Aging and the depth of binocular rivalry suppression

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Abstract

A single experiment was designed to examine the effect of aging upon the strength of binocular rivalry suppression. To initiate the onset of rivalry, orthogonally-oriented sine-wave luminance gratings were presented dichoptically to the observers' two eyes. On each trial, a small probe spot was presented in one of four randomly chosen locations to either the dominant or suppressed eye's view. The observers' task was to detect the location of the probe. The observers in both the younger and older age groups exhibited significant suppression (i.e., the probe was easily detected when presented to the dominant eye, but it was much more difficult to detect when presented to the suppressed eye), but the magnitude of the suppression was 75 percent greater in the older observers. The greater suppression of older observers was attributed to a deterioration in their ability to make judgments about the characteristics of unattended environmental stimuli.

Aging and the depth of binocular rivalry suppression

We human observers view the world with two eyes. The left and right eyes' retinal images are always slightly different, because our eyes view the same 3-dimensional (3-D) scene from two different vantage points. The differences between the positions of corresponding object features in the left and right eyes' retinal images, referred to as *binocular disparities*, greatly facilitate our ability to perceive depth and 3-D object shape (e.g., see Howard & Rogers, 1995; Julesz, 1971; Wheatstone, 1838). The ability to perceive depth and 3-D object shape from binocular disparity is called stereopsis. Recent research has demonstrated that stereopsis is largely preserved with increases in age, although modest quantitative differences do exist between the stereoscopic capabilities of younger and older adults (Norman, Dawson, & Butler, 2000; Norman, Crabtree, Herrmann, Thompson, Shular, & Clayton, 2006).

In normal visual situations, neural mechanisms within the brain "fuse" the two eyes' similar, but disparate, retinal images into a unified perception of the environment. Whenever the two eyes retinal images are highly discordant, however, fusion fails and binocular rivalry occurs: an observer may first see only the left eye's image, while the right eye's image is suppressed. After a few seconds of left-eye dominance, the right eye's image becomes visible and the left eye's image is simultaneously suppressed. This alternating pattern continues as long as the contradictory images are viewed. The phenomenon of binocular rivalry has been known for centuries (e.g., Breese, 1899; Wheatstone, 1838, pp. 386-387) and has been extensively studied over the past 40 years (Blake, Fox, & McIntyre, 1971; Blake & Lema, 1978; Blake & Camisa, 1979; Blake, Yu, Lokey, & Norman, 1998; de Weert & Wade, 1988; Fox & Herrmann, 1967; Fox & Check, 1972; Fukuda & Blake, 1992; Halpern, Patterson, & Blake, 1987; Hollins, 1980; Lee & Blake, 1999; Levelt, 1968; Mueller & Blake, 1989; Norman, Norman, & Bilotta, 2000;

O'Shea, Sims, & Govan, 1997; Wade, de Weert, & Swanston, 1984; Westendorf, 1989). It is therefore surprising that little research has investigated the effects of age upon binocular rivalry. The only previous research on aging and binocular rivalry indicated that the rate of binocular rivalry alternations slows with age (Jalavisto, 1964; Ukai, Ando, & Kuze, 2003). This effect, however, is apparently quite small: the results of Ukai et al. indicate that only 14 percent of the variance in their observers' alternation rates was due to differences in age. No other characteristic of binocular rivalry has been measured in older adults; little is therefore known at present about how binocular rivalry changes with increasing age. One purpose of our experiment was to fill this void.

