



Reduction in the retinotopic early visual cortex with normal aging and magnitude of perceptual learning



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ABSTRACT

Although normal aging is known to reduce cortical structures globally, the effects of aging on local structures and functions of early visual cortex are less understood. Here, using standard retinotopic mapping and magnetic resonance imaging morphologic analyses, we investigated whether aging affects areal size of the early visual cortex, which were retinotopically localized, and whether those morphologic measures were associated with individual performance on visual perceptual learning. First, significant age-associated reduction was found in the areal size of V1, V2, and V3. Second, individual ability of visual perceptual learning was significantly correlated with areal size of V3 in older adults. These results demonstrate that aging changes local structures of the early visual cortex, and the degree of change may be associated with individual visual plasticity.

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1. Introduction

During the last decade, the application of magnetic resonance imaging (MRI) techniques has enabled us to observe the brain structural changes with normal aging in vivo. Whole brain analyses using these techniques has revealed that normal aging manifests itself as an overall cerebral atrophy that includes the shrinkage of gray matter volume (Allen et al., 2005; Courchesne et al., 2000; Fotenos et al., 2005; Good et al., 2001; Lemaitre et al., 2012; Raz et al., 1997; Resnick et al., 2003; Sherwood et al., 2011; Walhovd et al., 2005), cortical thickness (Fjell et al., 2009; Kochunov et al., 2011; Lemaitre et al., 2012), cortical areal size (Lemaitre et al., 2012), white matter volume, or white matter integrity (Allen et al., 2005; Fotenos et al., 2005; Guttmann et al., 1998; Head et al., 2004; Kochunov et al., 2011; Raz et al., 1997; Resnick et al.,

2003; Salat et al., 2005; Sherwood et al., 2011; Walhovd et al., 2005), as well as the enlargement of cerebrospinal fluid spaces (Courchesne et al., 2000).

On the other hand, studies focused on regional analyses have shown that the brain structural reduction is not homogenous and may be affected differently across different brain regions (Sowell et al., 2003). For instance, aging effects are significantly stronger in frontal cortices (Allen et al., 2005; Brickman et al., 2007; Fjell et al., 2009; Lemaitre et al., 2012; Raz et al., 1997, 2004; Salat et al., 1999, 2004) but more moderate in the temporal (Cowell et al., 1994; Lemaitre et al., 2012; Sullivan et al., 1995) and parietal areas (Abe et al., 2008; Brickman et al., 2007; Good et al., 2001; Resnick et al., 2000; Salat et al., 2004).

One controversy, however, is whether the occipital area is affected by aging (Fjell et al., 2009). Some studies suggest that the occipital area is largely preserved with normal aging, including cortical areal size (Lemaitre et al., 2012), gray matter volume (Lemaitre et al., 2012; Raz, 2001; Raz et al., 1997), cortical thickness (Lemaitre et al., 2012), white matter-gray matter intensity contrast (Davatzikos and Resnick, 2002), white matter volume, and fractional anisotropy (Fjell et al., 2008; Good et al., 2001). However, other studies have found significant morphologic declination on

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gray matter volume (Allen et al., 2005; Resnick et al., 2003), cortical thickness (Salat et al., 2004), white matter volume, or white matter integrity (Allen et al., 2005; Head et al., 2004; Madden et al., 2004; Nusbaum et al., 2001; Resnick et al., 2003) in the occipital lobe.

To our knowledge, all the studies that examined effects of aging on the occipital lobe have defined the brain region by the anatomic landmarks including an automated parcellation technique (Fischl et al., 2002, 2004). However, the occipital lobe is functionally divided into several visual areas, each of which can be clearly defined by retinotopic representation including V1, V2, and V3 (Tootell et al., 1982; Wandell and Winawer, 2011; Whitney et al., 2003), where V1 denotes the primary visual cortex and V1, V2, and V3 are considered the early visual areas. Each of these areas has different functional properties including plasticity. Nevertheless, the effect of aging on each of these areas in the occipital lobe has, to our knowledge, never been examined. This raises the possibility that nonsignificant effects of aging on the anatomically defined occipital lobe does not necessarily indicate that there are significant morphologic changes in functionally defined divisions of the occipital lobe. If it is the case that there are indeed morphologic changes, this would raise the possibility that some functional changes with aging are related to possible morphological changes. To examine this possibility, we first measured the areal size of the early visual areas, because it has been shown that the size of visual areas is related to visual functions of younger subjects (Duncan and Boynton, 2003; Schwarzkopf and Rees, 2013; Schwarzkopf et al., 2011). Thus, we investigated the effect of aging on areal size of retinotopically defined early visual areas (morphologic aging effects), by comparing these regions in older and younger adults.

