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Aging and visual processing: Declines in spatial not temporal integration

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Abstract

Age-related declines in vision are well documented in the literature. In the present study we examined whether changes in spatial or temporal integration contribute to this decline. Younger (mean age of 21) and older (mean age of 745) subjects were asked to identify 2D shapes based on kinetic occlusion information—the accretion and deletion of texture during motion. The results of the first experiment indicated age-related decrements in spatial but not temporal integration. In the second experiment we manipulated the lifetime of motion stimuli to more directly examine temporal integration. The results indicated no differential effect of age on temporal integration. The results considered together suggest age related changes in recovering 2D shape from occlusion are the result of spatial but not temporal integration. Age-related changes in neural inhibition and ACh for regulating spatial integration are proposed as possible mechanisms for this decline.

Keywords: Aging; Motion perception; Spatial integration; Temporal integration; Shape perception

1. Introduction

Visual processing requires the integration of information over space and time. For example, consider how the visual system perceives a 2D form from fragmented image information. In order to perceive the form, the visual system must combine local fragments (e.g. line segments) across space to recover the shape of the form. Information for perception can also be available from different time intervals. For example, consider the perception of a moving object partly obscured by nearer objects. In order to perceive the form the visual system must integrate the different parts of the object visible at different time intervals. These examples highlight the role of spatial and temporal integration in vision.

Evidence of spatial and temporal integration has been shown in studies examining neuronal activity in the visual system. For example, at the earliest levels of visual processing cells respond to information present over a limited region of the visual field (e.g., Arnett, 1972; Barlow, 1953). The visual system spatially combines or integrates information from local receptive field regions via intracortical connections from other cells within a cortical region (e.g., Brown, Allison, Samonds, & Bonds, 2003; Das & Gilbert, 1999; Stettler, Das, Bennett, & Gilbert, 2000) and from cells in higher cortical regions (Bullier, Hupe, James, & Girard, 2001; Moore & Armstrong, 2003; see Roberts et al., 2005 for a detailed discussion). Spatial integration has been demonstrated to be important for visual processing including motion perception, (e.g., Ledgeway & Hess, 2002; Vaina & et al., 2003; Watamaniuk, McKee, & Gryzwacz, 1995) form perception (e.g., Aspell, Wattam-Bell, & Braddick, 2006; Field, Hayes, & Hess, 1993; Kovacs, 1996) and brightness induction (Hong & Shevell, 2004).

Neurophysiological studies have also examined the role of temporal integration by the visual system. For example, studies have examined the role of temporal integration for motion perception in primary visual cortex (V1) and extrastriate motion area (MT/V5) (e.g., Bair & Movshon,

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2004) and the role of the lateral interparietal area for perceptual decision regarding motion (Huk & Shadlen, 2005). Temporal integration at a neural level has been argued to be due to the synchronous activity of groups of neurons rather than the firing rate of a single neuron (Shadlen & Movshon, 1999; Shadlen & Newsome, 1994). Temporal integration has been shown to be important in visual processing in motion perception (Baker & Braddick, 1985) visual masking, (Breitmeyer, 1984; Enns & Di Lollo, 2000) and form perception (Andersen & Cortese, 1989; Blake & Lee, 2005; Kellman & Shipley, 1992; Lee & Blake, 1999).

A growing body of literature suggests that visual processing declines with age. These studies have shown decreased performance in motion perception (Atchley & Andersen, 1998; Bennett, Sekuler, & Sekuler, 2007; Gilmore, Wenk, Naylor, & Stuve, 1992; Trick & Silverman, 1991), surface detection (Andersen & Atchley, 1995), collision detection (Andersen, Cisneros, Saidpour, & Atchley, 2000; Andersen & Enriquez, 2006), binocular disparity (Norman, Crabtree, & Hermann, 2006), shape perception (Norman, Clayton, Shular, & Thompson, 2004) and shape from motion (Wist, Schrauf, & Ehrenstein, 2000). Furthermore, age-related declines in visual processing cannot be solely accounted for by changes in the optical characteristics of the eye (Ball & Sekuler, 1986; Sekuler, Bennett, & Mamelak, 2000). In the present study we used a novel perceptual task to examine whether age-related declines in visual processing were the result of changes in spatial or temporal integration. To assess this issue we used a visual task that requires both spatial and temporal integration—the recovery of 2D shape from kinetic occlusion. Kinetic occlusion can specify 2D shape by providing information regarding edge boundaries of an object based on the accretion and deletion of texture over time. Consider an opaque object positioned in front of a background (see Fig. 1). If the object and background have identical random texture (e.g., randomly positioned dots) then the object boundaries cannot be seen. However, if the object moves (or the background moves) then the accretion and deletion of the background texture can be used to define the boundaries of the object. In order to recover the object boundary the visual system must integrate the accretion and deletion of texture over space (i.e., discrete samples of the edge boundary are specified by the local disappearance/reappearance of texture) and time (i.e., the accretion and deletion of texture occur in local intervals of time).

Previous research (Andersen & Cortese, 1989) examined the importance of kinetic occlusion for specifying the shape of 2D objects. College-age subjects were presented with displays of a moving opaque object with random dot texture against a random dot texture background. The velocity and texture of the display was varied and subjects were asked to identify which of four shapes were present. The results indicated that an increase in velocity and density resulted in greater accuracy in shape identification. The results also indicated that density was the primary factor in determining performance. Indeed, the variance accounted for (ω^2) by the main effect of density was 35% compared to 4% for the main effect of velocity.

