# Aging and the integration of orientation and position in shape perception

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**The current experiments examined the effect of healthy aging on the integration of orientation and position information in shape perception. Following Day and Loffler (2009), conflicting contours were created by sampling the orientations of one shape (e.g., a rounded pentagon) with Gabors, and positioning them on the circumference of a different shape (e.g., a circle). In Experiment 1, subjects judged whether the conflicting contour looked more circular than a rounded pentagon of varying amplitude, which allowed us to estimate the perceived shape of the conflicting contour. The relative amount of position and orientation information was manipulated by varying the number of Gabors comprising the target contour. Orientation information dominated the percept for contours sampled with 15–40 elements, producing a strong shape illusion, but position information determined the shape with denser sampling. The magnitude of this orientation dominance effect was equal in younger and older subjects across all sampling levels. In Experiment 2, subjects discriminated five contours that differed in orientation and/or position information. Both groups showed poor discrimination between conflicting contours and their perceptually equivalent radial frequency patterns, confirming the main finding of Experiment 1. In addition, older subjects showed worse discrimination between two noncircular radial frequency patterns than younger subjects. In sum, integration of orientation and position information in shape perception is preserved with aging; however, older adults are less able to make fine shape discriminations between noncircular sampled contours.**

## Introduction

Healthy aging is accompanied by declines in multiple aspects of vision that cannot be ascribed to changes in optics and accommodation, but rather arise from changes in cortical function (for reviews see Faubert, 2002; Sekuler & Sekuler, 2000; Spear, 1993). Neurophysiological studies in aged cats and primates have revealed significant changes in the functioning of neurons in early visual areas, such as increased levels of spontaneous activity, decreased signal-to-noise ratios, reduced orientation and spatial frequency selectivity, and increased response latencies of V1 and V2 neurons (Schmolesky, Wang, Pu, & Leventhal, 2000; Y. Wang, Zhou, Ma, & Leventhal, 2005; Yu, Wang, Li, Zhou, & Leventhal, 2006). Although these neurophysiological changes would be expected to produce noticeable declines in pattern vision with aging, studies in older humans have found no evidence of broader orientation or spatial frequency tuning with aging (Delahunt, Hardy, & Werner, 2008; Govenlock, Sekuler, & Bennett, 2010; Govenlock, Taylor, Sekuler, & Bennett, 2009, 2010), and no evidence for decreased orientation and spatial frequency discrimination ability for single gratings (Delahunt et al., 2008; Bennett, Sekuler, McIntosh, & Della-Maggiore, 2001; Betts, Sekuler, & Bennett, 2007).

However, several studies have found age-related declines in visual tasks that require integration of information across space, such as contour integration (Del Viva & Agostini, 2007; Hadad, 2012; McKendrick, Weymouth, & Battista, 2010; Roudaia, Bennett, & Sekuler, 2008, 2013; Roudaia, Farber, Bennett, & Sekuler, 2011), curvature discrimination (Legault,

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Allard, & Faubert, 2007), bilateral symmetry detection (Herbert, Overbury, Singh, & Faubert, 2002), perceptual grouping (Kurylo, 2006), perceptual contour completion (Richards, Bennett, & Sekuler, 2006; Salthouse & Prill, 1988), and figure–ground segregation (Lass, Bennett, Peterson, & Sekuler, 2012). For example, when discriminating sampled contours, older subjects are significantly more affected by the addition of cluttering elements (Casco, Robol, Barollo, & Cansino, 2011), or by increases in the relative spacing of contour and noise elements (Del Viva & Agostini, 2007; Roudaia et al., 2013), and require longer stimulus durations to reach the same performance level as younger subjects (Roudaia, Farber, Bennett, & Sekuler, 2011). At the same time, disruptions in collinearity of contour elements and changes in contour element proximity have a similar effect on younger and older subjects (Hadad, 2012; McKendrick et al., 2010; Roudaia et al., 2013). Although declines in contour discrimination appear to be due to a reduced ability to segregate contours from cluttered backgrounds (Casco et al., 2011; Del Viva & Agostini, 2007; Roudaia et al., 2013), contour grouping deficits are also seen in the absence of background clutter (Casco et al., 2011; Roudaia et al., 2008). In a task that required subjects to discriminate isolated contours consisting of low-contrast elements, the alignment of local orientations along the contour path improved performance of younger subjects (Saarinen & Levi, 2001), but not older subjects (Roudaia et al., 2008), suggesting that the efficiency of integrating orientation information across space changes with aging.

Shape perception is an intermediate-level process that appears to integrate orientation information across space using both local and global mechanisms (e.g., Achtman, Hess, & Wang, 2003; Bell, Gheorghiu, Hess, & Kingdom, 2011; Hess, Wang, & Dakin, 1999; Loffler, 2008; Loffler, Wilson, & Wilkinson, 2003; Schmidtmann, Gordon, Bennett, & Loffler, 2013; Schmidtmann, Kennedy, Orbach, & Loffler, 2012; Wilkinson, Wilson, & Habak, 1998). Studies examining whether shape perception is altered in older age have found mixed results (Habak, Wilkinson, & Wilson, 2009; Mayhew & Kourtzi, 2013; McKendrick & Battista, 2013; McKendrick et al., 2010; Rivest, Kim, Intriligator, & Sharpe, 2004; Y. Z. Wang, 2001; Y. Z. Wang, Morale, Cousins, & Birch, 2009; Weymouth & McKendrick, 2012). Studies that have assessed shape perception by measuring texture coherence thresholds in Glass patterns consistently report that older subjects require higher texture coherence than younger subjects to detect or discriminate global shapes (Mayhew & Kourtzi, 2013; Weymouth & McKendrick, 2012), but studies examining shape perception using isolated contours have obtained less consistent results. Y. Z. Wang (2001) first measured shape discrimination thresholds in older subjects using radial frequency patterns (Wilkinson et al., 1998), which are continuous, luminance-defined closed contours whose shape is defined by the frequency and amplitude of radial modulation. Younger and older subjects showed equivalent thresholds for detecting low radial frequency modulations (Y. Z. Wang, 2001). Habak et al. (2009) replicated these results and found equivalent thresholds in younger and older subjects even for very brief stimulus presentations. Moreover, the increase in thresholds caused by lateral shape interactions also did not differ with aging. Habak et al. (2009) concluded that shape perception mechanisms were robust to the effects of aging. In contrast, Y. Z. Wang et al. (2009) reported a gradual decline in radial modulation thresholds of 0.035 logMAR per decade starting at 55 years of age. More recently, Weymouth and McKendrick (2012) also found higher radial frequency deformation thresholds in older subjects in a task that required discrimination between two different radial frequency patterns. Rivest et al. (2004) assayed the effects of aging on shape perception by measuring a shape distortion effect that occurs when the percept of a shape (e.g., circle) becomes distorted when another shape (e.g., rectangle) is presented immediately before it. Although there were no age differences in the basic perception of the circle shapes, older subjects showed a weaker shape distortion effect compared to younger subjects, suggesting that the interactions between shape selective neurons were less effective in older age. Finally, the ability to discriminate the shape of sampled contours appears to be only slightly impaired with aging, although older subjects require contours to be more densely sampled than younger subjects to discriminate their shape reliably (McKendrick et al., 2010). In sum, although several earlier studies found little or no change in shape perception mechanisms with aging, more recent studies have found evidence to the contrary.

