 16 kHz (Polak et al., 2004), pure tone stimuli were presented from 2 to 20 kHz systematically, starting at the lowest frequencies and increasing to the highest frequencies. Each ear was tested independently.

Neuronal recordings in the SC

Animal preparation. Prior the extracellular unit recordings in the SC of the rat, a period of two weeks was allowed for the rats to recover from the anesthesia following the DPOAE recordings. On the day of recording, the rat was first treated i.m. with atropine sulfate (0.5 mg/kg, Atro-sol; Ormond Veterinary Supply Ltd, Ancaster, ON, Canada) in order to reduce bronchial secretions and induce mydriasis. Afterward, surgical anesthesia was induced by an i.m. injection mixture of ketamine (75 mg/kg; Ketaset, Wyeth Animal Health, Guelph, ON, Canada) and xylazine (5 mg/kg; Rompun, Bayer, Toronto, ON, Canada). Dexamethasone sodium phosphate (10 mg/kg; Vetoquinol, Lavaltrie, QC, Canada) was also administered i.m. to reduce inflammation. Aged rats received about 80% of the drugs doses given to young adult animals to account for the lower level of liver function and altered metabolism due to aging (Palombi et al., 2001; Turner et al., 2005).

Once anesthetized, the rat's head was immobilized in a stereotaxic apparatus (David Kopf, model 963) set up with a gaseous mask. From this point on, surgical anesthesia was maintained with a gaseous mixture of isoflurane (0.5–1.5%; Baxter Corp., Mississauga, ON, Canada), nitrous oxide and oxygen ($N_2O:O_2$, 70:30). All pressure points and incision sites were routinely subcutaneously infiltrated with lidocaine 2% (Astra Pharma Inc., Mississauga, ON, Canada). An anchoring brass bar (length: 1.5 cm; diameter: 2 mm) was fixed on the rat's skull, anterior to the bregma, by means of

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