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Visual bandwidths for face orientation increase during healthy aging

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ABSTRACT

Perception of visual motion declines during healthy aging, and evidence suggests that this reflects decreases in cortical GABA inhibition that increase neural noise and motion bandwidths. This is supported by neurophysiological data on motion perception in senescent monkeys. Much less is known about deficits in higher level form vision. For example, face perception of frontal views remains relatively constant from adolescence through age 70 with a modest decline thereafter. However, we have shown recently that the elderly have a specific deficit in face matching when a transformation must be made between frontal and left or right side views. Here we use face view adaptation to demonstrate that this deficit results from significant broadening of cortical bandwidths for face orientation along with increased internal noise. A neural model shows that these bandwidths increase by a factor of 1.74 between age 26 and age 67 years. This is similar to the increase reported for motion bandwidths in senescent monkeys. Furthermore, the neural model demonstrates that head orientation bandwidth increases can arise from decreased cortical inhibition. Thus, high levels of form vision degrade in parallel with higher levels of motion perception and likely result from similar causes.

1. Introduction

Many low level aspects of vision decline with age, including contrast sensitivity (Owsley, Sekuler, & Siemsen, 1983). Except at low contrasts or in noise, however, there is little evidence of decline in orientation discrimination (Betts, Sekuler, & Bennett, 2007; Govenlock, Taylor, Sekuler, & Bennett, 2009), an attribute of primary visual cortex (V1). Contrast response functions in V1 neurons show much smaller effects of age than do neurons higher up the dorsal pathway in the middle temporal area (MT) (Yang et al., 2009). Several major aging defects are manifest in MT: increased bandwidths for motion direction (Liang et al., 2010), increased neural noise, decreased speed sensitivity (Yang et al., 2009), and decreased inhibition (Leventhal, Wang, Pu, Zhou, & Ma, 2003). Psychophysical studies of human motion processing also show high level motion deficits in the elderly (Betts, Taylor, Sekuler, & Bennett, 2005; Norman, Ross, Hawkes, & Long, 2003).

In contrast, deficits in the ventral visual pathway have been reported to be modest during aging. Face perception represents a key example of processing in the ventral stream in both monkeys (Gross, 1992) and humans (Kanwisher, McDermott, & Chun, 1997). Face discrimination in the elderly is reportedly normal except when stimuli are presented in noise or at low contrasts (Crook & Larrabee, 1992; Grady, 2002; Owsley, Sekuler, & Boldt, 1981). However, previous studies have primarily utilized front views of faces, although a key aspect of face perception is transformation of faces between views for comparison. In agreement, we recently demonstrated that the visually healthy elderly perform identically to young controls on a task restricted to faces in a single view (Habak, Wilkinson, & Wilson, 2008). However, when the task involved matching between front and 20° side head orientations, the elderly showed a persistent deficit at all stimulus durations (Habak et al., 2008). This task requires a transformation or association between head views, and there is evidence that associative memory related to faces is specifically compromised in aging (Naveh-Benjamin, Guez, Kilb, & Reedy, 2004). We therefore explored the nature of this face-view transformation deficit in healthy aging by asking whether bandwidths for face orientation broaden with age, similar to primate motion bandwidths (Liang et al., 2010). As fMRI adaptation studies indicate that multiple face views are represented in the human fusiform face area (FFA) (Grill-Spector & Malach, 2001), we hypothesized that a bandwidth increase for face orientation might explain elderly deficits in head view transformations. This hypothesis was tested using a recently introduced face adaptation aftereffect (Fang & He, 2005), which is analogous to the well-known tilt aftereffect (Gibson & Radner, 1937). Our data demonstrate that the aftereffect is more than twice as large in the elderly as in young controls and that internal noise is also greater. A neural model of face orientation tuning shows that a 1.74-fold increase in bandwidths in the elderly can explain these results and that these bandwidth increases can occur in consequence of decreased cortical inhibition between neural representations of different face views.

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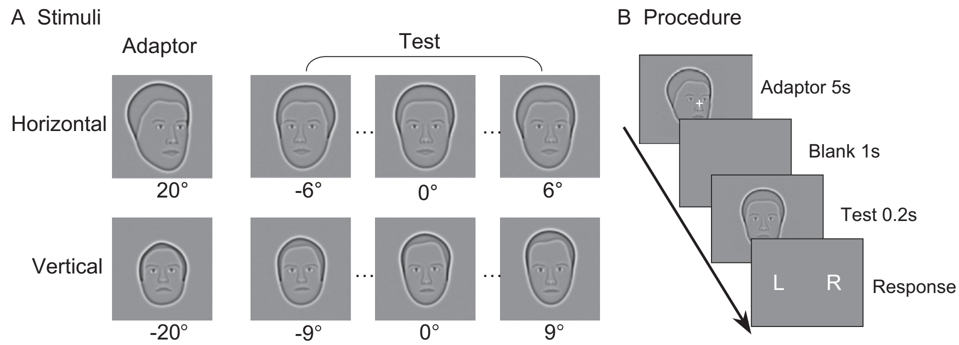

Fig. 1. Adapting and test stimuli (A) and stimulation sequence for each trial (B). (A) In left/right tests, adaptation was to a 20° side view synthetic face, and this was followed by one of seven test stimuli spanning a ±6° range around frontal. For vertical tests, adaptation was to a 20° upward stimulus, which was followed by a ±9° range of vertical stimuli centered on frontal. (B) Subjects fixated the white cross during 5.0 s of adaptation during which the adapting face shifted randomly every second (see Section 2). Following this, the screen returned to the mean luminance for 1.0 s, then a test face was flashed for 200 ms, and then the response options appeared (L R, or U D). The subject used the mouse to point to the appropriate response and clicked the mouse button.