To gain further insight into age-related changes in shape perception, we examined the role of local orientation in shape perception in younger and older subjects. Using a compelling shape illusion, Day and Loffler (2009) demonstrated that the perceived shape of a contour sampled with oriented elements is based on a weighted combination of the positions and orientations of its local elements. When elements whose orientations were consistent with a pentagon were positioned on a circle, the orientation information influenced the percept and a pentagon shape was perceived. With increasing number of elements, the position information became more dominant and a circular shape was perceived. Conversely, increasing the strength of orientation information by increasing the spatial frequency of the oriented elements resulted in a stronger shape illusion. Here, we employed this illusion

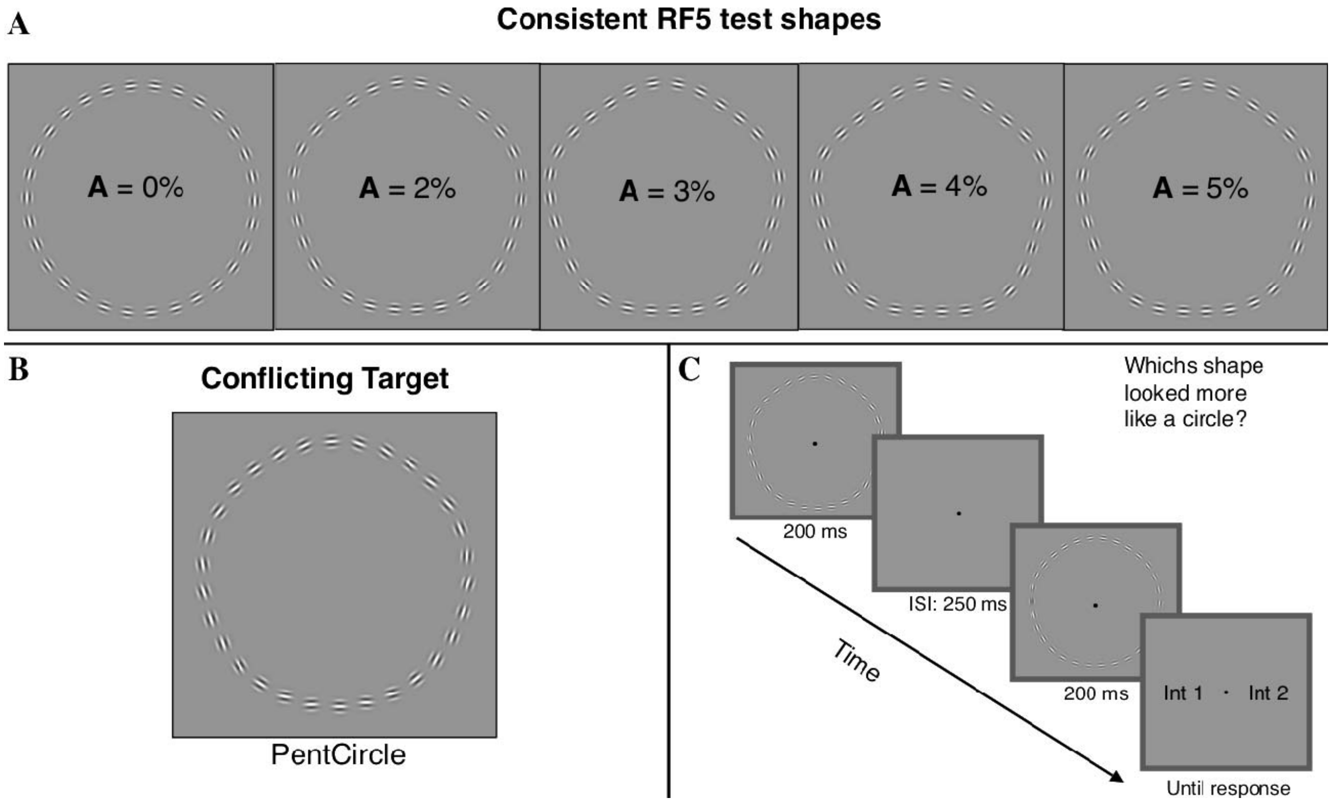

Figure 1. Stimuli used in Experiment 1. (A) Examples of sampled radial frequency 5 (RF5) shapes composed of Gabor elements collinear with the contour path. The amplitude of RF5 shapes varied from 0% to 5% of the mean radius. (B) The conflicting target shape, pentCircle, consisted of Gabor elements placed on the circumference of a circle, but having local orientations consistent with an RF5 shape with 5% amplitude (i.e., rightmost shape in A). Although linking the centers of the pentCircle Gabors traces out a circle, the Gabor orientations influence shape perception and the contour appears as a rounded pentagon. (C) Experiment 1 procedure: The pentCircle and an RF5 contour with varying amplitude were presented in two intervals on every trial. Subjects reported which interval contained the most circular shape.

to study whether orientation and position information are combined in a similar way in younger and older subjects in shape perception. In Experiment 1, we estimated the perceived shapes of contours comprised of a different number of elements whose position and orientation information were in conflict. In Experiment 2, we measured shape discrimination performance for contours differing either in orientation information, position information, or both.

## Experiment 1: Does the pentagon illusion change with age?

This experiment, which was based on experiment 2 of Day and Loffler (2009), examined whether the relative roles of orientation and position information in shape perception change with age. Conflicting target stimuli were created by sampling the orientation of a rounded pentagon with Gabors and positioning them on a circle (see Figure 1). Under certain circumstances, the Gabors are perceived as falling along a pentagon-shaped contour even though they are arranged on a circle. To measure the strength of this illusion, subjects were asked to compare the shape of the conflicting target to a series of rounded pentagons with varying amplitudes (with zero amplitude corresponding to a circle). The amplitude of the rounded pentagon that was judged to be perceptually equivalent to the target was taken as an estimate of the strength of the illusion. The number of Gabors comprising the contours was varied to manipulate the relative strength of position and orientation information and examine its effect on the strength of the illusion.

### Methods

#### *Subjects*

Twelve younger ($M = 25$ years; age range: 19–32; six males) and twelve older subjects ($M = 68$ years; age range: 62–75; six males) participated in Experiment 1.

| Group | $N$ | Age | Near acuity | Far acuity | Pelli-Robson | MMSE |
|---|---|---|---|---|---|---|
| Younger | 12 | 25.17 (4.51) | −0.13 (0.08) | −0.15 (0.08) | 1.95 (0.06) | |
| Older | 12 | 68.25 (4.29) | 0.01 (0.10) | −0.04 (0.08) | 1.94 (0.05) | 29.33 (1.15) |

Table 1. Mean (*SD*) age, near and far logMAR visual acuity, Pelli-Robson contrast sensitivity, and Mini-Mental State Examination (MMSE). Standard deviations are shown in parentheses.

Subjects were compensated for their time at a rate of \$10 per hour. We measured subjects' near visual acuity, distance visual acuity, and contrast sensitivity using the SLOAN Two Sided ETDRS Near Point Test, the 4 Meter 2000 Series Revised ETDRS charts, and the Pelli-Robson Contrast Sensitivity Test (Precision Vision, LaSalle, IL; Pelli, Robson, & Wilkins, 1988), respectively. Subjects wore their habitual optical correction for each distance during vision testing, if needed. All subjects' acuity and contrast sensitivity measures were normal for their age group (Elliott, Sanderson, & Conkey, 1990; Elliott, Yang, & Whitaker, 1995; Mäntyjärvi & Laitinen, 2001). We administered a general health questionnaire to screen for previous diagnoses of visual (e.g., cataracts, glaucoma) or neurological disorders. None of the subjects reported any known visual or neurological problems. Older subjects also completed the Mini-Mental State Examination to screen for cognitive impairment and none scored below the normal cut-off score of 26/30 (Crum, Anthony, Bassett, & Folstein, 1993; Folstein, Folstein, & McHugh, 1975). Table 1 summarizes the demographic information for all subjects.

### Apparatus

The experiment was programmed in the MATLAB environment (version 7.2) using the Psychophysics and Video Toolboxes (version 3.0.8; Brainard, 1997; Pelli, 1997) on a Macintosh G5 computer running OS X, version 10.4.11. Stimuli were presented on a 21-inch Sony Trinitron monitor with a 1280 × 1024 resolution (pixel size = 0.014 deg) and a refresh rate of 75 Hz. The display was the only light source in the room and had a mean luminance of 65 cd/m$^2$. Subjects viewed the display binocularly through natural pupils with their habitual distance correction, if needed, from a viewing distance of 114 cm. Their viewing position was stabilized with a chin/forehead rest. A standard QWERTY Macintosh keyboard was used to collect subjects' responses.