An important issue examined in their study was whether performance was based on the rate of occlusion events (the number of occlusion events per unit time). To examine this issue they compared performance across conditions in which velocity and density changed proportionally resulting in a constant rate of occlusion events. For example, an occlusion stimulus with a velocity of 0.8 deg/s and a density of 1.2 dots/deg^2 was compared to an occlusion stimulus with a velocity of 1.6 deg/s and a density of 0.6 dots/deg^2. These two conditions have identical rates of occlusion events (i.e. disappearance/reappearance of texture). The results indicated that performance varied across conditions with a constant rate of occlusion events, with performance increasing due to an increase in density. These findings led Andersen and Cortese to conclude that, although temporal integration from velocity was important, that spatial integration from texture density was the primary factor in shape perception from kinetic occlusion.

In the present study we examined conditions similar to those examined by Andersen and Cortese (1989). Subjects

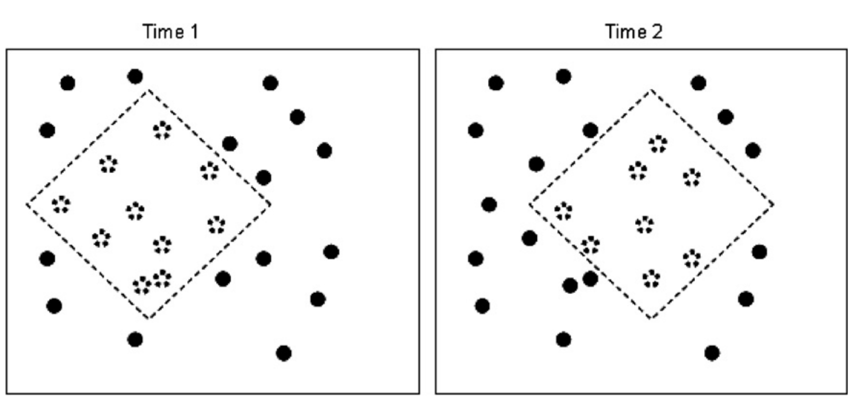

Fig. 1. Schematic illustration of the stimuli used in the present study. An implicit 2D shape (diamond) was presented and translated left and right. As the object moved texture on a background surface was occluded by the opaque object. The disappearance and reappearance of the texture provided kinetic occlusion information that could be used to recover the shape boundary.

were shown kinetic occlusion displays and were asked to identify the 2D shape of a moving form. Information for spatial and temporal integration was manipulated by changing velocity and texture density. Information for spatial and temporal integration was manipulated by changing the texture density of the display. Specifically, an increase in density will result in an increase in spatial and temporal information for the edge boundary. Information for temporal integration was manipulated by varying the speed of motion. If the velocity of the object is increased then the rate of accretion and deletion is increased, resulting in an increase in information for temporal integration. If age-related decrements in visual processing are due to changes in temporal integration, then we predict that object identification performance will be significantly worse for older observers as compared to younger observers at slower speeds.

To isolate the role of spatial integration we examined variations in performance when the rate of occlusion events was constant. If the velocity of the moving object is decreased and the texture density is increased proportionately then the spatial separation of accretion and deletion of texture that defines the object boundary is decreased while the rate of occlusion events is constant. If age related decrements in visual processing are due to changes in spatial integration then we predict that object identification performance will be significantly worse for older observers as compared to younger observers at lower texture densities with constant rates of occlusion.

2. Experiment 1

In the first experiment we examined age-related decrements in the perception of 2D shape from kinetic occlusion. The displays consisted of random dots projected onto either a 2D shape (circle, square, diamond, or 5 point star) or the background. The primary variables of interest were dot density, velocity of object, and the absence/presence of background texture (i.e. providing kinetic occlusion information when background texture was present). If older observers have a decreased capacity for spatially integrating kinetic occlusion information, then we expect poorer performance for older observers with a decrease in dot density when background texture is present, particularly when the rate of occlusion is constant. Of course observers may be able to determine the shape if a high level of texture density is present on the object. To address this issue we included conditions in which no background texture (and no kinetic occlusion information) was available.

2.1. Method

2.1.1. Observers

The observers were 18 younger subjects (9 women and 9 men) from the University of California, Riverside campus and 18 older subjects (9 women and 9 men) from the Life Society Program, a continuation education program at the University of California, Riverside. All were paid for their participation, had normal or corrected to normal vision, and were naïve with regard to the purpose of the experiment. All observers were screened using several perceptual and cognitive tests. Demographic information regarding all of the observers used in the present experiments, and the results of these screening tests, are presented in Table 1.

Table 1
Means and standard deviation (in parentheses) of demographic information and results from perceptual and cognitive tests

	Younger	Older
Age (years)[a]	21.3 (2.3)	74.7 (6.6)
Years of Education[a]	13.1 (1.5)	16.2 (2.4)
Snellen letter acuity	10/10.2 (1.5)	10/12.1 (2.3)
log contrast sensitivity[a,b]	1.75 (0.08)	1.45 (0.13)
Digit span forward	11.0 (1.8)	10.7 (1.8)
Digit span backward	8.1 (1.9)	6.8 (1.5)
Perceptual encoding		
Manual[a]	42.9 (5.1)	30.6 (4.9)
KBIT Vocabulary[a]	20.9 (2.1)	27.5 (3.4)

[a] Differences between age groups significant at the .05 level or less for both sets of age groups.
[b] Contrast sensitivity measured using Pelli-Robson test (Pelli, Robson, & Wilkins, 1988).

2.1.2. Design

Four within-subject independent variables were investigated: the presence of absence of kinetic occlusion, dot density (0.61, 1.22, 1.83, or 2.44 dots/deg^2), object velocity (1.0, 2.0, 4.0, or 8.0 deg/s), and size (objects subtended a square region that was either 4.2 or 6.5 deg horizontally and vertically). Age was run as a between subjects variable (mean age for the older and younger groups was 74.7 and 21.3, respectively).

2.1.3. Stimuli

The stimuli were computer generated displays of white dots (.012 deg by .012 deg) projected onto an opaque black object against a black background. The luminance of the dots and background were 28.7 and .08 cd/m^2, respectively, resulting in a Michelson contrast ratio of 0.99. Four different object shapes were examined—circle, 5 point star, square, or diamond. The objects were positioned in the center of the display, and translated from the center to the right, to the left, and then to the right to the original position. Only dots projected onto the object translated. Background dots remained stationary. Display duration was 5 s with a refresh rate of 60 Hz.

