CONTOUR INTEGRATION AND AGING

THE EFFECTS OF AGING ON VISUAL CONTOUR AND SHAPE PERCEPTION

By

EUGENIE ROUDAIA, B.Sc.

A Thesis

Submitted to the School of Graduate Studies

in Partial Fulfillment of the Requirements

for the Degree

Doctor of Philosophy

McMaster University

DOCTOR OF PHILOSOPHY (2013)	McMaster University
(Psychology, Neuroscience, & Behaviour)	Hamilton, Ontario

TITLE:	The effects of aging on visual contour and shape perception
AUTHOR:	Eugenie Roudaia, B.Sc. (McGill University)
SUPERVISOR:	Professors Patrick J. Bennett and Allison B. Sekuler
NUMBER OF PAGES:	xx, 177

Abstract

The effects of aging on visual contour and shape perception

Eugenie Roudaia
Doctor of Philosophy
Department of Psychology, Neuroscience, & Behaviour
McMaster University
2013

Human vision has an incredible ability to translate light reaching the retinae into a coherent, three-dimensional representation of the outside world in a fraction of a second. Much research has been devoted to understanding how local orientation information is integrated to form global contours and shapes - a crucial step in visual processing. This dissertation describes experiments examining how contour and shape perception are affected in healthy aging.

Chapter 2 examined contour grouping at low contrast and in the absence of distracters. Unlike younger subjects, older subjects did not benefit from co-alignment of local orientations with the contours outline, suggesting that grouping by orientation co-alignment is impaired in older age in low contrast. Chapters 3 and 4 examined the effects of aging on the ability to detect and discriminate high-contrast contours embedded in a dense field of distracters, as real life situations often require detecting objects among clutter, such as a snake hiding among tall grass. Results showed that older adults require significantly more time to discriminate contours in clutter, especially for less salient contours. Moreover, increasing the relative density of background clutter had a greater detrimental effect on older, compared to younger, subjects. However, aging did not seem to affect the ability to group contours across a range of spatial distances, or the sensitivity of contour integration to orientation misalignment. Lastly, Chapter 5 examined the influence of local orientation information on the perception of a contour's shape. Results revealed that older and younger subjects perceived the shape of a sampled contour in the same way, even when the contour's orientation and position information were in conflict. These findings indicated that the integration of orientation and position information in shape perception does not change with age.

Preface

`To my loving family and friends.`

This dissertation comprises 6 chapters and is written in the "sandwich" thesis format. Chapter 1 outlines the general theme and objectives of the work. Chapters 2-5 describe the research and are written in journal article format. Chapter 6 lays out the overall implications of the research and outlines future research directions.

Research presented in Chapter 2 was conducted in 2006 and was published in Vision Research in 2008. Research presented in Chapter 3 was conducted in 2007-2008 and was published in Vision Research in 2010. Both articles are reproduced here verbatim with full permission from Vision Research. Research presented in Chapters 5 and 4 was conducted between 2009 and 2011 and will be submitted for publication in Vision Research and Frontiers of Perception, respectively.

All work described in this dissertation was conducted in collaboration with my supervisors, Dr. Allison B. Sekuler and Dr. Patrick J. Bennett. As the primary author, I was responsible for all aspects of the research: the experimental design, stimulus generation and programming, data analysis, and writing of the first draft of the manuscripts. Later versions of all manuscripts were revised in collaboration with the co-authors. Two control experiments (4a and 4b) presented in Chapter 3 were conducted in collaboration with Lindsay E. Farber, who did the initial data analysis and wrote the methods section for those experiments. I wrote the necessary code for all the experiments, with the exception of Experiment 1 in Chapter 2 and Experiments 4a and 4b in Chapter 3 that were written by Patrick J. Bennett. Donna Waxman, the lab manager, provided invaluable assistance in recruiting and testing subjects who provided data presented in all the chapters.

This research was supported by grants from the Canada Research Chair programme, the Canadian Institute of Health Research and the National Science and Engineering Research Council to A.B.S. and P.J.B. Throughout my graduate studies, I was supported by the Prestige scholarship from McMaster University (2007-2008), the Ontario Graduate Scholarship Science and Technology (2008-2009), and the A.G. Bell NSERC Canada Graduate Scholarship (2009-2011).

Acknowledgements

I am deeply grateful to my supervisors, Patrick J. Bennett and Allison B. Sekuler, for providing the opportunity to engage in this research, for their wisdom and stimulating discussions, and for sharing their passion for good science and good science communication. I would like to thank Daniel Goldreich for his insightful feedback and discussions during my thesis committee meetings and Bruce Christensen for joining my supervisory committee at a short notice. I also thank Steven Dakin for sharing his experimental code that I adapted for use in Chapter 4.

I am sincerely grateful to Donna Waxman for her incredible work recruiting and testing younger and older subjects, for her unwavering dedication to research and to the lab, and for being a true friend. A special thank you to Zahra Hussain, Yaroslav Konar, Lia Tsotsos, Stanley Govenlock, Christopher Taylor, Carl Gaspar, Karin Pilz, Guillaume Rousselet, Lindsay Farber, and David McGovern for their helpful discussions on my work. Thank you to all the members of the Canada Institute of Health Research Strategic Research Training Program in Communication and Social Interaction in Health Aging for stimulating my interest in interdisciplinary research in aging. A big thanks to all past and present members of the Vislab family and to the wonderful Department of Psychology, Neuroscience, & Behaviour for creating an interesting and exciting place to work and learn. I am forever grateful to my parents, friends, and family for their invaluable support throughout these years. A very special thank you to my sister, Liya, for encouraging me to do research and to Ron Smid for being my inspiration.

Contents

List of Tables

List of Figures

Chapter 1

General Introduction

During the five years that spanned this dissertation, the proportion of Canadians aged 65 and over increased by 14%, growing faster than the proportions of children and of adults younger than 64 in the same period (Statistics Canada, 2011). The aging of the Canadian population is mirrored in many countries across the globe, where improvements in living conditions, nutrition, and healthcare have allowed people to live longer and healthier lives. Yet, even in the absence of disease, aging is accompanied by physiological declines. It is widely known that cognitive functions, such as working memory and processing speed, decline with aging (e.g., Birren and Fisher, 1995; Craik and Salthouse, 2000). It is also appreciated that sensory thresholds increase with aging, so that older subjects require a greater amount of sensory stimulation to detect stimuli reliably (Birren, 1964). However, much less is known about age-related changes in perception. Although the percept of a coherent, stable world is obtained quickly and effortlessly, it is the result of a complicated cascade of neural computations in multiple brain areas that combine sensory inputs with prior knowledge to arrive at the most likely interpretation of sensory input. Given that perception is a pre-requisite to most, if not all, cognitive and motor functions, understanding age-related changes in perceptual function is crucial for understanding behaviour across the lifespan. In addition, examining how perception changes with age can inform our understanding of perceptual mechanisms and how they adapt to neurophysiological and sensory decline.

1.1 Perceptual organization

When we look around, the world appears organized into coherent objects appearing against backgrounds (e.g., birds in the sky and flowers on the grass), not as a disjointed collection of dots, curves, and surfaces distributed across space. Perceptual organization is the process by which elements of the scene are grouped together into wholes. In the early 20th century, Gestalt psychologists observed that parts of the visual scene are often perceived as a whole, even though no explicit grouping is defined in the image. Indeed, the structure of the environment is not explicitly available in the patterns of light reaching our retinae and must instead be inferred from this signal. A priori, there exist infinite ways to group information across the visual field. Yet, we typically perceive only one grouping at a time, which is similar across individuals and often corresponds to the three-dimentional structure of the surrounding world. In his classic paper, Wertheimer (1923) formulated several principles by which elements may be organized, such as proximity, similarity, symmetry, closure, continuity, common fate, "good Gestalt", and past experience. These investigations laid the foundations for subsequent research aimed at discovering the ways in which the visual system discovers the structure of the outside world (e.g., Field, Hayes, and Hess, 1993; Kimchi, 2000; Kubovy, Holcombe, and Wagemans, 1998; Elder and Goldberg, 2002; Grossberg, Mingolla, and Ross, 1997; Roelfsema, 2006; Sasaki, 2007; Sekuler and Bennett, 2001).

The visual system analyses visual input in successive stages, beginning with a local analysis of luminance, contrast, colour, and local motion and progressively combining the local information to extract increasingly complex image structure, culminating with a complete three-dimensional representation of objects and scenes (Felleman and Van Essen, 1991; Marr, 1982). The size of the visual field sampled by the neurons – their receptive field – and the complexity of image structure to which neurons respond vary across visual areas (Felleman and Van Essen, 1991; Yoshor, Bosking, Ghose, and Maunsell, 2007). Neurons in the primary visual cortex (V1), the earliest cortical area receiving visual input, have small receptive fieelds and show tuning for orientation, spatial frequency, and spatial phase of luminance contrast (Hubel and Wiesel, 1962, 1968). Neurons in area V2 have larger receptive fields and are also selective for orientation and direction of motion, but unlike neurons in V1, V2 cells also show selectively for angles, curved arcs, and illusory contours (Sincich and Horton, 2005; Hegdé and Van Essen, 2000; Peterhans and von der Heydt, 1989). Further up the hierarchy, neurons in area V4 are no longer sensitive to cartesian orientation (Gallant, Connor, Rakshit, Lewis, and

Van Essen, 1996), but instead show systematic tuning for angles and arcs in specific locations with respect to the center of the global contour, providing the possibility to flexibly represent arbitrary contour outlines with a population code (Pasupathy and Connor, 1999, 2001, 2002; Pasupathy, 2006). Even further, the lateral occipital complex is sensitive to the global three-dimensional object shape and is invariant to the local contours that define the shape (Kourtzi and Kanwisher, 2001; Kourtzi, Erb, Grodd, and Bülthoff, 2003a). Other extrastriate areas appear to be specialized for processing particular types of objects, such as faces and bodies (e.g., Allison, Ginter, McCarthy, Nobre, Puce, Luby, and Spencer, 1994; Downing, Jiang, Shuman, and Kanwisher, 2001).

At each level of processing, the neuronal response is determined not only by its tuning profile and the image falling within its receptive field, but also by the surrounding context through short-range, long-range, and feedback connections (Gilbert and Wiesel, 1990; Gilbert, 1992; Fitzpatrick, 2000; Kapadia, Ito, Gilbert, and Westheimer, 1995; Kapadia, Westheimer, and Gilbert, 2000; Joo, Boynton, and Murray, 2012). Perceptual grouping can thus be mediated by non-linear interactions between different connected neural populations at the same processing level, or by activating cells in intermediate and high-level visual areas that are tuned for global structure (Roelfsema, 2006), or both. For example, grouping collinearly-arranged oriented elements may result from mutual interactions between orientation-tuned cells in V1 (Kapadia et al., 2000; Polat, Mizobe, Pettet, Kasamatsu, and Norcia, 1998), but a group of dots arranged in a circle can be grouped by virtue of activating a V4 cell tuned to detect circular structure (Pasupathy, 2006).

1.2 Aging of the visual system

What is known about the effects of aging at different levels of the visual system? At the sensory level, a reduced flexibility of the ocular lens causes one well-known sign of aging vision - presbyopia. Other signs of ocular aging include the yellowing of the lens, the accumulation of debris in the ocular medium, and a reduction in pupil size (Winn, Whitaker, Elliott, and Phillips, 1994; Weale, 1982, 1963). These changes lead to greater image blur and reduced retinal illuminance (Weale, 1963, 1988). However, replacing older crystalline lenses with artificial lenses and providing optical correction for presbyopia will not completely restore "young" vision to older observers, because aging also affects the function of visual cortical mechanisms (for reviews, see Sekuler and Sekuler, 2000; Spear, 1993; Owsley, 2011).

Detailed anatomical studies in non-human primates revealed that the volume, cortical thickness, and number of neurons in the LGN and primary visual cortex do not change with aging (Spear, 1993; Peters, Nigro, and McNally, 1997). However, there are changes in synaptic morphology in visual areas, as evidenced by less frequent synapses and shorter apical dendrites in pyramidal cells in V1 of older macaques (Peters, Moss, and Sethares, 2001) and fewer dentritic spines in extrastriate visual areas in older humans (Jacobs, Driscoll, and Schall, 1997). There is also widespread degeneration of myelin sheaths with aging, which likely affects the speed and fidelity of information transfer between cortical regions (Peters, Verderosa, and Sethares, 2008). A large cross-sectional study of structural images of the brains of adults 18 to 94 years old found significant age-related declines in cortical thickness of several brain areas, including the primary visual cortex (Salat, Buckner, Snyder, Greve, Desikan, Busa, Morris, Dale, and Fischl, 2004).

Neurophysiological studies in primates, cats, and rats have found significant declines in the functional properties of visual neurons with aging (Schmolesky, Wang, Pu, and Leventhal, 2000; Wang, Xie, Li, Chen, and Zhou, 2006; Hua, Li, He, Zhou, Wang, and Leventhal, 2006; Hua, Li, Tang, Wang, and Chang, 2009). V1 neurons of older macaques show higher levels of spontaneous activity, decreased signal-to-noise ratios, and poorer orientation and direction selectivity than neurons in young animals (Schmolesky et al., 2000). Spatial and temporal frequency selectivities are also reduced in V1 in older macaques (Zhang, Wang, Wang, Fu, Liang, Ma, and Leventhal, 2008). V2 neurons show even greater degradation of orientation and direction selectivity (Yu, Wang, Li, Zhou, and Leventhal, 2006), as well as greater firing latencies, suggesting that information transfer V2 to V1 may be delayed in older animals (Wang, Zhou, Ma, and Leventhal, 2005). Similar declines are found in motion-sensitive area MT (Yang, Liang, Li, Wang, Zhou, and Leventhal, 2008; Yang, Zhang, Liang, Li, Wang, Ma, Zhou, and Leventhal, 2009). These functional declines may be linked to reductions in the efficacy or the availability of inhibitory neurotransmitter GABA in the visual cortex (Leventhal, Wang, Pu, Zhou, and Ma, 2003; Hua, Kao, Sun, Li, and Zhou, 2008). Recent studies analysing postmortem tissue of human visual cortex showed that the relative proportions of different components of the GABAergic signaling system change across the lifespan (Pinto, Hornby, Jones, and Murphy, 2010; Williams, Irwin, Jones, and Murphy, 2010), indicating that the balance of excitation and inhibition in the visual cortex differs between younger and older subjects.

The only study that examined age-related changes on the efficacy of contextual modulation found reduced surround suppression in older V1 neurons (Fu, Wang, Wang, Zhang, Liang, Zhou, and Ma, 2010). The effects of aging on the efficacy of other types of contextual modulation, the efficacy of lateral and feedback interactions, or the selectivity of neurons in extrastriate visual areas are largely unknown.

1.3 Effect of aging on visual perception

Behavioural and psychophysical studies have revealed that many visual processes change with age. Visual acuity declines steadily after 30 years of age (Pitts, 1982; Elliott, Yang, and Whitaker, 1995) and contrast sensitivy for medium and high spatial frequencies starts to decline in the fourth decade of life (Owsley, Sekuler, and Siemsen, 1983; Sloane, Owsley, and Alvarez, 1988; Hardy, Delahunt, Okajima, and Werner, 2005). Temporal aspects of visual processing also decline with age, as evidenced by poorer sensitivity to spatial structure at high temporal frequencies (Elliott, Whitaker, and Macveigh, 1990; Tyler, 1989) and a lower flicker fusion rate (Coppinger, 1955; Misiak, 1951).

Many aspects of motion perception decline with aging, including detection and direction discrimination of translational motion (Wood and Bullimore, 1995; Snowden and Kavanagh, 2006; Gilmore, Wenk, Naylor, and Stuve, 1992; Betts, Taylor, Sekuler, and Bennett, 2005; Trick and Silverman, 1991; Bennett, Sekuler, and Sekuler, 2007; Norman, Ross, Hawkes, and Long, 2003), perception of optic flow (Andersen and Atchley, 1995; Atchley and Andersen, 1998; Warren, Blackwell, and Morris, 1989) and discrimination of biological motion (Legault, Troje, and Faubert, 2012; Norman, Payton, Long, and Hawkes, 2004; Pilz, Bennett, and Sekuler, 2010). The declines are not uniform, as some types of motion processing are not affected and others only show a gradual decline (Billino, Bremmer, and Gegenfurtner, 2008). Some of these changes may be due to changes in low-level motion detectors (Roudaia, Bennett, Sekuler, and Pilz, 2010; Tsotsos, 2012). However, impairments in local motion cannot account for all the observed effects, as aging also affects the ability to integrate local motion information to extract global form (Andersen and Ni, 2008; Legault et al., 2012; Pilz et al., 2010)

In form vision, older adults show poorer face recognition (Boutet and Faubert, 2006; Lott, Haegerstrom-Portnoy, Schneck, and Brabyn, 2005) and are less accurate at matching faces and objects across viewpoints (Habak, Wilkinson, and Wilson, 2008; Pilz, Konar, Vuong, Bennett, and Sekuler, 2011). Aging especially impairs performance in the presence of visual distractors (Sekuler and Ball, 1986) or in the presence of visual noise (Rousselet, Husk, Pernet, Gaspar, Bennett, and Sekuler, 2009; Rousselet, Gaspar, Pernet, Husk, Bennett, and Sekuler, 2010). However, contrary to motion perception, early-stage spatial vision appears to be relatively well preserved in older age. Psychophysical and electrophysiological studies in humans found no evidence of age-related changes in the tuning of orientation and spatial frequency channels (Govenlock, Taylor, Sekuler, and Bennett, 2009b, 2010; Delahunt, Hardy, and Werner, 2008; Govenlock, 2010), contrary to the broader tuning in individual neurons in primates and cats (Schmolesky et al., 2000; Hua et al., 2006; Zhang et al., 2008). Older adults also do not show any declines in local orientation discrimination, provided the stimuli are not difficult to detect (Betts, Sekuler, and Bennett, 2007; Delahunt et al., 2008). Moreover, the ability to indiscriminately pool orientation information across space also does not decline with age (Govenlock, Sekuler, and Bennett, 2009a).

To date, relatively few studies have examined how aging affects the intermediate stages of visual form processing where local information is integrated across space. In two studies on perceptual grouping, older subjects showed weaker perceptual grouping than younger subjects when grouping was based on local density, dot alignment, angle orientation, and flicker, but they showed no deficits when grouping was based on color or motion (Kurylo, 2006; Kurylo, Allan, Collins, and Baron, 2003). These studies indicated that perceptual organization may change with age, but that the effects depend on the type of stimulus and the type of grouping required. Another study found that older adults were less able to detect bilateral symmetry in dot patterns (Herbert, Overbury, Singh, and Faubert, 2002), a task that requires integrating information across space and relies primarily on extrastriate areas (Sasaki, 2007). Older subjects were also less sensitive at discriminating different types of curved arcs (Legault, Allard, and Faubert, 2007), a second-order task that requires the integration of several orientation detectors. In a task where subjects were required to discriminate two types of illusory contours, older subjects showed poorer performance when they were required to switch their attention between two different tasks (Richards, Bennett, and Sekuler, 2006). On the other hand, older and younger subjects were equally sensitive at discriminating between two different contour outlines, suggesting that shape discrimination mechanisms are unaffected in aging (Wang, 2001; Habak, Wilkinson, and Wilson, 2009). In sum, the limited evidence so far suggested that some aspects of perceptual organization change with age, however, the effects vary with the type of processing, stimulus, and task demands.

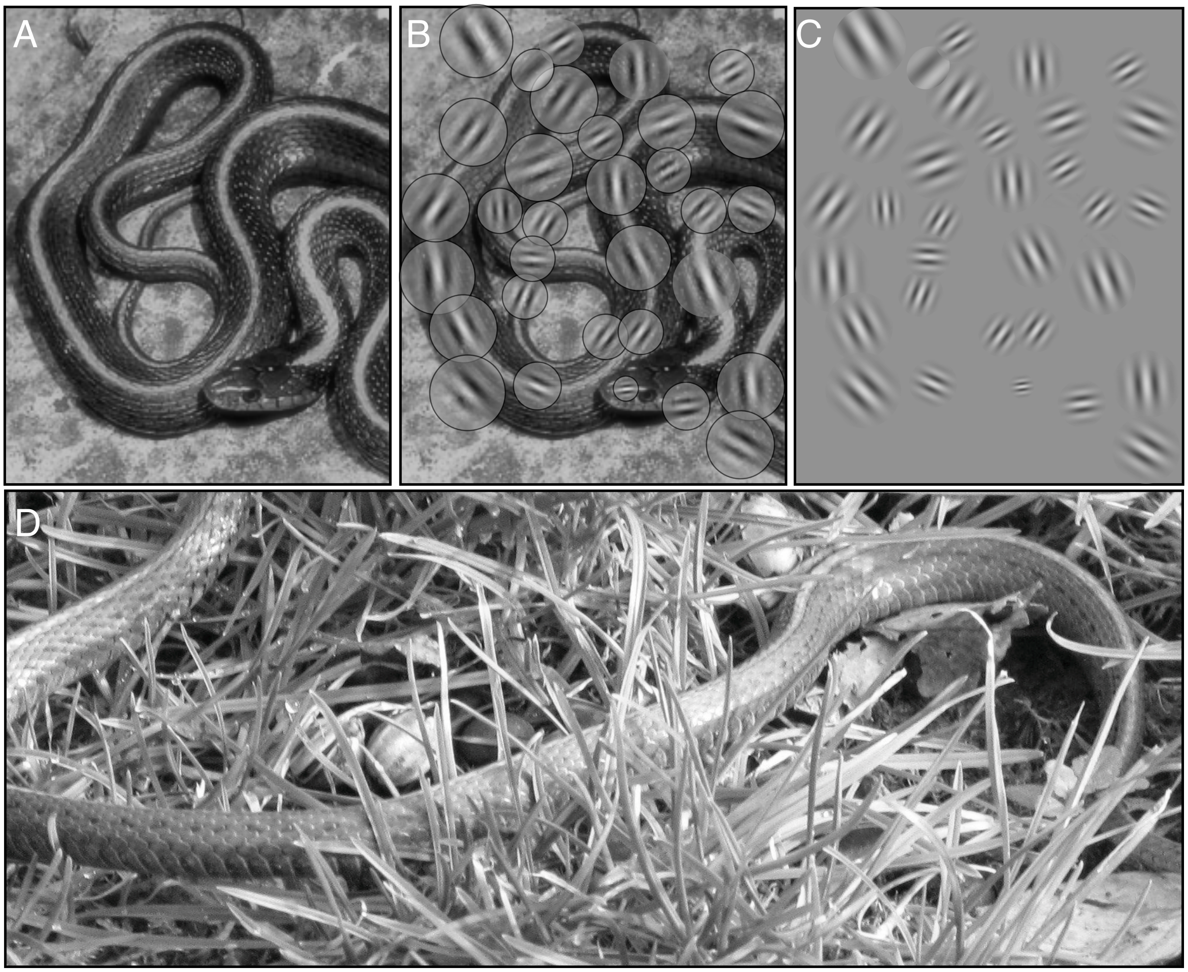


Figure 1.1: The problem of contour integration. A) Simple visual scene. B) Gabor elements (1D sinusoidal gratings multiplied by a Gaussian contrast enveloppe) are overlaid on image A to represent some of the receptive fields in early visual areas that will be activated by this image. C) When the underlying image is removed, it becomes apparent that information from several Gabor elements needs to be integrated in the appropriate way to extract the underlying contour of the snake. In the absence of prior knowledge of the underlying image, the principle by which to connect the local Gabor elements to represent the global object is not evident. D) In the real world, this task is often further complicated by the presence of occlusion and clutter, as when snakes are camouflaged by tall grass and leaves.

1.4 Contour integration

An important step in visual form processing is the perception of contours. To illustrate the problem of contour integration, consider the scene in Figure 1.1A. This visual scene is sampled by millions of simple-cells in the primary visual cortex that each monitor the contrast inside their receptive field. Neurons will fire depending on the extent to which information within the receptive field corresponds to their prefered orientation, spatial frequency, and spatial phase. These simple cells can be modeled as Gabor filters, or luminance-modulated 1D sinusoidal gratings multiplied by a 2D Gaussian. The orientation, phase, and spatial frequency of the Gabor carrier represent the type (odd- or even-symmetric), prefered orientation, and scale of the neuron. The Gabors shown in Figure 1.1B represent some of the early visual neurons that would be highly activated by the image in Figure 1.1A. In Figure 1.1C, only the Gabors are shown and the underlying image is removed. This disjointed collection of Gabors illustrates information available after the visual scene has been sampled by these local orientation filters. At the second stage, some computation is needed to combine, or integrate, the local orientation information to represent an extended contour. Looking at Figure 1.1C, it may become apparent that there is no easy rule to decide which Gabors should be linked together. Yet, our visual system has solved this binding problem and is capable of accomplishing this task in very complex and cluttered scenes, as in Figure 1.1D.

The development of the path paradigm by Field et al. (1993) has led to significant progress in understanding the mechanisms of contour integration. In this paradigm, Gabors were positioned on an imaginary path and embedded within a field of identical, but randomly oriented noise Gabors. All Gabors were spatially separated so that local orientation filters were unlikely to be stimulated by more than one Gabor and the average spacing of contour and background elements was equalized, to ensure that density or proximity cues could not be used to detect the path. Thus, detecting the contour path required integrating the responses of multiple orientation filters. On every trial, subjects were shown two patterns, one containing the path and the other just the noise Gabors, and were asked to report which pattern contained the path. Properties of contour integration mechanisms could be inferred by examining contour detection accuracy as a function of local parameters, such as the relative orientations, spatial phase, contrast, and scale of Gabors, or global parameters, such as the overall curvature or smoothness of the path (for review, see Hess, Hayes, and Field, 2003).

The path paradigm revealed that contour detection depended crucially on the relative position and orientation of contour elements: detection was best when contour elements were oriented tangentially to the contour path, so that adjacent elements on the path were collinear, or aligned, with each other. Contour detection was poorer, but still relatively good, when contour elements were oriented orthogonally (i.e., at 90°) to the contour path (Field et al., 1993). On the other hand, contour detection was very poor when contour elements were oriented obliquely (i.e., at 45°) to the contour path (Ledgeway, Hess, and Geisler, 2005). Given that Gabors are circularly symmetric, varying their orientations does not affect their proximity to each other. Thus, contours defined by Gabors oriented at 0°, 45°, or 90° to the path are statistically equivalent and can be detected by the lawful relationship between their orientations and the contour path. The fact that tangential contours were detected substantially better than orthogonal and oblique arrangements demonstrates that the visual system preferentially groups local orientated elements that are in collinear arrangements, reminiscent of the Gestalt principle of good continuation (Wertheimer, 1923). Collinearity also confers a benefit for perceiving the global shape of contours at low contrast and in the absence of visual clutter (Bonneh and Sagi, 1998; Saarinen and Levi, 2001) and for detecting a low contrast oriented target between high-contrast lateral flankers (Polat and Sagi, 1993). There is compelling evidence that this sensitivity to collinearity - as well as other grouping principles - may be related to the statistics of the natural environment (Sigman, Cecchi, Gilbert, and Magnasco, 2001; Geisler, Perry, Super, and Gallogly, 2001; Elder and Goldberg, 2002; Prodöhl, Würtz, and von der Malsburg, 2003).