2. Methods

2.1. Stimuli

Stimuli were created in Matlab™ and presented on a Macintosh computer with resolution of 1280 × 1024 pixels. At the viewing distance of 131 cm the screen subtended 14.8° by 11.8° with mean luminance of 80.0 cd/m^2. We used synthetic faces, constructed as previously described (Wilson, Loffler, & Wilkinson, 2002). These have been shown to stimulate human FFA very effectively (Loffler, Yourganov, Wilkinson, & Wilson, 2005). Adaptation and test faces were bandpass filtered to a spatial frequency optimal for face discrimination (Gold, Bennett, & Sekuler, 1999; Näsänen, 1999), which was 10.0 cycles/face width or 8.0 cpd at our viewing distance. The test faces near the frontal view (0°) were oriented at ±6°, ±4°, ±2°, and 0° for the left/right adaptation experiments. Seven views were also used for the up/down experiments, but with orientations of ±9°, ±6°, ±3°, and 0°, reflecting greater difficulty in the vertical task. See Fig. 1 for examples. Each test face was presented 10 times at random during an experiment for a total of 70 presentations. All subjects completed all experimental conditions.

2.2. Subjects

Fifteen older subjects (mean age 67 ± 5.4 years, range 58–70) and 15 younger subjects (mean age 26 ± 5.4 years, range 19–35) participated in the study. All had normal or corrected acuity of 20/20 or better. An eye examination was conducted on each older subject including refraction, ophthalmoscopy, biomicroscopy, tonometry, and stereoscopy. Subjects were also screened for general health and for use of any medications that might affect visual function. Older subjects used a 0.75D distance correction lens.

2.3. Experimental procedure

Each experimental trial began with fixation on a cross at the middle of the screen. The adapting face then appeared for a total of 5 s and jumped randomly within ±21.0 arc min each second to minimize low level contour adaptation. Following adaptation and a 1.0 s blank period at mean luminance, a test face was flashed for 200 ms positioned randomly within ±21.0 min. Letters "L" and "R" ("U" and "D" for the up/down experiment) then appeared on the screen and the subject indicated whether the test appeared left or right of frontal by clicking the appropriate letter (see Fig. 1). Trials were self-paced by the subject.

2.4. Modeling

Bandwidth models were implemented using Matlab™ software on a Macintosh computer. The effects of noise were estimated using a Monte Carlo simulation with 10,000 repetitions with a separate random noise sample for each.

3. Results

3.1. Face view adaptation

To measure bandwidths for horizontal face rotations, subjects were first adapted to either a frontal face view (control condition) or else a left/right 20° side view of a face for 5.0 s. Following adaptation for 5.0 s, one of seven faces near the frontal view was flashed for 200 ms (Fig. 1). In a two alternative forced choice task the subject indicated whether the flashed face was perceived as rotated left or right of a frontal view. The data were fit with a cumulative normal distribution, with the mean estimating the point of subjective equality (PSE), and the standard deviation, σ, estimating slope. Experiments were also run in which the adapting face was oriented 20° upward, and test faces were oriented slightly upward or downward relative to frontal.

To determine whether elderly subjects (age 67 ± 5.4 years) could perform these tasks as effectively as younger ones (age 26 ± 5.4 years), a control condition was first run in which subjects adapted to a frontal face view. The horizontal and vertical baseline responses averaged across subjects are depicted in Fig. 2A and B respectively. Mean PSEs were −0.04 ± 0.76° (young) and 0.25 ± 0.76° (elderly). A 2 × 2 repeated measures ANOVA showed no effect of either age ($p = 0.52$, n.s.) or rotation axis (left/right or up/down, $p = 0.39$, n.s.) and no interaction ($p = 0.31$, n.s.). Subsequent t-tests showed that the PSE did not differ significantly from the true frontal orientation of 0.0° for either group ($p > 0.22$). A similar analysis of σ from the individual fits revealed no significant difference between ages, with the averages being 1.15 ± 1.51° (elderly) and 1.35 ± 0.96° (young). However, σ for the up/down discrimination task was significantly larger ($F_{[1,20]} = 21.32$; $p < 0.0001$) than for left/right, averaging 3.53 ± 2.63° (elderly) and 2.95 ± 1.75° (young). This increased noise reflects the greater difficulty of the up/down task. Clearly, the elderly can perform face view adaptation experiments without difficulty and with comparable accuracy to the young in our control task.

Results following adaptation to a 20° left or right oriented face are plotted in Fig. 2C. The blue[1] lines and symbols show that adap-

[1] For interpretation of color in Fig. 3, the reader is referred to the web version of this article.