2.1.4. Apparatus

The displays were generated using a Dell Dimension XPS computer and presented, in a dark room, on a 58.8 cm (resolution 1024 × 768) non-interlaced color monitor. The total viewing distance to the monitor was 57 cm resulting in a visual angle of 40 deg. To control for age-related differences in accommodative focus the displays were viewed through a large (45.7 cm diameter) Fresnel lens (Edmund Scientific; 200 grooves per 2.56 cm) to reduce accommodative focus differences between older and younger observers. A Fresnel lens, as compared to a glass plano-convex lens, can introduce slight chromatic and spherical aberrations. Informal observations, comparing the Fresnel lens and a glass plano-convex lens (used in Andersen, Saidpour, & Braunstein, 1998), suggests that the effect of aberrations with the Fresnel lens on the perception of moving dots was negligible.

2.1.5. Procedure

Subjects were informed that they would be shown a series of displays of one of four moving objects—a circle, 5 point star, diamond or square. The four shapes were demonstrated with cardboard models. They subjects were informed that their task was to identify which shape appeared in the display.

After observers understood the task they were presented with 1 block of 16 practice trials. The practice trials consisted of two presentations of each object (without kinetic occlusion present) at the two size conditions under high dot density levels (2.44 dots/deg^2) and translating at 4.0 deg/s. Subjects were required to correctly identify a minimum of 15 of 16 practice trials before proceeding to the experiment. No feedback was used.

Following the presentation of the practice block the experiment was started. Observers participated in two single-hour sessions conducted on separate days. In each session observers were presented 4 blocks of trials, with each block consisting of 2 replications of all 256 displays (absence/presence of kinetic occlusion by 2 sizes by 4 dot densities by 4 speeds by 4 shapes) presented in random order for a total of 512 trials per block. The total number of trials for each observer was 4096. No feedback was used during the experiment.

2.2. Results

The proportion correct was tabulated for each subject in each condition and analyzed using a 2 (presence/absence of occlusion) by 4 (density) by 4 (velocity) by 2 (size) by 2 (age group) Analysis of Variance (ANOVA). To protect against positive biases in the F tests, we computed the significance levels with conservative degrees of freedom (Greenhouse & Geisser, 1959). Note that for each analysis, the actual (rather than the conservative) degrees of freedom are shown. However, the p values given are those of the conservative degrees of freedom.

The overall effect of age was significant, $F(1,31) = 12.6$, $MSE = 0.15$, $p < .01$ and varied according to the absence/presence of kinetic occlusion, $F(1,31) = 10.7$, $MSE = 0.077$, $p < .01$. The results of this interaction are shown in Fig. 2. According to this result, older and younger observers showed similar levels of performance for the kinetic-occlusion absent condition. When kinetic occlusion was added, both groups showed greater shape identification with a greater increase in performance occurring for the younger as compared to older observers. This result suggests that younger observers, as compared to older observers, had a greater capacity for integrating spatial and temporal information for determining the boundaries of the object.

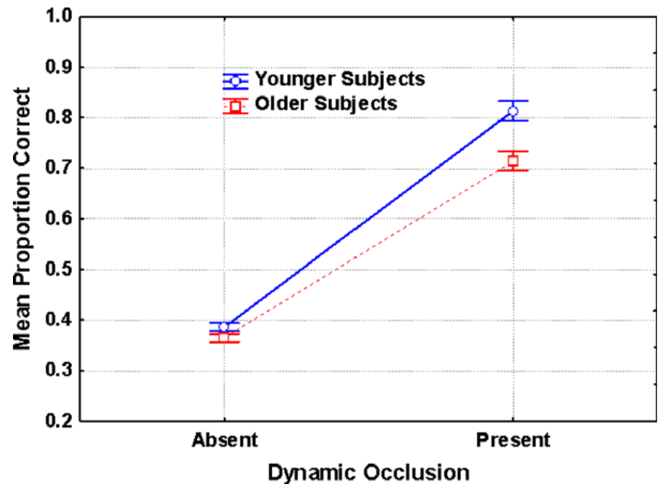

Fig. 2. Shape identification accuracy as a function of age and absence/presence of kinetic occlusion from Experiment 1. Error bars are ±1 standard error.

Based on these results we conducted several additional analyses of the data. The first analysis focused on age-related differences when kinetic occlusion information was absent. This analysis assessed how texture density, velocity, and size might be used for shape identification. The second analysis focused on age related differences when kinetic occlusion information was present. This analysis assessed (1) how texture density, velocity, and size might be used for shape identification and (2) how texture density, velocity, and size might provide spatial/temporal information of edge boundaries. The third analysis examined age-related effects of kinetic occlusion when spatial/temporal information was constant.

2.2.1. Kinetic occlusion absent

The proportion correct was tabulated for each subject in each occlusion absent condition and analyzed using a 4 (density) by 4 (velocity) by 2 (size) by 2 (age group) ANOVA. The main effect of age was not significant, $F(1,31) = 2.99$, $p > .05$. In addition, no significant interactions were obtained between age and velocity, age and density, or age and size, $p > .05$. The main effect of density was significant, $F(3,93) = 235.1$, $MSE = 0.01$, indicating that accuracy increased with an increase in texture density. The main effect of size was significant, $F(1,31) = 98.3$, $MSE = 0.01$, $p < .05$, indicating that greater accuracy in shape identification occurred for the larger size. Finally, the interaction of density and shape was significant, $F(3,93) = 7.4$, $MSE = 0.01$, $p < .05$. According to this result, the improved accuracy with increased density was greater for the larger size as compared to the smaller size. All other main effects and interactions were not significant, $p > .05$.