To model how contour integration may be implemented in the brain, Hess and Field (1999) proposed a so-called association field in which local contour elements are associated with each other if they are detected by local filters that have a) similar orientation preference and b) their receptive fields are co-axial with their preferred orientation in visual space. Conversely, local contours are weakly associated with each other if they are detected by local filters whose orientation preference and receptive fields do not form a collinear arrangement. Although more recent studies have highlighted several situations where the association field model fails to account for contour detection performance (e.g., Ledgeway et al., 2005; Dakin and Baruch, 2009), this simple model has been influential in proposing that contour integration may be mediated in a feedforward manner by local interactions between early visual filters. Several computational models incorporating biologically plausible computations of V1 neurons have been successful at predicting psychophysical data in contour detection experiments (Li, 1998; Yen and Finkel, 1998;

Pettet, McKee, and Grzywacz, 1998).

These ideas have been bolstered by neurophysiological recordings in V1 neurons of macaques showing response facilitation to their prefered stimulus when collinear flanking stimuli were presented outside the cell's receptive field (Kapadia et al., 1995; Polat et al., 1998). What's more, response facilitation of V1 neurons due to the presence of a contour was predictive of behavioural contour detection accuracy of monkeys in a contour detection task (Li, Piëch, and Gilbert, 2006). However, this contour facilitation response was not seen in monkeys naive to the contour detection task, nor when attention was diverted to a different task, suggesting that top-down attention may serve as a gating mechanism for contour related responses in V1 (Li, Piëch, and Gilbert, 2008). The source of contour-related response facilitation in V1 is still debated. This facilitation may be mediated by intrinsic horizontal connections between pyramidal neurons in V1 (Rockland and Lund, 1983; Gilbert and Wiesel, 1979), whose long-range axonal projections preferentially link regions with similar functional properties, including similar orientation specificity (Gilbert and Wiesel, 1989; Malach, Amir, Harel, and Grinvald, 1993; Stettler, Das, Bennett, and Gilbert, 2002). At the same time, neurons in area V2 that receive their inputs from V1 and whose anisotropic feedback connections cover a large spatial extent (Angelucci, Levitt, Walton, Hupe, Bullier, and Lund, 2002; Stettler et al., 2002) are also well placed to provide contextual modulation to V1 neurons (for review, see Angelucci and Bullier, 2003).

Finally, it is still not known what role higher-order areas and their feedback play in contour integration. An MEG study found that the earliest contour specific activity was localized outside V1, in the parieto-occipital sulcus and higher areas in cuneus and middle and superior occipital gyri (Tanskanen, Saarinen, Parkkonen, and Hari, 2008). Studies using fMRI have found greater BOLD activation in early visual areas (V1, V2, and V3), as well as higher-order occipitotemporal areas (LOC) for stimuli containing a contour, compared to only randomly oriented Gabors (Altmann, Bülthoff, and Kourtzi, 2003; Kourtzi, Tolias, Altmann, Augath, and Logothetis, 2003b). However, these areas showed differences in stimulus processing, with early areas showing a more transient activation that was sensitive to local contour information, and the LOC showing a more sustained activation that was sensitive to the global contour shape (Kourtzi and Huberle, 2005). Thus, it appears that both early, as well as later areas in the ventral occipitotemporal hierarchy are involved in contour integration.

Although contour integration has been extensively studied in healthy young adults, as well as in persons with neurological or developmental disorders (e.g., Silverstein, Hatashita-Wong, Schenkel, Wilkniss, Kovács, Fehér, Smith, Goicochea, Uhlhaas, Carpiniello, and Savitz, 2006; Bex, Simmers, and Dakin, 2001; Levi, Yu, Kuai, and Rislove, 2007), very few studies have examined how contour integration is affected in older age. To fill the gap in the literature, the current dissertation examined how aging affects the ability to integrate local orientation information across space to form contours and shapes.

1.5 Thesis summary

In our first set of experiments (Chapter 2), we examined the discrimination of a single contour presented against a blank background. In this way, age-related changes in contour grouping could be assessed in the absence of any effects of visual clutter. Adopting a paradigm introduced by Saarinen and Levi (2001), stimuli consisted of "C"-shaped contours composed of spatially separated Gabor elements. To examine the effect of local orientation on contour grouping, Gabor orientations were either all tangential to the contour path, all orthogonal, or alternating tangential and orthogonal orientations. Contour grouping performance was assessed by estimating the minimum contrast required to discriminate the global orientation of the contour. Younger subjects required less contrast to discriminate contours composed of tangentially-oriented Gabors, compared to contours composed of orthogonally-oriented Gabors, or Gabors of alternating orientations. The contrast facilitation seen for tangentially-oriented Gabors is consistent with previously reported benefits of collinearity for grouping local elements into extended shapes (Saarinen and Levi, 2001). In contrast, older subjects did not benefit from the collinear arrangement of contour elements, as their contrast thresholds did not differ as a function contour type. This first result indicated that grouping of low-contrast elements into global shapes may be impaired in older age.

In Chapter 3, we examined whether age-differences in contour grouping will also be evident at suprathreshold levels, as deficits observed at low contrast may not generalize to high contrast conditions. In addition, because natural scenes often contain large amounts of visual clutter, we examined older subjects' ability to discriminate contours in a noisy background. "C"-shaped contours were composed of high-contrast Gabors oriented tangentially or orthogonally to the contour path and were embedded within a uniform field of randomly oriented Gabors. Performance was assessed by estimating the minimum stimulus duration required to discriminate the global orientation of the contour.

Stimulus duration thresholds were significantly greater in older subjects than in younger subjects, especially when contours were composed of orthogonally-oriented Gabors. Control experiments showed that the increase in duration thresholds with aging could not be explained by reductions in retinal illuminance, or by slower processing of local elements and their orientations. Therefore, these findings suggested that age-related differences in performance were due to changes at the stage where local elements are grouped into contours and extracted from the background clutter.

In Chapter 4, we examined how the effect of aging on contour discrimination depends on parameters that primarily influence contour grouping (Experiments 1 and 2), and those that primarily influence the extraction of contours from the background (Experiment 3). In Experiments 1 and 2, we measured contour discrimination accuracy as a function of absolute contour element spacing and contour element collinearity for a range of stimulus durations. Although contour discrimination accuracy was lower in older subjects, the effect of aging did not vary with contour element spacing or level of collinearity. These results suggested that the spatial range and the sensitivity to collinearity for contour integration are not affected in aging. In Experiment 3, we measured contour discrimination accuracy in the context of iso-oriented and randomly-oriented background elements as a function of relative contour-distracter spacing. Older subjects showed no deficit in contour discrimination when background elements were iso-oriented. On the other hand, when background elements were randomly-oriented, increasing background density had a significantly greater detrimental effect on older subjects compared to younger subjects. Thus, age-differences in contour discrimination were greatest when background elements were spaced closer to each other than contour elements.

Performance in all previous experiments measured subjects' ability to report the global orientation of a contour, while disregarding how the contour may appear to the subjects. In Chapter 5, we examined whether the shape percept of sampled contours changes with aging as a function of contour element orientations and sampling density. When a contour is comprised of dots or non-oriented blobs, the perceived shape of the contour can be described by connecting the positions of its elements. However, when a contour is sampled with oriented elements, its perceived shape results from a weighted combination of the positions and local orientations of the elements comprising the contour (Day and Loffler, 2009). Using the paradigm of Day and Loffler (2009), we found that younger and older subjects combine orientation and position information in a similar way when extracting the shape of a sampled contour. In Experiment 2, we confirmed and extended this finding with a task requiring contour shape discrimination. Results in Experiment 2 also showed that the sensitivity for discriminating two suprathreshold radial frequency patterns decreases with aging, a result that was unexpected given previous reports that shape discrimination ability was unimpaired in older age (Wang, 2001; Habak et al., 2009).

The General Discussion in Chapter 6 re-analyses the above findings in the context of the latest findings in the research field, outlines some remaining questions, and provides several suggestions for future research. In sum, the following experiments demonstrate that aging significantly affects the processes responsible for extracting contours in visual scenes, which likely has negative consequences on the speed and efficiency of visual perception of older adults.

Bibliography

Allison, T., Ginter, H., McCarthy, G., Nobre, A. C., Puce, A., Luby, M., Spencer, D. D., 1994. Face recognition in human extrastriate cortex. Journal of Neurophysiology 71 (2), 821–5.

Altmann, C. F., Bülthoff, H. H., Kourtzi, Z., 2003. Perceptual organization of local elements into global shapes in the human visual cortex. Current Biology 13 (4), 342–349.

Andersen, G. J., Atchley, P., 1995. Age-related differences in the detection of three-dimensional surfaces from optic flow. Psychology and Aging 10 (4), 650–8.

Andersen, G. J., Ni, R., 2008. Aging and visual processing: declines in spatial not temporal integration. Vision Research 48 (1), 109–118.

Angelucci, A., Bullier, J., 2003. Reaching beyond the classical receptive field of V1 neurons: horizontal or feedback axons? Journal of physiology, Paris 97 (2-3), 141–54.

Angelucci, A., Levitt, J. B., Walton, E. J. S., Hupe, J.-M., Bullier, J., Lund, J. S., 2002. Circuits for local and global signal integration in primary visual cortex. The Journal of Neuroscience 22 (19), 8633–8646.

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 (2), 297–308.

Bennett, P. J., Sekuler, R., Sekuler, A. B., 2007. The effects of aging on motion detection and direction identification. Vision Research 47 (6), 799–809.

Betts, L. R., Sekuler, A. B., Bennett, P. J., 2007. The effects of aging on orientation discrimination. Vision Research 47 (13), 1769–80.

Betts, L. R., Taylor, C. P., Sekuler, A. B., Bennett, P. J., 2005. Aging reduces center-surround antagonism in visual motion processing. Neuron 45 (3), 361–366.

Bex, P. J., Simmers, A. J., Dakin, S. C., 2001. Snakes and ladders: the role of temporal modulation in visual contour integration. Vision Research 41 (27), 3775–3782.

Billino, J., Bremmer, F., Gegenfurtner, K. R., 2008. Differential aging of motion processing mechanisms: evidence against general perceptual decline. Vision Research 48 (10), 1254–61.

Birren, J. E., 1964. The psychology of aging. Prentice-Hall, Englewood Cliffs (N.J.).

Birren, J. E., Fisher, L. M., 1995. Aging and speed of behavior: possible consequences for psychological functioning. Annual Review of Psychology 46, 329–53.

Bonneh, Y., Sagi, D., 1998. Effects of spatial configuration on contrast detection. Vision Research 38 (22), 3541–3553.

Boutet, I., Faubert, J., 2006. Recognition of faces and complex objects in younger and older adults. Memory & Cognition 34 (4), 854–64.

Coppinger, N. W., 1955. The relationship between critical flicker frequency and chronologic age for varying levels of stimulus brightness. Journal of Gerontology 10 (1), 48–52.

Craik, F. I. M., Salthouse, T. A., 2000. The Handbook of Aging and Cognition. Lawrence Erlbaum Associates.

Dakin, S. C., Baruch, N. J., 2009. Context influences contour integration. Journal of Vision 9 (2), 13.1–13.

Day, M., Loffler, G., 2009. The role of orientation and position in shape perception. Journal of Vision 9, 1–17.

Delahunt, P. B., Hardy, J. L., Werner, J. S., 2008. The effect of senescence on orientation discrimination and mechanism tuning. Journal of Vision 8 (3), 1–9.

Downing, P. E., Jiang, Y., Shuman, M., Kanwisher, N., 2001. A cortical area selective for visual processing of the human body. Science 293 (5539), 2470–3.

Elder, J. H., Goldberg, R. M., 2002. Ecological statistics of Gestalt laws for the perceptual organization of contours. Journal of Vision 2 (4), 324–53.

Elliott, D., Whitaker, D., Macveigh, D., 1990. Neural contribution to spatiotemporal contrast sensitivity decline in healthy aging eyes. Vision Research 30 (4), 541–547.

Elliott, D. B., Yang, K. C., Whitaker, D., 1995. Visual acuity changes throughout adulthood in normal, healthy eyes: seeing beyond 6/6. Optometry and Vision Science 72 (3), 186–91.

Felleman, D. J., Van Essen, D. C., 1991. Distributed hierarchical processing in the primate cerebral cortex. Cerebral Cortex 1 (1), 1–47.

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 (2), 173–193.

Fitzpatrick, D., 2000. Seeing beyond the receptive field in primary visual cortex. Current Opinion in Neurobiology 10 (4), 438–43.

Fu, Y., Wang, X. S., Wang, Y. C., Zhang, J., Liang, Z., Zhou, Y. F., Ma, Y. Y., 2010. The effects of aging on the strength of surround suppression of receptive field of v1 cells in monkeys. Neuroscience 169 (2), 874–81.

Gallant, J. L., Connor, C. E., Rakshit, S., Lewis, J. W., Van Essen, D. C., 1996. Neural responses to polar, hyperbolic, and cartesian gratings in area v4 of the macaque monkey. Journal of Neurophysiology 76 (4), 2718–39.

Geisler, W. S., Perry, J. S., Super, B. J., Gallogly, D. P., 2001. Edge co-occurrence in natural images predicts contour grouping performance. Vision Research 41 (6), 711–24.

Gilbert, C. D., 1992. Horizontal integration and cortical dynamics. Neuron 9 (1), 1–13.

Gilbert, C. D., Wiesel, T. N., 1979. Morphology and intracortical projections of functionally characterised neurones in the cat visual cortex. Nature 280 (5718), 120–5.

Gilbert, C. D., Wiesel, T. N., 1989. Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. The Journal of Neuroscience 9 (7), 2432–2442.

Gilbert, C. D., Wiesel, T. N., 1990. The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. Vision Research 30 (11), 1689–701.

Gilmore, G., Wenk, H., Naylor, L., Stuve, T., 1992. Motion perception and aging. Psychology and Aging 7 (4), 654.

Govenlock, S., Sekuler, A., Bennett, P., 2009a. The effect of aging on the spatial pooling of local orientation signals. Journal of Vision 9 (8), 1069–1069.

Govenlock, S. W., 2010. The effect of aging on visual orientation and spatial frequency channels. Ph.D. thesis, McMaster University.

Govenlock, S. W., Taylor, C. P., Sekuler, A. B., Bennett, P. J., 2009b. The effect of aging on the orientational selectivity of the human visual system. Vision Research 49 (1), 164–172.

Govenlock, S. W., Taylor, C. P., Sekuler, A. B., Bennett, P. J., 2010. The effect of aging on the spatial frequency selectivity of the human visual system. Vision Research 50 (17), 1712–9.

Grossberg, S., Mingolla, E., Ross, W. D., 1997. Visual brain and visual perception: how does the cortex do perceptual grouping? Trends in Neurosciences 20 (3), 106–11.

Habak, C., Wilkinson, F., Wilson, H. R., 2008. Aging disrupts the neural transformations that link facial identity across views. Vision Research 48 (1), 9–15.

Habak, C., Wilkinson, F., Wilson, H. R., 2009. Preservation of shape discrimination in aging. Journal of Vision 9 (12), 18.1–8.

Hardy, J. L., Delahunt, P. B., Okajima, K., Werner, J. S., 2005. Senescence of spatial chromatic contrast sensitivity. i. detection under conditions controlling for optical factors. Journal of the Optical Society of America. A 22 (1), 49–59.

Hegdé, J., Van Essen, D. C., 2000. Selectivity for complex shapes in primate visual area v2. The Journal of Neuroscience 20 (5), RC61.

Herbert, A. M., Overbury, O., Singh, J., Faubert, J., 2002. Aging and bilateral symmetry detection. The Journals Of Gerontology Series B Psychological Sciences And Social Sciences 57 (3), P241–P245.

Hess, R. F., Field, D., 1999. Integration of contours: new insights. Trends in Cognitive Science 3 (12), 480–486.

Hess, R. F., Hayes, A., Field, D. J., 2003. Contour integration and cortical processing. Journal of Physiology – Paris 97 (2-3), 105–119.

Hua, T., Kao, C., Sun, Q., Li, X., Zhou, Y., 2008. Decreased proportion of gaba neurons accompanies age-related degradation of neuronal function in cat striate cortex. Brain Research Bulletin 75 (1), 119–125.

Hua, T., Li, G., Tang, C., Wang, Z., Chang, S., 2009. Enhanced adaptation of visual cortical cells to visual stimulation in aged cats. Neuroscience Letters 451 (1), 25–8.

Hua, T., Li, X., He, L., Zhou, Y., Wang, Y., Leventhal, A. G., 2006. Functional degradation of visual cortical cells in old cats. Neurobiology of Aging 27 (1), 155–162.

Hubel, D. H., Wiesel, T. N., 1962. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. The Journal of Physiology 160, 106–54.

Hubel, D. H., Wiesel, T. N., 1968. Receptive fields and functional architecture of monkey striate cortex. The Journal of Physiology 195 (1), 215–43.

Jacobs, B., Driscoll, L., Schall, M., 1997. Life-span dendritic and spine changes in areas 10 and 18 of human cortex: a quantitative golgi study. Journal of Comparative Neurology 386 (4), 661–80.

Joo, S. J., Boynton, G. M., Murray, S. O., 2012. Long-range, pattern-dependent contextual effects in early human visual cortex. Current Biology 22 (9), 781–6.

Kapadia, M. K., Ito, M., Gilbert, C. D., Westheimer, G., 1995. Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in v1 of alert monkeys. Neuron 15 (4), 843–56.

Kapadia, M. K., Westheimer, G., Gilbert, C. D., 2000. Spatial distribution of contextual interactions in primary visual cortex and in visual perception. Journal of Neurophysiology 84 (4), 2048–62.

Kimchi, R., 2000. The perceptual organization of visual objects: a microgenetic analysis. Vision Research 40 (10-12), 1333–47.

Kourtzi, Z., Erb, M., Grodd, W., Bülthoff, H. H., 2003a. Representation of the perceived 3-d object shape in the human lateral occipital complex. Cerebral Cortex 13 (9), 911–20.

Kourtzi, Z., Huberle, E., 2005. Spatiotemporal characteristics of form analysis in the human visual cortex revealed by rapid event-related fmri adaptation. Neuroimage 28 (2), 440–52.

Kourtzi, Z., Kanwisher, N., 2001. Representation of perceived object shape by the human lateral occipital complex. Science 293 (5534), 1506–9.

Kourtzi, Z., Tolias, A. S., Altmann, C. F., Augath, M., Logothetis, N. K., 2003b. Integration of local features into global shapes: monkey and human fmri studies. Neuron 37 (2), 333–46.

Kubovy, M., Holcombe, A. O., Wagemans, J., 1998. On the lawfulness of grouping by proximity. Cognitive Psychology 35 (1), 71–98.

Kurylo, D., Allan, W., Collins, T., Baron, J., 2003. Perceptual organization based upon spatial relationships in Alzheimer's disease. Behavioural Neurology 14 (1/2), 19–28.

Kurylo, D. D., 2006. Effects of aging on perceptual organization: efficacy of stimulus features. Experimental Aging Research 32 (2), 137–152.

Ledgeway, T., Hess, R. F., Geisler, W. S., 2005. Grouping local orientation and direction signals to extract spatial contours: empirical tests of ”association field” models of contour integration. Vision Research 45 (19), 2511–2522.

Legault, I., Allard, R., Faubert, J., 2007. Normal aging and the perception of curvature shapes. Optometry and vision science : official publication of the American Academy of Optometry 84 (12), 1087–92.

Legault, I., Troje, N. F., Faubert, J., 2012. Healthy older observers cannot use biological-motion point-light information efficiently within 4 m of themselves. i-Perception 3 (2), 104–111.

Leventhal, A. G., Wang, Y. C., Pu, M. L., Zhou, Y. F., Ma, Y. Y., 2003. GABA and its agonists improved visual cortical function in senescent monkeys. Science 300 (5620), 812–815.

Levi, D. M., Yu, C., Kuai, S.-G., Rislove, E., 2007. Global contour processing in amblyopia. Vision Research 47 (4), 512–24.

Li, W., Piëch, V., Gilbert, C. D., 2006. Contour saliency in primary visual cortex. Neuron 50 (6), 951–62.

Li, W., Piëch, V., Gilbert, C. D., 2008. Learning to link visual contours. Neuron 57 (3), 442–51.

Li, Z., 1998. A neural model of contour integration in the primary visual cortex. Neural computation 10 (4), 903–40.

Lott, L. A., Haegerstrom-Portnoy, G., Schneck, M. E., Brabyn, J. A., 2005. Face recognition in the elderly. Optometry and Vision Science 82 (10), 874–81.

Malach, R., Amir, Y., Harel, M., Grinvald, A., 1993. Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primate striate cortex. Proceedings of the National Academy of Sciences of the United States of America 90 (22), 10469–10473.

Marr, D., 1982. Vision. The MIT Press, Cambridge, MA.

Misiak, H., 1951. The decrease of critical flicker frequency with age. Science 113 (2941), 551–2.

Norman, J. F., Payton, S. M., Long, J. R., Hawkes, L. M., 2004. Aging and the perception of biological motion. Psychology and Aging 19 (1), 219–225.

Norman, J. F., Ross, H. E., Hawkes, L. M., Long, J. R., 2003. Aging and the perception of speed. Perception 32 (1), 85–96.

Owsley, C., 2011. Aging and vision. Vision Research 51 (13), 1610–22.

Owsley, C., Sekuler, R., Siemsen, D., 1983. Contrast sensitivity throughout adulthood. Vision Research 23 (7), 689–699.

Pasupathy, A., 2006. Neural basis of shape representation in the primate brain. Progress in Brain Research 154, 293–313.

Pasupathy, A., Connor, C. E., 1999. Responses to contour features in macaque area v4. Journal of Neurophysiology 82 (5), 2490–502.

Pasupathy, A., Connor, C. E., 2001. Shape representation in area v4: position-specific tuning for boundary conformation. Journal of Neurophysiology 86 (5), 2505–19.

Pasupathy, A., Connor, C. E., 2002. Population coding of shape in area V4. Nature Neuroscience 5 (12), 1332–8.

Peterhans, E., von der Heydt, R., 1989. Mechanisms of contour perception in monkey visual cortex. ii. contours bridging gaps. The Journal of Neuroscience 9 (5), 1749–63.

Peters, A., Moss, M. B., Sethares, C., 2001. The effects of aging on layer 1 of primary visual cortex in the rhesus monkey. Cerebral Cortex 11 (2), 93–103.

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 (1), 29–36.

Peters, A., Verderosa, A., Sethares, C., 2008. The neuroglial population in the primary visual cortex of the aging rhesus monkey. Glia 56 (11), 1151–61.

Pettet, M. W., McKee, S. P., Grzywacz, N. M., 1998. Constraints on long range interactions mediating contour detection. Vision Research 38 (6), 865–79.

Pilz, K. S., Bennett, P. J., Sekuler, A. B., 2010. Effects of aging on biological motion discrimination. Vision Research 50 (2), 211–9.

Pilz, K. S., Konar, Y., Vuong, Q. C., Bennett, P. J., Sekuler, A. B., 2011. Age-related changes in matching novel objects across viewpoints. Vision Research 51 (17), 1958–65.

Pinto, J. G. A., Hornby, K. R., Jones, D. G., Murphy, K. M., 2010. Developmental changes in gabaergic mechanisms in human visual cortex across the lifespan. Frontiers in Cellular Neuroscience 4, 16.

Pitts, D. G., 1982. Visual acuity as a function of age. Journal of the American Optometric Association 53 (2), 117–24.

Polat, U., Mizobe, K., Pettet, M. W., Kasamatsu, T., Norcia, A. M., 1998. Collinear stimuli regulate visual responses depending on cell's contrast threshold. Nature 391 (6667), 580–4.

Polat, U., Sagi, D., 1993. Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. Vision Research 33 (7), 993–9.

Prodöhl, C., Würtz, R. P., von der Malsburg, C., 2003. Learning the Gestalt rule of collinearity from object motion. Neural computation 15 (8), 1865–96.

Richards, E. D., Bennett, P. J., Sekuler, A. B., 2006. The effects of task switching on age-related differences in shape perception. Journal of Vision 6 (6), 325–325.

Rockland, K. S., Lund, J. S., 1983. Intrinsic laminar lattice connections in primate visual cortex. Journal of Comparative Neurology 216 (3), 303–18.

Roelfsema, P. R., 2006. Cortical algorithms for perceptual grouping. Annual Revire Neuroscience 29, 203–27.

Roudaia, E., Bennett, P. J., Sekuler, A. B., Pilz, K. S., 2010. Spatiotemporal properties of apparent motion perception and aging. Journal of Vision 10 (14), 5.

Rousselet, G. A., Gaspar, C. M., Pernet, C. R., Husk, J. S., Bennett, P. J., Sekuler, A. B., 2010. Healthy aging delays scalp eeg sensitivity to noise in a face discrimination task. Frontiers in Psychology 1, 19.

Rousselet, G. A., Husk, J. S., Pernet, C. R., Gaspar, C. M., Bennett, P. J., Sekuler, A. B., 2009. Age-related delay in information accrual for faces: evidence from a parametric, single-trial eeg approach. BMC Neuroscience 10, 114.

Saarinen, J., Levi, D. M., 2001. Integration of local features into a global shape. Vision Research 41 (14), 1785–1790.

Salat, D. H., Buckner, R. L., Snyder, A. Z., Greve, D. N., Desikan, R. S. R., Busa, E., Morris, J. C., Dale, A. M., Fischl, B., 2004. Thinning of the cerebral cortex in aging. Cerebral Cortex 14 (7), 721–30.

Sasaki, Y., 2007. Processing local signals into global patterns. Current Opinion in Neurobiology 17 (2), 132–9.

Schmolesky, M. T., Wang, Y., Pu, M., Leventhal, A. G., 2000. Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. Nature Neuroscience 3 (4), 384–390.

Sekuler, B. A., Bennett, P. J., 2001. Generalized common fate: grouping by common luminance changes. Psychological Science 12 (6), 437–444.

Sekuler, R., Ball, K., 1986. Visual localization: age and practice. Journal of the Optical Society of America. A 3 (6), 864–7.

Sekuler, R., Sekuler, A. B., 2000. Visual perception and cognition. In: Evans, J., Williams, T., Beattie, B., Michel, J.-P., Wilcock, G. (Eds.), Oxford Textbook of Geriatric Medicine, 2nd Edition. Oxford University Press, New York, pp. 753–756.

Sigman, M., Cecchi, G. A., Gilbert, C. D., Magnasco, M. O., 2001. On a common circle: natural scenes and gestalt rules. Proceedings of the National Academy of Sciences of the United States of America 98 (4), 1935–40.

Silverstein, S. M., Hatashita-Wong, M., Schenkel, L. S., Wilkniss, S., Kovács, I., Fehér, A., Smith, T., Goicochea, C., Uhlhaas, P., Carpiniello, K., Savitz, A., 2006. Reduced top-down influences in contour detection in schizophrenia. Cognitive neuropsychiatry 11 (2), 112–32.

Sincich, L. C., Horton, J. C., 2005. The circuitry of v1 and v2: integration of color, form, and motion. Annual Review Neuroscience 28, 303–26.

Sloane, M. E., Owsley, C., Alvarez, S. L., 1988. Aging, senile miosis and spatial contrast sensitivity at low luminance. Vision Research 28 (11), 1235–46.

Snowden, R. J., Kavanagh, E., 2006. Motion perception in the ageing visual system: minimum motion, motion coherence, and speed discrimination thresholds. Perception 35 (1), 9–24.

Spear, P. D., 1993. Neural bases of visual deficits during aging. Vision Research 33 (18), 2589–2609.

Stettler, D. D., Das, A., Bennett, J., Gilbert, C. D., 2002. Lateral connectivity and contextual interactions in macaque primary visual cortex. Neuron 36 (4), 739–50.

Tanskanen, T., Saarinen, J., Parkkonen, L., Hari, R., 2008. From local to global: Cortical dynamics of contour integration. Journal of Vision 8 (7), 15.1–12.

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 (9), 1437–1440.