From recent neurophysiological findings, it is clear that many areas within the brain are involved in binocular rivalry, from subcortical areas such as the lateral geniculate nucleus to primary visual cortex to extrastriate and frontal cortex (e.g., Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Lumer, Friston, & Rees, 1998; Polonsky, Blake, Braun, & Heeger, 2000; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Tong & Engel, 2001; Wunderlich, Schneider, & Kastner, 2005). Many prominent theories of binocular rivalry (e.g., Blake, 1989; Mueller, 1990; Wilson, 2003; also see Tong, 2001) have postulated that monocular neurons in early cortical areas, such as primary visual cortex, detect significant inconsistencies between the two eyes' views and then initiate the onset of binocular rivalry through reciprocal inhibition. Recent research using single-unit recording on senescent macaque and rhesus monkeys (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky, Wang, Pu, & Leventhal, 2000) has indicated that aging leads to deterioration in the functionality of inhibitory synapses within primary visual cortex. Given this age-related degradation in inhibition within primate primary visual cortex and the presumed importance of this inhibition for the onset of binocular rivalry, one would therefore expect that increases in age would lead to significant changes in binocular rivalry suppression. In particular, in the absence of any other available information, one might expect that the depth or magnitude of older observers' binocular rivalry suppression would be less than that of younger observers, given that they have less inhibition present within their primary visual cortices. An additional purpose of our experiment was to evaluate whether older human observers do in fact show age-related changes in the depth of binocular rivalry suppression.

Method

Apparatus. The rivalrous stimuli were created by a dual-processor Apple PowerMacintosh G4 computer (1.42 GHz) and displayed on a 22-inch Mitsubishi Diamond Plus 200 color monitor. The resolution of the monitor was 1280 x 1024 pixels. The dichoptic displays were presented to the observers using CrystalEyes3 LCD-shuttered glasses (StereoGraphics, Inc.). The viewing distance from the observer to the monitor was 100 cm.

Stimulus displays. Sine-wave luminance gratings were presented to both eyes: a vertically-oriented grating was presented to the observers' left eye, while an otherwise identical horizontally-oriented grating was simultaneously presented to their right eye. The contrast and spatial frequency of the gratings was set to 50 percent and 1.75 cycles/degree visual angle, respectively. A sample dichoptic stimulus is illustrated in Figure 1. The projected width and height of the gratings in each eye's half-image was 1.15 deg. Each grating was surrounded by a pair of gray square-shaped contours that helped the observers to maintain appropriate convergence. The spatial phase of the depicted gratings was randomly varied across trials. A small black square (6.9 minutes arc both in width and height) was presented at the center of each grating, and the observers were required to maintain steady fixation upon it during each trial.

Procedure. Each observer participated in two experimental sessions, with each session containing 50 trials; therefore the observers judged a total of 100 rivalrous stimuli. On each trial, a small (6.9 minutes arc) probe square was briefly (200 ms) presented at one of four randomly determined locations within the stimulus pattern (near the top, bottom, left, or right edges). While viewing the rivalrous patterns of a particular trial, each observer was required to continuously report whether they perceived exclusive (i.e., they only saw either the left eye's stimulus or only the right eye's stimulus) or piecemeal rivalry (i.e., they saw a mosaic containing "pieces" of each eye's stimuli; some pieces coming from the left eye's stimulus, with other pieces coming from the right eye's stimulus). If the observers perceived exclusive rivalry, they were asked to indicate whether they saw the horizontally-oriented grating only or the vertically-oriented grating only. On half of the trials, the probe was presented to a grating when it was exclusively dominant (i.e., visible), and on the remaining half of the trials, the probe was presented to a grating when it was exclusively suppressed (i.e., not currently visible at all). The probe was presented immediately at the beginning of a particular phase of rivalry alternation. The observers' task on each trial was to judge the location of the probe (left, right, top, bottom).

If we had used a probe with a fixed brightness, its visibility would have depended upon the location where it was presented within the stimulus pattern. For example, a light probe spot would be easily detected if it were placed against a dark region within the pattern, but would be difficult to detect if placed against a lighter region within the stimulus. Rather than using a fixed-intensity probe, we used probes that had a brightness that was determined by the intensity of the background region it was placed against. In particular, all probes had an intensity that was a fixed increment from the intensity of the background. Prior to the start of the experiment, pilot testing with non-rivalrous stimuli (identical gratings of the same orientations were presented to both eyes) was conducted for each individual observer to determine the probe brightness increment needed for a performance of 80 percent correct judgments.

Observers. Sixteen observers participated in the experiment: eight older observers (mean age was 66.4 years, SD = 4.8; the range of their ages was 60 to 74 years) and eight younger observers (mean age was 22.4 years, SD = 2.1; the range of their ages was 20 to 26 years). Two potential older observers were excluded: one could not see the probe spot even under the best of circumstances, while the other had a rate of rivalry alternation that was so fast that we could not reliably present the probe to the desired eye's view. One potential younger observer was excluded because she always perceived piecemeal rivalry, while the results of another younger observer were excluded because she was stereoblind.

