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NORMAL AGING SLOWS SPONTANEOUS SWITCHING IN AUDITORY AND VISUAL BISTABILITY

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Abstract—Age-related changes in auditory and visual perception have an impact on the quality of life. It has been debated how perceptual organization is influenced by advancing age. From the neurochemical perspective, we investigated age effects on auditory and visual bistability. In perceptual bistability, a sequence of sensory inputs induces spontaneous switching between different perceptual objects. We used different modality tasks of auditory streaming and visual plaids. Young and middle-aged participants (20–60 years) were instructed to indicate by a button press whenever their perception changed from one stable state to the other. The number of perceptual switches decreased with participants' ages. We employed magnetic resonance spectroscopy to measure non-invasively concentrations of the inhibitory neurotransmitter (γ-aminobutyric acid, GABA) in the brain regions of interest. When participants were asked to voluntarily modulate their perception, the amount of effective volitional control was positively correlated with the GABA concentration in the auditory and motion-sensitive areas corresponding to each sensory modality. However, no correlation was found in the prefrontal cortex and anterior cingulate cortex. In addition, effective volitional control was reduced with advancing age. Our results suggest that sequential scene analysis in auditory and visual domains is influenced by both age-related and neurochemical factors.

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Key words: perceptual organization, age, attention, awareness, scene analysis, MRS.

INTRODUCTION

Normal aging impairs speech communication in noisy environments or multitalker situations. This reflects changes in peripheral and central auditory processing, as well as more general changes in cognitive and attentional processing (Working Group on Speech Understanding and Aging, 1988). The difficulty in speech comprehension is probably derived from age-related declines in listener's abilities of perceptual organization (see Alain et al., 2006 for a review). The purpose of perceptual organization is to structure a mixture of sensory inputs into meaningful perceptual objects. For hearing, this task is termed auditory scene analysis (Bregman, 1990). The principles of auditory scene analysis are based on sequential cues, such as similarity in acoustic features over time, and concurrent cues, such as harmonicity. In the laboratory, it has been found that concurrent scene analysis declines with age (Alain et al., 2001; Snyder and Alain, 2005), whereas sequential scene analysis is preserved in the elderly (Trainor and Trehub, 1989; Alain et al., 1996; Snyder and Alain, 2007). In the context of auditory streaming, a recent study has demonstrated that older listeners do not benefit more from background (i.e., unattended) predictable cues than younger listeners do (Rimmele et al., 2012a). Therefore, there is the possibility that advancing age impairs the ability to exploit sequential information outside the focus of attention.

A parallel exists in vision. In the absence of disease or injury, we can suffer from age-related impairments of spatial vision, motion perception, and object recognition (Ball and Sekuler, 1986; Spear, 1993; Sekuler and Sekuler, 2000). Surprisingly, there are rather few studies investigating age effects on visual perceptual organization. Most previous studies have used binocular rivalry, where monocular images are presented to different eyes, and shown that the rate of rivalry alternations slows down with age (Jalavisto, 1964; Ukai et al., 2003; Tarita-Nistor et al., 2006). The present study investigated whether visual motion perception is influenced by advancing age, because visual motion provides sequential information to segregate objects from the background.

We focused on bistable stimuli to clarify age effects on perceptual organization. In perceptual bistability, a physically unchanging stimulus induces spontaneous switching of conscious perception (Schwartz et al.,

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Abbreviations: AC, auditory cortex; ACC, anterior cingulate cortex; ANOVA, analysis of variance; GABA, γ-aminobutyric acid; MRS, magnetic resonance spectroscopy; MT, motion-sensitive area; PFC, prefrontal cortex.

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2012). To compare two sensory modalities, we employed auditory streaming as an auditory stimulus (Pressnitzer and Hupé, 2006; Kondo and Kashino, 2009) and moving plaids as a visual stimulus (Adelson and Movshon, 1982; Hupé and Rubin, 2003) (Fig. 1A). The two types of stimuli have an advantage for probing perceptual organization, because they involve a basic competition between a one-object (grouped) and a two-object (split) interpretation. In daily life, we frequently have difficulty taking signals from sensory inputs due to spatial and temporal occluders. From the perspective of adaptive behavior, it is thus important for the brain to create some possible percepts from insufficient information and fluctuate its perceptual interpretations (Kondo et al., 2017a).

We not only collected spontaneous bistable reports, but also manipulated the volition (or sometimes called selective attention) of participants during the task. Perception and attention interact dynamically to facilitate information processing. In general, if the relevant information is perceptually salient, attentional demand would be low (Desimone and Duncan, 1995). Even when observers select what to attend based on low-level features, attention operates on perceptual objects (Shinn-Cunningham, 2008). In a bistability paradigm, the predictability of sequential information gives no priority to either of the percepts (Bendixen, 2014). Thus, we can expect that bottom-up attention is essentially required for the formation and selection of perceptual objects and that spontaneous switching in perceptual bistability is sensitive to attentional abilities for each individual.