Tsotsos, L. E., 2012. Tsotsos, lia e. "the effects of aging on motion perception in healthy older adults." (2012). Ph.D. thesis, McMaster University.

Tyler, C. W., 1989. Two processes control variations in flicker sensitivity over the life span. Journal of the Optical Society of America. A 6 (4), 481–90.

Wang, H., Xie, X., Li, X., Chen, B., Zhou, Y., 2006. Functional degradation of visual cortical cells in aged rats. Brain Research 1122 (1), 93–8.

Wang, Y., Zhou, Y., Ma, Y., Leventhal, A. G., 2005. Degradation of signal timing in cortical areas v1 and v2 of senescent monkeys. Cerebral Cortex 15 (4), 403–8.

Wang, Y. Z., 2001. Effects of aging on shape discrimination. Optometry and vision science : official publication of the American Academy of Optometry 78 (6), 447–54.

Warren, Jr, W. H., Blackwell, A. W., Morris, M. W., 1989. Age differences in perceiving the direction of self-motion from optical flow. Journal of Gerontology 44 (5), P147–53.

Weale, R. A., 1963. The Aging Eye. Lewis, London.

Weale, R. A., 1982. Senile ocular changes, cell death, and vision. In: Sekuler, R., Kline, D., Dismukes, K. (Eds.), Aging and visual function. Liss, New York, pp. 161–171.

Weale, R. A., 1988. Age and the transmittance of the human crystalline lens. Journal of Physiology 395, 577–587.

Wertheimer, M., 1923. Untersuchungen zur lehre von der gestalt. ii. Psychologische Farschung 4, 301–350.

Williams, K., Irwin, D. A., Jones, D. G., Murphy, K. M., 2010. Dramatic loss of ube3a expression during aging of the mammalian cortex. Frontiers in Aging Neuroscience 2, 18.

Winn, B., Whitaker, D., Elliott, D. B., Phillips, N. J., 1994. Factors affecting light-adapted pupil size in normal human subjects. Investigative Ophthalmology & Visual Science 35 (3), 1132–1137.

Wood, J. J., Bullimore, M., 1995. Changes in lower displacement limit for motion with age. Ophthalmic and Physiological Optics 15 (1), 31–36.

Yang, Y., Liang, Z., Li, G., Wang, Y., Zhou, Y., Leventhal, A. G., 2008. Aging affects contrast response functions and adaptation of middle temporal visual area neurons in rhesus monkeys. Neuroscience 156 (3), 748–57.

Yang, Y., Zhang, J., Liang, Z., Li, G., Wang, Y., Ma, Y., Zhou, Y., Leventhal, A. G., 2009. Aging affects the neural representation of speed in macaque area mt. Cerebral Cortex 19 (9), 1957–1967.

Yen, S. C., Finkel, L. H., 1998. Extraction of perceptually salient contours by striate cortical networks. Vision Research 38 (5), 719–41.

Yoshor, D., Bosking, W. H., Ghose, G. M., Maunsell, J. H. R., 2007. Receptive fields in human visual cortex mapped with surface electrodes. Cerebral Cortex 17 (10), 2293–302.

Yu, S., Wang, Y., Li, X., Zhou, Y., Leventhal, A. G., 2006. Functional degradation of extrastriate visual cortex in senescent rhesus monkeys. Neuroscience 140 (3), 1023–1029.

Zhang, J., Wang, X., Wang, Y., Fu, Y., Liang, Z., Ma, Y., Leventhal, A. G., 2008. Spatial and temporal sensitivity degradation of primary visual cortical cells in senescent rhesus monkeys. European Journal of Neuroscience 28 (1), 201–7.

Chapter 2

Effect of aging on contour integration at low contrast

2.1 Preamble

The contents of this chapter has been previously published (Roudaia, E., Bennett, P. J., and Sekuler, A. B. (2008). The effect of aging on contour integration. Vision Research, 48(28), pp 2767 – 2774) and is reproduced here with full permission from Vision Research.

2.2 Abstract

Perception of global patterns requires the integration of local orientation information across space. The present study examined whether this integration ability declines in older age. We measured contrast thresholds for discriminating the global orientation of a "C" shaped contour against a blank background in younger and older subjects. Performance of younger subjects improved when the elements composing the "C" were aligned along the contour path, as opposed to being orthogonal to it or of mixed orientations. However, older subjects' performance was not affected by the orientation of the local elements. This indicates an age-related decline in contour integration.

2.3 Introduction

Age-related changes in visual function have an important impact on the lives of an ever-growing number of healthy elderly persons. Declining visual function has been found to be associated with decline in perceptual as well as cognitive abilities of older adults (Salthouse, Hancock, Meinz, and Hambrick, 1996; Skeel, Schutte, van Voorst, and Nagra, 2006). Although the optics of the eye change considerably with age (Savage, Haegerstrom-Portnoy, Adams, and Hewlett, 1993; Weale, 1988, 1963; Winn, Whitaker, Elliott, and Phillips, 1994), they are insufficient to account for age-related declines in visual function such as acuity, spatial or chromatic contrast sensitivity or orientation discrimination (Atchley and Andersen, 1998; Bennett, Sekuler, and Ozin, 1999; Betts, Sekuler, and Bennett, 2007; Betts, Taylor, Sekuler, and Bennett, 2005; Elliott, Whitaker, and Macveigh, 1990a; Hardy, Delahunt, Okajima, and Werner, 2005; Weale, 1982). Observed age-related declines in motion perception, bilateral symmetry perception, spatial integration, and orientation discrimination are thought to be related to changes in cortical mechanisms (Andersen and Ni 2008; Bennett, Sekuler, and Sekuler 2007; Betts et al. 2007; Del Viva and Agostini 2007; Delahunt, Hardy, and Werner 2008; Herbert, Overbury, Singh, and Faubert 2002; Norman, Ross, Hawkes, and Long 2003; for reviews see Faubert, 2002; Sekuler and Sekuler, 2000; Spear, 1993; Werner, Peterzell, and Scheetz, 1990). When asked to describe their visual problems, older adults tend not to report difficulty in simply detecting objects, but often report having slower visual processing capacities, difficulty perceiving the meaning of complex scenes, and organizing parts of the visual scene into a meaningful whole (NRC, 1987, p.7, as cited in Sekuler and Sekuler 2000).

To derive a meaningful percept of a scene, the visual system must perform several important steps, including integrating individual features into global shapes, segregating objects from their background, and filling in missing information caused by occlusion. Detecting and discriminating contours is a critical process in all of these tasks. The visual system's ability to perceive contours has been extensively researched in young adults. For example, there have been numerous studies examining the detection of contours embedded in a cluttered background (e.g., Achtman, Hess, and Wang 2003; Altmann, Bülthoff, and Kourtzi 2003; Field, Hayes, and Hess 1993; Hess, Beaudot, and Mullen 2001; Hess and Dakin 1997; Kovács and Julesz 1993; Mathes and Fahle 2007; Nikolaev and van Leeuwen 2007; see Hess and Field 1999; Hess, Hayes, and Field 2003 for reviews). These studies typically show that people are best at detecting contours composed of elements whose local orientations are aligned along the global contour path, suggesting that contour detection relies on the integration of orientation information across space. Local orientation information also appears to be important when identifying a global shape in the absence of background noise (Bonneh and Sagi, 1998; Saarinen and Levi, 2001). For example, Saarinen and Levi (2001) measured the contrast needed to identify the location of a gap in a "C"-shaped contour composed of locally-oriented Gabor elements that were either all aligned tangential to the "C"-contour path, all orthogonal to the path, or of mixed orientations (randomly oriented tangential or orthogonal). Thresholds were lowest when the local elements were tangential to the global contour path, suggesting that the perception of a global shape or contour is facilitated by the alignment of local orientations along the contour path.

Despite the large number of previous studies on contour integration, little is known about how contour integration is affected by aging. Previous research using psychophysical methods showed that the tuning of human orientation channels remains intact in older age (Delahunt et al., 2008; Govenlock, Taylor, Sekuler, and Bennett, submitted, 2006), suggesting that older adults encode local orientations just as well as younger adults. However, older subjects appear to be impaired at tasks that require the integration of local information across space, such as curvature discrimination (Legault, Allard, and Faubert, 2007), bilateral symmetry (Herbert et al., 2002), and perceptual completion (Richards, Bennett, and Sekuler, 2006; Salthouse and Prill, 1988). A recent study (Del Viva and Agostini, 2007) examined the effect of aging on contour integration by comparing younger and older subjects' ability to detect closed circular shapes embedded in noisy backgrounds. Subjects had to locate a chain of Gabors with the elements oriented tangentially to a circle in a field of distracter Gabor elements with random positions and orientations. Detection thresholds were obtained for circles with different inter-element distances by varying the relative density of distracter Gabors. The older group was found to have lower sensitivity than the younger group for all inter-element distances tested and this impairment was not correlated with age-related declines in contrast sensitivity. This finding provides preliminary evidence for an age-related decline in cortical processes involved in contour integration. However, it is not clear whether the age-related changes were due to changes in contour integration mechanisms *per se*. It has been shown that contours composed of tangentially aligned elements that are also in a single spatial phase, like those used by Del Viva and Agostini (2007), may be detected by using simple linear filters (Hess and Dakin, 1997; Hess and Field, 1999) rather than mechanisms that integrate information across different orientations. Moreover, some evidence suggests that higher-order grouping strategies are involved in the detection of closed contours (Kovács and Julesz, 1993; Mathes and Fahle, 2007). Additionally, Del Viva and Agostini presented stimuli for relatively long durations (approximately 1 s), and therefore it is not clear whether age differences in attentional search strategies or eye movements contributed to the observed age differences. Finally, the study by Del Viva & Agonstini does not examine the effect of background clutter on age differences in contour integration. In particular, it is not clear if age differences persist in the absence of clutter.

The goal of the present study is to investigate the effect of aging on contour integration in the absence of background noise, under conditions that let us disentangle the relative roles of contour integration and higher-order linear filtering and grouping. For this purpose, we adapted the paradigm used by Saarinen and Levi (2001) to measure contrast detection thresholds for younger and older subjects discriminating among "C" shaped patterns composed of Gabor elements. By varying the orientation of Gabor elements along the "C" contour, we examined the effect of local orientation on global shape identification.

2.4 Experiment 1: "C" Orientation Discrimination

2.4.1 Methods

Subjects

Twelve younger (M = 21.3 years; SD = 2.54) and 12 older (M = 68.4 years; SD = 3.5) adults were recruited from our bank of subjects to take part in the study, and were compensated for their time at a rate of $10/hour. Near and far Snellen acuities and contrast sensitivity were measured for each subject prior to testing and appropriate corrective lenses were used when required (Table 3.1). All subjects had normal or corrected-to-normal acuity, and contrast sensitivity was also normal for each age group as measured by the Pelli-Robson Contrast Sensitivity Test (Elliott, Sanderson, and Conkey, 1990b; Mäntyjärvi and Laitinen, 2001; Pelli, Robson, and Wilkins, 1988). A general health questionnaire was administered prior to testing, and none of the subjects reported having any visual disorders or major health problems. All except one younger and two older subjects visited their optometrist and/or ophthalmologist less than three years prior

Table 2.1: Mean ± 1 SD age, near and far Snellen decimal acuity, Pelli-Robson contrast sensitivity, and Mini-Mental State Exam (MMSE).

	N	Age	Near Acuity	Far Acuity	Pelli-Robson	MMSE
Expt 1	12	68.5 ± 3.5	1.21 ± 0.29	1.14 ± 0.31	1.93 ± 0.09	29.3 ± 1.15
	12	21.3 ± 2.5	1.57 ± 0.29	1.27 ± 0.27	1.95	
Control	12	68.5 ± 3.5	1.21 ± 0.29	1.14 ± 0.31	1.93 ± 0.09	29.3 ± 1.15
	11	22.9 ± 2.8	1.55 ± 0.31	1.34 ± 0.35	1.95	

to the experiment. Older subjects also completed the Mini-Mental State Examination (Folstein, Folstein, and McHugh, 1975) to assess their cognitive abilities. All scores were within the normal ranges for subjects' age and education levels (Crum, Anthony, Bassett, and Folstein, 1993). Two older subjects were left handed, and there were six males and six females in each age group. All the subjects gave their written informed consent to participate in the study.

Apparatus

The experiment was programmed in the Matlab environment (version 7.2) using software from the Psychophysics and Video Toolboxes (version 3) (Brainard, 1997; Pelli, 1997). Stimulus generation and presentation were controlled by a Macintosh G5 computer using a NVIDIA GeForce 6600 video card and a BITS++ Digital Video Processor (Cambridge Research Systems Ltd, UK) which provided 14-bit luminance resolution. Mean luminance of the display was 109 cd/m^2. The stimuli were presented in a dark room on a 20-inch (51 cm) Sony Trinitron monitor with 1280 x 1024 resolution (pixel size: 0.014 deg) and refresh rate of 75 Hz. The full display subtended 17.2 x 13.5 degrees of visual angle at a viewing distance of 114 cm. Head position and viewing distance were stabilized with a chin/forehead rest. Subjects responded with a standard QWERTY Macintosh keyboard.

Stimuli

Stimuli consisted of 14 Gabor elements presented against a uniform grey background and arranged in a global pattern in the shape of a "C". Gabor elements were created by dampening a sine wave grating with a spatial frequency of 3 cpd and with either positive or negative sine phase by a circular Gaussian envelope whose full width at half its maximum value was 0.25 deg. The global "C" shape was created by placing 16 Gabors on an imaginary circle that was centred on the screen and had a radius of 1.5 deg. The Gabors were equally spaced around the circle, resulting in an inter-element distance of ≈ 0.59 deg, or ≈ 1.77 spatial periods of the carrier grating. The gap in the "C"-shaped pattern was created by removing two adjacent patches in one of four locations: upper left, upper right, lower left, lower right. The contrast of the Gabors was varied on every trial by a staircase procedure.

There were four stimulus conditions in this experiment (Figure 3.1). In three conditions, element orientation was varied to determine the effect of local orientation on contour integration. In the aligned condition, all Gabor elements were oriented tangentially to the contour path; in the radial condition, elements were oriented orthogonally to the contour path; and in the mixed condition, the tangential and orthogonal orientations alternated. The elements in the above three conditions all had positive sine phase. The mixed condition used Gabors with alternating aligned and radial orientations instead of randomly assigning Gabors to be aligned or radial (as in Saarinen and Levi, 2001) to avoid situations where two or more Gabors would be aligned with each other by chance. A fourth condition was added, which was not included in Saarinen and Levi's original study, where the "C" was composed of elements with tangential orientation, but the phase alternated from positive to negative sine phase. This condition was included to examine the possibility that performance in the aligned condition may result from summation in a simple linear detector with an elongated receptive field (Hess and Field, 1999).

Procedure

Subjects completed the experiment in a single session lasting approximately 60 minutes. Stimuli were blocked by condition, and the order of the blocks was randomized for each subject. Each block contained 100 trials. The first block was preceded by an adaptation period of 60 sec, during which time subjects adapted to the mean luminance of the screen. Each trial started by presenting a uniform grey screen with a black fixation point in the centre of the screen. The fixation point then flickered (alternated between black and white) for 300 ms at a rate of 10 Hz to attract the subject's attention to the centre of the display. After a delay of 500 ms, the "C" shape appeared for 200 ms. To reduce temporal and positional uncertainty, the stimulus was surrounded by a

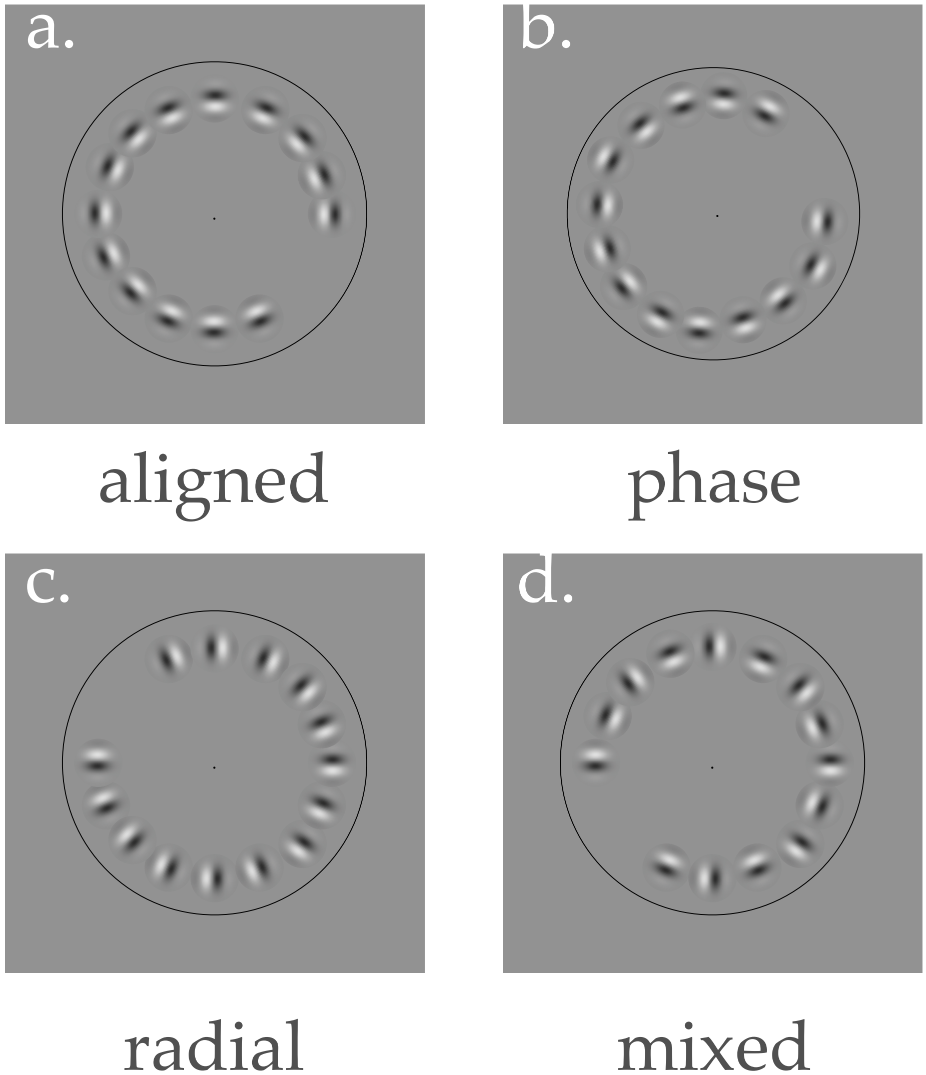


Figure 2.1: Examples of stimulus conditions. In the aligned condition (a), elements were oriented tangentially to the global contour, and all elements were presented in +sine phase. In the phase condition (b), elements were also oriented tangentially to the global contour, but the phase alternated between +sine and sine. In the radial condition (c), all elements were oriented orthogonally to the global contour and, finally, in the mixed condition (d), the elements alternated between being tangential and orthogonal to the global contour path. In the last two conditions, all elements had +sine phase.

high-contrast black circle that was centered on the fixation point and had a radius of 2 deg. The location of the gap in the "C" was randomized on every trial. A uniform grey screen with a fixation point in the centre then appeared for 500 ms followed by a response screen (Figure 3.2). The response screen consisted of numbers 1, 2, 3, and 4, placed in the four possible locations of the gap (LL, UL, UR, LR respectively). The subject then indicated the location of the gap by pressing one of four labelled keys on the keyboard. Auditory feedback was provided with a high-pitched tone indicating a correct answer and a low-pitched tone indicating an incorrect answer. The next trial began immediately after the subject's response.

Two interleaved staircases modulated stimulus contrast in steps of 0.05 log units across trials. A four-down/one-up staircase and a two-down/one-up staircase converged on the contrasts needed to correctly identify the location of the gap with 84% and 71% accuracy, respectively. Contrast threshold, defined as the contrast needed to perform with 75% accuracy, was determined for each condition by fitting a Weibull function to combined data obtained from the two staircases.

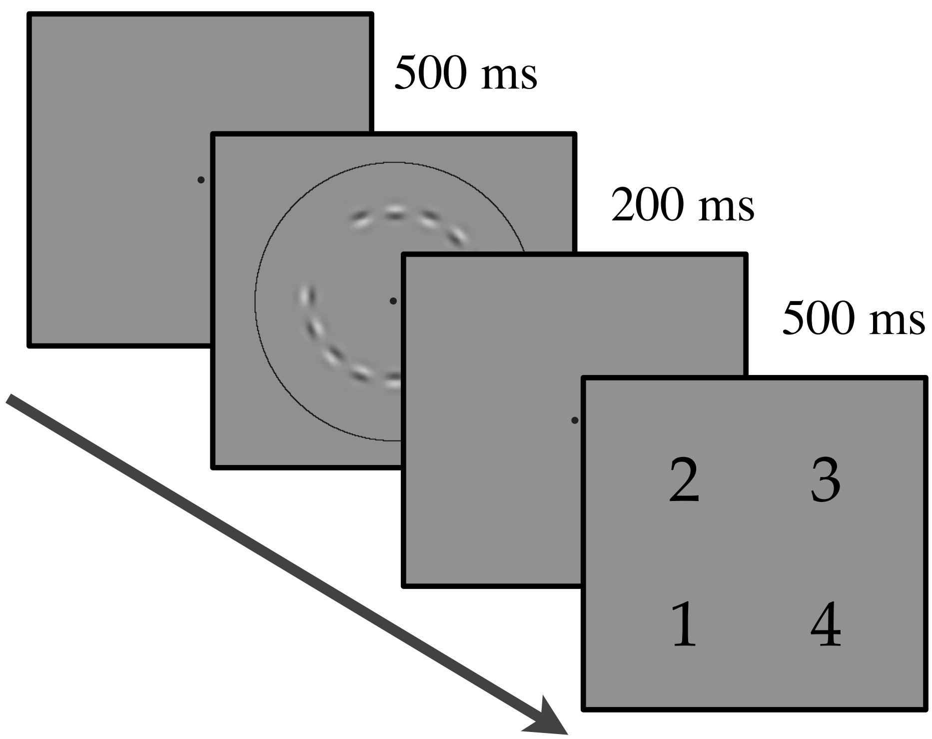


Figure 2.2: Procedure used in the "C" orientation discrimination experiment.

Results

All analyses were performed on log-transformed data using the statistical computing environment R (R Development Core Team, 2007).

Mean contrast thresholds for both age groups and for the four conditions are plotted in Figure 2.3. An Analysis of Variance revealed a significant main effect of age ($F(1, 21) = 70.2, p < 0.001$), indicating that thresholds were, on average, higher in older subjects. To assess the effect of element orientation, we performed three planned linear contrasts. The first contrast compared thresholds in the aligned and phase conditions to thresholds in the radial and mixed conditions: the comparison was significant in younger subjects ($t(11) = 7.39, p < 0.001$) but not in older subjects ($t = -0.55, df = 11, p = 0.60$), and an ANOVA confirmed that the Comparison x Group interaction was significant ($F(1, 22) = 17.591, p < 0.001$). These results indicate that thresholds in younger subjects, but not older subjects, were significantly lower in the aligned and phase conditions than in the radial and mixed conditions. The second contrast compared thresholds in the aligned and phase conditions: the comparison was not significant in younger subjects ($t(11) = 1.84, p = 0.093$) or older subjects ($t(11) = 0.53, p = 0.61$), and an ANOVA found that the Comparison x Group interaction was not significant ($F(1, 22) = 0.12, p = 0.73$). Hence, thresholds in the aligned and phase conditions did not differ significantly in either age group. The third contrast compared thresholds in the aligned and radial conditions: The comparison was significant in the younger group ($t(11) = 4.75, p < 0.001$) but not the older group ($t(11) = 0.40, p = 0.70$), and an ANOVA found that Comparison x Group interaction was significant ($F(1, 22) = 6.24, p = 0.02$).

Discussion

This study examined whether the effect of local orientation on global shape identification is affected by aging in the absence of cluttering background elements. We found that aligning local elements along the contour path facilitated the identification of the global shape in younger adults, but had no effect on the performance of older adults. Our results for the younger group are consistent with previous research (Saarinen and Levi, 2001), where young subjects showed consistently lower contrast thresholds for “C” shapes in the aligned condition using different Gabor patch densities and with varying gap sizes. Here, however, we also showed that younger subjects’ advantage for aligned elements was not due simply to the use of a higher order linear filter, as thresholds for the

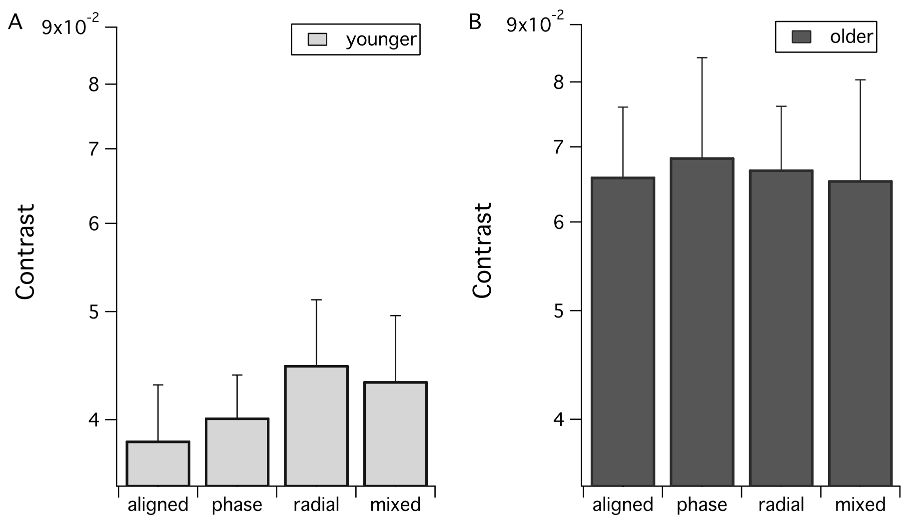


Figure 2.3: Results of the "C" orientation discrimination experiment. Mean thresholds for (A) younger subjects and (B) older subjects are shown for each condition. Error bars represent one standard deviation.

contours composed of either aligned or phase-alternating Gabors were lower than those composed of radial or mixed-orientation Gabors. Instead, the advantage seems to be an indication of a non-linear contour integration process (Hess and Dakin, 1997; Hess and Field, 1999).

The pattern of results is quite different for older subjects. Discrimination thresholds were overall higher for older subjects than for younger subjects, a result that may be caused by overall reductions in sensitivity with age (e.g., Bennett et al. 1999; Elliott et al. 1990a; Owsley, Sekuler, and Siemsen 1983). More interesting, however, is the critical finding of a significant interaction of age with element orientation in the discrimination task. To the extent that older subjects can perceive the orientation of individual Gabors, the absence of facilitation for discriminating aligned contours cannot be due to reduced sensitivity overall. Instead, the lack of facilitation implies that the mechanisms involved in contour integration are impaired in older subjects. The following control experiment was designed to confirm that older subjects can discriminate the orientation of individual Gabor elements at near-threshold contrast.

2.5 Experiment 2: Control Experiment

2.5.1 Methods

Subjects

Twelve younger (M = 22.9 years; SD = 2.81) and 12 older (M = 68.5 years; SD = 3.48) adults participated in this experiment. All except three younger subjects had also participated in the previous experiment. Visual acuity and contrast sensitivity means for these groups are shown in Table 3.1. None of the subjects reported having any visual disorders or major health problems. Two older and no younger subjects were left-handed and there were five females in the younger group and six females in the older group. All the subjects gave their written informed consent to participate in the study.