### Stimuli

Stimuli consisted of closed sampled contours presented against a uniform gray background. The contour shapes were created by applying a sinusoidal deviation to the radius of a circle with a frequency of 5 cycles per radius (Wilkinson et al., 1998). The radius of each shape can be described by the formula

$$r(\theta) = R_0[1 + A\sin(5\theta + \phi)] \tag{1}$$

where $R_0$ is the mean radius of the contour and $A$ is the amplitude of radial deviation in units of $R_0$. For $A = 0$, no radial modulation is applied and the formula describes a circle. The magnitude of radial modulation increases with increasing $A$, creating five-pointed shapes with progressively sharper lobes that resemble rounded pentagons. Accordingly, a contour defined by the above formula with, for example, an amplitude $A = 0.05$ will be referred to as a *5% pentagon* or a *5% RF5 pattern*. The overall orientation of the shape was kept constant by setting the phase parameter to $\pi$. To preclude subjects from using particular locations on the screen for their decisions, the mean radius $R_0$ varied between 3.48°–3.68° and the position of the center of the shape varied randomly within a 0.56° diameter circle in the middle of the screen. The shapes were sampled with oriented Gabor patches created by multiplying a 6 c/deg sine wave grating with 98% contrast by a circular Gaussian envelope ($\sigma = 0.1°$). All Gabors had positive cosine phase with respect to the centre of the Gaussian envelope. The number of Gabor elements sampling each contour was varied across blocks and the elements were equally spaced along the contour path.

Following Day and Loffler (2009), there were two types of shape stimuli: consistent test stimuli and conflicting target stimuli. Consistent test shapes were constructed with contours that were created by placing Gabors on the radius of an RF5 contour at equally spaced polar angles and setting the Gabor orientations to be tangent to the RF5 contour at each location. In these contours, the local orientations in these contours were aligned with the contour path defining the RF5 shape (Figure 1). Conflicting target shapes were constructed from contours comprising Gabors whose positions were consistent with one shape but whose orientations were consistent with another shape. The pentCircle, used in Experiment 1, consisted of Gabor patches placed on the circumference of a circle at equally spaced polar angles, but each Gabor's orientation was determined by the tangent to an RF5 contour with $A = 5\%$ evaluated at the polar angle of its position (Figure 1). Thus, the positions of this contour describe a circle, but the orientations come from a 5% RF5 shape.

### Procedure

The McMaster University Research Ethics Board approved the experimental protocol, and written informed consent was obtained from all subjects prior to their participation. The ethical approval ensured compliance with the tenets of the Declaration of Helsinki.

Following Day and Loffler (2009), a two-interval forced choice procedure was used to determine the amplitude of an RF5 contour whose shape was perceptually equivalent to the perceived shape of the conflicting pentCircle target. Two shapes were shown on every trial in random order: a conflicting pentCircle shape and a consistent RF5 shape with varying amplitude. Subjects were asked to report "which interval contained the shape that looked more like a circle." The experiment began with an adaptation period of 60 s during which subjects adapted to the mean luminance of the screen, which remained constant throughout the experiment. The task was then explained, and two examples of RF5 shapes with different amplitudes were shown to get subjects familiar with the shapes. Each trial began with the presentation of a black fixation point in the center of the screen: Subjects were instructed to fixate this location throughout each trial. The fixation point, which flickered at 10 Hz to attract the subject's attention, was extinguished after 300 ms and, after a delay of 250 ms, was followed by two 200 ms stimulus intervals separated by an interstimulus interval (ISI) of 250 ms (Figure 1). The (nonflickering) fixation point was presented in the center of the display during the ISI to help subjects maintain proper fixation. A response screen containing a "1" on the left side and a "2" on the right side was shown following the second interval until the subject's response. Subjects pressed the key labeled "1" with their left hand to indicate the first interval, or the key labeled "2" with their right hand to indicate the second interval. No response feedback was given. The next trial began 1500 ms after the response. All subjects reported that they understood the instructions and had no problems completing the task.

To manipulate the relative amount of orientation and position information, the number of Gabors sampling the contour varied from 15, 20, 30, 40, 50, to 60 Gabors. These six conditions (labeled 15G, 20G, etc.) were tested in separate blocks in random order. In the seventh block, the conflicting target consisted of a "random" contour: 30 Gabors were positioned on the circumference of a circle and their orientations were random. Given that the random contours do not carry any consistent orientation information, the shape perception in the random condition should be largely determined by the element positions, which are consistent with a circle.

### Analysis

Three interleaved staircases manipulated the amplitude of the consistent test stimulus: for each condition: a 3-up/1-down, a 3-down/1-up, and a 1-up/1-down staircase converged, respectively, on the 79%, 50%, and 21% points on the psychometric function. Amplitude varied between 0 and 0.05 using adaptive step sizes that began at 0.016 and were progressively reduced to 0.002 after reaching six reversals. Each staircase terminated after 33 trials or after 19 reversals, whichever came first, resulting in a maximum of 99 trials per condition.

We used two different methods to estimate the amplitude of the RF5 contour that produced a shape that was perceptually equivalent to the conflicting target in each condition. In the first method, we fit a cumulative Gaussian function to the combined data from all three staircases and then determined the RF5 amplitude yielding 50% on the fitted curve. The second method consisted of calculating the mean of the last four reversal points of the 1-up/1-down staircase. The thresholds obtained with the two methods were comparable. The mean and median absolute differences were, respectively, 0.0024 and 0.017 in the older group and 0.0028 and 0.019 in the younger group. Out of a total of 168 thresholds, only 26 thresholds (15%) differed by 0.005 or more, and these differences occurred primarily in the random orientation ($n = 9$) and the 60 Gabors ($n = 10$) conditions. In the majority of these cases (20/26), the data showed a significant response bias, whereby the conflicting stimulus was judged as more circular than an RF5 contour with $A = 0$ (i.e., a true circle) on a majority of trials. This bias led to poor fits of the psychometric function. For this reason, we opted to conduct our analyses on the thresholds obtained using the second method (i.e., averaging the last four reversals of the 1-up/1-down staircase). Note that the main statistical results are the same when thresholds obtained in the first method are used.

Statistical analyses were conducted using R (R Development Core Team, 2011). When appropriate, the Geisser-Greenhouse correction ($\hat{\varepsilon}$) was used to adjust the degrees of freedom to correct for violations of the sphericity assumption underlying $F$ tests for within-subject variables (Maxwell & Delaney, 2004). Generalized eta squared, $\eta_g^2$, was used as a measure of effect size where appropriate (Bakeman, 2005; Olejnik & Algina, 2003).