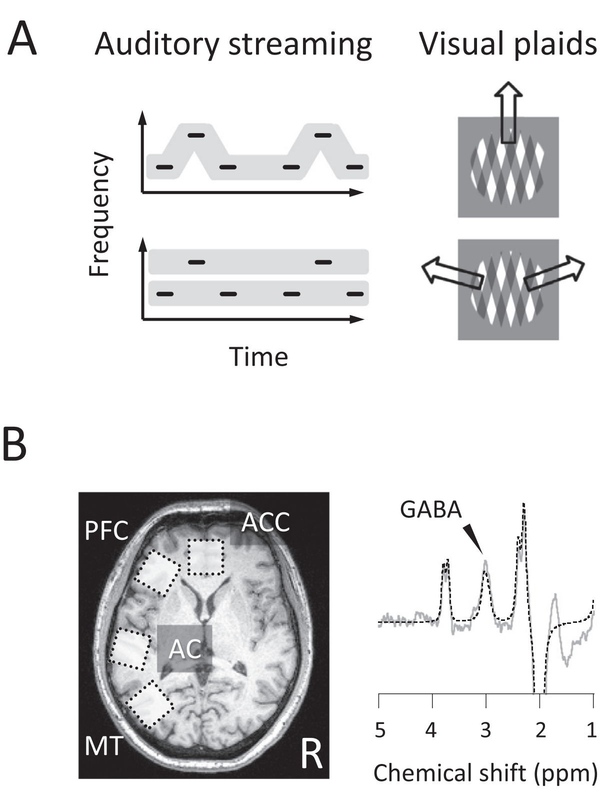

Fig. 1. Perceptual tasks and MRS data acquisition. (A) A sound sequence of triplet tones was presented in auditory streaming. The auditory stimulus produced perceptual switches between one and two streams. Two rectangular gratings were moving in visual plaids. The visual stimulus led to perceptual switches between upward grouped and sideward split motion. (B) The size and location of voxels (left) and the edited GABA spectrum of one representative participant (right). The voxel in the auditory cortex (AC) included the Heschl gyrus and the anterior part of the temporal plane. The voxel in the motion-sensitive area (MT) was placed at the ventrolateral occipital cortex. The voxel in the prefrontal cortex (PFC) was located at the anterior part of the middle frontal gyrus. The voxel in the anterior cingulated cortex (ACC) was centered on the interhemispheric fissure. The γ-aminobutyric acid (GABA) peak was obtained from the differences in spectra by editing radio frequency on/off pulses and fitted by a Gaussian function (dashed line).

We hypothesized that participants' ages would affect perceptual organization and volitional control. What neural mechanisms contribute to the age effects? One possibility is that the efficacy of cortical inhibition based on γ-aminobutyric acid (GABA) mediates neurophysiological changes in perception and attention (Leventhal et al., 2003), because the GABAergic system plays a critical role in all sorts of brain functions, such as sharpening tuning curves of sensory neurons and orienting the focus of attention (Tadin and Blake, 2005). We used magnetic resonance spectroscopy (MRS) to obtain a non-invasive, *in vivo* measurement of GABA in the human brain (Puts and Edden, 2012). Previous studies have shown that the GABA concentration in different cortical areas predicts individual differences in orientation discrimination (Edden et al., 2009), visual awareness (van Loon et al., 2013), visual attention (Kihara et al., 2016), and auditory multistability (Kondo et al., 2017a). The interest in the MRS technique has grown in recent years, but few studies have investigated the relationship between GABA levels and age-related changes in brain functions (see Duncan et al., 2014 for a review). The present study specified GABA levels in a broad range of young and middle-aged people.

In MRS studies, *a priori* assumptions are important for regional specificity (Duncan et al., 2014). From the perspective of neurochemical measures, we here explore the outstanding issue of whether the bistable selection process is supported by low-level sensory areas or high-level cognitive ones. Auditory streaming has neural correlates in the auditory cortex (AC) (Gutschalk et al., 2005; Micheyl et al., 2007; Kondo and Kashino, 2009), whereas moving plaids induce activity in the motion-sensitive area (MT) of the visual cortex (Huk and Heeger, 2001; Castelo-Branco et al., 2002). In addition, it has long been argued that the prefrontal cortex (PFC) and anterior cingulate cortex (ACC) are involved in perceptual switching in visual bistability (Lumer et al., 1998; Sterzer and Kleinschmidt, 2007), but this has been recently disputed (Brascamp et al., 2015). We clarified whether GABA concentrations in the four cortical regions are linked with individual differences in auditory and visual bistability.

EXPERIMENTAL PROCEDURES

Participants

Thirty-eight young and middle-aged participants were recruited for this study (22 males and 16 females; M_{age} = 36.6, SD_{age} = 10.8, range 20–60 years). The pool of the participants consisted of the following age