2.5.2 Apparatus and Stimuli

The apparatus and stimuli were the same as those used in the previous experiment, except that only the aligned and radial stimuli were included.

Procedure

A two interval forced-choice procedure (2-IFC) was used to measure thresholds in three conditions: detecting an aligned "C", detecting a radial "C" and discriminating between an aligned and a radial "C". To reduce temporal and positional uncertainty, each interval contained a high-contrast black circle that was centered on the fixation point and had a radius of 2 deg. In the two detection conditions, one interval contained an aligned or a radial "C", and the subject's task was to determine which interval contained the stimulus. In the discrimination condition, one interval contained an aligned "C" and the other interval contained a radial "C", and the subject determined which interval contained the aligned "C". In the detection conditions, the location of the gap in the "C" was chosen randomly on every trial among four different locations. In the discrimination condition, the location of the gap also varied randomly across trials, but was the same for each interval on any given trial.

Each trial began with a uniform grey screen with a fixation point in the middle. The fixation point alternated between black and white for 300 ms at a rate of 10 Hz to attract the viewer's attention to the centre of the display. The fixation point then remained black for 500 ms, after which the two stimulus intervals were presented in succession for 200 ms each, separated by a 500 ms inter-stimulus-interval when only the fixation point remained on the screen. The response screen was then presented 500 ms later until the subject pressed one of two keys, labelled 1 or 2, that corresponded to the interval containing the target (Figure 2.4).

Two interleaved staircases modulated stimulus contrast in steps of 0.05 log units across trials. A four-down/one-up staircase and a two-down/one-up staircase converged on the contrasts needed to correctly identify the location of the gap with 84% and 71% accuracy, respectively. Contrast threshold, defined as the contrast needed to perform with 75% accuracy, was determined for each condition by fitting a Weibull function to combined data obtained from the two staircases. Two thresholds were obtained for each condition in separate blocks of trials, resulting in six randomized blocks of 100 trials each. Analyses were performed on the average of the two thresholds obtained for each condition.

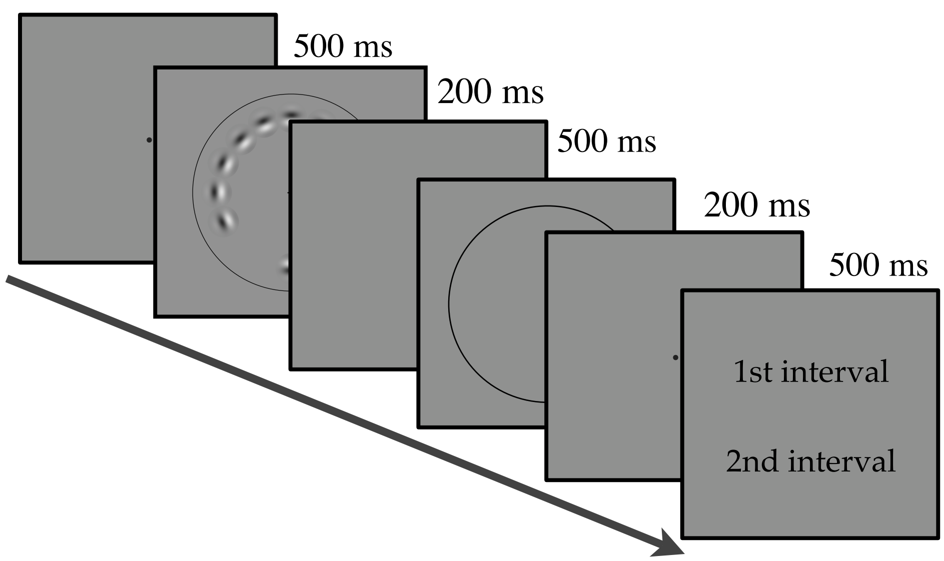


Figure 2.4: Procedure used in the control experiment.

Results

All analyses were performed on log-transformed data using the statistical computing environment R (R Development Core Team, 2004). One young subject was excluded from all analyses because two of their thresholds were outside of the range of contrasts that were presented during the experiment.

Thresholds for both groups are shown in Figure 2.5. Thresholds were higher in older subjects than younger subjects ($F(1, 21) = 23.01, p < 0.001$) and varied significantly across conditions ($F(2, 42) = 18.9, p < 0.001$). The Age x Condition interaction was not significant ($F(2, 42) = 1.76, p = 0.19$). The effect of condition was analyzed with two planned linear contrasts. The first contrast compared detection thresholds in the aligned and radial conditions: In both age groups, detection thresholds were lower in the aligned condition than the radial condition (younger: $t(10) = 4.8, p < 0.001$; older: $t(11) = 3.70, p = 0.003$), and an ANOVA indicated that the value of the comparison did not differ across age groups ($F(1, 21) = 0.24, p = 0.63$). Note that this lack of a Comparison x Group interaction differs from the result obtained in Experiment 1, which found that the the comparison of aligned and radial conditions differed significantly across groups. The second planned contrast compared discrimination thresholds and detection thresholds in the aligned condition: The comparison was not significant in younger subjects ($t(10) = 1.51, p = 0.16$) or older subjects ($t(11) = 0.59, p = 0.56$), and an ANOVA found that the Comparison x Group interaction was not significant ($F(1, 21) = 2.32, p = 0.14$).

Examination of Figure 2.3 shows that the average "C" orientation discrimination threshold was approximately 0.065 in older subjects, a value that is much higher than the thresholds shown in Figure 2.5. This observation was confirmed by t tests: in older subjects, thresholds in the aligned-detection ($t(11) = -23.2,\ p < 0.001$), radial-detection ($t(11) = -14.5, p < 0.001$), and aligned-radial discrimination ($t(11) = -28.6, p < 0.001$) conditions were all significantly lower than the average threshold obtained from older subjects in Experiment 1.

2.5.3 Discussion

Our control experiment demonstrated that detection thresholds for aligned and radial "C" stimuli were significantly higher (i.e. ≈ 0.14 log units) in older subjects. However,

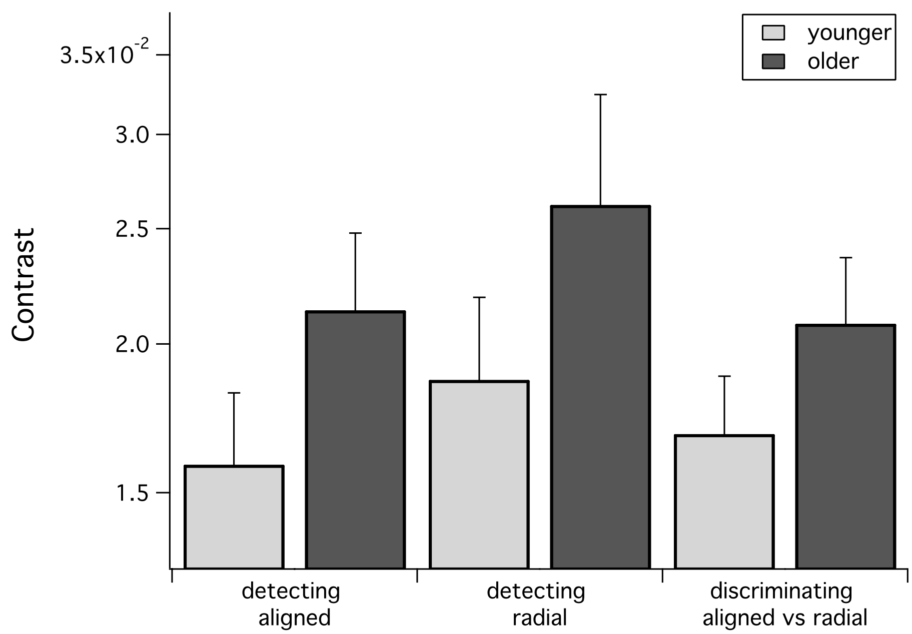


Figure 2.5: Results of the control experiment. Mean thresholds for younger (grey bars) and older (black bars) subjects are shown for each condition. Error bars represent one standard deviation.

it is unlikely that this difference in sensitivity can account for the age differences found in Experiment 1. First, detection thresholds obtained in the control experiment were much lower than the "C" orientation discrimination thresholds measured in Experiment 1. Therefore, stimulus detectability almost certainly was not a constraint on performance in Experiment 1. Second, the control experiment found that detection thresholds were significantly lower in the aligned condition than the radial condition, and that the threshold difference was the same in both age groups. This result differs from Experiment 1, which found that the radial-aligned difference was significantly larger in younger subjects. Hence, the results of the control experiment indicated that the greater sensitivity to the "C" contour that was found in the aligned condition in Experiment 1 only in young subjects cannot be explained by positing that younger subjects, but not older subjects, are more sensitive to aligned Gabors than to radial Gabors.

Another possible explanation of the finding that older subjects in Experiment 1 performed similarly in all conditions is that older subjects simply could not discriminate the orientations of the Gabor elements. The results of the control experiment are inconsistent with this explanation. The control experiment found that the ratio between thresholds measured in the aligned detection and aligned/radial discrimination conditions did not differ across groups, and that discrimination thresholds were significantly lower than the "C" orientation discrimination thresholds measured in Experiment 1. Both of these results suggest that discrimination of Gabor orientation was not a strong constraint on the performance of older subjects in Experiment 1.

The current experiment found that contrast sensitivity was higher in the aligned condition – in which the Gabor patterns were oriented tangentially – than in the radial condition. Previous studies, on the other hand, have shown that contrast sensitivity and acuity for sine wave gratings presented in the peripheral visual field are higher for radially-oriented patterns than for tangentially-oriented patterns (Johnston, 1987; Rovamo, Virsu, Laurinen, and Hyvarinen, 1982; Temme, Malcus, and Noell, 1985). However, those previous studies used relatively small, isolated gratings, rather than circular arrangements of Gabors like the ones used in the current experiment. The different results obtained in the current experiment are another indication of how detection thresholds for the "C" patterns were influenced significantly by the spatial arrangement of the Gabor elements, rather than being determined solely by the elements themselves.

2.6 General Discussion

In our main experiment, we found that younger subjects showed increased sensitivity for discriminating "C" contours composed of elements aligned tangentially to the contour path, as compared to contours composed of orthogonally oriented elements or elements with alternating aligned and orthogonal orientations. In contrast, older subjects obtained equivalent thresholds in all conditions, showing no effect of local orientation on their sensitivity for contour discrimination. Our control experiment indicated that older subjects could discriminate the orientation of local elements as soon as they could detect the stimulus. However, discrimination of the global orientation of the contour required a three-fold increase in contrast. These results indicate that the performance of older subjects in the "C" orientation discrimination experiment was not limited by an inability to detect the local elements and/or orientations. Instead, our results suggest that aging is associated with a change in the mechanisms responsible for contour integration.

According to the association field theory of Field et al. (1993), the strongest contour linking occurs between elements of similar orientation that are positioned along their orientation axis and the strength of association weakens as the relative orientation of the elements increases or their spatial location becomes inappropriate. Similarly, Kellman and Shipley (1991) suggested that relatable elements (elements linked along contours without acute angles) are more readily integrated into contours than other non-relatable elements (but see Guttman, Sekuler, and Kellman 2003 for a notable exception to the theory of relatability). Our findings for younger adults are consistent with these ideas. Interestingly, the findings for older adults suggest that aging affects the functioning of orientation-tuned cells that form the association field, resulting in similar performance when discriminating contours composed of elements with different relative orientations. The nature of changes that would lead to such a pattern of results remains to be determined.

The effects of aging on different perceptual abilities vary greatly. Some visual functions show significant declines with age (e.g., optic flow: Atchley and Andersen 1998; motion perception: Bennett et al. 2007; Norman et al. 2003; Snowden and Kavanagh 2006; Trick and Silverman 1991; stereopsis: Wright and Wormald 1992), whereas other functions remain virtually intact (e.g., blur adaptation: Elliott, Hardy, Webster, and Werner 2007; temporal integration: Andersen and Ni 2008; shape perception: Norman, Crabtree, Norman, Moncrief, Herrmann, and Kapley 2006; Wang 2001; visual short-term memory: Bennett, Sekuler, McIntosh, and Della-Maggiore 2001; Della-Maggiore, Sekuler, Grady, Bennett, Sekuler, and McIntosh 2000; McIntosh, Sekuler, Penpeci, Rajah, Grady, Sekuler, and Bennett 1999; Sara and Faubert 2000). One theory proposed to explain this variation suggests that age-related changes in visual function are more pronounced in functions requiring complex and multiple stages of processing (Bennett et al., 2001; Faubert, 2002; Habak and Faubert, 2000). The reasoning behind this theory is that any age-related functional declines in processing, however subtle, will accumulate as the processing complexity increases; thus, age-related changes will become noticeable in sufficiently complex tasks. A related theory suggests that the effects of aging may be masked by compensatory mechanisms in relatively simple tasks, but when tasks requirements are increased, the compensatory mechanisms break down and age effects become apparent (Bennett et al., 2001; Della-Maggiore et al., 2000; McIntosh et al., 1999; Richards et al., 2006). Consistent with these predictions, Habak and Faubert (2000) found an age-related decline in the detection of static and moving gratings for complex, second-order stimuli, but not for simple, first-order, stimuli. Standard models of contour integration (eg., Field et al. 1993; Altmann et al. 2003) posit that contour integration is an intermediate level task that requires multiple stages of non-linear processing. Thus, the age-related declines in contour integration mechanisms observed in our study are consistent with the processing complexity hypothesis.

Aging also has been found to affect other intermediate level processing tasks. For example, Andersen and Ni (2008) examined the effects of age on spatial and temporal integration using a task requiring subjects to extract the shape of an object from moving dots. Andersen and Ni found that spatial, but not temporal, integration was impaired in older age. Kurylo (2006) examined the effect of age on perceptual organization using several visual components and found that grouping abilities of older subjects were impaired for patterns defined using line-orientation and flicker, but not colour or motion. Mechanisms involved in luminance-defined shape perception also appear to be affected by age: Rivest, Kim, Intriligator, and Sharpe (2004) found that, although perception of simple elementary shapes is unimpaired, older subjects show a reduced shape distortion effect compared to young subjects. This effect is thought to be caused by a decline in the interaction of shape selective neurons in the ventral stream. Finally, a recent study found that, under divided attention conditions, older subjects showed a reduced capacity to complete partly occluded contours (Richards et al., 2006).

Given that the physiology underlying contour integration is not fully understood, hypotheses on the causes of age-related impairment in contour integration are necessarily speculative. However, a reduction in the efficiency of inhibitory mechanisms could be involved (Leventhal, Wang, Pu, Zhou, and Ma, 2003; Schmolesky, Wang, Pu, and Leventhal, 2000; Yu, Wang, Li, Zhou, and Leventhal, 2006). Existing theories of contour integration suggest that it is mediated by long-range interactions among orientation selective columns, which are characterized by facilitation among cells with similar orientation preference and having collinear receptive fields, accompanied by inhibition among cells with similar orientation preference and having flanking receptive fields (Hess and Field, 1999; Hess et al., 2003; Polat, 1999). A dysfunction in the dynamics of these long-range connections could be responsible for the age-related impairment that we observed in our study. Betts et al. (2005) showed that older subjects have reduced spatial suppression for large, high contrast moving targets, which is consistent with the hypothesized reduced efficacy of intracortical inhibition in older age. Interestingly, inhibitory deficits have also been suggested as possible mechanisms for the observed age-related declines in bilateral symmetry detection and spatial integration (Andersen and Ni, 2008; Herbert et al., 2002), as well as a possible cause for increased binocular rivalry suppression (Norman, Norman, Pattison, Taylor, and Goforth, 2007).

In conclusion, we have shown that older adults, unlike younger adults, do not benefit from the alignment of local elements along the contour path when discriminating low contrast contours. This result suggests that contour integration mechanisms in older adults are impaired. Further research is needed to assess the boundaries of this impairment, and to determine the direct link between age-related changes in intracortical inhibition and the age-related decline in contour integration.

2.6.1 Acknowledgments

We thank Donna Waxman for collecting the data for this study, and all the subjects for their dedicated participation. This work was supported by the Canada Institute of Health Research Grant and Canada Research Chair Program to A.B.S. and P.J.B., and the CIHR Training Program in "Communication and Social Interaction in Healthy Aging" grant and Ontario Graduate Scholarship in Science and Technology to E.R.

Bibliography

Achtman, R. L., Hess, R. F., Wang, Y.-Z., 2003. Sensitivity for global shape detection. Journal of Vision 3 (10), 616–624.

Altmann, C. F., Bülthoff, H. H., Kourtzi, Z., 2003. Perceptual organization of local elements into global shapes in the human visual cortex. Current Biology 13 (4), 342–349.

Andersen, G. J., Ni, R., 2008. Aging and visual processing: declines in spatial not temporal integration. Vision Research 48 (1), 109–118.

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 (2), 297–308.

Bennett, P. J., Sekuler, A. B., McIntosh, A. R., Della-Maggiore, V., 2001. The effects of aging on visual memory: evidence for functional reorganization of cortical networks. Acta Psychologica 107 (1-3), 249–273.

Bennett, P. J., Sekuler, A. B., Ozin, L., 1999. Effects of aging on calculation efficiency and equivalent noise. Journal of the Optical Society of America. A 16 (3), 654–668.

Bennett, P. J., Sekuler, R., Sekuler, A. B., 2007. The effects of aging on motion detection and direction identification. Vision Research 47 (6), 799–809.

Betts, L. R., Sekuler, A. B., Bennett, P. J., 2007. The effects of aging on orientation discrimination. Vision Research 47 (13), 1769–80.

Betts, L. R., Taylor, C. P., Sekuler, A. B., Bennett, P. J., 2005. Aging reduces center-surround antagonism in visual motion processing. Neuron 45 (3), 361–366.

Bonneh, Y., Sagi, D., 1998. Effects of spatial configuration on contrast detection. Vision Research 38 (22), 3541–3553.

Brainard, D. H., 1997. The psychophysics toolbox. Spatial Vision 10 (4), 433–436.

Crum, R. M., Anthony, J. C., Bassett, S. S., Folstein, M. F., 1993. Population-based norms for the mini-mental-state-examination by age and educational-level. JAMA – J Am Med Assoc 269 (18), 2386–2391.

Del Viva, M. M., Agostini, R., 2007. Visual spatial integration in the elderly. Investigative Ophthalmology & Visual Science 48 (6), 2940–2946.

Delahunt, P. B., Hardy, J. L., Werner, J. S., 2008. The effect of senescence on orientation discrimination and mechanism tuning. Journal of Vision 8 (3), 1–9.

Della-Maggiore, V., Sekuler, A. B., Grady, C. L., Bennett, P. J., Sekuler, R., McIntosh, A. R., 2000. Corticolimbic interactions associated with performance on a short-term memory task are modified by age. The Journal of Neuroscience 20 (22), 8410–8416.

Elliott, D., Whitaker, D., Macveigh, D., 1990a. Neural contribution to spatiotemporal contrast sensitivity decline in healthy aging eyes. Vision Research 30 (4), 541–547.

Elliott, D. B., Sanderson, K., Conkey, A., 1990b. The reliability of the pelli-robson contrast sensitivity chart. Ophthalmic & Physiological Optics 10 (1), 21–24.

Elliott, S. L., Hardy, J. L., Webster, M. A., Werner, J. S., 2007. Aging and blur adaptation. Journal of Vision 7 (6), 1–9.

Faubert, J., 2002. Visual perception and aging. Canadian Journal of Experimental Psychology 56 (3), 164–176.

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 (2), 173–193.

Folstein, M. F., Folstein, S. E., McHugh, P. R., 1975. ”Mini-mental state”. a practical method for grading the cognitive state of patients for the clinician. Journal of Psychiatric Research 12 (3), 189–198.

Govenlock, S. W., Taylor, C. P., Sekuler, A. B., Bennett, P. J., 2006. Orientation tuning channels in old and young observers. Journal of Vision 6 (6), 196–196.

Govenlock, S. W., Taylor, C. P., Sekuler, A. B., Bennett, P. J., submitted. The effect of aging on the orientational selectivity of the human visual system. Vision Research.

Guttman, S., Sekuler, A., Kellman, P., 2003. Temporal variations in visual completion: a reflection of spatial limits? Journal of Experimental Psychology: Human Perception & Performance 29 (6), 1211 – 1227.

Habak, C., Faubert, J., 2000. Larger effect of aging on the perception of higher-order stimuli. Vision Research 40 (8), 943–950.

Hardy, J. L., Delahunt, P. B., Okajima, K., Werner, J. S., 2005. Senescence of spatial chromatic contrast sensitivity. i. detection under conditions controlling for optical factors. Journal of the Optical Society of America. A 22 (1), 49–59.

Herbert, A. M., Overbury, O., Singh, J., Faubert, J., 2002. Aging and bilateral symmetry detection. The Journals Of Gerontology Series B Psychological Sciences And Social Sciences 57 (3), P241–P245.

Hess, R. F., Beaudot, W. H., Mullen, K. T., 2001. Dynamics of contour integration. Vision Research 41 (8), 1023–1037.

Hess, R. F., Dakin, S. C., 1997. Absence of contour linking in peripheral vision. Nature 390 (6660), 602–604.

Hess, R. F., Field, D., 1999. Integration of contours: new insights. Trends in Cognitive Science 3 (12), 480–486.

Hess, R. F., Hayes, A., Field, D. J., 2003. Contour integration and cortical processing. Journal of Physiology – Paris 97 (2-3), 105–119.

Johnston, A., 1987. Spatial scaling of central and peripheral contrast-sensitivity functions. Journal of the Optical Society of America. A 4 (8), 1583–1593.

Kellman, P. J., Shipley, T. F., 1991. A theory of visual interpolation in object perception. Cognitive Psychology 23, 141–221.

Kovács, I., Julesz, B., 1993. A closed curve is much more than an incomplete one: effect of closure in figure-ground segmentation. Proceedings of the National Academy of Sciences of the United States of America 90 (16), 7495–7497.

Kurylo, D. D., 2006. Effects of aging on perceptual organization: efficacy of stimulus features. Experimental Aging Research 32 (2), 137–152.

Legault, I., Allard, R., Faubert, J., 2007. Normal aging and the perception of curvature shapes. Optometry and vision science : official publication of the American Academy of Optometry 84 (12), 1087–92.

Leventhal, A. G., Wang, Y. C., Pu, M. L., Zhou, Y. F., Ma, Y. Y., 2003. GABA and its agonists improved visual cortical function in senescent monkeys. Science 300 (5620), 812–815.

Mäntyjärvi, M., Laitinen, T., 2001. Normal values for the Pelli-Robson contrast sensitivity test. Journal of Cataract and Refractive Surgery 27 (2), 261–266.

Mathes, B., Fahle, M., 2007. Closure facilitates contour integration. Vision Research 47 (6), 818–827.

McIntosh, A. R., Sekuler, A. B., Penpeci, C., Rajah, M. N., Grady, C. L., Sekuler, R., Bennett, P. J., 1999. Recruitment of unique neural systems to support visual memory in normal aging. Current Biology 9 (21), 1275–1278.

Nikolaev, A. R., van Leeuwen, C., 2007. Collinearity, curvature interpolation, and the power of perceptual integration. Psychological Research 71 (4), 427–437.

Norman, J. F., Crabtree, C. E., Norman, H. F., Moncrief, B. K., Herrmann, M., Kapley, N., 2006. Aging and the visual, haptic, and cross-modal perception of natural object shape. Perception 35 (10), 1383–1395.

Norman, J. F., Norman, H. F., Pattison, K., Taylor, M. J., Goforth, K. E., 2007. Aging and the depth of binocular rivalry suppression. Psychology and Aging 22 (3), 625–631.

Norman, J. F., Ross, H. E., Hawkes, L. M., Long, J. R., 2003. Aging and the perception of speed. Perception 32 (1), 85–96.

NRC, 1987. Work, aging, and vision: report of a conference. National Academy Press, Washington, DC.

Owsley, C., Sekuler, R., Siemsen, D., 1983. Contrast sensitivity throughout adulthood. Vision Research 23 (7), 689–699.

Pelli, D., Robson, J., Wilkins, A., 1988. The design of a new chart for measuring contrast sensitivity. Clinical Vision Science 2 (3), 187–199.

Pelli, D. G., 1997. The videotoolbox software for visual psychophysics: transforming numbers into movies. Spatial Vision 10 (4), 437–442.

Polat, U., 1999. Functional architecture of long-range perceptual interactions. Spatial Vision 12 (2), 143–162.

R Development Core Team, 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (http://www.R-project.org).

Richards, E. D., Bennett, P. J., Sekuler, A. B., 2006. The effects of task switching on age-related differences in shape perception. Journal of Vision 6 (6), 325–325.

Rivest, J., Kim, J. S., Intriligator, J., Sharpe, J. A., 2004. Effect of aging on visual shape distortion. Gerontology 50 (3), 142–151.

Rovamo, J., Virsu, V., Laurinen, P., Hyvarinen, L., 1982. Resolution of gratings oriented along and across meridians in peripheral vision. Investigative Ophthalmology & Visual Science 23 (5), 666–670.

Saarinen, J., Levi, D. M., 2001. Integration of local features into a global shape. Vision Research 41 (14), 1785–1790.

Salthouse, T. A., Hancock, H. E., Meinz, E. J., Hambrick, D. Z., 1996. Interrelations of age, visual acuity, and cognitive functioning. The journals of Gerontology. Series B, Psychological Sciences and Social Sciences 51 (6), P317–30.

Salthouse, T. A., Prill, K. A., 1988. Effects of aging on perceptual closure. The American Journal of Psychology 101 (2), 217–238.

Sara, M., Faubert, J., 2000. Aging, perception, and visual short-term memory for luminance-defined form. Ophthalmic & Physiological Optics 20 (4), 314–322.

Savage, G., Haegerstrom-Portnoy, G., Adams, A., Hewlett, S., 1993. Age changes in the optical density of human ocular media. Clinical Vision Science 8, 97–108.

Schmolesky, M. T., Wang, Y., Pu, M., Leventhal, A. G., 2000. Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. Nature Neuroscience 3 (4), 384–390.

Sekuler, R., Sekuler, A. B., 2000. Visual perception and cognition. In: Evans, J., Williams, T., Beattie, B., Michel, J.-P., Wilcock, G. (Eds.), Oxford Textbook of Geriatric Medicine, 2nd Edition. Oxford University Press, New York, pp. 753–756.

Skeel, R. L., Schutte, C., van Voorst, W., Nagra, A., 2006. The relationship between visual contrast sensitivity and neuropsychological performance in a healthy elderly sample. Journal of Clinical and Experimental Neuropsychology 28 (5), 696–705.

Snowden, R. J., Kavanagh, E., 2006. Motion perception in the ageing visual system: minimum motion, motion coherence, and speed discrimination thresholds. Perception 35 (1), 9–24.

Spear, P. D., 1993. Neural bases of visual deficits during aging. Vision Research 33 (18), 2589–2609.

Temme, L. A., Malcus, L., Noell, W. K., 1985. Peripheral visual field is radially organized. American Journal of Optometry and Physiological Optics 62 (8), 545–554.

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 (9), 1437–1440.

Wang, Y. Z., 2001. Effects of aging on shape discrimination. Optometry and vision science : official publication of the American Academy of Optometry 78 (6), 447–54.

Weale, R. A., 1963. The Aging Eye. Lewis, London.

Weale, R. A., 1982. Senile ocular changes, cell death, and vision. In: Sekuler, R., Kline, D., Dismukes, K. (Eds.), Aging and visual function. Liss, New York, pp. 161–171.

Weale, R. A., 1988. Age and the transmittance of the human crystalline lens. Journal of Physiology 395, 577–587.

Werner, J. S., Peterzell, D. H., Scheetz, A. J., 1990. Light, vision, and aging. Optometry and Vision Science 67 (3), 214–229.