Next, we examined whether observed changes in areal size retinotopically defined as early visual areas in the occipital lobe, if any, were associated with individual differences among older adults for visual perceptual learning, as one of the possible functions of the visual cortex. Perceptual learning is defined as long-term improvement on a visual task and is regarded as a manifestation of visual plasticity (Doshier et al., 2013; Ooi et al., 2013; Sagi, 2011; Sasaki et al., 2010; Seitz and Watanabe, 2003; Shibata et al., 2011; Watanabe et al., 2001, 2002). Recent studies have shown that perceptual learning is possible with older individuals with learning effects that are similar to younger adults (Andersen et al., 2010; Bower and Andersen, 2012). This finding suggests that visual plasticity is preserved for visual training in older adults, which is in contrast to studies that found limited effects of training for cognitive tasks (Jones et al., 2006; Lustig et al., 2009; Owen et al., 2010; Verhaeghen et al., 1992; Yesavage et al., 1990). However, it remains unclear whether the underlying mechanism of perceptual learning in older adults is the same as that in younger adults. We thus tested whether areal sizes of the early visual area were correlated with the magnitude of visual perceptual learning in the older and younger individuals.

2. Methods

2.1. Subjects

Subjects were recruited into 2 age groups: 18 older adults (6 males and 12 females; the average age, 71.8 ± 5.13 years; mean \pm SD, ranging between 65 and 86 years old), and 21 younger adults (14 males and 7 females; the average age, 23.3 ± 3.5 years; mean \pm SD, ranging between 19 and 32 years old). One older subject was dropped, because we could not collect retinotopic mapping for this individual. The older subjects were recruited through the Harvard Cooperative on Aging and Brookline Senior Center. The younger subjects were recruited from Keio University and Boston University. All subjects had normal or corrected to normal vision

(see Supplementary Note 1 and Tables 1 and 2). The older subjects were evaluated by preexperiment screen session (including WAIS sub-tests: digit span, digit symbol coding, Mini Mental Status Examination, and activity level) to ensure normal cognitive and memory function (Andersen et al., 2010). All subjects gave informed consent for their participation to the experiments. The experiment procedure was approved by the Institutional Review Board at Brown University, Massachusetts General Hospital, Keio University, and Boston University where the experiments took place.

2.2. Magnetic resonance imaging

2.2.1. Anatomic image acquisition

All images were scanned by 3 Tesla scanners (Trio, Siemens, Erlangen, Germany) at Massachusetts General Hospital or Keio University. For anatomic images, 2 T1-weighted MR images (magnetization prepared rapid gradient echo: repetition time = 2.531 seconds, echo time = 3.28 ms, flip angle = 70° , inversion time = 1100 ms, 256 slices, voxel size = $1.3 \times 1.3 \times 1.0$ mm³, resliced during analysis to 1 mm³) were acquired from each subject.

2.2.2. Functional image acquisition for the retinotopic mapping scans

V1, V2, and V3 areas were localized functionally using a standard retinotopic mapping technique (Engel et al., 1994; Fize et al., 2003; Yotsumoto et al., 2008). All functional MR images were acquired using gradient echo planar imaging sequences (repetition time = 2 seconds, echo time = 30 ms, flip angle = 90°) with the standard 12-channel head coil. Thirty-three contiguous slices ($3 \times 3 \times 3.5$ mm³) oriented parallel to the AC-PC plane were acquired to cover the entire brain by automatic slice alignment method (van der Kouwe et al., 2005). During the retinotopic mapping scans, 5 different visual stimuli were presented on a gray background: (1) horizontal condition (12 degree wedge-shaped checkerboards centered on the horizontal meridian axis); (2) vertical condition (24 degree wedge-shaped checkerboards centered on the vertical meridian axis); (3) foveal condition (a small 168 degree wedge-shaped checkerboard placed between 0 and 3 degree eccentricity from the fixation); (4) parafoveal condition (a large 168 degree wedge-shaped checkerboard where the area within 3–7 degree eccentricity was filled with gray color as background); and (5) fixation condition. All conditions were presented in the counterbalanced order by blocked design during 4 times of the retinotopic mapping scans (12 seconds/block; 240 seconds/scan).

The activation of the functional localizer was projected on individual flattened format of cortical surface to allow us to functionally define V1, V2, and V3 areas with varied eccentricity. By contrast of horizontal and vertical checkerboard conditions, we defined the boundary of V1, V2, and V3 from the meridian of the activations (Engel et al., 1994; Fize et al., 2003; Yotsumoto et al., 2008). The foveal region was defined as the cortical part from the fovea to 3 degree eccentricity and the parafoveal region as 3–7 degree eccentricity for each of V1, V2, and V3.

2.2.3. Image processing

All imaging data were analyzed by FreeSurfer 4.5 version (<http://surfer.nmr.mgh.harvard.edu/>). The T1-weighted images were processed to reconstruct cortical surface (Dale et al., 1999; Fischl et al., 1999) and segmented into gray and white matter. The cortical surface information will be processed by FreeSurfer surface-based stream for the morphologic analysis (Dale et al., 1999). The functional images were analyzed by FreeSurfer Functional Analysis Stream package for preprocessing motion correction (Cox and Jesmanowicz, 1999), spatial smoothing (a Gaussian kernel of

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