2.2.2. Kinetic occlusion present

The proportion correct was tabulated for each subject in each occlusion present condition and analyzed using a 4 (density) by 4 (velocity) by 2 (size) by 2 (age group) ANOVA. The main effect of age was significant, $F(1,31) = 13.7$, $MSE = 0.19$, $p < .05$. According to this result, accuracy was lower for older subjects (mean proportion correct of .71) as compared to younger observers (mean proportion correct of .81). In addition, the interaction between age group and density was significant, $F(3,93) = 8.85$, $MSE = 0.01$, $p < .05$, and is shown in Fig. 3. For comparison purposes we have included the age group and density interaction results from the occlusion absent condition. According to this result, there was a decrease in performance for older observers, as compared to younger observers, at lower density levels. These results suggest that age-related decrements in recovering shape from kinetic occlusion might be due to a decreased ability to spatially integrate information. An important issue is whether this interaction is the result of ceiling effects for younger observers at the highest density levels. For the 1.83 density condition the number of younger and older subjects with performance greater than or equal to 95% was 1 and 0, respectively. For the 2.44 dot density condition the number of younger and older subjects with performance greater than or equal to 95% was 12 and 9, respectively. Furthermore, if we exclude the highest density condition from the analysis (focusing on the effects of density at the other 3 levels) the age by density interaction is also significant, $F(2,62) = 5.4$. These results suggest that the age by density interaction was not due to ceiling effects for younger subjects.

No significant interactions were obtained between age and velocity, age and size, or any other higher order interactions with age, $p > .05$. The non-significant age by velocity interaction is shown in Fig. 4. For comparison purposes we have included the age by velocity interaction for the occlusion absent condition. As is shown in Fig. 4, age-related decrements in shape identification were approximately constant across variations in velocity. The lack of a significant interaction of age and velocity, $F(3,93) = 1.09$, $p > .05$, indicates that the present study failed to find evidence of an age-related decline in temporal integration.

The main effect of density was significant, $F(3,93) = 592.8$, $MSE = 0.01$, $p < .05$, indicating increased accuracy with increased density. The main effect of velocity was significant, $F(3,93) = 287.2$, $MSE = 0.01$, $p < .05$, indicating increased accuracy with increased velocity. The main effect of size was significant, $F(1,31) = 179.1$, $MSE = 0.01$, $p < .05$, indicating increased accuracy for the larger as compared to the smaller size. The two way interactions of density and velocity ($F(9,279) = 29.6$, $MSE = 0.008$) and density and size ($F(3,93) = 11.1$, $MSE = 0.01$) were significant, $p < .05$. These findings are consistent with the results previously reported in Andersen and Cortese (1989).

2.2.3. Age-effects and spatial integration

To isolate the effects of spatial integration we examined whether the age-related differences in performance varied across conditions in which spatial/temporal information was constant. Four different analyses were conducted that compare display conditions (combinations of velocity and density) with constant spatial/temporal information. The displays that were compared in the four analyses were:

Analysis 1: 2.0 deg/s velocity with 0.61 dots/deg^2 density and 1.0 deg/s velocity with 1.22 dots/deg^2 density;

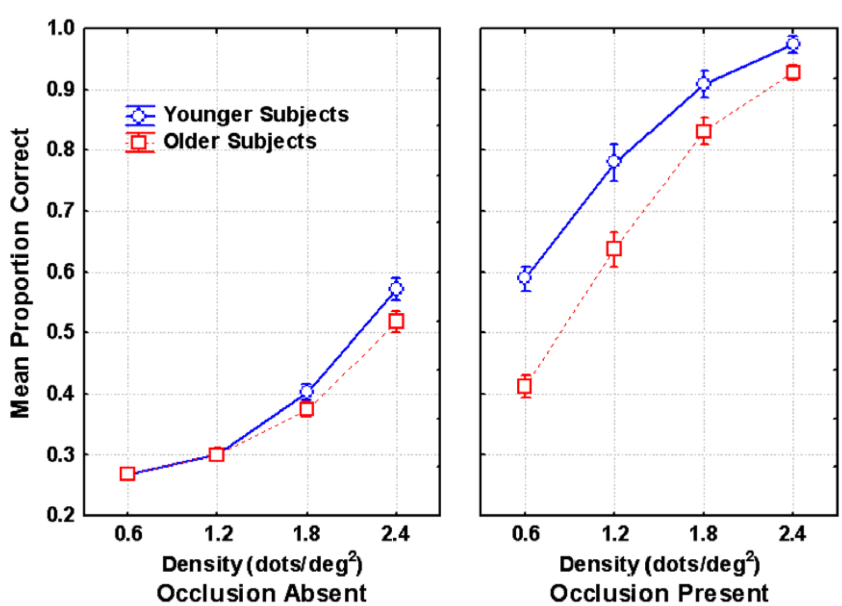

Fig. 3. Interaction of age and density on shape identification accuracy from Experiment 1. Graphs are presented for occlusion absent and occlusion present conditions. Error bars are ±1 standard error.