Winn, B., Whitaker, D., Elliott, D. B., Phillips, N. J., 1994. Factors affecting light-adapted pupil size in normal human subjects. Investigative Ophthalmology & Visual Science 35 (3), 1132–1137.

Wright, L. A., Wormald, R. P., 1992. Stereopsis and ageing. Eye 6 (Pt 5), 473–476.

Yu, S., Wang, Y., Li, X., Zhou, Y., Leventhal, A. G., 2006. Functional degradation of extrastriate visual cortex in senescent rhesus monkeys. Neuroscience 140 (3), 1023–1029.

Chapter 3

The effect of aging on contour discrimination in clutter

3.1 Preamble

The contents of this chapter has been previously published (Roudaia, E., Farber, L. E., Bennett, P. J., and Sekuler, A. B. (2011). The effects of aging on contour discrimination in clutter. Vision research, 51(9), pp 1022 – 1032) and is reproduced here with full permission from Vision Research.

3.2 Abstract

The present study examined the effect of aging on the detection and discrimination of contours embedded in a dense field of distractors. The minimum stimulus duration required to correctly discriminate (Experiment 1) and detect (Experiment 2) three types of "C" shaped contours was measured. Overall, older subjects required longer stimulus durations than younger subjects in all conditions. Comparing performance for contours comprising elements oriented tangentially to the contour path (aligned) and those oriented orthogonally to the contour (radial) revealed that the effect of local orientation on contour discrimination is slightly greater in older than younger subjects. Control experiments showed that these age differences were not due to differences in retinal illuminance, or the detectability or discriminability of the elements comprising the contours. These

findings suggest that the ability to extract global contours embedded in clutter declines in older age.

3.3 Introduction

It is well established that neurons in the early stages of visual processing respond primarily to information falling within a limited location in the visual field, termed the classical receptive field of the neuron. Nevertheless, our visual world is not a disjointed collection of features, but consists of global objects and shapes embedded in a background. To achieve this percept, the visual system needs to integrate information across space to extract global contours and shapes.

Two important factors that influence the grouping of local elements into elongated contours are element proximity and the alignment of element orientations (Field, Hayes, and Hess, 1993; Hess, Hayes, and Field, 2003), both of which are characteristic of local parts of contours in natural scenes (Geisler, Perry, Super, and Gallogly, 2001; Geisler and Perry, 2009). Although the neural mechanisms underlying contour integration are not well understood, it appears that contour integration may be mediated by long-range horizontal connections within early visual areas (Gilbert and Wiesel, 1989; Bosking, Zhang, Schofield, and Fitzpatrick, 1997; Malach, Amir, Harel, and Grinvald, 1993), as well as feedback projections from higher visual areas (Angelucci, Levitt, Walton, Hupe, Bullier, and Lund, 2002; Altmann, Bülthoff, and Kourtzi, 2003; Kourtzi, Tolias, Altmann, Augath, and Logothetis, 2003).

Only a few studies have examined the effects of aging on perceptual grouping and contour integration. Salthouse and Prill (1988) showed that older adults are are less able to perceptually complete simple line drawings. Compared to younger subjects, older subjects also have difficulty perceptually grouping elements when line-orientation and flicker rate are used as grouping cues, but show no impairment in grouping by color of motion cues (Kurylo, 2006). Roudaia, Bennett, and Sekuler (2008) also suggested that contour integration was impaired in older adults.

To examine the effects of aging on contour integration mechanisms, Roudaia et al. (2008) measured the minimum contrast required for subjects to discriminate contours that were presented against a uniform background and composed of elements whose orientations were aligned along the contour path, were orthogonal to it, or that alternated between aligned and orthogonal orientations. Consistent with previous research (Saarinen and Levi, 2001) and the principle of good continuation, younger adults performed better when discriminating aligned contours compared with the other types. Surprisingly, older subjects were not influenced by the local orientation of the elements, showing equal performance for the three types of contour.

Roudaia et al. (2008) argued that their results demonstrated that aging alters contour integration mechanisms, but it is not clear whether this impairment generalizes to supra-threshold stimuli and/or to contours presented in background elements, or clutter. The influence of clutter on contour integration was demonstrated recently by Dakin and Baruch (2009), who showed that contour perception requires the suppression of irrelevant background information as well as the integration of local elements. Two studies have examined the effect of aging on the detection and discrimination of contours embedded in visual clutter. Del Viva and Agostini (2007) assessed the ability of older and younger subjects to detect closed circular contours, comprising equally spaced aligned Gabors elements, that were embedded in a field of randomly oriented distractor Gabors. They found that the maximum number of distractors that older subjects could tolerate was lower than that for younger subjects, suggesting that aging impairs the integration of contours in clutter. The study by McKendrick, Weymouth, and Battista (2010) examined older subjects' ability to make fine shape discriminations of similar circular contours, with and without the presence of distractor elements. Interestingly, older and younger subjects did not differ in their ability to discriminate the contour shapes, even in the presence of clutter. Thus, it appears that aging may impair the ability to extract contours among clutter, but it does not seem to influence shape discrimination once the contour has been detected.

To further examine the effects of aging on contour integration, the current study examined the subjects' ability to discriminate open contours embedded in a cluttered background. Importantly, this study also examined the roles of orientation and phase of local contour elements on contour integration ability of younger and older adults. Stimuli consisted of contours defined by Gabors arranged in the shape of a "C" that were placed within a field of randomly oriented Gabors. The relative density of the contour and background Gabors was equalized such that only the relative orientations of the Gabors signaled the contour. The contours were randomly rotated across trials and subjects were asked to report the location of the gap in the "C‘", which required the discrimination of the full contour. Performance was assessed by estimating the minimum stimulus exposure duration required to discriminate the contour. The first type of contour, aligned, comprised Gabors that were oriented tangentially to the contour path, and all having the same spatial phase. The second type, phase, also comprised tangentially oriented Gabors, but the phase polarity of the Gabors alternated along the contour. The third type, radial, was composed of Gabors that were oriented orthogonally to the contour path. Consistent with previous research (e.g., Field et al., 1993; Dakin and Baruch, 2009), we expected performance in the aligned and phase conditions to be better than in the radial condition, due to the benefit of co-linearity for contour perception. In addition, we hypothesized that the consistent phase of local elements in the aligned condition would improve discrimination performance compared to the phase condition, also in keeping with previous findings (e.g., Field, Hayes, and Hess, 2000).

3.4 Experiment 1: Contour Discrimination in Clutter

3.4.1 Methods

Subjects

Twelve younger ($M = 23$ years; range: $20 - 32$) and 15 older ($M = 70$ years; range: $64 - 79$) subjects participated in this study, and were compensated at a rate of $10/hour. Near and far visual acuities were measured in all subjects using the SLOAN Two Sided ETDRS Near Point Test and the 4 Meter 2000 Series Revised ETDRS charts (Precision Vision, LaSalle, Illinois, USA). Contrast sensitivity was estimated using the Pelli-Robson Contrast Sensitivity Test. Subjects wore their habitual optical correction during the vision testing and during the experiment. Although older subjects on average showed poorer visual acuity than younger subjects, all subjects had normal or corrected-to-normal near and far Snellen visual acuity (range: -0.23 to 0.18 logMAR). All subjects showed normal contrast sensitivity for their age group, as measured by the Pelli-Robson Contrast Sensitivity Test (Elliott, Sanderson, and Conkey, 1990; Mäntyjärvi and Laitinen, 2001; Pelli, Robson, and Wilkins, 1988). In addition, we administered the Mini-Mental State Examination assessment (Folstein, Folstein, and McHugh, 1975) to all older subjects to screen for any cognitive decline. All scores were within the normal range for the subjects' age and education levels (Crum, Anthony, Bassett, and Folstein, 1993). All subjects also completed a general health questionnaire to screen for any his-

Table 3.1: Mean ± 1 SD age, near and far logMAR acuity, Pelli-Robson contrast sensitivity, and Mini-Mental State Examination (MMSE).

Experiment	N (M:F)	Age	Near Acuity	Far Acuity	Pelli-Robson	MMSE
"C" Orientation	11 (4:7)	23.0 ± 3.48	-0.16 ± 0.08	-0.12 ± 0.06	1.95 ± 0	
Discrimination	11 (5:6)	69.6 ± 5.41	0.00 ± 0.13	-0.04 ± 0.14	1.94 ± 0.05	28.7 ± 1.19
"C" Detection	8 (4:4)	22.0 ± 3.55	-0.12 ± 0.07	-0.11 ± 0.06	1.93 ± 0.05	
	8 (3:5)	69.3 ± 4.33	-0.02 ± 0.14	-0.09 ± 0.13	1.95 ± 0	28.5 ± 1.31
Retinal Illuminance						
Control	7 (4:3)	20.0 ± 1.41	-0.13 ± 0.08	-0.11 ± 0.06	1.95 ± 0	

tory of visual pathology, such as cataracts, glaucoma, and retinopathy. One older subject reported having a cataract and was not included in the experiment. None of the other subjects reported any visual disorders or major health problems. One younger and three older subjects were later excluded from all analyses because they failed to obtain thresholds in at least one condition (see section 3.4.1 for criteria for valid thresholds). Table 3.1 summarizes the relevant demographic information for all subjects included in the analyses.

Apparatus

The stimuli were generated and presented using a Macintosh G5 computer equipped with a NVIDIA GeForce 6600 video card and a BITS++ Digital Video Processor (Cambridge Research Systems Ltd, UK), which provided 14-bit luminance resolution. The experiment was programmed using the Psychophysics and Video Toolboxes (version 3) (Brainard, 1997; Pelli, 1997) in the Matlab environment (version 7.2). The stimuli were presented on a 20-inch (51 cm) 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 an average luminance of 120 cd/m^2. Head position and viewing distance were stabilized with a chin/forehead rest.

Stimuli

The stimuli consisted of a square region of pseudo-randomly distributed Gabor patches that contained a global pattern in the shape of a C in the center. All Gabors were created by multiplying a 3 c/deg sine wave grating of 60% contrast by a circular Gaussian envelope whose full width at half height was 0.25 deg.

The following algorithm was used to construct stimulus arrays in which the presence of a contour was defined by the relative orientations of the Gabor elements comprising the target. First, an invisible 12×12 grid was created with a cell size of 0.59 deg. The position of the grid was jittered horizontally and vertically relative to the center of the display by selecting random displacements from a Normal distribution ($\sigma = 3$ pixels). Next, the position of 16 target Gabors was determined by placing them on an imaginary circle (radius = 1.5 deg) with a constant distance between adjacent Gabors of 0.59 deg ($\approx$ 1.77 spatial periods). To create the C, two adjacent Gabor patches were removed either in the upper left, upper right, lower left or lower right quadrant. The imaginary circle was positioned in the centre of grid and then displaced horizontally and vertically by random amounts selected from a Normal distribution ($\sigma = 2$ pixels). It was then verified that each target Gabor was located in a separate cell in the grid. If more than one Gabor fell within a single cell, the contour was redrawn. The distractor Gabors were then placed in all remaining cells in the grid: the center of each distractor was displaced horizontally and vertically relative to the cell's center by amounts drawn from a Normal distribution ($\sigma = 4$ pixels). When two distractors overlapped, one of the overlapping elements was removed. This procedure reduced the possibility the local density of Gabors could serve as a cue for detecting the contour. The mean number of elements removed was 7.3 and ranged from 0 to 16 elements across trials. The number of elements discarded on each trial was recorded and subsequent analyses confirmed that the average number of elements removed was the same across conditions and age groups.

The orientation and phase of the contour Gabor elements varied across three stimulus conditions (Figure 3.1). In the aligned condition, all target Gabors were oriented tangentially to the contour path and all had positive sine phase with respect to the center of the element. In the phase condition, Gabor orientations were the same as in the aligned condition, but their phase alternated from positive to negative sine phase. Summation by a simple linear detector with an elongated receptive field may contribute significantly to grouping in the aligned condition, but not in the phase condition (Hess and Field, 1999). Finally, all Gabors in the radial condition were oriented orthogonally to the contour path and had positive sine phase.

A mask was shown after each stimulus presentation. The mask was created by taking the frequency spectrum of a typical stimulus array and randomizing the phase of its frequency components. This procedure ensured that the mask and stimulus contained the same contrast energy and spatial frequency content.

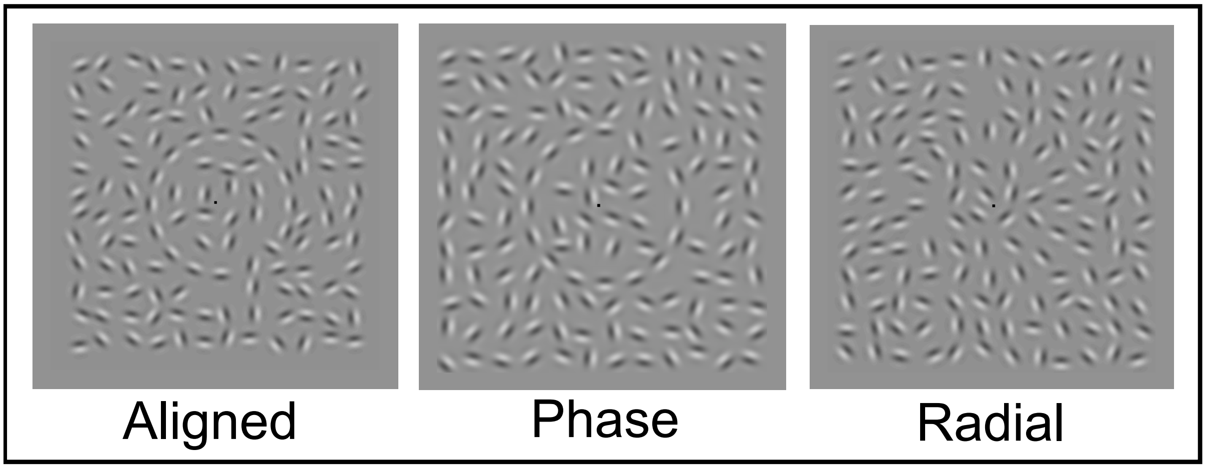


Figure 3.1: Examples of stimulus conditions. In the aligned condition (a), elements had +sine phase and were oriented tangentially to the global contour. In the phase condition (b), elements were also oriented tangentially to the global contour, but the phase alternated between +sine and -sine. In the radial condition (c), all elements were oriented orthogonally to the global contour and all had +sine phase.

Procedure

The McMaster University Research Ethics Board approved the experimental protocol. Written informed consent was obtained from all subjects prior to their participation in the experiment.

A four-alternative forced-choice (4-AFC) procedure was used to measure the stimulus exposure duration needed to discriminate the global orientation of the "C" contour with 75% accuracy. Each of the three conditions was tested in one block of 130 trials, and the order of conditions was randomized for every subject. The experiment began with a light adaptation period of 60 s , followed by 10 practice trials in the beginning of each block, where stimuli were presented for 2 s and the contrast of the distractor elements was reduced by 20% to make it easier for the subjects to see the contour and to ensure that they understood the task. The experimental trials immediately followed the practice trials. A black fixation point was presented in the center of the blank screen of mean luminance. Subjects were instructed to fixate the fixation point, which remained in the center throughout the trial. At the beginning of each trial, the fixation point flickered a rate of 10 Hz for 0.3 s. The stimulus array was then presented for a stimulus duration that varied across trials. The location of the gap in the C was randomized on each trial. The stimulus was then followed by a mask for duration: 0.5 s. Finally, a blank screen replaced the mask for 0.5 s before the response screen appeared (Figure 3.2). The response screen consisted of numbers 1, 2, 3, and 4, placed in the four possible locations of the gap (lower left, upper left, upper right, lower right, respectively). The subjects reported the location of the gap by pressing one of four labeled keys on the keyboard. Auditory feedback was given on every trial with a high pitch tone indicating a correct response and a low pitch tone indicating an error. The subsequent trial began after a 1.5 sec inter-trial interval.

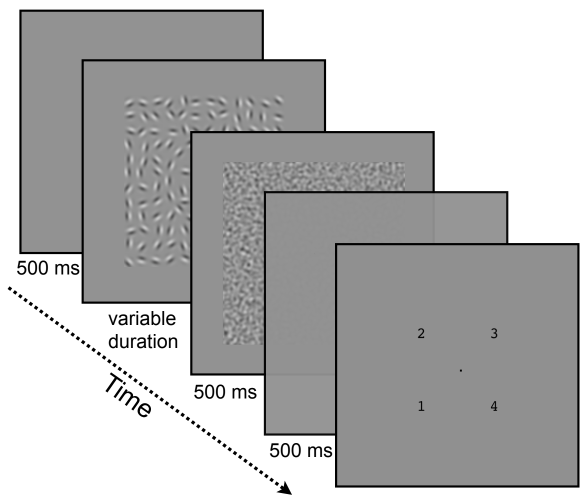


Figure 3.2: Procedure used in the C orientation discrimination experiment.

Analysis

Two interleaved staircases manipulated the stimulus exposure duration across trials. A four-down/one-up staircase and a two-down/one-up staircase converged on the duration needed to correctly identify the location of the gap with 84% and 71% accuracy, respectively (Levitt, 1971; Schlauch and Rose, 1990). The initial staircase step size was 0.133 s (i.e., 10 frames), then it was reduced to 0.107, 0.080, 0.053, and 0.027 s (i.e., 8, 6, 4, and 2 frames) after 1, 2, 3 and 4 reversals respectively. The range of possible durations was limited to 0.013–2 s. Each staircase terminated after 65 trials. Psychometric functions were then obtained by fitting the combined data from both staircases using `psignifit` (v 2.5.6) for Matlab (see http://bootstrap-software.org/psignifit/). This software applied the maximum-likelihood method to determine the best fitting Weibull function (Wichmann and Hill, 2001) F such that

$$\psi(x; \alpha, \beta, \gamma, \lambda) = \gamma + (1 - \gamma - \lambda)F(x; \alpha, \beta).$$

where $\psi(x)$ is the proportion of correct responses at duration x, γ is the guessing rate (fixed at 0.25 for this experiment), α and β are two parameters defining the shape of the psychometric function F, and λ is a lapse rate parameter that was constrained to lie between 0 and 5%. The stimulus exposure duration that corresponded to the 75% accuracy point on the fitted psychometric function was defined as the *duration threshold* for each condition. If the fitted psychometric function had a zero or negative slope, or if threshold was higher than the maximum presented duration, then the threshold was deemed invalid and was excluded from the statistical analyses. One younger subject and 13 older subjects failed to obtain valid thresholds in the radial condition with maximum duration set to 2 s . To obtain valid measures for that condition, we retested nine older subjects only in the radial condition, with the maximum duration set to 2, 4 and 6 s in three randomized blocks. The average of all valid thresholds obtained in this second experimental session was used as the subject's threshold for the radial condition. Finally, one younger subject obtained a threshold lower than the minimum presented duration (1 frame) in the aligned condition (i.e., response accuracy with a one frame exposure duration was greater than 75% correct). To retain this subjects' data for the analyses, their threshold for the aligned condition was set arbitrarily to 1 frame. Note that this value is an overestimate of this subject's threshold, and therefore slightly reduces the true age difference in this condition.

3.4.2 Results

All analyses were performed using the statistical computing environment R (R Development Core Team, 2008). We applied a log transformation to all duration thresholds to ensure that the data satisfy the assumptions of normality and constant variance. When within-subjects tests were performed, the Geisser-Greenhouse correction was used to adjust the degrees-of-freedom to correct for violations of the sphericity assumption

(Maxwell and Delaney, 2004). In such cases, the adjusted p-values are reported. Finally, effect sizes are reported either as Cohen's d or Cohen's f (Maxwell and Delaney, 2004).

Figure 3.3 shows mean duration thresholds for younger and older subjects for the three types of contour. Overall, older subjects showed higher duration thresholds than younger subjects. Compared to younger subjects, thresholds in older subjects were elevated by 0.47, 0.45, and 0.62 $\log_{10}$ units in the aligned, phase, and radial conditions respectively. A mixed repeated-measures ANOVA confirmed these observations, as it revealed a significant main effect of Age ($F(1, 20) = 68.5, p < 0.0001$, $f = 1.75$, MSE = 0.07).

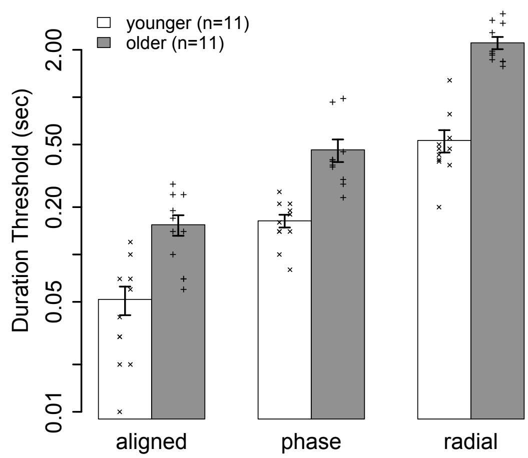


Figure 3.3: Results of the C orientation discrimination experiment. Mean duration thresholds for (A) younger subjects and (B) older subjects are shown for each condition. Error bars represent standard error of duration threshold. The points, which represent data from individual subjects, have been displaced horizontally to improve visibility.

To analyze the effect of condition, we performed three focused comparisons. First, we examined the effect of element orientation by comparing performance in the aligned and phase conditions with performance in the radial condition. The linear contrast was significant for both younger ($t(10) = 14.6$, $p < 0.001$, $d = 4.41$) and older ($t(10) = 12.6$, $p < 0.001$, $d = 3.79$) subjects. Both groups of subjects had lower thresholds in the conditions where contour elements were oriented tangentially to the contour path, compared to contours comprising orthogonally oriented elements. The Contrast × Age interaction approached, but did not reach, conventional levels of statistical significance

($F(1, 20) = 3.53$, $p = 0.07$, $d = 0.80$).

Second, we examined the effect of alternating the phase of successive Gabors in contours comprising tangentially oriented elements. As depicted in Figure 3.3, performance in the phase condition was worse than in the aligned condition. The difference in thresholds in the aligned and phase conditions was significant in both groups (younger: $t(10) = 5.47$, $p < 0.001$, $d = 1.65$; older: $t(10) = 8.08$, $p < 0.001$, $d = 2.44$). Furthermore, the difference between conditions was similar in both groups, as the Contrast × Age interaction was not significant ($t(20) = 0.64$, $p = 0.43$, $d = 0.34$). Thus, alternating the phase of successive elements impairs performance relative to when element phase is constant, and the magnitude of this effect does not change with age.

Finally, we compared performance in the phase and radial conditions to examine the effect of local orientation, without the additional benefit conferred by phase alignment in the aligned condition. This comparison was also significant in both groups (younger: $t(10) = 6.3$, $p < 0.001$, $d = 1.89$; older: $t(10) = 8.42$, $p < 0.001$, $d = 2.54$), indicating that both groups exhibited poorer performance in the radial condition. Again, the Contrast × Age interaction approached, but did not reach, conventional levels of statistical significance ($F(1, 20) = 3.8$, $p = 0.07$, $d = 0.83$).

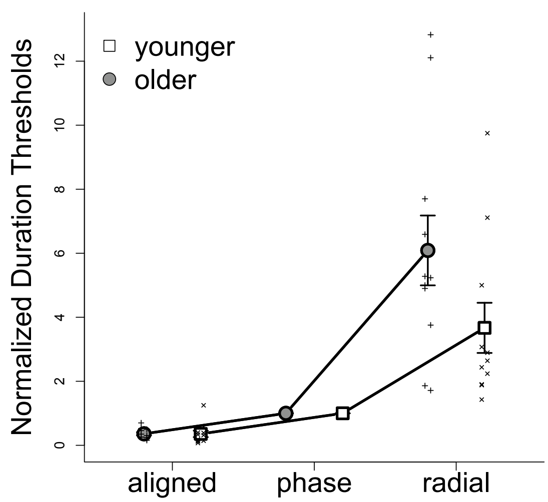


Figure 3.4: Duration thresholds for younger and older subjects normalized by performance in the phase condition. Thresholds from each subject were divided by the threshold obtained in the phase condition. Error bars represent ± standard error. The points represent data from individual subjects.

In both linear comparisons examining the effect of local orientation, the Contrast × Age interaction approached, but did not reach, statistical significance. However, in both cases the effect size (Cohen's d) was approximately 0.8, which according to Cohen's criteria is a large effect (Maxwell and Delaney, 2004). This result suggests that there may be a difference between age groups in the way that performance was affected by element alignment but that our experiment lacked sufficient power to detect it. To examine this possibility, we visually inspected the relationship between the aligned, phase, and radial conditions in the two groups by normalizing each individual's thresholds by threshold in the phase condition. Mean normalized thresholds are plotted in Figure 3.4. Older and younger subjects exhibit a similar improvement in thresholds for the aligned condition compared to the phase condition. On the other hand, older subjects show, on average, a greater increase in thresholds in the radial condition compared to the phase condition, as the slope between the phase and radial conditions is steeper in the older group than the younger group.

3.4.3 Discussion

This experiment examined the ability of younger and older subjects to discriminate the global orientation of three types of contours embedded in a cluttered background. Overall, older subjects required longer stimulus presentations to discriminate all types of contours. Subjects in both age groups performed better with contours composed of elements oriented tangentially to the contour path, compared to contours comprising orthogonally oriented elements. This result is consistent with previous studies showing better contour integration for aligned contours compared to radial contours in younger subjects (e.g. Field et al., 1993; Saarinen and Levi, 2001; Ledgeway, Hess, and Geisler, 2005; Dakin and Baruch, 2009; Bex, Simmers, and Dakin, 2001). Moreover, there is some indication that the effect of element orientation may be even greater in older subjects. Older subjects required 4.2 times longer stimulus presentation than younger subjects to discriminate the "C" in the radial condition, compared to just 2.8 times longer duration in the phase condition. In addition, we found that alternating the phase of the tangentially oriented elements along the path reduces performance in both younger and older subjects by a similar factor. Previous studies with younger subjects also found worse performance with phase-alternating, as opposed to same phase, contours (Field et al., 2000; Hess, Beaudot, and Mullen, 2001; Hess and Dakin, 1999). This effect of phase has been explained by proposing that contour integration is mediated by two processes, one which is sensitive to phase information and another that is indifferent to the phase of the elements (Field et al., 2000). Our results provide no evidence that aging affects the phase-sensitive component of the contour integration process.

3.5 Experiment 2: Contour Detection in Clutter

The contour discrimination task in Experiment 1 required the subjects to extract the entire shape of the contour in order to correctly identify the orientation of the "C". The inability to correctly perform that task may have resulted either from a failure to detect the contour entirely, or alternatively, subjects may have detected the presence of a contour, but failed to completely extract it from the background to locate the gap. In the following experiment, we examine whether aging also influences the ability to simply detect the presence of a contour in clutter. Using a two alternative forced-choice procedure, we measure the minimum stimulus exposure duration required to detect the presence of the "C" contour in the aligned, phase, and radial conditions.

3.5.1 Methods

Subjects

Eight older and two younger subjects who participated in Experiment 1 participated in this experiment. In addition, seven naïve younger subjects were recruited to participate in this experiment. In total, eight older and nine younger subjects participated in Experiment 2 and were compensated for their time at a rate of $10/hour. One younger subject was later excluded from analyses due to invalid thresholds in two conditions. Demographic information for all subjects included in the analyses is summarized in Table 3.1. Finally, after completing Experiment 2, five of the seven new younger subjects – who had not participated in the previous experiment – were tested in the "C" orientation discrimination task used in Experiment 1.

Apparatus

The apparatus was the same as in Experiment 1.