## Results

The perceived shape of the pentCircle was determined by measuring the perceptually equivalent pentagon (PEP), which was defined as the amplitude of an RF5 contour that was judged to be more circular than

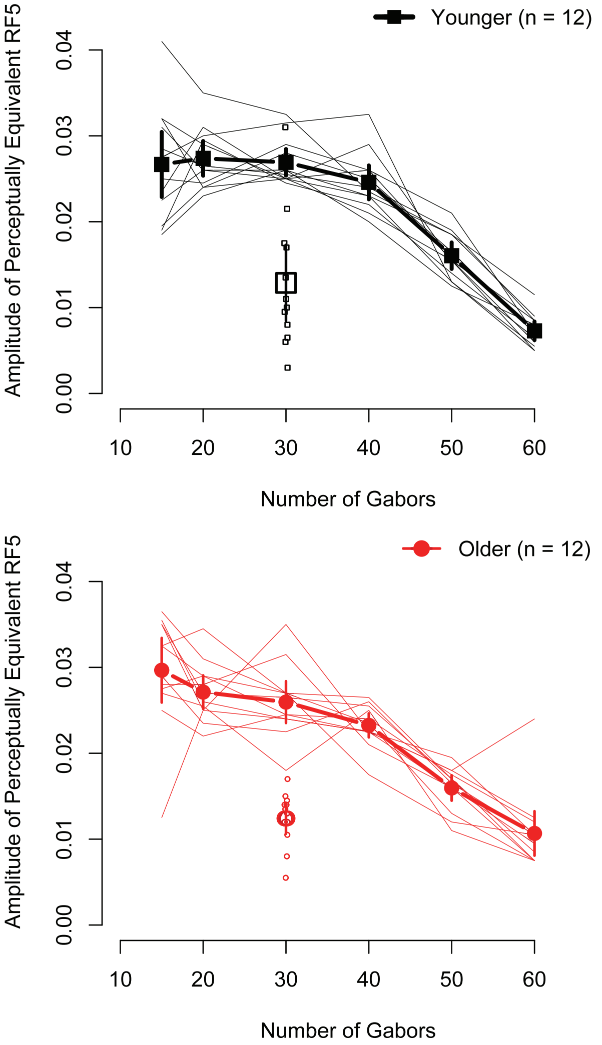

Figure 2. Mean amplitudes of the perceptually equivalent pentagon are shown as a function of the number of Gabors comprising the conflicting pentCircle contour for younger subjects (top) and older subjects (bottom). Higher amplitude represents a stronger shape illusion engendered by the local orientations. Thick lines and filled symbols show the group average data. Error bars represent the 95% confidence interval. Thin lines show individual subjects' performance. The open symbols show data in the random condition (contour comprising 30 randomly oriented Gabors positioned on a circle).

the pentCircle on 50% of the trials. Figure 2 plots the mean amplitude of the PEP for each subject as a function of the number of Gabors comprising the conflicting contour. A high amplitude represents a strong shape illusion engendered by the local orientations in the pentCircle. As can be seen in Figure 2, the illusion was present for contours sampled with 15–40 Gabors and diminished when more than 40 elements sampled the contour. Interestingly, the strength of the illusion was the same in older and younger subjects for all contours, as the curves in the older and younger groups lie on top of each other.

A mixed-model ANOVA revealed a significant main effect of number of elements, $F(5, 110) = 91.9$, $\hat{\varepsilon} = 0.50$, $p < 0.0001$, $\eta_g^2 = 0.77$, confirming that the strength of the illusion varied with the number of contour elements. Neither the main effect of age, $F(1, 22) = 0.66$, $p = 0.42$, $\eta_g^2 = 0.01$, nor the interaction between age and number of elements, $F(5, 110) = 1.62$, $\hat{\varepsilon} = 0.50$, $p = 0.20$, $\eta_g^2 = 0.05$, were significant. Older and younger subjects also showed equivalent PEP amplitudes in the random condition, $F(1, 22) = 0.04$, $p = 0.85$, $\eta_g^2 = 0.001$.

Pairwise comparisons were conducted to compare performance between conditions. The Holm's Sequential Bonferroni procedure was used to maintain a family-wise Type I error at 0.05. For the younger group, PEP amplitudes in the 15G, 20G, 30G, and 40G conditions differed significantly from the random condition ($p_{adj} < 0.01$), but the 50G and 60G conditions did not ($p_{adj} > 0.5$). For the older group, the PEP amplitude in the 15G, 20G, 30G, 40G, and 50G conditions different significantly from the random condition ($p_{adj} < 0.05$), and only the 60G condition did not differ from the random condition ($p_{adj} = 0.55$). Thus, the shape illusion was present for contours comprising 15–40 Gabors in younger subjects, and contours comprising 15–50 Gabors in older subjects. The strength of the illusion was comparable for contours with 15–40 Gabors, as PEP amplitudes did not differ significantly between 15G and 20G ($p_{adj} > 0.55$), 20G and 30G ($p_{adj} > 0.46$), and 30G and 40G ($p_{adj} > 0.18$) conditions in both groups. However, PEP amplitudes were significantly lower in the 50G compared to the 40G condition ($p_{adj} < 0.001$), and in the 60G compared to the 50G condition ($p_{adj} < 0.007$) in both groups. This result indicates that orientation information had a diminished effect on the perception of shape when contours were sampled with more than 40 elements.

The presence of a shape illusion for conflicting contours sampled with 15–40 Gabors is consistent with findings of Day and Loffler (2009). However, subjects in Day and Loffler's study consistently experienced the strongest illusion in the 30 Gabor condition and showed a significantly weaker illusion in the 15 and 40 Gabor conditions, exhibiting an inverted U-shaped function. In the current results, this U-shaped function was less pronounced and the number of contour elements that produced the strongest illusion varied substantially across subjects between 15 and 40 Gabors (see individual subjects' data in Figure 2).

Although more older than younger subjects showed the strongest illusion with 15 Gabors, the proportion of subjects with the maximum illusion in each condition did not differ between older and younger subjects, $\chi^2(3)$

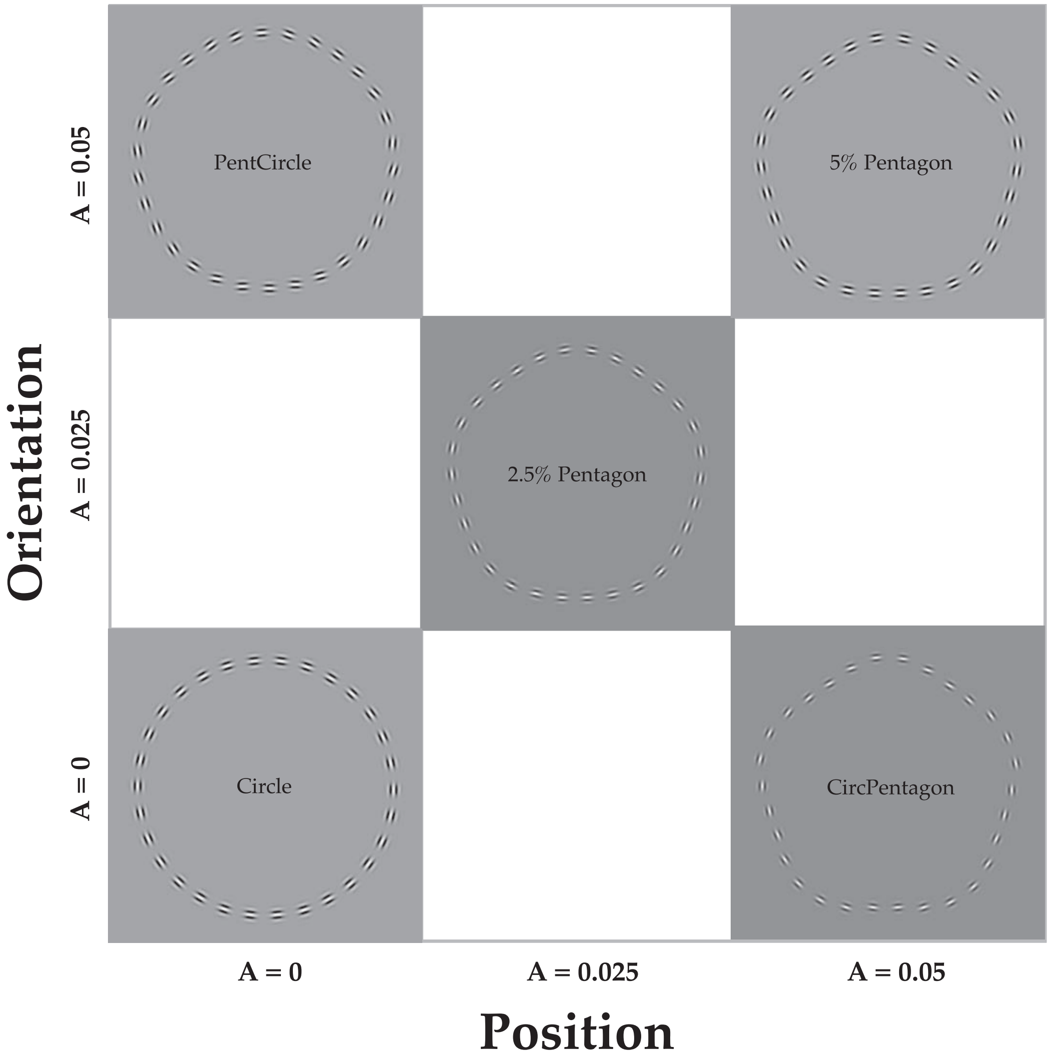

Figure 3. The five patterns used in Experiment 2. Shapes on the same row but in different columns only differ by the positions of the Gabors. Shapes in the same column but in different rows only differ by the orientations of the Gabors. The amplitude of the RF5 used to generate the positions and orientations of the shapes is indicated beside each row and column.