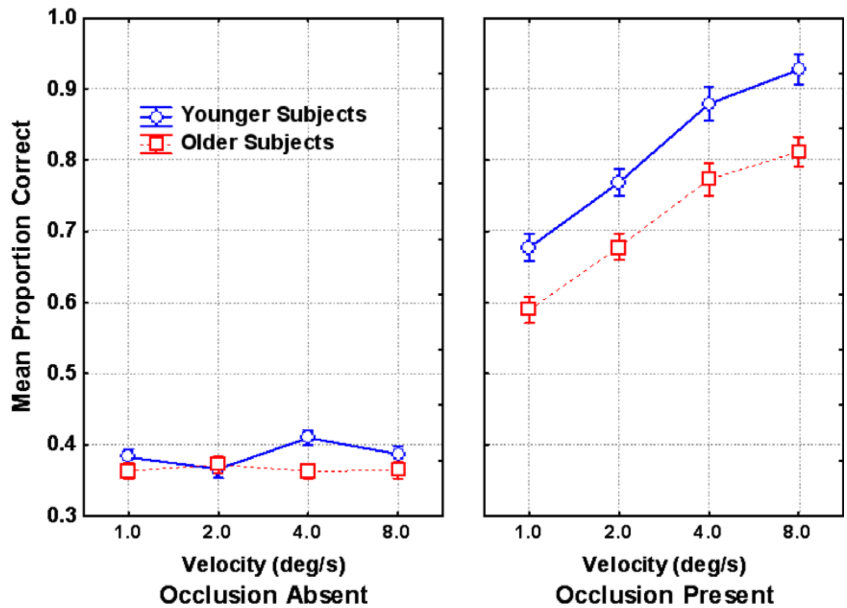

Fig. 4. Interaction of age and velocity on shape identification accuracy from Experiment 1. Graphs are presented for occlusion absent and occlusion present conditions. Error bars are ±1 standard error.

Analysis 2: 4.0 deg/s velocity with 0.61 dots/deg^2 density, 2.0 deg/s velocity with 1.22 dots/deg^2 density, and 1.0 deg/s velocity with 2.44 dots/deg^2 density;
Analysis 3: 8.0 deg/s velocity with 0.61 dots/deg^2 density, 4.0 deg/s velocity with 1.22 dots/deg^2 density, and 2.0 deg/s velocity with 2.44 dots/deg^2 density;
Analysis 4: 8.0 deg/s velocity with 1.22 dots/deg^2 density and 1.0 deg/s velocity with 2.44 dots/deg^2 density.

An age by display condition ANOVA was conducted for each analysis. For example, analysis 1 was a 2 (age group) by 2 (display condition) ANOVA whereas analysis 2 was a 2 (age group) by 3 (display condition). The F ratios for analysis 1 ($F(1,31) = 4.9$; MSE = 0.029), analysis 2 ($F(2,62) = 4.8$; MSE = 0.01), analysis 3 (F(2,62) = 12.7; MSE = 0.008), and analysis 4 ($F(1,31) = 4.2$; MSE = 0.005) were significant ($p < .05$). All analyses showed the same general pattern of results. For the purpose of brevity we will discuss in detail the pattern of results for analysis 3. As is shown in Fig. 5, proportion correct increased across the 3 display conditions for both older and younger observers. An important question is what factor accounts for the greater decrease in performance for older as compared to younger observers across the three display conditions. Note that performance increased as velocity decreased across the three display conditions (8.0, 4.0, and 2.0 deg/s). This pattern is inconsistent with the highly significant effect of increased accuracy with increased velocity reported earlier. Thus we conclude that the significant age by display condition observed in analysis 2 was not due to variations in velocity. However, performance increased with an increase in density across the three display conditions (0.61, 1.22, and 2.44 dots/deg^2). This pattern of results indicates that performance decreased at lower density levels for both older and younger observers, with a greater decrease occurring for older observers. All four analyses showed the same pattern of age-related effects—performance for older observers, as compared to younger observers, decreased at a greater rate with decreased density but did not decrease with a decrease in velocity. We conclude that these results are evidence of age related decrements in spatial integration.

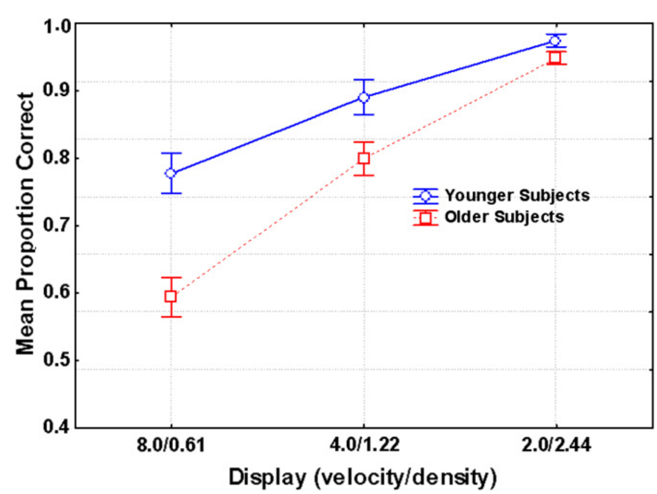

Fig. 5. Interaction of age and display condition on shape identification accuracy from Experiment 1 when the rate of occlusion events is constant. Error bars are ±1 standard error.

3. Experiment 2

In Experiment 1 we determined that decreased performance for older observers in using kinetic occlusion information was due to spatial rather than temporal processing. Our conclusion that age-related effects were not the result of temporal integration was based on the lack of an interaction of age and velocity. In Experiment 2 we used a different approach to provide converging evidence that age-related effects were not due to temporal integration. Observers were presented with the same displays as those used in Experiment 1 with the following exception. In Experiment 2 we used limited lifetime stimuli in which the duration of individual dots was restricted. Consider the information available to determine shape under these conditions compared to the conditions examined in Experiment 1. In Experiment 1 the object moved against a stationary background with the object boundary defined by a discontinuity in motion and stationary regions. When limited lifetime displays are used the object and background dots in the display would appear for a limited period of time and be randomly repositioned in the display. As a result the salience of the edge boundary is considerably reduced because the background consists of scintillating noise and there is no boundary defined by a discontinuity of motion and stationary regions. In order to recover the boundary, the visual system must determine regions of local motion of limited duration and regions of no motion of limited duration. As a result, variations in the duration of the limited lifetime dots allows one to more directly assess the integration of information over time.

If the age-related decrements in using kinetic occlusion information were due to a loss in temporal integration, then decreasing the duration of local dot motion should result in greater limits on temporal integration, resulting in a subsequent decrease in performance for older observers.