Stimuli

There were two types of stimuli in this experiment: target stimuli containing a "C" contour and noise stimuli that did not contain a contour. The target stimuli were created as described in Experiment 1 and were presented in the aligned, phase, and radial conditions. The noise stimuli was created by generating a target stimulus and then randomizing the orientations of the Gabors comprising the contour. Once the orientations were randomized, the contour was no longer present.

Procedure

A two-interval forced-choice (2-IFC) procedure was used to measure the stimulus exposure duration needed to detect the presence of the "C" contour with 75% accuracy. Subjects completed each condition in a separate block and the order of the blocks was randomized across subjects. The experiment began with an adaptation period of 60 s and five practice trials were presented before each block. Each trial began with a flickering (10 Hz) fixation point that was presented in the middle of a uniform gray screen for 0.3 s. Two intervals then followed, separated by an inter-stimulus-interval consisting of a uniform blank field that lasted 0.5 s. Each interval consisted of a stimulus whose duration varied across trials, followed immediately by a mask lasting 0.5 s. The target stimulus appeared in the first or the second interval with equal probability. A response screen, containing the words "1st interval" on the left and "2nd interval" on the right, appeared 0.25 s after the offset of the mask at the end of the second interval. Subjects pressed a key labeled "1" with their left index finger or a key labeled "2" with their right index finger to indicate the interval that contained the "C". The next trial began $\approx$ 4 s after the subject's response.

Analysis

Stimulus duration was varied across trials using two interleaved staircases. A four-down/one-up staircase and a two-down/one-up staircase converged on the duration needed to detect the contour with 84% and 71% accuracy, respectively. Each staircase terminated after 50 trials, resulting in 100 trials per condition. Psychometric functions were fit to the combined data from all trials as described in 3.4.1. Duration thresholds were defined as the stimulus duration that corresponded to 75% accuracy on the psychometric function.

In the contour detection task, younger and older subjects showed very high accuracy in the aligned condition, even at the shortest exposure duration presented. As such, data from all younger subjects and six older subjects were not well fit by a psychometric function in the aligned condition, and duration thresholds could not be estimated. In addition, two other thresholds – one in the phase condition and another in the radial condition – in the younger group were lower than 1 frame. In order to keep the two subjects in the analyses, we set these two thresholds to 1 frame, which is an underestimation of their performance.

3.5.2 Results

All statistical analyses were performed in the the statistical computing environment R (R Development Core Team, 2008). Duration threshold values were log-transformed to ensure that data satisfy the assumptions of normality and homogeneity of variance.

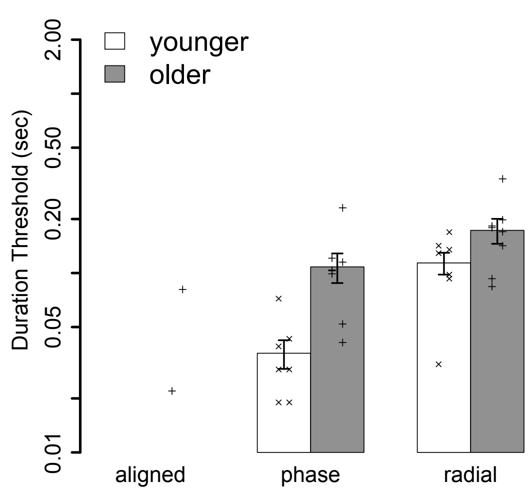


Figure 3.5: Barplots and error bars show the mean ± SE of the valid thresholds in the phase and radial conditions. The points represent individual data for younger (×) and older (+) subjects. Thresholds of only two older subjects are shown in the aligned condition, as all the other thresholds were shorter than the minimum stimulus duration used (1 frame or 0.013 s).

Figure 3.5 shows mean duration thresholds for detecting the "C" contour in the phase and radial conditions. Thresholds from only two older subjects could be estimated in the aligned condition and they are depicted individually in the figure. All other subjects had a very good performance in the aligned condition even at the shortest stimulus duration of 1 frame, so their duration thresholds could not be estimated.

Overall, older subjects again showed higher thresholds than younger subjects. Duration thresholds also varied with condition: performance was best in the aligned condition and worst in the radial condition. To analyze the results, we performed an Age × Condition (phase and radial) mixed repeated-measures ANOVA on log-transformed duration threshold values. The main effect of Age was significant ($F(1, 14) = 24.64$, $p < 0.001$, $f = 1.21$). The main effect of condition was also significant ($F(1, 14) = 9.26$, $p = 0.009$, $f = 0.59$), but the Age × Condition interaction was not significant ($F(1, 14) = 1.03$, $p < 0.33$, $f = 0.04$). These analyses indicate that both groups showed higher duration thresholds in the radial condition than in the phase condition, and that the phase – radial difference was similar in the two groups.

It is interesting to compare the performance in the detection task to performance measured in the same subjects in the discrimination task used in Experiment 1. In the phase condition, the group difference was only slightly larger in the discrimination than the detection task: the log-ratio of older to younger group's thresholds was 0.57 for discrimination and 0.49 for detection. This result suggests that much of the age difference in contour discriminability in the phase condition could be linked to differences in contour detectability. In the radial condition, however, the log threshold ratio was 0.71 for discrimination but only 0.23 for detection. The much larger impairment in the discrimination task suggests that differences in radial contour detectability did not produce the age difference in radial contour discriminability. To investigate this point further, we computed the log-transformed ratio between contour discrimination and detection thresholds for each of the seven young and eight older subjects who completed both sets of tasks used in Experiments 1 and 2. In the phase condition, the log discrimination/detection ratios in older and younger subjects were, respectively, 0.59 and 0.50, and these values did not differ significantly from each other ($t(13) = 0.85$, $p = 0.41$, $d = 0.44$). In the radial condition, the log discrimination/detection ratios in older and younger subjects were 1.13 and 0.69, and these values did differ significantly ($t(13) = 3.31$, $p = 0.006$, $d = 1.71$).

3.5.3 Discussion

Contour detection thresholds were higher for older subjects than younger subjects, but we found no evidence that the effect of element alignment differed between groups: for both younger and older subjects, detection was best for aligned contours, followed by phase contours, and worst for radial contours. This pattern is consistent with results from other studies using the path detection paradigm with younger subjects (Field et al., 2000; Ledgeway et al., 2005; Field et al., 1993; Dakin and Baruch, 2009). It is interesting to note that aligned contours were much easier to detect than phase contours. This findings supports the existence of a phase-sensitive component in contour integration (Hess et al., 2001; Field et al., 2000; Hess and Dakin, 1999), or the involvement of simple linear filters (Hess and Dakin, 1997). Comparisons of contour detection and discrimination thresholds suggests that age differences in contour detection may account for differences in contour discrimination when the elements are aligned but not when they are orthogonal (i.e., the radial condition). Thus, it appears that older subjects can detect the regularity in local orientations of the Gabors signaling the presence of the radial contour. However, they have difficulty completely segregating the radial contour from the background elements in order to locate the gap.

It may be surprising that subjects could detect the contours with such brief exposure durations, especially in the aligned condition. Hess et al. (2001) studied the dynamics of aligned contours and found critical stimulus durations of 0.2 s for contours with similar curvature. However, Hess et al. used a stimulus that was preceded and followed by a mask containing Gabors with random orientations. In contrast, the current experiment did not use a forward mask, and the backward mask did not contain Gabor elements. Moreover, the contours in this experiment were highly predictable and always presented in the center. Thus, top-down processing likely contributed to the surprisingly short duration thresholds obtained in this experiment.

3.6 Experiment 3: Retinal Illuminance Control

It is well established that retinal illuminance affects the spatial and temporal summation properties of the visual system (Barlow, 1958; van Nes, Koenderink, Nas, and Bouman, 1967; Rovamo and Raninen, 1984). Due to a decrease in pupil size and increased density of the ocular media, the average 60 year old receives 2-3 times less light on their retina than the average twenty year old (Weale, 1963). In this experiment, we tested younger subjects with different luminance levels to determine the effect of decreased retinal illuminance on performance in the contour discrimination task.

3.6.1 Methods

Subjects

Seven naive young subjects (μ: 20 years, range: 19-22) were recruited to participate in this experiment and were compensated for their time at a rate of $10/hour. All subjects had normal or corrected-to-normal acuity, normal contrast sensitivity, and were free of any visual disorders or health problems. There were four males and three females in the group. Their demographic information is summarized in Table 3.1.

Apparatus

The apparatus was the same as in Experiment 1. Display luminance was varied by placing neutral density filters in front of the screen. Placing two and three neutral density filters reduced the display luminance from 120 cd/m^2 to 26 cd/m^2 (22%) and 12 cd/m^2 (10%), respectively. Previous studies have shown that such reductions in display luminance reduce retinal illuminance in younger subjects by approximately 0.5 and 0.75 log units (Betts, Sekuler, and Bennett, 2007; Winn, Whitaker, Elliott, and Phillips, 1994).

Stimuli and Procedure

The stimuli and procedure were the same as in Experiment 1. Subjects discriminated the orientation of the "C" contour in the aligned, phase, and radial conditions at three different mean luminance levels in a 3 $\times$ 3 within-subjects design. The order of luminance levels was counterbalanced across subjects and the order of conditions was randomized within each luminance level. There was one block per condition and all nine blocks were tested in one experimental session lasting $\approx$90 minutes. As in Experiment 1, two interleaved staircases manipulated the duration of stimulus presentation to estimate a duration threshold for each condition. Each staircase contained 55 trials, totaling 110 trials per condition. The range of stimulus duration was restricted to 0.013-2 sec.

Psychometric functions were fit to the combined data from the two staircases using the method described in Experiment 1.

3.6.2 Results

As in Experiment 1, a threshold was deemed invalid if it was greater than the maximum duration level presented, or if the slope of the psychometric function was equal to or less than zero. Four thresholds obtained from three subjects in the radial condition were deemed invalid; at least one invalid threshold was obtained at each luminance level. The three subjects who had an invalid threshold were not included in the statistical analyses. In addition, four estimated thresholds in the aligned condition – 3 and 1 in the lowest and highest luminance conditions, respectively – were lower than the minimum value presented (1 frame). As in Experiment 1, these thresholds were set to 1 frame, which was the shortest possible duration that could be displayed on our apparatus. Note that this procedure results in an overestimate of threshold in the aligned condition.

The means and individual data points of all valid duration thresholds, including those from the three subjects not included in the statistical analyses, are shown in Figure 3.6 for each mean luminance level. Data in Figure 3.6 suggest that performance was unaffected by large changes in retinal illuminance. A within-subjects ANOVA on log-transformed duration thresholds supported this observation: there was a significant main effect of Condition ($F(2, 6) = 43.2$, $p = 0.007, \hat{\epsilon} = 0.77$), but the main effect of Luminance ($F(2, 6) = 1.66$, $p = 0.28$, $\hat{\epsilon} = 0.51$) and the Luminance × Condition interaction ($F(4, 12) = 1.30$, $p = 0.34$, $\hat{\epsilon} = 0.38$) were not significant.

3.6.3 Discussion

This experiment revealed that decreasing the mean luminance of the stimulus by a factor of ten did not increase younger subjects' duration thresholds in any condition. This result suggests that a decrease in retinal illuminance alone cannot be responsible for the increased duration thresholds observed in older subjects in Experiment 1.

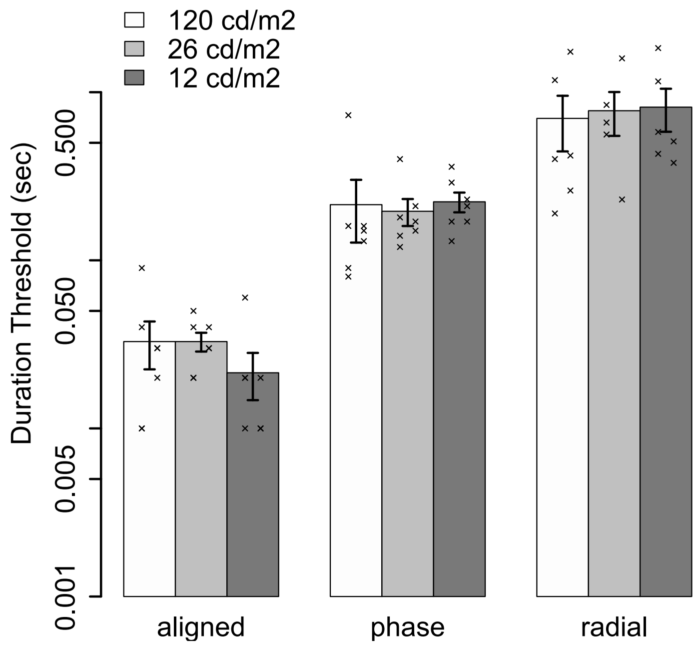


Figure 3.6: Results of the retinal illuminance control experiment. All valid duration thresholds and their means are shown for each condition at three mean luminance levels (120, 26, and 12 cd/m^2). Error bars are ± SEM.

3.7 Experiments 4a and 4b: Effect of Duration on Processing of Individual Elements.

To reduce the effects of age differences in contrast sensitivity (e.g. Owsley, Sekuler, and Siemsen, 1983), Experiments 1 and 2 used Gabor elements set to 60% contrast, a value that is much higher than previously-reported contrast detection thresholds. However, studies of the effects of aging on contrast sensitivity typically have used stimulus durations that are significantly longer than the ones used here. Hence, it is possible that age differences in contrast sensitivity for very brief stimuli may have contributed to age differences in contour detection and discrimination. Results presented by Zhang and Sturr (1995), who showed that age differences in contrast sensitivity for 0.5 c/deg gratings are invariant across stimulus durations ranging from 10 to 1000 ms, are inconsistent with this idea. Nevertheless, our experiment used a considerably higher spatial frequency than the one used by Zhang and Sturr, and therefore it remains possible that age differences in contrast sensitivity contributed to age differences in contour detection and discrimination. Experiment 4a examines this idea by measuring contrast detection thresholds for 3.5

Table 3.2: Mean ± 1 SD age, near and far logMAR visual acuity, Pelli-Robson contrast sensitivity, and Mini-Mental State Examination (MMSE).

Experiment	N (M:F)	Age	Near Acuity	Far Acuity	Pelli-Robson	MMSE
Contrast	10 (5:5)	22.9 ± 2.02	-0.14 ± 0.07	-0.14 ± 0.07	1.95 ± 0	
Detection	10 (5:5)	71.6 ± 3.53	-0.03 ± 0.09	-0.05 ± 0.07	1.91 ± 0.1	27.7 ± 1.7
Orientation	10 (5:5)	21.6 ± 2.41	-0.16 ± 0.09	-0.13 ± 0.07	1.92 ± 0.06	
Discrimination	10 (5:5)	66.4 ± 5.66	-0.03 ± 0.08	-0.03 ± 0.09	1.89 ± 0.1	29.2 ± 0.79

c/deg Gabor patterns at various stimulus durations.

Contour detection and discrimination presumably depends, in part, on an accurate representation of the orientations of the Gabor elements. Orientation discrimination performance has been shown to be similar in older and younger subjects for high contrast gratings (Betts et al., 2007; Delahunt, Hardy, and Werner, 2008; Govenlock, Taylor, Sekuler, and Bennett, 2009b). However, previous studies of the effects of aging have used stimulus durations that were much longer than the ones used in the current experiments, large differences in sensitivity to local orientations at very brief durations may have influenced the results in Experiments 1 and 2. Experiment 4b examines this idea by measuring orientation discrimination thresholds for 3.5 c/deg Gabor patterns at various stimulus durations.

3.7.1 General Methods

Subjects

A separate group of ten younger and ten older subjects participated in each experiment and were compensated for their time at a rate of $10/hr. Visual acuity and contrast sensitivity were normal or corrected-to-normal in all subjects. The older subjects did not show signs of cognitive decline as assessed by the MMSE (Folstein et al., 1975) and reported no major visual or health problems. All demographic information and visual and cognitive measures are summarized in Table 3.2.

Apparatus

The experiments were programmed in MATLAB, version R2010a, using the Psychophysics and Video Toolboxes (Brainard, 1997; Pelli, 1997) on a Macintosh G5 computer. Stimuli were displayed on a 21-inch Apple Studio Display monitor (model M6204) with a 1024 x 768 resolution (pixel size: 0.029 deg) and a 100 Hz refresh rate. The average luminance of the display was 29.05 cd/m^2 and was the only source of light in the room during the experiment. Subjects were seated at a distance of 60 cm from the computer display, which subtended a 25.2 deg $\times$ 29.8 deg visual angle at that distance. Each subjects' head position was stabilized using a chin/forehead rest. A standard Macintosh keyboard was used to record the subjects' responses.

Stimulus

The target stimulus was a sine wave grating with a spatial frequency of 3.5 c/deg. Contrast was modulated by a circular envelope (diameter = 1.07 deg), and the spatial phase of the grating was 0 deg (i.e., cosine phase) relative to the center of the circular envelope. In the detection experiment (4a), the grating's orientation was horizontal and contrast was varied across trials to estimate detection threshold. In the discrimination experiment (4b), the grating's contrast was 60% and orientation was varied around horizontal to estimate orientation discrimination threshold.

3.7.2 Experiment 4a: Contrast Detection as a Function of Duration

This experiment measured contrast detection thresholds for a small sine wave grating presented in the center of the display as a function of stimulus duration.

Methods

A two-interval forced-choice (2-IFC) procedure was used to measure detection thresholds for five stimulus durations ranging from 0.02 to 0.54 s. Each trial began with a circular (diameter = 4 pixels) black fixation point presented in the center display against a mean luminance background. The fixation point flickered three times at 16.7 Hz to attract the subjects' attention, then disappeared. After a delay of 0.5 s, the two intervals were presented, separated by a 0.5 s interstimulus interval (ISI), during which the display remained blank. The fixation point re-appeared in the middle of the screen 0.5 s after the end of the second interval and remained visible until the subject's response. The subject indicated which interval contained the target by pressing a key labeled "1" with their left index finger and a key labeled "2" with their right index finger. Subjects were told that the target was equally likely to appear in the first or second interval. Auditory feedback (i.e., low-pitch tone) was given after incorrect responses. The subsequent trial began automatically 1.5 s after the subject's response.

Typically, auditory tones are used as cues that mark the stimulus intervals in a 2-IFC visual task. We were concerned that such cues might be less effective in older subjects when the stimulus durations were very brief, and therefore the current experiment also examined the effectiveness of three different types of cues: a visual cue, an auditory cue, or a combination of visual and auditory cues. The visual cue was a 1 pixel wide ring 3.73 deg in diameter, centered in the middle of the display. The auditory cue was a clearly audible tone. The combination cue consisted of the circular ring and the tone presented simultaneously. The onset and offset of each type of cue coincided with the onset and offset of each interval.

Trials were blocked by interval cue type and the order of the cue types was randomized across subjects. Stimulus contrast was varied across trials with a three-down/one up adaptive staircase procedure, which converged on the contrast needed to achieve 79% correct responding. Five staircases – one for each stimulus duration – were randomly interleaved. A staircase ended after reaching 10 reversals or 75 trials, whichever came first, and testing ended when all five staircases were completed. Contrast thresholds for each duration were obtained by averaging the last four reversals in each staircase. Subjects were adapted to the average luminance of the display for 60 s prior to the start of the first block of trials. The total number of trials in the experiment ranged from 650 to 750. Subjects completed the experiment in one session that lasted approximately one hour.

Results and Discussion

Log-transformed thresholds were analyzed using a Age × Duration × Cue Type mixed-model analysis of variance (ANOVA). There was a main effect of Age, indicat-

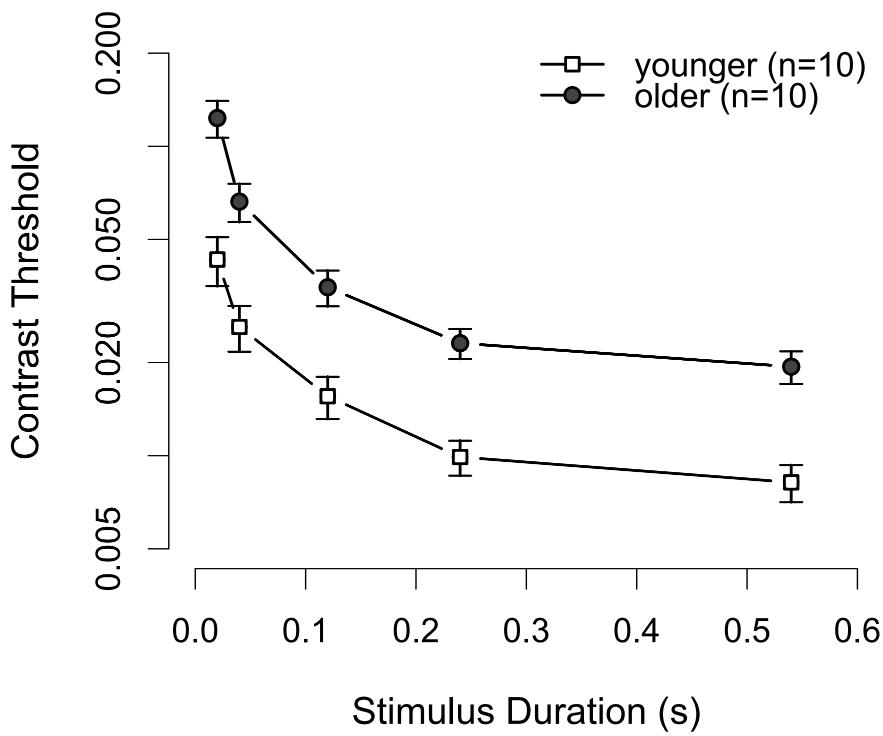


Figure 3.7: Contrast thresholds for detecting a horizontal grating in the center of the display for younger and older subjects at different levels of exposure duration. Error bars represent ± SEM.

ing that thresholds were higher in older subjects ($F(1, 18) = 32.4$, $p < 0.001$, $f = 1.25$). Thresholds also decreased as a function of increasing exposure duration, as evidenced by a significant main effect of Duration ($F(4, 72) = 2.73$, $\hat{\epsilon} = 0.26$, $p < 0.001$, $f = 1.71$). The main effect of Cue Type was not significant ($F(2, 26) = 2.43$, $\hat{\epsilon} = 0.84$, $p = 0.19$, $f = 0.08$), nor did it interact significantly with any other variable (Duration × Cue: $F(8, 144) = 0.54$, $\hat{\epsilon} = 0.26$, $p = 0.62$, $f = 0$; Age × Cue:$F(2, 36) = 1.78$, $p = 0.18$, $\hat{\epsilon} = 0.84$, $f = 0.06$; Duration×Cue×Age: $F(8, 144) = 0.98$, $\hat{\epsilon} = 0.27$, $p = 0.39$, $f = 0$). Finally, and most importantly, the Duration × Age interaction was not significant ($F(4, 72) = 2.73$, $\hat{\epsilon} = 0.26$, $p = 0.11$, $f = 0.09$).

The failure to find a significant Duration × Age interaction implies that the effect of duration on detection threshold was similar in the two age groups. This finding is illustrated in Figure 3.7, which plots threshold (averaged across cue type) as a function of stimulus duration for each age group. The threshold-vs.-duration curves are approximately parallel, which indicates that the effect of age on detection threshold is approximately independent of stimulus duration. These results are consistent with previous studies using a lower spatial frequency (Zhang and Sturr, 1995), and suggest that the temporal processes involved in a single grating pattern detection are not affected in healthy aging.

3.7.3 Experiment 4b: Orientation Discrimination as a Function of Duration

This experiment measured orientation discrimination thresholds as a function of stimulus duration.

Methods

Orientation discrimination thresholds were measured using a 2-IFC procedure that was similar to the one used in Experiment 4a. Subjects were told that two gratings would be presented on every trial, and that their task was to decide which of the two intervals contained a grating tilted counterclockwise relative to horizontal. Because stimulus contrast (60%) was well above detection threshold, the gratings themselves clearly marked the onset and offset of each interval, and therefore no additional cues were used in this experiment.

Grating orientation was varied across trials with a three-down/one-up staircase procedure. Orientation discrimination threshold was determined for gratings presented at five different exposure durations ranging 0.01–0.36 s using a separate staircase procedure for each duration. Each staircase completed upon reaching 10 reversals or 75 trials, whichever came first. Discrimination threshold was defined as the average of the last four reversals. All duration trials were randomly intermixed. An optional break was allowed after every 150 trials. Subjects completed the experiment in approximately 30 minutes.

Results and Discussion

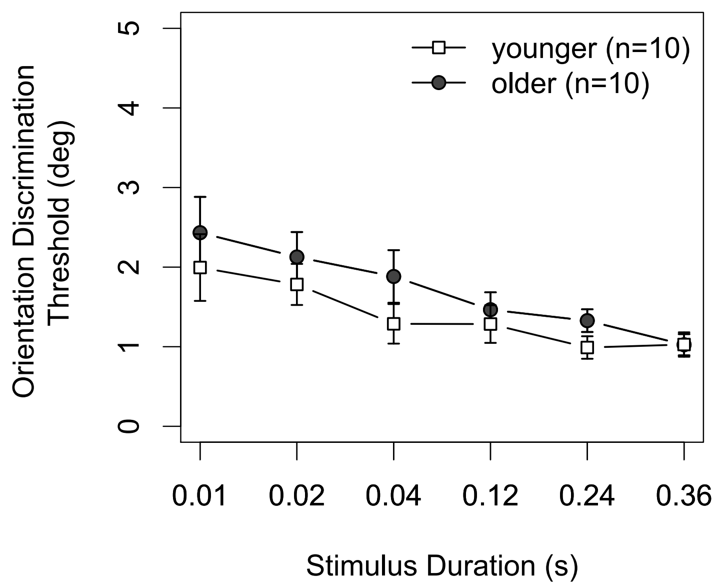


Figure 3.8: Orientation discrimination thresholds for a horizontal grating in the center of the display as a function of stimulus exposure duration. Bars represent ± SEM.

Figure 3.8 shows orientation discrimination thresholds plotted as a function of the stimulus exposure duration for both groups of subjects. In both age groups, threshold decreased approximately linearly as a function of log stimulus duration. At the shortest stimulus duration, thresholds in older subjects were (on average) approximately 0.5 deg higher than thresholds in younger subjects, but at the longest stimulus duration thresholds in the two age groups were equal.

Thresholds were analyzed using a Age × Duration mixed-model ANOVA. The main effect of Age was not significant ($F(1, 18) = 1.07$, $p = 0.32$, $f = 0.06$). There was a significant main effect of Duration ($F(5, 90) = 12.5$, $\hat{\epsilon} = 0.52$, $p < 0.001$, $f = 0.48$), indicating that threshold decreased significantly with increasing duration. Importantly, the Age × Duration interaction was not significant ($F(5, 90) = 0.63$, $\hat{\epsilon} = 0.52$, $p = 0.58$, $f = 0$), which implies that stimulus duration affected thresholds similarly in the two age groups.

Previous studies have found very small or no age differences in orientation discrimination threshold. Using a high-contrast 4 c/deg Gabor pattern displayed for 750 ms, Delahunt et al. (2008) found that orientation discrimination thresholds were ≈ 0.5 deg higher in older subjects. Even smaller age differences were found by Betts et al. (2007, Experiment 2), who reported no age difference in orientation discrimination threshold for a high-contrast 1.5 c/deg Gabor pattern displayed for 500 ms. The current findings are consistent with these previous reports and extend them to very brief stimulus durations: using a 3.5 c/deg Gabor stimulus, we found no evidence for an age difference in orientation discrimination threshold for stimulus durations ranging from 0.01 to 0.36 s. Other experiments have shown that orientation selectivity of pattern masking (Delahunt et al., 2008; Govenlock et al., 2009b) also does not differ between older and younger subjects, suggesting that aging does not alter bandwidths of orientation-selective visual mechanisms. Finally, Govenlock, Sekuler, and Bennett (2009a) found no age differences in an orientation discrimination task that required subjects to integrate orientation signals from 128 Gabors spatially distributed in an annulus (inner and outer radii = 0.5 and 3.4 deg, respectively) centered on the fixation point. The available evidence suggests, therefore, that processes that encode orientation are not altered significantly by aging. Based on these findings, it is unlikely that group differences in performance in contour discrimination and contour detection experiments stem from age-related deficits in the ability to discriminate local orientation signals.