$= 2.36$, $p = 0.50$. Moreover, the maximum PEP amplitudes of younger subjects ($\mu = 3.05\%$) and older subjects ($\mu = 3.21\%$) also did not differ from each other, $F(1, 22) = 1.00$, $p = 0.33$, $\eta_g^2 = 0.043$.

## Experiment 2: Discriminating between the real and illusory pentagon shapes

Results from Experiment 1 suggest that older and younger subjects perceive the pentCircle to be as circular as a rounded pentagon with an amplitude of ≈2.6%. However, it is not clear to what extent the two contours are perceptually similar on other dimensions.

The current experiment attempted to better quantify the illusion by measuring subjects' ability to discriminate between the conflicting target contours and consistent pentagon contours of different amplitudes. Subjects were presented with two contours on every trial and were asked to report whether the contour shapes were the same or different. If the illusion is not present, a conflicting target contour and consistent pentagon contours should be easily discriminable and sensitivity (i.e., *d′*) should be high. Conversely, if the illusion is very strong, then these contours should be difficult to discriminate and *d′* should be low. Experiment 2 measured the discriminability of five closed contours differing by either Gabor positions or orientations, or by both positions and orientations (see Figure 3).

## Methods

### *Subjects*

Eleven older and nine younger subjects from Experiment 1 participated in this experiment.

### *Apparatus*

The apparatus was the same as in Experiment 1.

### *Stimuli*

Five shapes were constructed using Gabor elements that had the same parameters as in Experiment 1. Three shapes had consistent contours: a 0% pentagon (circle), a 2.5% pentagon, and a 5% pentagon. In addition, there were two shapes constructed with conflicting contours: the pentCircle, which was the same as in Experiment 1, and the circPentagon. The circPentagon consisted of Gabor patches placed along the radius of an RF5 shape with $A = 5\%$, but the Gabor orientations were tangential to a circle. Hence, linking the Gabor centers of the circPentagon traced out a path corresponding to a 5% RF5 shape, but the local orientations of the Gabors were not collinear with the path.

All five contours were sampled with 30 equally spaced Gabor elements. The elements in the five contours differed in terms of their positions, orientations, or both positions and orientations (Figure 3). For example, the circle and the pentCircle shared the same Gabor positions, but differed in their orientations; the same was true for the circPentagon and the 5% pentagon. Conversely, the circle and the circPentagon shared the same orientations, but differed in the Gabor positions; the same was true for the pentCircle and the 5% pentagon. Finally, the 2.5% pentagon differed from the others in both element positions and orientations, but the magnitude of the difference was the same for all four shapes.

### *Procedure*

A same–different task was used to measure sensitivity for discriminating the five shapes. Two shapes were shown sequentially on every trial and subjects were asked to indicate whether they were the same or different. Subjects were informed that there would be an equal number of same and different trials.

The experiment began with an adaptation period of 60 s during which subjects adapted to the mean luminance of the screen. Three examples of trials with same and different shapes were then shown to familiarize the subjects with the task. The temporal sequence of a single trial was identical to the one used in Experiment 1. A response screen, containing an "S" on the one side of the screen and a "D" on the other, was presented at the end of each trial. Subjects indicated their response by pressing one of two keys on a computer keyboard. The "same" response was on the right side of the display and keyboard for half of the subjects and was on the left side for the other half of the subjects. Subjects had unlimited time to respond and the following trial started 2500 ms after their response. Unlike Experiment 1, auditory feedback was provided on every trial, with correct and incorrect responses were indicated by high- and low-pitched tones, respectively.

Each shape was paired with itself on 60 trials and with every other shape on 30 trials. Given that there are 10 possible pairs, this resulted in 300 same trials (60 trials × 5 contours) and 300 different trials (30 trials × 10 pairs). All trials were interleaved and split into six blocks of 100 trials. The experiment took approximately 60 minutes to complete. The global orientation of the shapes (i.e., the phase of radial modulation) was randomized across trials, but stayed constant across the two intervals in each trial. The mean radius and the center of the contour was jittered slightly across trials and intervals as in Experiment 1 to preclude subjects from basing their judgments on local changes occurring at particular locations on the screen.

### *Analysis*

The differencing strategy for same–different tasks was used to calculate $d'$ (Kaplan, Macmillan, & Creelman, 1978; Macmillan & Creelman, 1991). Hit rate was defined as $p$("different" | different trial) and False Alarm rate was defined as $p$("different" | same trial). One-way ANOVAs were used to compare younger and older subjects' performance for the ten pairs of contours and the Holm-Bonferroni method was used to control the family-wise error rate at 0.05.

## Results

Figure 4A shows mean $d'$ values for discriminating consistent contours: the circle, the 2.5% pentagon, and the 5% pentagon. Subjects in both age groups showed very good discrimination performance for the pairs containing the circle and somewhat poorer sensitivity for the 2.5% and 5% pentagon pair. Better discrimination performance for pairs containing the circle compared to two noncircular contours is consistent with previous studies showing a gradual increase in radial modulation thresholds with increasing amplitude of the test contour (Bell, Wilkinson, Wilson, Loffler, & Badcock, 2009; Schmidtmann et al., 2012). For example, whereas the Weber fraction for discriminating an RF5 from a circle is $<0.004$ (Schmidtmann et al., 2012; Wilkinson et al., 1998), it increased to $\approx 0.005$ for an RF5 with 2% amplitude (Schmidtmann et al., 2012).