All of the observers, both younger and older, possessed excellent acuity; all of their acuities were 1.0 min^{-1} or better (1.0 min^{-1} is equivalent to 20/20 vision measured at 20 feet). Similarly, all observers possessed good stereopsis and were able to perceive and spontaneously describe the depth and shape of 3-dimensional surfaces depicted in random-dot stereograms (cf., Julesz, 1964, 1971). The observers were asked (i.e., self report) whether they possessed eye or retinal problems, such as macular degeneration, glaucoma, or cataracts (none were reported). If the observers typically wore corrective lenses (e.g., bifocals, trifocals), they used the correction that gave the best acuity to view the experimental stimuli.

Results

The results are shown in Figure 2 for both the older and younger observers. As can be clearly seen in the figure, there was a large effect of rivalry suppression: the observers' spatial discrimination performance was good when the probe was presented to the dominant eye's view, and was greatly reduced when it was presented to the suppressed eye's view ($F(1, 14) = 231.0$, $p < .0001$, $MSE = 37.7$, $\eta^2 = .94$). The main effect of age was not significant ($F(1, 14) = 4.1$, $p > .05$), but there was a highly significant age x suppression interaction ($F(1, 14) = 17.2$, $p = .001$, $MSE = 37.7$, $\eta^2 = .55$). The depth or magnitude of the younger observers' suppression is almost identical to that which was obtained in a similar earlier experiment from our laboratory (H. F. Norman et al., 2000, see Figure 2b). The older observers' depth of suppression was 75 percent larger than that exhibited by the younger observers.

Despite the larger depth of rivalry suppression experienced by the older observers, they performed just as well in the spatial discrimination task as the younger observers when the probe was presented to the dominant eye. In order to obtain this equal performance in the dominant eye's view (80 percent correct), the older observers required larger luminance increments than the younger observers (i.e., a brighter probe spot; $t(14) = -4.1$, $p = .001$, 2-tailed). This was expected. Weale (1963) has shown that the retina of a typical 60-year old receives only one-third of the light that the retina of a 20-year old would receive. It is therefore not surprising that in order to create equivalent performance (in the dominant condition) for both age groups that the probe needed to be brighter for the older observers.

Discussion

Given the neurophysiological findings of less inhibition in the primary visual cortex (V1) of senescent monkeys (Leventhal et al., 2003; Schmolesky et al., 2000), and the fact that many prominent theories and computational models of binocular rivalry (e.g., Blake, 1989; Mueller, 1990; Wilson, 2003) postulate reciprocal inhibition within V1, one might have therefore expected to find that increasing age in human observers would lead to less rivalry suppression. Instead, our results conclusively indicate the opposite: the strength of older observers' rivalry suppression is much greater than that of the younger observers. In our experiment, when the probe was presented to the dominant eye's view, all observers, both younger and older, performed equally well; in contrast, when the probe was presented to the suppressed eye's view, the younger observers were able to detect the location of the probe much more accurately than the older observers (55.8 vs. 38.0 percent correct, respectively). Despite the reduced performance of the older observers in the suppressed condition, their ability to detect the location of the probe was significantly better than chance ($\chi^2 = 40.5$, $p < .0001$).

At first glance, the results of the current experiment are somewhat puzzling (i.e., there are good reasons to expect less suppression with age, but our results conclusively indicate that older observers have stronger rivalry suppression). The current results, however, are understandable within the context of the wider literature on aging. It is possible to view rivalry suppression as a "withdrawal of attention" (see Blake, Tadin, Sobel, Raissian, & Chong, 2006). For example, during a particular phase of binocular rivalry the observer is "attending" to the stimulus presented to the dominant eye, while at the same time they definitely cannot attend to the stimulus presented to the suppressed eye (because it is not visible). A variety of studies (Czigler, Csibra, & Csontos, 1992; Mitchell & Perlmutter, 1986; Owsley, Burton-Danner, & Jackson, 2000; Plude & Hoyer, 1986) have shown that older observers perform more poorly when asked to judge the properties of an unattended stimulus (analogous to judging the "unattended" or suppressed stimulus in our experiment).