3.8 General Discussion

Experiments 1 and 2 found that the stimulus durations required for detecting and discriminating sampled open contours embedded in a dense field of distractors were significantly longer for older than younger subjects. The effect of local orientation on contour perception was present in both groups: younger and older subjects showed better performance with contours whose Gabor orientations were co-aligned with the contour path compared to contours whose Gabor elements were oriented orthogonally to the path, a consistent finding in the literature (e.g. May and Hess, 2007; Dakin and Baruch, 2009; Field et al., 1993). Interestingly, this effect of local orientation may be slightly greater in older compared to younger subjects in the contour discrimination task. In addition, our results also revealed an effect of contrast polarity alternation on contour detection and discrimination. There was a significant drop in performance between the aligned contours, where spatial phase was fixed, and the contours in the phase condition, which had the same orientations as the aligned condition, but where the spatial phase of alternating elements differed by 180 deg. This finding replicates previous work showing that, although contour integration is possible for phase-alternating contours, performance is best when path elements all have the same phase (Hess et al., 2001; Field et al., 2000; Hess and Dakin, 1999). The drop in performance associated with phase-alternation was similar in older and younger subjects, suggesting that the phase-sensitive contour integration mechanism is preserved in older age.

What are the potential causes of the increase in processing time required for contour perception in aging? First, it is not the case that older subjects generally show higher exposure duration thresholds than younger subjects. Previous studies examining motion direction discrimination of simple gratings have found that older subjects sometimes show equivalent or even shorter duration thresholds than younger subjects (Betts, Taylor, Sekuler, and Bennett, 2005; Betts, Sekuler, and Bennett, 2009). Similarly, Habak, Wilkinson, and Wilson (2009) did not find any age-related delays in processing time in a shape discrimination task. Thus, it is unlikely that increased thresholds in the contour integration tasks result from an overall general slowing of processing speed (Salthouse, 1996). Second, results from the retinal illumination control experiment refute the possibility that differences in retinal illuminance between groups account for the observed effects of age, as younger subjects did not show increased duration thresholds when display luminance was decreased by as much as 90%. Third, age-related changes in contrast sensitivity also are an unlikely cause. Experiment 4a revealed that decreasing the stimulus duration to 0.02 s does not differentially affect older and younger subjects' contrast thresholds for detecting a small grating. Moreover, the contrast of the Gabor elements in the contour detection and discrimination experiments was five times higher than the average contrast threshold of the older group at an exposure duration of 0.02 s. Thus, it is unlikely that the increase in duration thresholds is due to age-related changes in sensitivity to the luminance profiles of the Gabor elements. In addition, Hess et al. (2001) previously showed that local element contrast does not affect the dynamics of contour integration. Thus, even if retinal contrast changed with age, the processing time of contours would not be expected to suffer.

Finally, it also is unlikely that contour detection and discrimination were affected by age differences in the ability to encode the orientation of the Gabor elements. Experiment 4b failed to find evidence of age-related changes in orientation discrimination for a range of stimulus exposure durations, including very brief presentations. These results are consistent with previous experiments(Betts et al., 2007; Delahunt et al., 2008; Govenlock et al., 2009b,a) that suggest that processing of local orientation information is not affected significantly by aging.

Thus, our results suggest that age-related increase in duration thresholds in the contour detection and discrimination tasks are not caused by problems processing individual elements, and instead indicate a deficit at the stage where elements are grouped into contours. Del Viva and Agostini (2007) found that older subjects were less sensitive at detecting circular contours comprising aligned Gabors that were embedded among randomly oriented distractor Gabors. The current experiments show that older subjects are also impaired at detecting and discriminating non-closed contours, and also contours comprised of orthogonally oriented elements.

Dakin and Baruch (2009) demonstrated that the context in which a contour appears influences its detection. In other words, performance in contour integration tasks reflects both the ability to group elements along a contour and the ability to suppress the influence of the surrounding elements. Thus, it is possible that the age-related declines in our task are caused by an inability to suppress the cluttering elements, as opposed to problems with grouping contour elements together. This hypothesis is plausible given that suppression likely involves inhibitory processes (Adini, Sagi, and Tsodyks, 1997; Gilbert, Das, Ito, Kapadia, and Westheimer, 1996; Kapadia, Ito, Gilbert, and Westheimer, 1995), whose functioning has been shown to degrade in senescent primates and cats (Leventhal, Wang, Pu, Zhou, and Ma, 2003; Hua, Kao, Sun, Li, and Zhou, 2008). Reduced surround-suppression in older subjects has been demonstrated in a study that used a motion direction discrimination task (Betts et al., 2005, 2009). On the other hand, Karas and McKendrick (2009) found the opposite effect in a study that used a static center-surround stimulus and a contrast discrimination task: Older subjects showed higher, not lower, surround suppression in this task. Thus, it is not clear how aging may affect the ability to suppress the surround in our task, as the influence of the surround greatly depends on the nature of the stimulus and task.

The current experiments were not designed to determine if deficits in contour discrimination are due to an inability to integrate orientation information across elements on the contour versus poorer suppression of the surrounding elements. The existing evidence is also equivocal. On the one hand, older subjects show evidence of impaired contour integration in a task where the contour elements are presented without clutter (Roudaia et al., 2008). Also, the addition of cluttering elements appears to affect contour shape discrimination ability of older and younger subjects equally (McKendrick et al., 2010). On the other hand, Del Viva and Agostini (2007) find that older subjects can tolerate less distractors than younger subjects, especially for contours with short inter-element distances. If the deficit were only due to integration ability, then older subjects would be expected to show greater declines with large inter-element distances, which are more difficult to integrate. Also, Govenlock et al. (2009a) found no age difference in a orientation discrimination task that required subjects to pool orientation signals across space, indicating that older subjects are able to integrate information across space. In sum, the contribution of these two mechanisms to the age-related declines in contour perception remains to be determined.

Habak et al. (2009) investigated shape discrimination using continuous contours defined by a first-order luminance modulation and also by a second-order texture pattern. Interestingly, shape discrimination thresholds did now show any declines with aging for luminance defined contours, even at very brief stimulus exposure durations. However, when the contours were defined by a second-order texture pattern, older subjects consistently showed poorer shape discrimination thresholds than younger subjects. The authors suggested that this was caused by impoverished contour information arriving from earlier stages. In this case, a second stage filter was required to detect the contour. Thus, it appears that mechanisms that group edge information into contours, or extract contour boundaries from second-order structure, are affected by aging. Yet, once the contour has been determined, the perception of its shape can be acquired successfully. McKendrick et al. (2010) examined shape discrimination using sampled contours comprising aligned Gabor elements. Again, older subjects performed as well as younger subjects when required to discriminate whether the contour was a circle or an ellipse. Although contour integration and shape perception are both so-called “intermediate stage” processes, the difference in their susceptibility to the effects of aging is an intriguing phenomenon.

In sum, the current experiment showed that duration thresholds of detecting and discriminating contours in a cluttered background are increased in older age. Age-related changes in sensitivity to local elements in the display cannot explain the obtained pattern of results, and thus our findings point to impairments in the cortical mechanisms responsible for contour integration.

3.8.1 Acknowledgments

A special thanks to Donna Waxman for testing all the subjects, and to all the subjects for their dedicated participation. This work was supported by the Canada Institute of Health Research Grant and Canada Research Chair Program to A.B.S. and P.J.B., and the Alexander Graham Bell Canada Graduate Scholarship to E.R.

Bibliography

Adini, Y., Sagi, D., Tsodyks, M., 1997. Excitatory-inhibitory network in the visual cortex: psychophysical evidence. Proceedings of the National Academy of Sciences of the United States of America 94 (19), 10426–31.

Altmann, C. F., Bülthoff, H. H., Kourtzi, Z., 2003. Perceptual organization of local elements into global shapes in the human visual cortex. Current Biology 13 (4), 342–349.

Angelucci, A., Levitt, J. B., Walton, E. J. S., Hupe, J.-M., Bullier, J., Lund, J. S., 2002. Circuits for local and global signal integration in primary visual cortex. The Journal of Neuroscience 22 (19), 8633–8646.

Barlow, H. B., 1958. Temporal and spatial summation in human vision at different background intensities. Journal of Physiology 141 (2), 337–350.

Betts, L. R., Sekuler, A. B., Bennett, P. J., 2007. The effects of aging on orientation discrimination. Vision Research 47 (13), 1769–80.

Betts, L. R., Sekuler, A. B., Bennett, P. J., 2009. Spatial characteristics of center-surround antagonism in younger and older adults. Journal of Vision 9 (1), 25.1–15.

Betts, L. R., Taylor, C. P., Sekuler, A. B., Bennett, P. J., 2005. Aging reduces center-surround antagonism in visual motion processing. Neuron 45 (3), 361–366.

Bex, P. J., Simmers, A. J., Dakin, S. C., 2001. Snakes and ladders: the role of temporal modulation in visual contour integration. Vision Research 41 (27), 3775–3782.

Bosking, W. H., Zhang, Y., Schofield, B., Fitzpatrick, D., 1997. Orientation selectivity and the arrangement of horizontal connections in tree shrew striate cortex. The Journal of Neuroscience 17 (6), 2112–2127.

Brainard, D. H., 1997. The psychophysics toolbox. Spatial Vision 10 (4), 433–436.

Crum, R. M., Anthony, J. C., Bassett, S. S., Folstein, M. F., 1993. Population-based norms for the mini-mental-state-examination by age and educational-level. JAMA – J Am Med Assoc 269 (18), 2386–2391.

Dakin, S. C., Baruch, N. J., 2009. Context influences contour integration. Journal of Vision 9 (2), 13.1–13.

Del Viva, M. M., Agostini, R., 2007. Visual spatial integration in the elderly. Investigative Ophthalmology & Visual Science 48 (6), 2940–2946.

Delahunt, P. B., Hardy, J. L., Werner, J. S., 2008. The effect of senescence on orientation discrimination and mechanism tuning. Journal of Vision 8 (3), 1–9.

Elliott, D. B., Sanderson, K., Conkey, A., 1990. The reliability of the pelli-robson contrast sensitivity chart. Ophthalmic & Physiological Optics 10 (1), 21–24.

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 (2), 173–193.

Field, D. J., Hayes, A., Hess, R. F., 2000. The roles of polarity and symmetry in the perceptual grouping of contour fragments. Spatial Vision 13 (1), 51–66.

Folstein, M. F., Folstein, S. E., McHugh, P. R., 1975. ”Mini-mental state”. a practical method for grading the cognitive state of patients for the clinician. Journal of Psychiatric Research 12 (3), 189–198.

Geisler, W. S., Perry, J. S., 2009. Contour statistics in natural images: grouping across occlusions. Visual Neuroscience 26 (1), 109–21.

Geisler, W. S., Perry, J. S., Super, B. J., Gallogly, D. P., 2001. Edge co-occurrence in natural images predicts contour grouping performance. Vision Research 41 (6), 711–24.

Gilbert, C. D., Das, A., Ito, M., Kapadia, M., Westheimer, G., 1996. Spatial integration and cortical dynamics. Proceedings of the National Academy of Sciences of the United States of America 93 (2), 615–22.

Gilbert, C. D., Wiesel, T. N., 1989. Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. The Journal of Neuroscience 9 (7), 2432–2442.

Govenlock, S., Sekuler, A., Bennett, P., 2009a. The effect of aging on the spatial pooling of local orientation signals. Journal of Vision 9 (8), 1069–1069.

Govenlock, S. W., Taylor, C. P., Sekuler, A. B., Bennett, P. J., 2009b. The effect of aging on the orientational selectivity of the human visual system. Vision Research 49 (1), 164–172.

Habak, C., Wilkinson, F., Wilson, H. R., 2009. Preservation of shape discrimination in aging. Journal of Vision 9 (12), 18.1–8.

Hess, R. F., Beaudot, W. H., Mullen, K. T., 2001. Dynamics of contour integration. Vision Research 41 (8), 1023–1037.

Hess, R. F., Dakin, S. C., 1997. Absence of contour linking in peripheral vision. Nature 390 (6660), 602–604.

Hess, R. F., Dakin, S. C., 1999. Contour integration in the peripheral field. Vision Research 39 (5), 947–59.

Hess, R. F., Field, D., 1999. Integration of contours: new insights. Trends in Cognitive Science 3 (12), 480–486.

Hess, R. F., Hayes, A., Field, D. J., 2003. Contour integration and cortical processing. Journal of Physiology – Paris 97 (2-3), 105–119.

Hua, T., Kao, C., Sun, Q., Li, X., Zhou, Y., 2008. Decreased proportion of gaba neurons accompanies age-related degradation of neuronal function in cat striate cortex. Brain Research Bulletin 75 (1), 119–125.

Kapadia, M. K., Ito, M., Gilbert, C. D., Westheimer, G., 1995. Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in v1 of alert monkeys. Neuron 15 (4), 843–56.

Karas, R., McKendrick, A. M., 2009. Aging alters surround modulation of perceived contrast. Journal of Vision 9 (5), 11.1–9.

Kourtzi, Z., Tolias, A. S., Altmann, C. F., Augath, M., Logothetis, N. K., 2003. Integration of local features into global shapes: monkey and human fmri studies. Neuron 37 (2), 333–46.

Kurylo, D. D., 2006. Effects of aging on perceptual organization: efficacy of stimulus features. Experimental Aging Research 32 (2), 137–152.

Ledgeway, T., Hess, R. F., Geisler, W. S., 2005. Grouping local orientation and direction signals to extract spatial contours: empirical tests of "association field" models of contour integration. Vision Research 45 (19), 2511–2522.

Leventhal, A. G., Wang, Y. C., Pu, M. L., Zhou, Y. F., Ma, Y. Y., 2003. GABA and its agonists improved visual cortical function in senescent monkeys. Science 300 (5620), 812–815.

Levitt, H., 1971. Transformed up-down methods in psychoacoustics. The Journal of the Acoustical Society of America 49 (2), Suppl 2:467+.

Malach, R., Amir, Y., Harel, M., Grinvald, A., 1993. Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primate striate cortex. Proceedings of the National Academy of Sciences of the United States of America 90 (22), 10469–10473.

Mäntyjärvi, M., Laitinen, T., 2001. Normal values for the Pelli-Robson contrast sensitivity test. Journal of Cataract and Refractive Surgery 27 (2), 261–266.

Maxwell, S. E., Delaney, H. D., 2004. Designing experiments and analyzing data: a model comparison perspective, 2nd Edition. Lawrence Erlbaum Associates, Mahwah, N.J.

May, K. A., Hess, R. F., 2007. Ladder contours are undetectable in the periphery: a crowding effect? Journal of Vision 7 (13), 9.1–15.

McKendrick, A. M., Weymouth, A. E., Battista, J., 2010. The effect of normal aging on closed contour shape discrimination. Journal of Vision 10 (2).

Owsley, C., Sekuler, R., Siemsen, D., 1983. Contrast sensitivity throughout adulthood. Vision Research 23 (7), 689–699.

Pelli, D., Robson, J., Wilkins, A., 1988. The design of a new chart for measuring contrast sensitivity. Clinical Vision Science 2 (3), 187–199.

Pelli, D. G., 1997. The videotoolbox software for visual psychophysics: transforming numbers into movies. Spatial Vision 10 (4), 437–442.

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (http://www.R-project.org).

Roudaia, E., Bennett, P. J., Sekuler, A. B., 2008. The effect of aging on contour integration. Vision Research 48 (28), 2767–2774.

Rovamo, J., Raninen, A., 1984. Critical flicker frequency and m-scaling of stimulus size and retinal illuminance. Vision Research 24 (10), 1127–31.

Saarinen, J., Levi, D. M., 2001. Integration of local features into a global shape. Vision Research 41 (14), 1785–1790.

Salthouse, T. A., 1996. The processing-speed theory of adult age differences in cognition. Psychological Review 103 (3), 403–28.

Salthouse, T. A., Prill, K. A., 1988. Effects of aging on perceptual closure. The American Journal of Psychology 101 (2), 217–238.

Schlauch, R. S., Rose, R. M., 1990. Two-, three-, and four-interval forced-choice staircase procedures: estimator bias and efficiency. Journal of the Acoustical Society of America 88 (2), 732–40.

van Nes, F. L., Koenderink, J. J., Nas, H., Bouman, M. A., 1967. Spatiotemporal modulation transfer in the human eye. Journal of the Optical Society of America 57 (9), 1082–8.

Weale, R. A., 1963. The Aging Eye. Lewis, London.

Wichmann, F. A., Hill, N. J., 2001. The psychometric function: I. fitting, sampling, and goodness of fit. Perception & Psychophysics 63 (8), 1293–1313.

Winn, B., Whitaker, D., Elliott, D. B., Phillips, N. J., 1994. Factors affecting light-adapted pupil size in normal human subjects. Investigative Ophthalmology & Visual Science 35 (3), 1132–1137.

Zhang, L., Sturr, J. F., 1995. Aging, background luminance, and threshold-duration functions for detection of low spatial frequency sinusoidal gratings. Optometry and Vision Science 72 (3), 198–204.

Chapter 4

Contour integration and aging: the effects of contour and distracter inter-element spacing, orientation alignment, and stimulus duration

Contour integration mechanisms appear to decline with healthy aging, however, the reasons for these changes are poorly understood. In three experiments, we examined the effects of aging on contour discrimination as a function of contour and distracter inter-element spacing, local orientation, and stimulus duration. Younger and older subjects were required to report the global orientation of spiral-shaped contours embedded in a uniform field of distracters. In Experiment 1, contour element spacing and orientation alignment were manipulated. Older subjects showed lower accuracy than younger subjects, but the effects of contour spacing and orientation jitter were not affected by aging. Experiment 2 manipulated the stimulus duration and revealed that older subjects require longer stimulus duration to discriminate less salient contours than younger subjects. Experiment 3 manipulated the relative spacing of contour and distracter elements. Results revealed that decreasing distracter spacing while maintaining contour spacing constant greatly reduced contour discrimination accuracy. However, this effect was significantly more pronounced in older than in younger subjects. Together, these results indicate that aging does not affect the sensitivity of contour integration mechanisms to proximity or collinearity of contour elements, however, contour integration in older adults is slower and less resistant to high contour-distracter relative spacing.

4.1 Introduction

Extracting contours is an important step in the process of translating incoming visual information into a meaningful percept. Since visual scenes often contain multiple objects that overlap and partially occlude each other, grouping different features into contours is not a trivial task, as features belonging to a single contour need to be grouped with one another and not grouped with other objects, or with elements of the background. Contours in natural scenes contain important statistical regularities (Elder and Goldberg, 2002; Geisler, Perry, Super, and Gallogly, 2001; Sigman, Cecchi, Gilbert, and Magnasco, 2001) and human observers appear to use the statistical properties of contours in natural images to detect contours (Field, Hayes, and Hess, 1993; Hess, Hayes, and Field, 2003; Geisler and Perry, 2009).

The rules governing contour grouping have been studied successfully using variations on the path paradigm, introduced by Field et al. (1993), in which subjects detect a contour whose path is defined by a group of discrete, oriented elements (e.g., Gabors) that are embedded within a field of similar distracters. Several studies have shown that contour saliency strongly depends on the alignment of local element orientations along the contour path and, to a lesser extent, on the separation of contour elements (Field et al., 1993; Saarinen and Levi, 2001; Kovács and Julesz, 1993). Other factors known to influence contour detection are contour curvature, length, eccentricity, spatial scale and phase alignment of contour elements (Beaudot and Mullen, 2001, 2003; Hess and Dakin, 1997; Kuai and Yu, 2006; Dakin and Hess, 1998; Ledgeway, Hess, and Geisler, 2005; Hess et al., 2003), as well as characteristics of the surrounding context, closure, and contour object identity (Braun, 1999; Kovács and Julesz, 1993; Dakin and Baruch, 2009; Mathes and Fahle, 2007; Nygaard, Sassi, and Wagemans, 2011). The most likely neural substrate for contour integration is the network of intrinsic horizontal connections in the primary visual cortex that link neurons with similar orientation preference and with spatially non-overlapping receptive fields (Gilbert and Wiesel, 1989; Malach, Amir, Harel, and Grinvald, 1993; Rockland and Lund, 1983; Amir, Harel, and Malach, 1993; Stettler, Das, Bennett, and Gilbert, 2002). This hypothesis is supported by the response facilitation of V1 neurons to oriented lines presented in the context of a contour (Kapadia, Ito, Gilbert, and Westheimer, 1995; Li, Piëch, and Gilbert, 2006), and by computational models that successfully detect contours in natural images employing only bottom-up processes that rely on the architecture and computation of the primary visual neurons (Li, 1998; Yen and Finkel, 1998). Nevertheless, contour selective responses in V1 neurons in primates have been shown to be affected by learning and spatial attention, and are completely abolished with anesthesia (Li, Piëch, and Gilbert, 2008; Gilbert, Ito, Kapadia, and Westheimer, 2000), indicating that contour selective responses are also modulated by top-down influences. Several behavioural and neuroimaging studies in humans have highlighted the role of top-down processing, as well as the involvement of both early and extrastriate visual areas in contour integration (Altmann, Bülthoff, and Kourtzi, 2003; Kourtzi, Tolias, Altmann, Augath, and Logothetis, 2003; Kourtzi and Huberle, 2005; Ciaramelli, Leo, Del Viva, Burr, and Ladavas, 2007; Verghese, 2009; Tanskanen, Saarinen, Parkkonen, and Hari, 2008).

Growing evidence suggests that contour integration declines with healthy aging (Del Viva and Agostini, 2007; Roudaia, Bennett, and Sekuler, 2008; Roudaia, Farber, Bennett, and Sekuler, 2011; McKendrick, Weymouth, and Battista, 2010; Casco, Robol, Barollo, and Cansino, 2011). Del Viva and Agostini (2007) first showed that older subjects were able to tolerate fewer distracters than younger subjects when detecting closed circular contours embedded among distracters. Roudaia et al. (2011) found that older subjects required longer stimulus durations than younger subjects to successfully discriminate the location of the gap in a "C"-shaped contour embedded among distracters. In another study, closed circular contours were used to examine the effect of aging on shape discrimination (McKendrick et al., 2010). Contrary to the previous contour detection and discrimination tasks, the ability to discriminate the closed contour shapes was only slightly (and not significantly) worse in older subjects compared to younger subjects. Moreover, the addition of background elements or the addition of orientation jitter to contour elements did not have a differential effect on both age-groups. On the other hand, older subjects required more contour elements (or smaller contour spacing) than younger subjects to make the contour shape discrimination, suggesting that older subjects had greater difficulty extracting the shape of contours containing large inter-element spacings. In a similar study, younger and older subjects were asked to detect the radial displacement of a single Gabor belonging to a circular contour (Casco et al., 2011): When the contour was composed of aligned Gabors and presented against a blank background, the minimum radial displacement that could be detected reliably was the same for younger and older subjects. However, older subjects required a larger displacement than younger subjects when the Gabors composing the contour were alternating between aligned and orthogonal orientations, or when the contour was embedded among randomly-oriented distracter Gabors.

The reasons for the observed age-related changes in contour integration are not well understood. Previous research has demonstrated that performance in contour integration tasks requires the integration of contour elements, as well as the suppression of the distracters in the background (Dakin and Baruch, 2009; Machilsen, Novitskiy, Vancleef, and Wagemans, 2011; Sassi, Vancleef, Machilsen, Panis, and Wagemans, 2010; Schumacher, Quinn, and Olman, 2011). Casco et al. (2011) argued that the age-related deficit in contour integration is caused by a decreased ability to suppress distracters with irrelevant orientations, as opposed to an inability to integrate contour elements. Although this hypothesis may be consistent with the pattern of results obtained in their task, it is not clear to what extent this conclusion generalizes to other stimuli and tasks. For example, Roudaia et al. (2008) examined the perception of contours presented against a blank background (i.e., in the absence of distracters) and found that older subjects failed to show a benefit for discriminating contours composed of aligned Gabors, compared to orthogonally-oriented Gabors, or contours containing mixed orientations, a result which cannot be explained by deficits in suppressive mechanisms alone.

In the following studies, we further characterized the effects of aging on contour integration by examining contour discrimination performance for a range of stimuli varying in contour inter-element spacing, distracter inter-element spacing, as well as for contours with different levels of local orientation alignment. Contour element spacing has been shown to influence contour detection (Kovács and Julesz, 1993; Li and Gilbert, 2002; Beaudot and Mullen, 2003; Watt, Ledgeway, and Dakin, 2008) and it has been suggested that contour integration mechanisms operate over a limited spatial range that scales with the spatial frequency of the contour elements (Beaudot and Mullen, 2003). In Experiment 1, we examined whether the spatial range of contour integration may be reduced with aging by measuring contour discrimination performance for contours with varying inter-element spacing. Moreover, we examined the sensitivity to contour element collinearity as a function of contour spacing by disrupting the alignment of contour element orientations with orientation jitter. Knowing that older subjects require longer stimulus durations than younger subjects to integrate contours (Roudaia et al., 2011), any effects of aging on performance in Experiment 1 were expected to depend on stimulus duration. To examine this relationship, a subset of representative conditions from Experiment 1 were repeated in Experiment 2 with a range of stimulus durations. In addition to contour element spacing, contour detection is also known to be influenced by the relative spacing of contour and distracter elements (Kovács, Kozma, Fehér, and Benedek, 1999; Li and Gilbert, 2002). In Experiment 3, we examined the effect of relative contour and distracter spacing on contour discrimination in older and younger subjects. Finally, we also measured contour discrimination against a background of iso-oriented Gabors, to examine whether aging affects the ability to segregate contours from a relatively uniform background.

In all 3 experiments, stimuli consisted of spiral shaped contours sampled with Gabor elements and embedded in a uniform field of distracter Gabors. Subjects were required to report the global orientation of the spiral contour on every trial in a four alternative forced-choice task. Spiral contours were chosen because i) we wanted to avoid closed or circular contours, due to possible additional detection benefits for closure and circularity (Kovács and Julesz, 1993; Dumoulin and Hess, 2007), ii) we wanted to use smooth contours that would be comparable to previous studies that have used open "C" shaped contours (Roudaia et al., 2008, 2011) and closed circular and ellipsoid shapes (Del Viva and Agostini, 2007; Casco et al., 2011; Hadad, 2012), iii) using a familiar spiral shape allowed us to devise an easily-understood task that assessed global contour discrimination, as opposed to contour detection; and iv) drawing spiral contours, as opposed to straight contours, allowed for a greater range of contour spacings.

4.2 Experiment 1: Effects of contour element spacing and local orientation alignment

This experiment examined the effects of contour element separation and local orientation alignment on contour integration in younger and older subjects. The separation between adjacent elements comprising the contour was varied across blocks, while the relative contour and distracter separation was kept constant. Within blocks, alignment of contour element orientations was manipulated by the addition of varying amounts of orientation jitter.