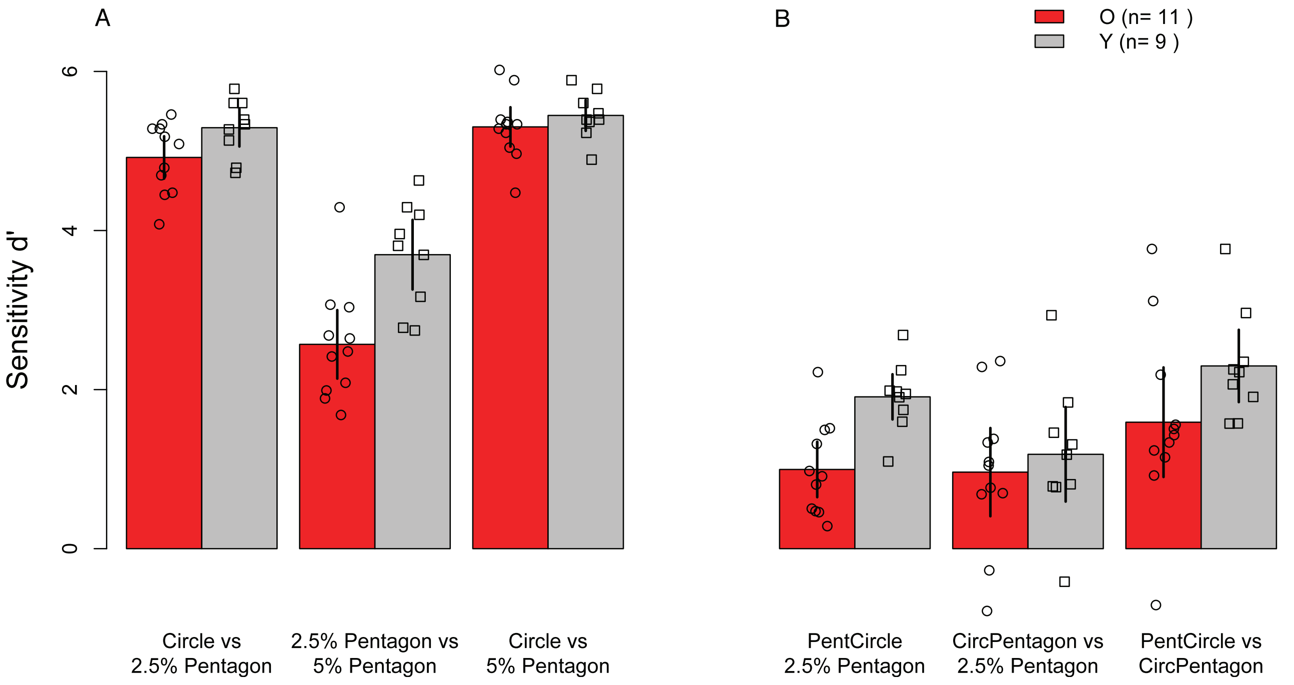

Figure 4. (A) Mean sensitivity, *d*′, of younger (gray bars) and older (red bars) subjects for discriminating consistent shapes: circle and 2.5% pentagon, 2.5% pentagon and 5% pentagon, and circle and 5% pentagon. (B) Mean sensitivity, *d*′, of younger (gray bars) and older (red bars) subjects for discriminating the following pairs: 2.5% pentagon and the pentCircle, the 2.5% pentagon and the circPentagon, and the pentCircle and the circPentagon. Error bars represent 95% confidence intervals and small open symbols show individual subjects' data. See Figure 3 for shape examples.

Comparing younger and older subjects' $d'$s for each pair revealed no effect of age for the circle and 5% pentagon pair, $F(1, 18) = 0.76$, $p = 0.40$, $\eta_g^2 = 0.04$, nor did the circle and 2.5% pentagon pair, $F(1, 18) = 4.07$, $p = 0.06$, $\eta_g^2 = 0.18$. However, the effect of age was significant for the 2.5% pentagon and 5% pentagon pair, $F(1, 18) = 12.72$, $p = 0.002$, $\eta_g^2 = 0.41$, with older subjects showing significantly lower $d'$ than younger subjects. Thus, whereas older subjects were as sensitive as younger subjects at discriminating the circle from the two rounded pentagon contours, they were less sensitive than younger subjects at discriminating between the 2.5% pentagon and the 5% pentagon.

Figure 4B shows mean $d'$ values for discriminating the 2.5% pentagon and the two conflicting contours—the circPentagon and pentCircle. Sensitivity for discriminating these three contours was worse than sensitivity for all other contour pairs, $F(1, 18) = 451.7$, $p < 0.001$. The relatively poor discrimination of these contours indicates that the contours appeared similar in shape. Thus, consistent with Experiment 1 and the study by Day and Loffler (2009), the orientations of the pentCircle shifted its shape from a circle to a rounded pentagon. Similarly, the orientations in the circPentagon made the pentagon appear more circular. As a result, discrimination of the pentCircle and the circPentagon was also poor (younger: $d' = 2.30$; older: $d' = 1.59$). Examining the effect of age for these pairs revealed a significant effect of age for the pentCircle and 2.5% pentagon pair, $F(1, 18) = 14.9$, $p = 0.001$, $\eta_g^2 = 0.45$, no significant effect of age for the circPentagon and 2.5% pentagon pair, $F(1, 18) = 0.29$, $p = 0.60$, $\eta_g^2 = 0.02$, and no effect for the pentCircle and the circPentagon pair, $F(1, 18) = 2.56$, $p = 0.13$, $\eta_g^2 = 0.12$.

Figure 5 shows mean $d'$ values for the remaining four pairs. Figure 5A shows discrimination performance for pairs of contours that have the same element orientations, but different element positions, and Figure 5B shows pairs of contours that have the same element positions, but differ by their element orientations. Comparing performance in the two groups for these four pairs revealed lower $d'$s in older subjects in the circle and circPentagon pair, $F(1, 18) = 4.9$, $p = 0.04$, $\eta_g^2 = 0.21$, and the circle and pentCircle pair, $F(1, 18) = 5.53$, $p = 0.03$, $\eta_g^2 = 0.24$; however, these effects did not pass the criterion for statistical significance after controlling the family-wise error rate. Younger and older subjects showed similar $d'$s for the circPentagon and 5% pentagon pair, $F(1, 18) = 1.96$, $p = 0.18$, $\eta_g^2 = 0.10$, and the pentCircle and 5% pentagon pair, $F(1, 18) = 1.28$, $p = 0.27$, $\eta_g^2 = 0.07$.

Y. Z. Wang and Hess (2005) previously reported that orientation information exerts a greater influence on the perceived shape than position information. We

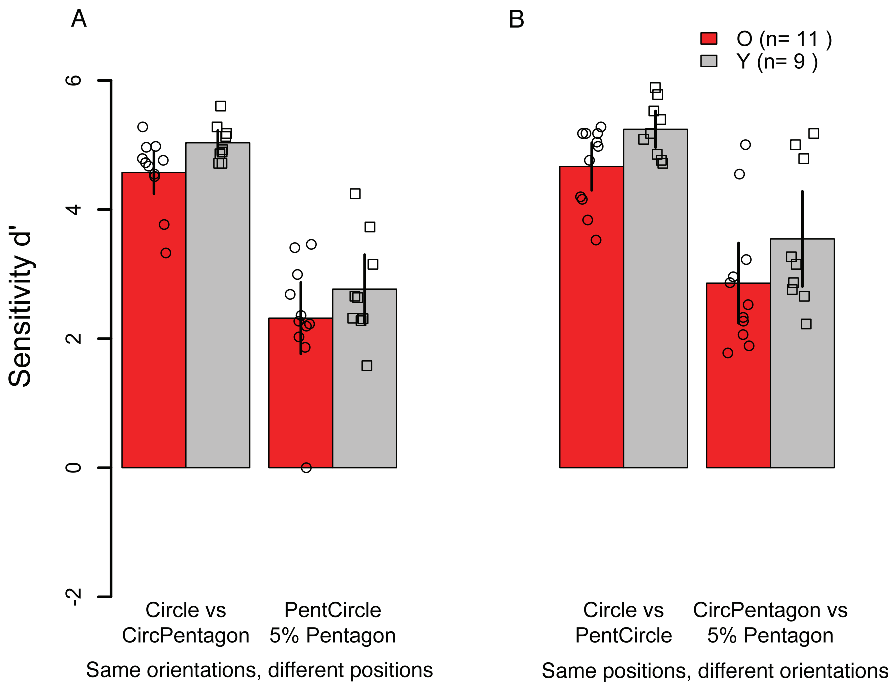

Figure 5. Mean sensitivity, *d*′, of younger (gray bars) and older (red bars) subjects for discriminating (A) pairs of contours that differ by their Gabor positions only, but whose local orientations are the same, and (B) pairs of contours that differ by their Gabor orientations only, but whose element positions are the same. Error bars represent 95% confidence intervals and small open symbols show individual subjects' data.

tested for this effect by carrying out a focused comparison, which revealed that *d*′s for the contour pairs that differed by the Gabor positions only (Figure 5A) were significantly lower than *d*′s for contour pairs that differed by their Gabor orientations only, $F(1, 18) = 7.9$, $p = 0.01$, $\eta_g^2 = 0.13$ (Figure 5B). This effect did not interact with age, $F(1, 18) = 0.38$, $p = 0.55$, $\eta_g^2 = 0.01$. Thus, two contours that differed only in their element orientations were more discriminable than two contours that differed only in their element positions for both age groups.