3.1. Methods

3.1.1. Observers

The observers were 9 older and 9 younger volunteers who had participated in Experiment 1. The subjects were paid for their participation and were naïve regarding the purpose of the experiment.

3.1.2. Design

Three within-subject independent variables were investigated: the presence of absence of kinetic occlusion information (determined by the absence or presence of background texture), motion duration (16, 33, 66, or 100 ms) and size (objects subtended a square region that was either 4.2 or 6.5 deg horizontally and vertically). Age was run as a between subjects variable (mean age for the older and younger groups was 20.5 and 72.1, respectively).

3.1.3. Stimuli

The stimuli were identical to those used in Experiment 1 with the following exception. The presentations of individual dots were shown for durations of 16, 33, 66, or 100 ms based on presentations of 2, 3, 4, or 6 frames. The proportion of dots repositioned from frame to frame varied as a function of lifetime. Specifically, for the 2 frame lifetime stimuli 50% of the dots were repositioned on each frame, for the 3 frame lifetime stimuli 33% were repositioned, etc. We examined a high texture density (2.44 dots/deg^2) to ensure that any age related performance differences would be due to temporal rather than spatial integration. The velocity of the dots was 8.0 deg/s.

3.1.4. Apparatus

The apparatus was the same as that used in Experiment 1.

3.1.5. Procedure

The procedure was identical to Experiment 1 with the following exception. Observers participated in two single-hour sessions conducted on separate days. In each session observers were presented 5 blocks of trials, with each block consisting of 2 replications of all 64 displays (absence/presence of kinetic occlusion by 2 sizes by 4 motion duration by 4 shapes) presented in random order for a total of 128 trials per block. The total number of trials for the entire experiment was 1280. No feedback was used during the experiment.

3.2. Results

The proportion correct was tabulated for each subject in each condition and analyzed using an Analysis of Variance (ANOVA). The main effect of age was not significant, $F(1,16) = 1.37$, MSE = 0.039, $p > .05$. The main effects of presence/absence of kinetic occlusion ($F(1,16) = 477.7$, MSE = 0.024) was significant, indicating that observers could easily identify the object when background texture was absent (mean proportion correct of 0.98) compared to when background texture was present (mean proportion correct of 0.78). The high level of performance in the background texture absent condition is due to the high density of the stimuli (2.44 dots/deg^2; the highest density examined in Experiment 1). This result indicates that density was sufficiently high to easily identify the shape when no background texture was present. To examine age related differences in temporal integration we examined the effects of dot lifetime duration and size when background texture (i.e. kinetic occlusion information) was present. The main effect of duration ($F(3,48) = 716.3$, MSE = 0.009), and size ($F(1,16) = 59.8$, MSE = 0.003) were significant ($p < .05$), indicating that an increase in duration or an increase in size resulted in increased detection performance. Surprisingly, no significant interaction were found between age and these variables, $p > .05$. To illustrate the similar performance of older and younger observers the results of the interaction of age and duration for the kinetic occlusion condition are shown in Fig. 6. Planned comparisons of the effect of age at each duration condition indicated no significant effects [$F(1,16) = 1.24$; $F(1,16) = 1.07$; $F(1,16) = 1.63$; and $F(1,16) = 0.02$]. These results, which are consistent with the result of Experiment 1, suggest that age-related

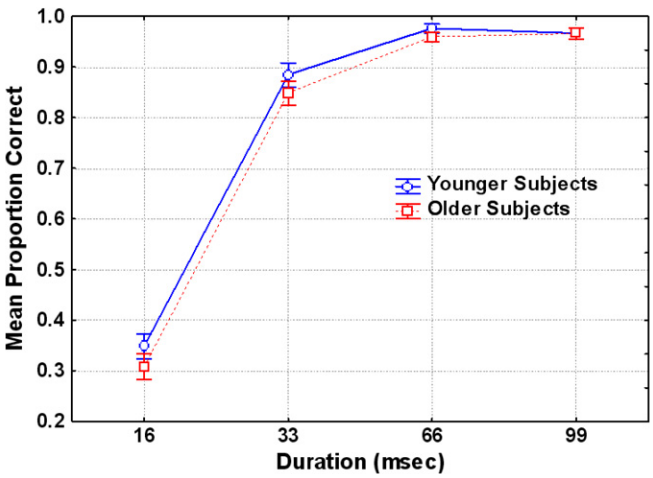

Fig. 6. Shape identification accuracy as a function of age and motion duration from Experiment 2. Error bars are ±1 standard error.

changes in visual processing are not the result of changes in temporal integration.

4. General discussion

The results of the present study indicate age related decrements in spatial but not temporal integration in identifying 2D shape from kinetic occlusion. In Experiment 1 we found that older observers had significantly worse performance than younger observers at identifying shape at lower texture densities. Consider the results at the lowest texture density condition. Younger observers had a 32% increase in detection performance when kinetic occlusion information was present. In contrast, older observers had an 11.5% increase in detection performance when kinetic occlusion information was present. An analysis of conditions in which the rate of occlusion events was constant, suggests that age-related differences were greater with lower density levels, indicating age-related decrements in spatial integration.

With regard to temporal integration, the main effect of velocity was significant, indicating increased temporal integration for both older and younger observers with an increase in speed. However, velocity did not interact with age. This result suggests no age-related differences in temporal integration.

To provide converging evidence that age-related decrements in the present task were not due to temporal integration, we conducted a second experiment in which we used limited lifetime motion stimuli. The results indicated a significant effect of lifetime duration. However no age effects were observed. As is shown in Fig. 6 the range of performance for lifetime duration was from near chance levels to 100% accuracy at the longest duration examined. These results are consistent with the results of Experiment 1 which suggest no age related differences in temporal integration.