The participants in the study by Czigler et al. (1992) were asked to read a book (of their own preference) during experimental sessions that lasted 2.5 hours. While reading, the participants were presented with auditory tones that normally had a frequency of 950 Hz. On a random 10 percent of the presentations, however, a higher frequency (1045 Hz) tone was substituted in place of the lower-pitched tone. Auditory event-related brain potentials (ERP's) were measured during the presentation of the tones. The participants were instructed to ignore the tones and focus their attention on reading the book. The deviations in frequency of the non-attended tones triggered smaller negative ERP's (i.e., there was less of a brain response) in the older as compared to the younger participants (e.g., see their Figure 3).

Mitchell and Perlmutter (1986) visually presented target and flanking words (the target words were displayed in red, while the flankers were black). The participants were instructed to attend to only the target words and to ignore the flankers. The participants performed both semantic (was the target animate or inanimate?) and nonsemantic (was the target printed in uppercase or lowercase letters?) tasks. The participants were later asked to recall the target and flanker words. Mitchell and Perlmutter found that when the recall test was expected, the older participants recalled fewer nonattended (i.e., flanker) words than the younger participants.

In the search condition of Experiment 1 of Plude and Hoyer (1986), the participants attended to a fixation cross and were then presented with a visual array of five letters. On half of the trials, a target consonant was presented in an unattended randomly chosen location (one target plus four nontargets). In the remaining trials, the target was not present in the array (all five letters were nontargets). The participants were required to judge on each trial whether the target was present or absent. The results showed that the task was much more difficult for the older participants (i.e., they took a much longer time to make their yes/no decision).

The observers in the experiment conducted by Owsley et al. (2000) attended to a central fixation cross. A stimulus display containing a target (a red bar) and distractors (green bars) was then displayed for 80 msec. The target was unattended (at least at the beginning of the stimulus display), because the observers were required to focus their attention upon a centrally-located fixation marker, and when the target did appear, it was located at an unknown and random location. The observers' task was to indicate the location where the target appeared on each trial. Owsley et al. concluded that "older adults in this study made more localization errors during feature search than did young adults, and their mislocalizations deviated by greater distances on average than those of younger adults."

In this review, we have seen that age-related deficits occur in: 1) the recall of an unattended visual item (Mitchell & Perlmutter, 1986), 2) judging the presence or absence of an unattended target (Plude & Hoyer, 1986), and 3) judging the location of an unattended target (Owsley et al., 2000). The findings of our current experiment most closely resemble those of Owsley et al. In our experiment (as in theirs), our older observers had much more difficulty (see Figure 2) than younger observers in detecting the spatial location of an unattended target. At least at the beginning of the stimulus display, the observers of Owsley et al. were not attending to the target because when it appeared, the target was presented at an unexpected random location. The observers' attention may have been drawn to the target after its appearance, but initially at least, the target location was unattended. In our experiment when the target was unattended (because it was presented to the suppressed eye's view during binocular rivalry), a large effect of age upon spatial localization was apparent as well. Perhaps the current finding of age-related effects upon the magnitude of binocular rivalry suppression is a reflection of a more general phenomenon that occurs whenever older observers are required to make judgments about the presence, location, or other characteristics of an unattended perceptual stimulus. When seen in this light, a suppressed eye's view during binocular rivalry is the ultimate unattended stimulus.

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Figure captions

Figure 1 -- An example of the sine-wave luminance gratings that were used as the rivalrous experimental stimuli. The gratings were viewed dichoptically so that the vertically-oriented grating was viewed by the observers' left eye while the horizontally-oriented grating was viewed by the right eye. The small central black square was used as a fixation marker. The small grey square shown against the vertically-oriented grating is a example of a probe stimulus (towards the right edge of the grating in this example).

Figure 2 -- Experimental results for both the younger and older observers. The observers' spatial discrimination accuracy is plotted for both the dominant and suppressed experimental conditions. The horizontal line indicates chance performance (i.e., 25 percent correct). The error bars indicate ± 1 SE.