Furthermore, many previous studies have shown that human vision is highly sensitive to circular shape (e.g., Achtman et al., 2003; Dumoulin & Hess, 2007; Hess et al., 1999; Kurki & Saarinen, 2004; Levi & Klein, 2000; Wilkinson et al., 2000). A focused comparison of four pairs that contained a circle versus the remaining six pairs was significant, $F(1, 18) = 402.7$, $p < 0.001$, and this effect did not interact with age, $F(1, 18) = 1.07$, $p = 0.31$. Thus, discrimination sensitivity was highest for pairs containing a circle in both age groups.

Finally, we were concerned that older subjects may have had a higher probability of making "finger errors" than younger subjects, which may have influenced their *d*′ estimates. To examine how a higher finger-error rate, or lapse rate, would affect *d*′ values in this task, we computed the accuracy of simulated observers displaying different lapse rates. The simulated observers responded with the same accuracy as younger subjects on most trials, except that they responded randomly on a certain percentage of the trials determined by the lapse rate. As the model's lapse rate increased, *d*′ values decreased more for conditions with high *d*′ values and less for conditions with lower *d*′. This pattern of results does not match the observed effects of aging, indicating that the observed age-related difference in shape discrimination cannot be explained by a higher lapse rate in older compared to younger subjects.

## Discussion

Using a shape illusion discovered by Day and Loffler (2009), Experiment 1 revealed that the way local orientation and position information are combined in shape perception does not change with aging. Consistent with Day and Loffler, the strength of the illusion, or the extent to which orientation information influenced the percept, depended on the number of elements composing the contour: when contours were densely sampled, the perceived shape corresponded to the shape of the underlying contour (i.e., a circle); when the contour was sampled more sparsely, the element orientations influenced the percept and generated the illusion of a pentagon shape. Day and Loffler found that the illusion was strongest when contours were sampled with 30 Gabors and declined for contours with sparser or denser sampling; however, in the current experiment, the number of Gabors associated with the strongest illusion varied across subjects and, on average, the strength of the illusion was comparable for contours composed of 15–40 Gabors. Importantly, the magnitude of the illusion and the effect of contour element number on the illusion did not differ with aging. By varying the number of elements and the element carrier frequency independently, Day and Loffler (2009) had shown that the strength of the illusion depends on the interelement separation relative to carrier wavelength, rather than on the number of elements per se. Interelement spacing of sampled contours was also found to be a critical factor for detecting a heterogeneity in a shape's contour (Kempgens, Loffler, & Orbach, 2013), further emphasizing the importance of interelement spacing in shape processing. The current results reveal that the dependence of shape perception on interelement spacing is not altered in aging. This result is consistent with a study by McKendrick et al. (2010) that examined the effect of aging on shape discrimination thresholds of contours sampled with different numbers of elements. Their results showed that the minimum aspect ratio required to discriminate an ellipse from a circle decreased with increasing contour sampling at the same rate for younger and older subjects. Interelement spacing has also been shown to affect the detectability and discriminability of elongated contours embedded in cluttered backgrounds (e.g., Beaudot & Mullen, 2003; Kovács & Julesz, 1993; Li & Gilbert, 2002). Interestingly, similar to the current results, the effect of interelement spacing on contour grouping was the same in younger and older subjects (Hadad, 2012; Roudaia et al., 2013), even though overall ability to detect and discriminate contours in noise declines with aging (Del Viva & Agostini, 2007; Roudaia et al., 2011, 2013). Although Day and Loffler (2009) speculated that the shape illusion is generated by integration by a global pooling mechanism, as opposed to local contour integration mechanisms thought to underlie detection of elongated contours in noise (e.g., Field, Hayes, & Hess, 1993), there is growing evidence suggesting that global shape mechanisms do not operate directly on individual contour elements, but instead pool information from intermediate-stage mechanisms that integrate local orientation information to encode curved contour segments and inflection points (e.g., Bell et al., 2011; Bell, Hancock, Kingdom, & Peirce, 2010; Kempgens et al., 2013; Schmidtmann et al., 2012). To the extent that there may be shared, overlapping mechanisms that contribute to performance in different tasks that involve the integration of orientation information in sampled contours, the current results are consistent with previous studies (Hadad, 2012; McKendrick et al., 2010; Roudaia et al., 2013) in finding no differential effect of interelement spacing on performance with aging.

To obtain a quantitative assessment of the shape illusion, Experiment 2 measured the discriminability of shapes described by consistent and conflicting contours using a same–different shape discrimination task. Results revealed that, just as a circle whose orientations are modified can be made to appear as a rounded pentagon, a pointed pentagon contour (5% pentagon) can be made to appear more rounded by making its element orientations consistent with that of a circle. Low discrimination performance between the pentCircle, the circPentagon, and the consistent 2.5% RF5 contour confirmed that these three contours appeared similar in shape to each other. Younger and older subjects showed similar $d'$ for two of these pairs, but younger subjects showed better discrimination for the pentCircle and the 2.5% pentagon than older subjects. It is not clear why the effect of age varied for the different pairs, but it may be due to differences in the strength or the consistency of the pentCircle illusion for the two groups. We also noted that discrimination performance for all three pairs of stimuli was significantly better than chance, suggesting that the contours did not appear identical to each other. What cues may have served to differentiate these contours? One possibility is that the perceived amplitude of radial deformation of the conflicting contours was not exactly 2.5% for all subjects, thereby allowing subjects to discriminate the contours based on slight differences in the amplitude of radial modulation. Alternatively, subjects may have used the variation in collinearity of the elements to distinguish between the conflicting and consistent contours. Day and Loffler (2009) suggested that the presence of the shape illusion implies that "observers perceive a smooth contour, despite the fact that strict collinearity is violated" (p. 14). However, this assumption does not need to be true. For example, the conflicting contour may appear to have the same shape as the 2.5% pentagon, but the former may appear "jagged" whereas the latter appears "smooth." If the collinearity cue was being used to discriminate these contours, then the addition of a small amount of orientation noise to the orientations of the 2.5% pentagon should greatly reduce the discriminability of the contours.

Experiment 2 demonstrated that for contours where orientations and positions were consistent with different shapes, a change in orientations had a greater influence on the perceived shape of the contour than a similar change in positions. This result is consistent with a previous study that examined the contribution of orientation and position information to shape discrimination (Y. Z. Wang & Hess, 2005). Radial frequency contours were sampled with Gabors such that either their positions or their orientations differentiated the contour from a true circle. Radial deformation thresholds for patterns defined by element orientations were found to be lower than deformation thresholds for patterns defined by element positions, indicating that shape perception mechanisms are more sensitive to changes in local contour orientation information compared to position information. Nevertheless, deformation thresholds were lowest when both orientation and position information were available, suggesting that both cues are used in shape discrimination. Similarly, the detectability of global shape contours embedded in noise appears to be more affected by the addition of orientation jitter to contour elements than by jittering contour element positions (Schmidtmann et al., 2013).

Experiment 2 also measured discrimination performance for the circle, the 2.5% pentagon, and 5% pentagon contours. Whereas there were no age differences in sensitivity for discriminating the circle from the 2.5% pentagon or the 5% pentagon, older subjects were less sensitive than younger subjects at discriminating the two pentagon contours from each other. What may account for this difference? Given that *d*′s for the pairs containing a circle were very high in both groups, a ceiling effect may have masked a true age difference in performance. Furthermore, discriminating a circle from a noncircle may be an easier task than discriminating two noncircular contours with different radial modulation. However, several studies that measured radial modulation thresholds for discriminating between a circle and an ellipse (McKendrick et al., 2010), a rounded square (RF4; Y. Z. Wang, 2001), and a rounded pentagon (RF5; Habak et al., 2009) in younger and older subjects failed to find any age differences in sensitivity. In one exception, Y. Z. Wang et al. (2009) reported a gradual decline in shape discrimination thresholds starting at age 55.