The results of these studies suggest considerable changes in spatial integration in recovering 2D shape as a function of age. What neurophysiological changes might account for age related decrements in spatial integration? One hypothesis is that changes in the physiology of the visual cortex accounts for age-related changes in visual processing. Previous studies based on aging and cognition have shown that the size of specific cortical regions, for example prefrontal cortex, decrease with increased age (e.g., Anderson, Hubbard, Coghill, & Sliders, 1983; Raz & et al., 2004). However, the evidence regarding age-related changes in visual cortex is quite different. Studies examining both neural morphology and neural density have found no significant differences in visual cortex with increased age (Peters, Feldman, & Vaughan, 1983; Peters, Nigro, & McNally, 1997). A second possibility concerns intracortical inhibition in visual cortex. Recent research (Schmolesky, Wang, Pu, & Leventhal, 2004) examined stimulus selectivity of cells in primary visual cortex (V1) of old and young macaques and found an age-related decrease in orientation selectivity of cells with increased age accompanied by increased responsiveness to all orientations and an overall increase in spontaneous activity. These results are consistent with an age-related degeneration in intracortical inhibition. Similar results have also been found by studies examining visual cortical cells of aged rats (Wang, Xie, Li, Chen, & Zhou, 2006). Recent psychophysical studies on motion perception and aging have found evidence in support of an aging and inhibition hypothesis (Betts, Taylor, Sekuler, & Bennett, 2005). A third possibility concerns biochemical changes in visual neurons. Recent research (Roberts et al., 2005) has found that acetycholine (ACh) regulates spatial integration in primary visual cortex. Specifically, local application of ACh in primate primary visual cortex reduced the extent of spatial integration. This finding suggests that age-related differences in the regulation of ACh may account for the spatial integration effects observed in the present study. An important issue for future research will be to determine the role of intracortical inhibition and ACh in spatial integration in 2D shape perception.

A possible explanation for some of the age-related effects is that the age-related differences in shape from kinetic occlusion may be due to differences in retinal illuminance. Specifically, a decrease in the number of dots in the stimuli may have changed factors such as pupil diameter resulting in changes in retinal illuminance. Thus, variations in pupil diameter may have occurred as a function of dot density. It is worth noting that recent research (Betts, Sekuler, & Bennett, 2007) examined the issue of retinal illuminance on age-related differences in orientation discrimination, and concluded that age-related differences in orientation discrimination were not solely due to differences in retinal illumination. We believe it is unlikely that retinal illuminance could account for the present results, given that the dots were high luminance and high contrast. Nevertheless, an important issue for future research would be to rule out this possibility.

The results of the present study suggest age-related changes in visual processing are the result of changes in spatial integration. An important question is whether other aspects of visual processing, that are known to change with age (e.g., motion perception, pattern recognition, face recognition, etc), may be due to decreased spatial integration. Age-related changes have also been found in visual attention tasks that involve spatial information (Greenwood & Parasuraman, 2004; McCarley, Mounts, & Kramer, 2004; Thorton & Raz, 2006). Spatial integration may not only explain age related effects in visual perception, but may be an important factor in age related changes in visual-spatial attention.

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References

Andersen, G. J., & Atchley, P. (1995). Age-related differences in the detection of three dimensional surfaces from optic flow. *Psychology and Aging, 10*, 650–658.

Andersen, G. J., Cisneros, J., Saidpour, A., & Atchley, P. (2000). Age-related differences in collision detection during deceleration. *Psychology and Aging, 15*, 241–252.

Andersen, G. J., & Cortese, J. M. (1989). 2-D contour perception resulting from kinetic occlusion. *Perception & Psychophysic, 46*, 49–55.

Andersen, G. J., & Enriquez, A. (2006). Aging and the detection of observer and moving object collisions. *Psychology and Aging, 21*, 74–85.

Andersen, G. J., Saidpour, A., & Braunstein, M. L. (1998). Effects of collimation on perceived layout in 3-D scenes. *Perception, 27*, 1305–1315.

Anderson, J. M., Hubbard, B. M., Coghill, G. R., & Sliders, W. (1983). The effect of advancing age on the neurone content of the cerebral cortex. *Journal of Neurological Science, 58*, 233–244.

Arnett, DW. (1972). Spatial and temporal integration properties of units in first optic ganglion of dipterans. *Journal of Neurophysiology, 35*, 429–444.

Aspell, J. E., Wattam-Bell, J., & Braddick, O. (2006). Interaction of spatial and temporal integration in global form processing. *Vision Research, 46*, 2834–2841.

Atchley, P., & Andersen, G. J. (1998). The effect of age, retinal eccentricity, and speed on the detection of optic flow components. *Psychology and Aging, 13*, 297–308.

Bair, W., & Movshon, J. A. (2004). Adaptive temporal integration in direction-selection neurons in Macaque visual cortex. *Journal of Neuroscience, 24*, 7305–7323.

Baker, C. L., & Braddick, O. J. (1985). Temporal properties of the short-range process in apparent motion. *Perception, 14*, 181–192.

Ball, K., & Sekuler, R. (1986). Improved visual perception in older observers. *Journal of Gerontology, 41*, 176–182.

Barlow, H. B. (1953). Summation and inhibition in the frog's retina. *Journal of Physiology, 119*, 69–88.

Bennett, P. J., Sekuler, R., & Sekuler, A. B. (2007). The effects of aging on motion detection and direction identification. *Vision Research, 47*, 799–809.

Betts, L. R., Taylor, C. P., Sekuler, A. B., & Bennett, P. J. (2005). Aging reduces center-surround antagonism in visual motion processing. *Neuron, 45*, 361–366.

Betts, L. R., Sekuler, A. B., & Bennett, P. J. (2007). Aging and orientation discrimination. *Vision Research, 47*, 1769–1780.

Blake, R., & Lee, S.-H. (2005). The role of temporal structure in human vision. *Behavioral and Cognitive Neuroscience Review, 4*, 21–42.

Breitmeyer, B. G. (1984). *Visual masking: An integrative approach*. New York: Oxford University press.