Author notes

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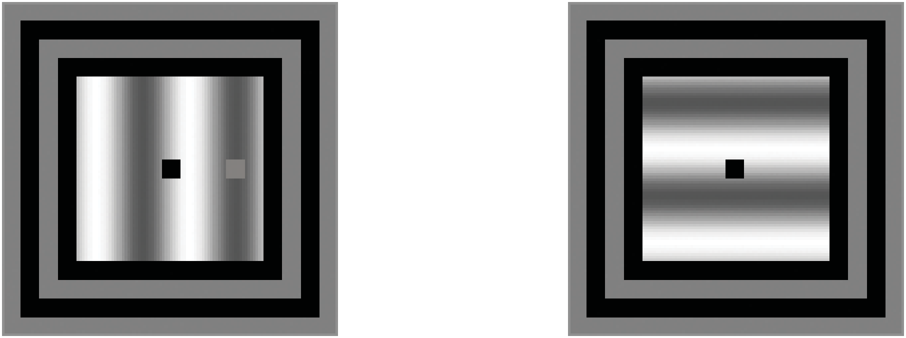

Figure 1

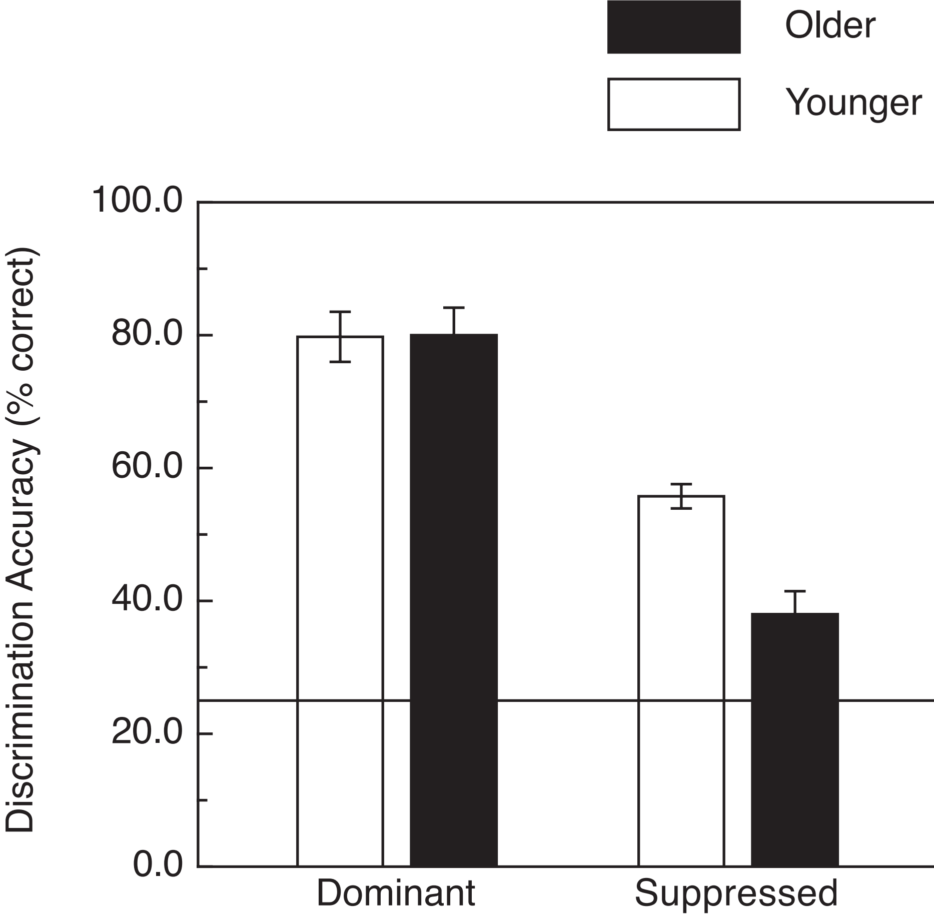
Older
Younger
Discrimination Accuracy (% correct)
100.0
80.0
60.0
40.0
20.0
0.0
Dominant
Suppressed

Figure 2