Furthermore, the finding of an age difference in discrimination of two noncircular contours is consistent with a recent study by Weymouth and McKendrick (2012), who found that older subjects required greater radial modulation than younger subjects to discriminate between two noncircular shapes: an RF3 (triangular) contour and an RF4 (square) contour. Thus, it appears that age differences in shape discrimination are more apparent in tasks involving two noncircular contours, as opposed to detection of deviations from circularity.

What type of mechanisms may account for the observed age-related changes in shape perception? The high sensitivity for discriminating amplitude modulations of radial frequency patterns provides strong evidence that shape perception is driven by a global mechanism that combines information across the circumference of the contour (Bell & Badcock, 2008, 2009; Habak, Wilkinson, & Wilson, 2006; Hess et al., 1999; Jeffrey, Wang, & Birch, 2002; Loffler et al., 2003; Schmidtmann et al., 2012; Wilkinson et al., 1998). This global pooling mechanism appears to be restricted to shapes with low radial frequency modulation (Schmidtmann et al., 2012; Wilkinson et al., 1998) and to be tuned to a specific type of shape and amplitude of radial modulations (Bell, Dickinson, & Badcock, 2008; Bell & Kingdom, 2009; Bell et al., 2009; Habak, Wilkinson, Zakher, & Wilson, 2004; Schmidtmann et al., 2012, 2013). Furthermore, several studies have shown that the inputs to the global pooling stage are themselves outputs of intermediate stage curvature detectors that integrate local orientation information to encode curvature and inflection points along the contour (Bell et al., 2008, 2010, 2011). A biologically-plausible model developed by Kempgens et al. (2013), based on an earlier model by Poirier and Wilson (2006), consists of five stages: In the first three stages, local contour information, the size and center of the shape are determined and, in the fourth stage, multiple local curvature units integrate information from local orientation channels in a nonlinear fashion, and outputs of one or more of these curvature units are combined with the earlier stages of the model to represent the curvature signals in relation to the center of the shape. In the final stage, a global mechanism pools the inputs of the various arc units from the fourth stage and a population code of these convexities and concavities in different locations around the shape combine to represent different shape types. The global pooling stage is based on neurophysiological recordings in primate area V4, where neurons are known to be sensitive to polar gratings, curves and angles, as well as complex combinations of curves (Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996; Pasupathy, 2006; Pasupathy & Connor, 1999, 2001). Moreover, it has been shown that a population of neurons with these properties is sufficient to encode complete shapes using a population code (Cadieu et al., 2007; Pasupathy, 2006). Similarly, neuroimaging studies in humans have revealed preferential activation of area V4 to concentric shapes and circularity (Dumoulin & Hess, 2007; Wilkinson et al., 2000).

The age difference in discrimination of the two noncircular contours observed in the current study may be due to declines at the stage where curvature detectors integrate contour elements together. Curvature discrimination is known to deteriorate with increasing curvature (Wilson & Richards, 1992), which would predict greater deficits with increasing amplitudes of radial modulation. Previous research found that older subjects showed impaired curvature discrimination with quadratic and compressed arcs, but not for bell-shaped curves, which were the easiest to discriminate (Legault et al., 2007). These results suggested that aging affects the sensitivity of curvature detectors, which are thought to rely primarily on responses of neurons in earlier visual areas (V1 and V2; Dobbins, Zucker, & Cynader, 1987, 1989; Wilson, 1985; Wilson & Richards, 1989). The idea that age-related declines in curvature detectors may account for age differences in shape discrimination was suggested previously by Habak et al. (2009), who found that older subjects showed worse shape discrimination thresholds for texture-defined contours, but not for luminance-defined contours. Given that radial modulation thresholds require optimal global pooling of information along the contour (Schmidtmann et al., 2012; Wilkinson et al., 1998), this pattern of results was consistent with the idea that aging reduces the ability to extract curvature from texture-defined contours, but does not affect the global pooling of curvature signals by shape detectors. To confirm this hypothesis, future studies should attempt to measure sensitivity to curvature and the extent of global pooling in radial frequency patterns in the same younger and older individuals.

Neurophysiological studies in monkeys and cats have found broader tuning for orientation and direction in V1 neurons of older animals (Hua et al., 2006; Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky et al., 2000), and this detuning was even more pronounced in V2 (Yu et al., 2006). Moreover, neurons in older macaques also showed delays in response latencies within and between V1 and V2 (Y. Wang et al., 2005). To date, there have not been any neurophysiological studies on the effects of aging on neuronal function in higher-order areas in the ventral stream. Given that shape selective neurons in area V4 receive their inputs from areas V1 and V2, age-related differences in shape perception may result from impoverished input arriving to V4 from V1 and V2, or from changes in the function of shape selective neurons in V4. That said, observed neurophysiological changes have not always been found to be associated with parallel behavioral changes. For example, in contrast to the above-mentioned degradation of neuronal function of early visual neurons in older cats and primates, psychophysical and electrophysiological studies in older humans have found no evidence for age-related changes in orientation perception or the tuning of orientation channels (Betts, Sekuler, & Bennett, 2007; Delahunt et al., 2008; Govenlock, 2010; Govenlock et al., 2009).

Finally, it is important to consider the contribution of optical factors on the observed age differences in performance. Although all subjects had normal or corrected-to-normal visual acuity, older subjects' lack of accommodation (due to presbyopia) would be expected to produce 0.87D of blur at our viewing distance. Given this amount of blur, subjects would be expected to resolve gratings with spatial frequency as high as 10.6 cpd (Benjamin & Borish, 2006). The Gabors comprising the contours in our stimuli had a spatial frequency of 6.5 cpd and $\approx$2 cycles were visible. Thus, even with greater optical blur, older subjects likely were able to perceive the Gabor orientations. The fact that we didn't observe any differences in the shape illusion in Experiment 1 further corroborates this hypothesis. If older subjects' ability to perceive the Gabor orientations was seriously affected, it would predict that orientations would have a reduced effect in older subjects, which we did not observe in Experiment 1.

Another factor that is worth considering is whether the relatively brief stimulus duration (200 ms) may have differentially affected performance in the two age groups. The stimulus duration was chosen to match previous studies, as well as to preclude any eye movements when performing the shape judgments. In a previous study, we showed that reducing stimulus duration to 40 ms does not have a differential effect on older subjects' orientation discrimination thresholds for single Gabors (Roudaia et al., 2011), and Habak et al. (2009) showed that younger and older subjects' radial modulation thresholds for RF5 contours are equally affected by changes in stimulus duration over a range from 40–500 ms. Thus, the current results are likely to generalize to longer stimulus durations.

In sum, the current experiments revealed that the magnitude of a shape illusion generated by conflicting orientation and position information does not change with aging, suggesting that orientation and position cues are integrated in a similar way in younger and older adults. However, older subjects were less able to discriminate between two noncircular radial frequency contours, indicating that shape discrimination performance is affected in older age, especially for noncircular shapes. Changes in the processing of shape in older age may play a role in the age-related changes in higher-order visual processing, such as face and object perception (Boutet & Faubert, 2006; Daniel & Bentin, 2012; Konar, Bennett, & Sekuler, 2013; Lott, Haegerstrom-Portnoy, Schneck, & Brabyn, 2005; Pilz, Konar, Vuong, Bennett, & Sekuler, 2011; Rousselet et al., 2009; Wilson, Mei, Habak, & Wilkinson, 2011). In addition, changes in shape discrimination ability may also impact visual working memory for shapes (Hayden & Gallant, 2013; Salmela, Lähde, & Saarinen, 2012). Further studies are needed to tease apart the relative contributions of different hierarchical stages of processing and different physiological mechanisms to the age-related changes in shape processing.

*Keywords: shape perception, orientation, position, aging*

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