Brown, H. A., Allison, D. D., Samonds, J. M., & Bonds, A. B. (2003). Nonlocal origin of response suppression from stimulation outside the classical receptive field in area 17 of the cat. *Visual Neuroscience, 20*, 85–96.

Bullier, J., Hupe, J. M., James, A. C., & Girard, P. (2001). The role of feedback connections in shaping the responses of visual cortical neurons. *Progress in Brain Research, 134*, 193–204.

Das, A., & Gilbert, C. D. (1999). Topography of contectural modulations mediated by short-range interactions in primary visual cortex. *Nature, 399*, 655–661.

Enns, J. T., & Di Lollo, V. (2000). What's new in visual masking. *Trends in Cognitive Science, 5*, 16–25.

Field, D. J., Hayes, A., & Hess, R. F. (1993). Contour integration by the human visual system: Evidence for a local 'association field'. *Vision Research, 33*, 173–193.

Greenhouse, S., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika, 24*, 95–112.

Greenwood, P. M., & Parasuraman, R. (2004). The scaling in visual search and its modification in healthy aging. *Perception & Psychophysics, 66*, 3–22.

Gilmore, G. C., Wenk, H. E., Naylor, L. A., & Stuve, T. A. (1992). Motion perception and aging. *Psychology and Aging, 7*, 654–660.

Hong, S. W., & Shevell, S. K. (2004). Brightness induction: Unequal spatial integration with increments and decrements. *Visual Neuroscience, 21*, 353–357.

Huk, A. C., & Shadlen, M. N. (2005). Neural activity in Macaque parietal cortex reflects temporal integration of visual motion signals during perceptual decision making. *Journal of Neuroscience, 25*, 10420–10436.

Kellman, P. J., & Shipley, T. F. (1992). Perceiving objects across gaps in space and time. *Current Directions in Cognitive Science, 1*, 193–199.

Kovacs, I. (1996). Gestalten of today: Early processing of visual contours and surfaces. *Behavioral and Brain Research, 82*, 1–11.

Ledgeway, T., & Hess, R. F. (2002). Rules for combining the outputs of local motion detectors to define simple contours. *Vision Research, 42*, 653–659.

Lee, S.-H., & Blake, R. (1999). Visual form created solely from temporal structure. *Science, 284*, 1165–1168.

McCarley, J. S., Mounts, J. R., & Kramer, A. F. (2004). Age-related differences in localized attentional interference. *Psychology and Aging, 19*, 203–210.

Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature, 421*, 370–373.

Norman, F. J., Clayton, A. M., Shular, C. F., & Thompson, S. R. (2004). Aging and the perception of depth and shape from motion parallax. *Psychology and Aging, 19*, 506–514.

Norman, F. J., Crabtree, C. E., & Hermann, D. (2006). Aging and the perception of 3-D shape from kinetic patterns of binocular disparity. *Perception & Psychophysics, 68*, 94–101.

Pelli, D. G., Robson, J. G., & Wilkins, A. J. (1988). Designing a new letter chart for measuring contrast sensitivity. *Clinical Visual Neuroscience, 2*, 187–199.

Peters, A., Feldman, M. L., & Vaughan, D. W. (1983). The effect of aging on the neuronal population within area 17 of adult rat cerebral cortex. *Neurobiology of Aging, 4*, 273–282.

Peters, A., Nigro, N. J., & McNally, K. J. (1997). A further evaluation of the effect of age on striate cortex of the Rhesus monkey. *Neurobiology of Aging, 18*, 29–36.

Raz, N. et al. (2004). Differential aging of the medial temporal lobe: A study of a five year change. *Neurology, 62*, 433–438.

Roberts, M. J., Zinke, W., Guio, K., Robertson, R., McDonald, J. S., & Thiele, A. (2005). Acetylcholine kinetically controls spatial integration in Marmoset primary visual cortex. *Journal of Neurophysiology, 93*, 2062–2072.

Schmolesky, M. T., Wang, W., Pu, M., & Leventhal, A. G. (2004). Degradation of stimulus selectivity of visual cortical cells in senescent Rhesus monkeys. *Nature Neuroscience, 3*, 384–390.

Sekuler, A. B., Bennett, P. J., & Mamelak, M. (2000). Effects of aging on the useful field of view. *Experimental Aging Research, 26*, 103–120.

Shadlen, M. N., & Movshon, J. A. (1999). Synchrony unbound: A critical evaluation of the temporal binding hypothesis. *Neuron, 24*, 67–77.

Shadlen, M. N., & Newsome, W. T. (1994). Noise, neural codes and cortical organization. *Current Opinions in Neurobiology, 4*, 569–579.

Stettler, D. D., Das, A., Bennett, J., & Gilbert, C. D. (2000). Lateral connectivity and contextual interactions in macaque primary visual cortex. *Neuron, 36*, 739–750.

Thorton, W. J. L., & Raz, N. (2006). Aging and the role of working memory resources in visuospatial attention. *Aging, Neuropsychology and Cognition, 13*, 36–61.

Trick, G. L., & Silverman, S. E. (1991). Visual sensitivity to motion: Age-related changes and deficits in senile dementia of the Alzheimer type. *Neurology, 41*, 1437–1440.

Vaina, L. M. et al. (2003). Can spatial and temporal motion integration compensate for deficits in local motion mechanisms? *Neuropsychologia, 41*, 1817–1836.

Wang, H., Xie, X., Li, X., Chen, B., & Zhou, Y. (2006). Functional degradation of visual cortical cells in aged rats. *Brain Research, 1122*, 93–98.

Watamaniuk, S. N. J., McKee, S. P., & Gryzwacz, N. M. (1995). Detecting a trajectory embedded in random direction motion noise. *Vision Research, 35*, 65–77.

Wist, E. R., Schrauf, M., & Ehrenstein, W. H. (2000). Dynamic vision based on motion contrast: changes with age in adults. *Experimental Brain Research, 134*, 295–300.