4.2.1 Methods

Subjects

Seventeen younger ($M = 25$ years; range: $22 - 33$ y.) and 16 older ($M = 66$ years; range: $60 - 82$ y.) subjects participated in this study and were compensated at a rate of $10/hour. Near and far visual acuities were measured in all subjects using the SLOAN

Table 4.1: Mean ± 1 SD age, near and far logMAR acuity, Pelli-Robson contrast sensitivity, and Mini-Mental State Examination (MMSE).

N (M:F)	Age	Near Acuity	Far Acuity	Pelli-Robson	MMSE
17 (11:6)	24.9 ± 3.20	-0.15 ± 0.08	-0.11 ± 0.09	1.95 ± 0.05	
16 (9:7)	65.9 ± 6.37	0.03 ± 0.11	-0.07 ± 0.10	1.92 ± 0.06	28.9 ± 1.06

Two Sided ETDRS Near Point Test and the 4 Meter 2000 Series Revised ETDRS charts (Precision Vision, LaSalle, Illinois, USA). Contrast sensitivity was estimated using the Pelli-Robson Contrast Sensitivity Test (Pelli, Robson, and Wilkins, 1988). Subjects wore their habitual optical correction during the vision testing and during the experiment. All subjects had normal or corrected-to-normal near and far Snellen visual acuity (range: $-0.29 - 0.16$ logMAR), although, on average, older subjects showed poorer acuity than younger subjects. All subjects showed normal contrast sensitivity for their age group (Elliott, Sanderson, and Conkey, 1990; Mäntyjärvi and Laitinen, 2001). The Mini-Mental State Examination assessment (Folstein, Folstein, and McHugh, 1975) was used to screen for cognitive impairment among older subjects and all scored above the normal cut-off score of 25/MM30. All subjects were free of visual pathology such as cataracts, glaucoma, and retinopathy, as assessed by a self-report questionnaire. One subject underwent successful bilateral cataract surgery four years prior to the experiment. Table 4.1 summarizes the relevant demographic information for the two groups.

Apparatus

The experiment was programmed using the Psychophysics and Video Toolboxes (v. 3; Brainard, 1997; Pelli, 1997) in the Matlab environment (v. 7.5) driven by a Macintosh G5 computer. The stimuli were presented on a 20-inch (51 cm) 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 an average luminance of 52 cd/m^2. Subjects viewed the display binocularly through natural pupils from a viewing distance of 114 cm. Viewing position was stabilized with a chin/forehead rest.

Stimuli

The stimulus consisted of a spiral-shaped contour sampled with Gabor micropatterns and embedded in a square region (9.5×9.5 deg) of randomly oriented distracter Gabors (Figure 4.1). Gabor micropatterns were created by multiplying a 3.33 cycles/deg sine wave grating ($\lambda = 0.30$ deg, 20 pixels/cycle) of 90% contrast by a circular Gaussian envelope with a standard deviation (σ) of 0.11 deg (≈ 1.4 visible cycles). All Gabors were in positive sine phase with respect to the center of the Gaussian window. The shape of the contour was defined by the formula for a logarithmic spiral,

$$r = ae^{b(t+t_j)} \tag{4.1}$$

where $a = 1.18$ deg, $b = 0.20$, and $1.25 < t < 3$. The position of the first contour Gabor relative to the beginning of the spiral path was jittered with t_j, a uniform random variable ranging from -0.1 to 0.1. Subsequent Gabors were placed at the appropriate locations along the spiral path such that the inter-element distance between all elements remained constant. The long axis of the spiral spanned ≈ 6.9 deg.

The center of the spiral was placed in the center of the 9.5 deg square and then displaced horizontally and vertically by random amounts selected from a Normal distribution with $\sigma = 1.5$ deg. An iterative procedure was used to fill the remaining portion of the square region with distracter Gabors. Gabors were placed in random locations subject to the contstraint that all neighbouring Gabors were not closer than a pre-determined minimum inter-element distance and the procedure continued until no more elements could be placed (Dakin and Baruch, 2009). On half the trials, the pattern was reflected along the vertical axis to create clockwise and counterclockwise spirals. Finally, the pattern was rotated by 90, 180, or 270 deg to create spirals of four different global orientations (see Figure 4.1).

The inter-element distance between neighbouring Gabor elements was varied across blocks. Inter-element distance were set to be 2, 4, 6 or 8 times the Gabor wavelength (λ), corresponding to 0.6, 1.2, 1.8, or 2.4 deg. Setting the minimum distance between distracter elements equal to the contour inter-element spacing created, by definition, a background with the smallest number of distracters needed to avoid any density or spacing cues as to the location of the contour. The approximate ratios of the number of contour and distractor Gabors for the 2λ, 4λ, 6λ, and 8λ inter-element spacings were 26:240, 13:60, 9:25, and 7:14 Gabors respectively. Due to the random nature of the iterative process, the number of background elements varied slightly from trial to trial.

For each inter-element spacing condition, contour discrimination performance was measured for different levels of contour element collinearity. Collinearity was manipulated by adding varying amounts of orientation jitter to the contour element orientations. Collinear (or aligned) contours were created by setting the orientation of each element to equal the tangent to the contour path at that position. An independent orientation jitter angle was then added to each element by picking random numbers from a uniform distribution spanning ranges of $\pm 15°$, $\pm 30°$, $\pm 45°$, or $\pm 60°$.

Procedure

The McMaster University Research Ethics Board approved the experimental protocol. Written informed consent was obtained from all subjects prior to their participation in the experiment.

A four-alternative forced-choice (4-AFC) procedure was used to measure contour discrimination accuracy. A stimulus containing a spiral contour was presented on every trial and subjects were asked to report whether the tail of the spiral was located in the top-center, bottom-center, right-middle, left-middle locations in the display. At the beginning of the experiment, each subject was shown examples of stimuli where the spiral contour was made clearly visible by reducing the contrast of background elements. After adapting to the luminance of the display for 60 s, subjects completed five practice trials. The experimenter ensured that all subjects understood the task before proceeding to the experimental trials.

Each trial began with a black fixation point (diameter = 0.12 deg) presented in the center of the blank screen of mean luminance. Subjects were instructed to fixate the fixation point, which remained in the center throughout the trial. The fixation point flickered a rate of 10 Hz for 0.3 s at the beginning of each trial, after which the stimulus array was presented for a 1 s, followed by a blank screen for 0.5 s. The fixation point was then displayed until the subject's response. The global orientation of the spiral was randomized across trials and the subjects reported the location of the end of the spiral by pressing either the up, down, left, or right arrow key. Auditory feedback was given on every trial with a high pitch tone indicating a correct response and a low pitch tone indicating an error. The subsequent trial began after a 1.5 s inter-trial interval. The four inter-element distance conditions were tested in separate blocks in randomized order. Each block consisted of 25 trials at orientation jitter levels of $0°$, $\pm 15°$, $\pm 30°$, $\pm 45°$, and

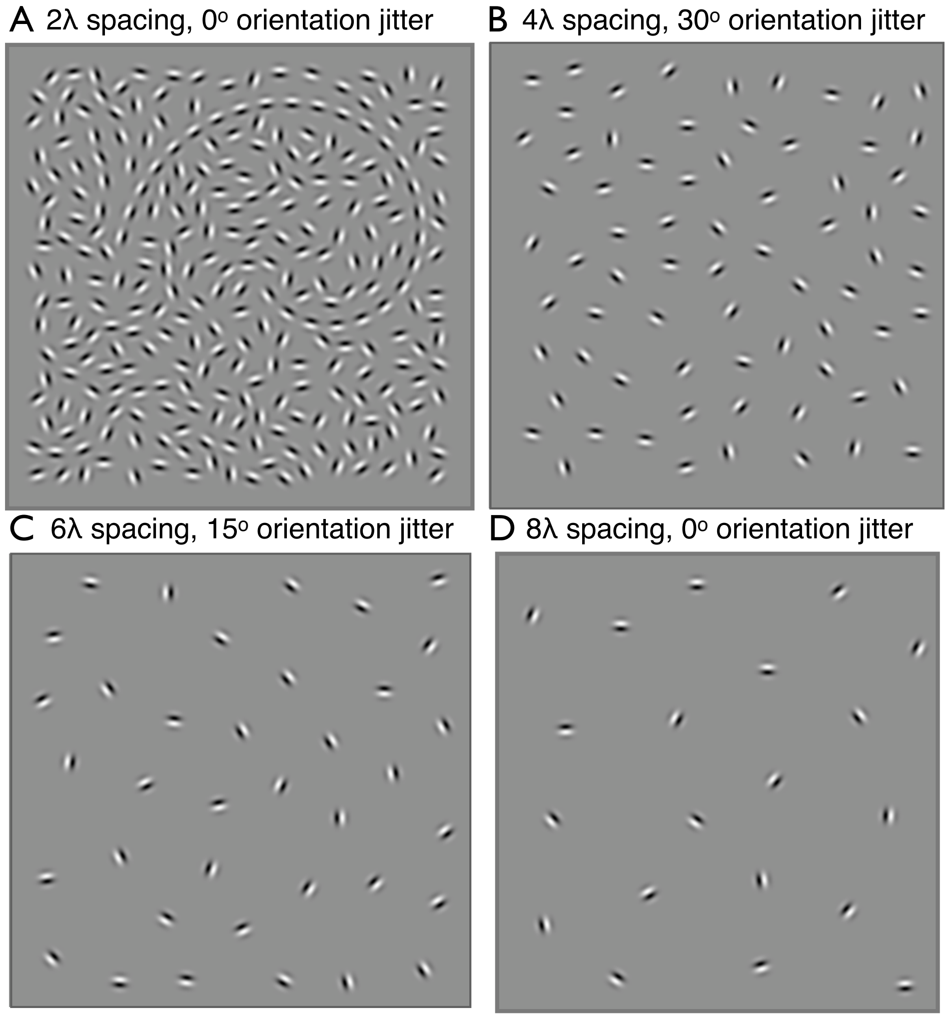


Figure 4.1: Stimuli were spiral-shaped contours sampled with Gabors ($\lambda = 0.30\,\text{deg}$, $\sigma = 0.11\,\text{deg}$) and embedded in a field of randomly oriented distracter Gabors. The shape and size of the spiral, which could be clockwise or counter-clockwise, remained constant throughout the experiment, but its global orientation and position varied randomly across trials. Subjects reported the global orientation of the spiral by indicating the location of its tail. The minimum inter-element distance varied across blocks and ranged from 0.6 deg to 2.4 deg, or 2λ - 8λ. Within each block, contour element orientations were jittered by the addition of local orientation jitter ranging from 0° to 60°. Four stimulus examples are shown: A) 2λ distance, 0° jitter, tail is on the left; B) 4λ distance, 30° jitter, tail is on the right; C) 6λ spacing, 15° jitter, tail is at the top; D) 8λ spacing, 0° jitter, tail is at the bottom.

$\pm 60°$.

Preliminary Control Experiment

The stimuli and task used in the main experiments assessed subjects' ability to perceive the spiral's global shape/orientation by requiring them to report the location of the spiral's tail. To examine whether this task could be performed on the basis of local contour information, a preliminary control experiment measured the minimum number of contour elements required to locate the tail of the spiral contour.

The stimuli and methods used in that control experiment were created using the same procedure described above, except that the distracter elements were removed and, on every trial, a staircase procedure determined the number of adjacent contour elements that would be displayed. The location of the adjacent elements on the spiral path was randomly chosen on every trial to be either the head, tail, or middle of the spiral. The two young subjects who participated in this experiment were shown the full shape of the spiral prior to the experiment and were told that only portions of the spiral contour would be visible on any given trial. Their task was to report whether the tail of the complete spiral would be at the top-center, bottom-center, right-middle, left-middle locations of the square pattern.

4.2.2 Results

For all of the current experiments, statistical analyses were performed using the statistical computing environment R (R Development Core Team, 2008; Lawrence, 2011). Mean accuracy and sensitivity (i.e., d') were obtained for each level of orientation jitter and inter-element distance. Since the pattern of results was similar for accuracy and d', only accuracy data are presented here. When conducting ANOVA, an arcsine transformation was applied to accuracy values to ensure the data satisfied the assumption of normality. For all within-subjects tests, the Geisser-Greenhouse correction was used to adjust the degrees-of-freedom to correct for violations of the sphericity assumption (Maxwell and Delaney, 2004). In such cases, the adjusted p-values are reported. Generalized eta-squared, η_g^2, is reported as a measure of association strength for all significant effects (Bakeman, 2005; Olejnik and Algina, 2003).

Our preliminary experiment experiment found that 11 Gabors were required to locate

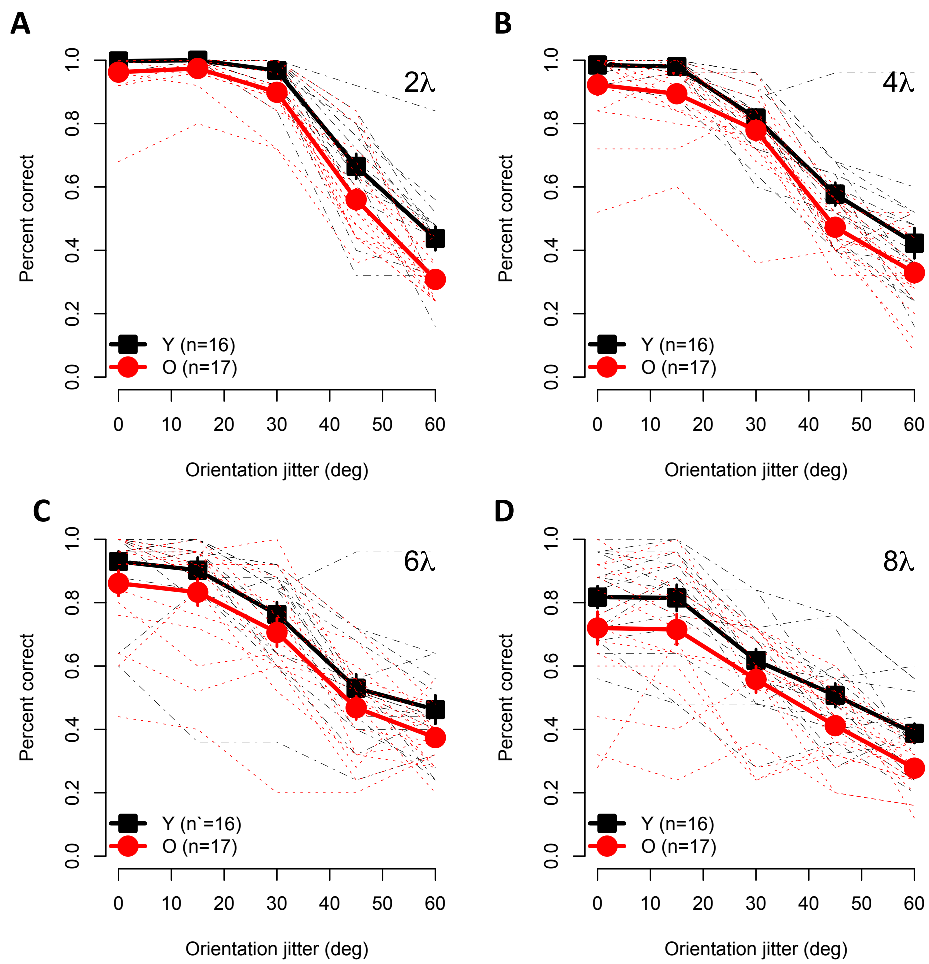


Figure 4.2: Contour discrimination accuracy in Experiment 1 is shown as a function of contour element orientation jitter for the four inter-element spacing conditions (A - D). Black squares show mean accuracy of younger subjects and red circles show mean accuracy of older subjects. Error bars represent ±1 SEM. Individual subjects' data are shown in black dashed line for younger subjects and dotted red lines for older subjects.

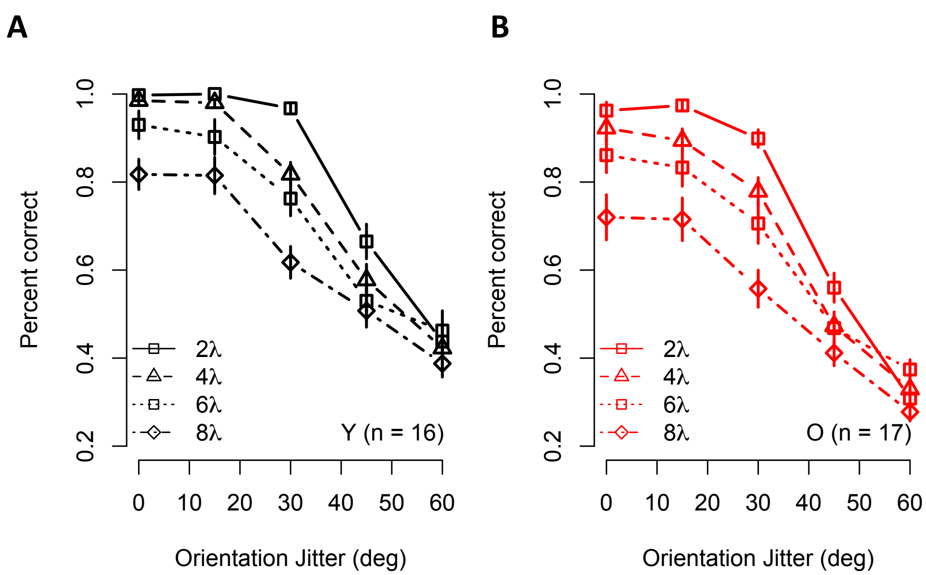


Figure 4.3: Effect of inter-element spacing on contour discrimination accuracy in Experiment 1 is shown as a function of orientation jitter for younger subjects (A) and older subjects (B). Different symbols show accuracy for $2\lambda - 8\lambda$ conditions separately (see legend). Error bars represent ± 1 SEM.

the tail for contours with 2λ spacing, and 4.5 Gabors were required for contours with 6λ spacing. Thus, reporting the location of the tail of the spiral (without distracters) with 75% accuracy in our stimuli requires grouping approximately half of the contour elements composing the contour.

Figure 4.2 shows mean accuracy for contour discrimination as a function of orientation jitter for all contour spacing conditions separately. As expected, accuracy in both groups declined with increasing orientation jitter at each level of element spacing. Furthermore, at any fixed level of orientation jitter, response accuracy in both groups decreased with increasing separation between elements. Accuracy in both groups was at ceiling when discriminating aligned (0° jitter) contours with 2λ spacing. However, accuracy was lower in older subjects than younger subjects in all other conditions. A mixed-model 2 (age) $\times$ 4 (spacing) $\times$ 5 (orientation jitter) ANOVA revealed significant main effects of age ($F(1,31) = 10.5$, $p = 0.0028$, $\eta_g^2 = 0.10$), spacing ($F(3,93) = 54.4$, $\hat{\epsilon} = 0.92$, $p < 0.0001$, $\eta_g^2 = 0.29$), and orientation jitter ($F(4,124) = 480.3$, $\hat{\epsilon} = 0.49$, $p < 0.0001$, $\eta_g^2 = 0.72$). The Spacing $\times$ Orientation jitter interaction also was significant ($F(12,372) = 17.0$, $\hat{\epsilon} = 0.63$, $p < 0.0001$, $\eta_g^2 = 0.14$), indicating that the effect of orientation jitter varied with inter-element spacing. Importantly, none of the interactions with age were

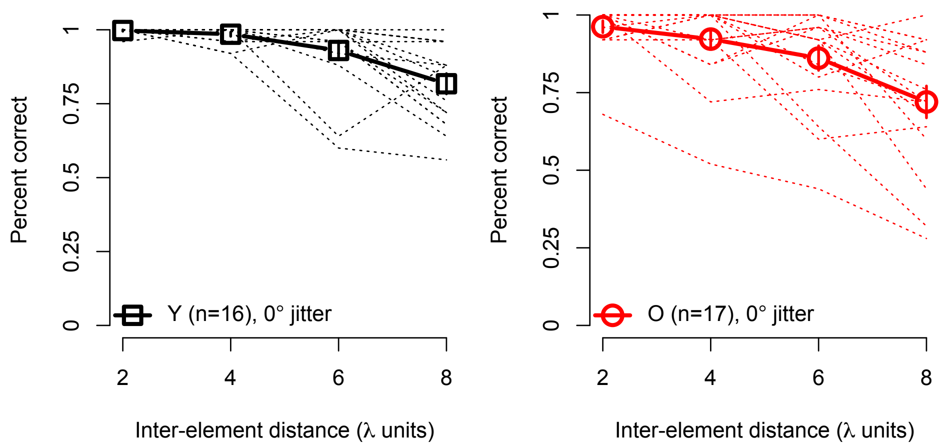


Figure 4.4: Experiment 1 results: Contour discrimination accuracy is shown a function of inter-element distance for contours with 0° orientation jitter (collinear). Dashed lines show individual subjects' data, solid lines are show mean accuracy, and error bars represent ±1 SEM.

significant (Age × Spacing: $F(3, 93) = 0.08$, $\hat{\epsilon} = 0.92$, $p = 0.96$; Age × Orientation Jitter: $F(4, 124) = 0.53$, $\hat{\epsilon} = 0.49$, $p = 0.57$; Age × Spacing × Orientation Jitter: $F(12, 372) = 0.74$, $\hat{\epsilon} = 0.63$, $p = 0.65$). These results indicate that the effect of age on contour integration did not vary significantly with inter-element spacing or orientation jitter.

To visualize the Spacing × Orientation Jitter interaction, the data were redrawn in Figure 4.3 to compare the effect of orientation jitter on contours with different inter-element spacings. The data show that accuracy achieved with low levels of jitter decreased with increasing inter-element spacing, but that the effect of spacing declined as jitter increased beyond ≈ 30 deg. In other words, contour discrimination showed greater resistance to small amounts of orientation jitter when inter-element separations were small.

Figure 4.4 shows the effect of element spacing for collinear contours (i.e., 0° orientation jitter) for younger and older subjects separately. The average accuracy in the two groups declined monotonically with increasing spacing and the rate of decline was similar for both groups. However, not all subjects showed the same rate of decline with spacing. As can be seen in Figure 4.4, several subjects in each group showed consistently high accuracy at all spacings. On the other hand, other subjects showed sharp declines in accuracy, even with spacing as small as $4\,\lambda$. Moreover, the number of subjects who showed poor performance ($\leq 75\%$) at larger spacings was greater in the older group than in the younger group.

4.2.3 Discussion

This experiment examined the effects of contour-element separation and collinearity on contour discrimination in younger and older subjects. Overall, contour discrimination was poorer in older subjects, but the age difference did not vary significantly with element separation or collinearity.

Field et al. (1993) found that contour detection accuracy declined to chance level with orientation jitter of only 30°, whereas subjects in the current experiment were able to tolerate much greater levels of orientation jitter. The reason for this discrepancy lies in the definitions of orientation jitter used in the two studies: A 30° orientation jitter in Field et al. signifies that each contour element's orientation either increased or decreased by 30°, whereas 30° orientation jitter in our experiment means that the jitter angle applied to any individual contour element can take on any value between −30° and 30°. Hence, the effects of orientation jitter in the two studies are not comparable.

Beaudot and Mullen (2003) estimated the spatial limit of contour integration by determining the maximum inter-element distance at which observers could reliably detect contours embedded in a field of randomly oriented Gabors. They found that the critical separation was proportional to spatial frequency and was unaffected by contour curvature. The average spatial limit for the achromatic mechanism of their four younger subjects was $\approx 6.8\lambda$. Kuai and Yu (2006) reported a similar estimate (6.9λ) in a contour detection task and a smaller (4.4λ) limit in a contour shape discrimination task.

Although the maximum element separation in the current experiment was 8λ, we did not observe a sharp decline in performance at the largest contour spacing in either group. Instead, average contour discrimination performance decreased gradually with element spacing, with some subjects showing a steeper decline and others maintaining high discrimination accuracy even at 8λ. Interestingly, Beaudot and Mullen (2003) also reported that some subjects showed constant performance as a function of contour-element separation. Thus, the spatial range for contour integration may not have a sharp boundary and may vary across individuals. However, if the spatial range of contour integration was reduced with aging, the age-difference in contour discrimination accuracy would be greater for contours with larger spacings, compared to smaller spacings. This pattern was not observed as the effect of age was approximately constant across all contour spacing conditions. Hence, the spatial range of contour integration does not appear to change with age.

Consistent with the idea that proximity increases overall contour salience (Li and Gilbert, 2002), the asymptotic level of performance decreased with increasing contour spacing for younger and older subjects. Contours with small spacing were also more resistant to orientation jitter than contours with large spacing. These results are consistent with previous studies showing that co-alignment of local orientation is required to group elements spaced far apart, but is less important for grouping elements that are placed close together (Nikolaev and van Leeuwen, 2007; Hadad, Maurer, and Lewis, 2010). In the current study, the effect of orientation jitter was the same for younger and older subjects across all contour spacing conditions. This finding is consistent with McKendrick et al. (2010) who examined the effect of orientation jitter on closed contour shape discrimination and found that younger and older subjects showed a similar increase in shape discrimination thresholds with orientation jitter. Similarly, Hadad (2012) found that disruption of collinearity had a similar effect on closed contour shape discrimination in younger and older subjects for stimuli with high and low proximity levels. Interestingly, using a similar paradigm, Hadad et al. (2010) previously found that the ability to use collinearity as a cue to group distant elements develops slowly and is not fully efficient even at fourteen years of age. In sum, converging evidence from several studies shows that aging does not affect the ability to use collinearity for grouping contours and extracting the contour shape.

4.3 Experiment 2: Effect of stimulus duration as a function of contour spacing and local orientation alignment

Previous research has shown that older subjects require longer stimulus durations than younger subjects to discriminate contours (Roudaia et al., 2011). A 1 s stimulus duration was used in Experiment 1 to ensure that older subjects had sufficient time to group the contours, so that the effects of contour spacing and collinearity could be observed independently of differences in processing time. Processing time for detecting contours in clutter increases with curvature (Beaudot and Mullen, 2001; Hess, Beaudot, and Mullen, 2001) and appears to increase with contour element spacing (Beaudot and Mullen, 2003). Similarly, the stimulus duration required for collinear facilitation – i.e., the reduction of contrast threshold for a target Gabor when flanked by high contrast, collinear flanker Gabors (Polat and Sagi, 1993) – has been shown to increase proportionally to the distance between target and flankers (Cass and Spehar, 2005). Thus, the dynamics of contour discrimination in Experiment 1 may also vary with inter-element separation and collinearity, and these dynamics may change with age in a non-linear way. In the current experiment, we tested contour discrimination for a range of stimulus durations to examine how the effect of aging for contours with different spacing and collinearity levels may be affected by the stimulus duration.

4.3.1 Methods

Subjects

Fourteen younger and fourteen older subjects who participated in Experiment 1 were tested. Subjects were compensated ($10/hour) for participating. One older subject completed only three out of four conditions in the experiment. For this reason, their data were excluded from statistical analyses, however, their data are included in the data plots. Demographic information is presented in Table 4.1.

Apparatus

The apparatus was the same as in Experiment 1.

Stimuli

The stimuli were generated using the same procedure as described in Experiment 1. Only two levels of inter-element spacing (2λ and 6λ) and two levels of orientation jitter ($0°$ and $30°$) were used in this experiment.

Procedure

The task and trial sequence was the same as in Experiment 1, except that the stimulus duration was randomized on every trial. The stimulus durations were 0.04, 0.093, 0.20, 0.40, or 0.80 seconds (i.e., 3, 7, 15, 30, or 60 frames). The trials were blocked by inter-element spacing and orientation jitter and the order of the blocks was randomized across subjects. Each block contained 150 trials, with 30 trials at each stimulus duration. As in Experiment 1, accuracy and d' were calculated for each subject. The pattern of results was similar for accuracy and d' and only accuracy data are shown here.

4.3.2 Results

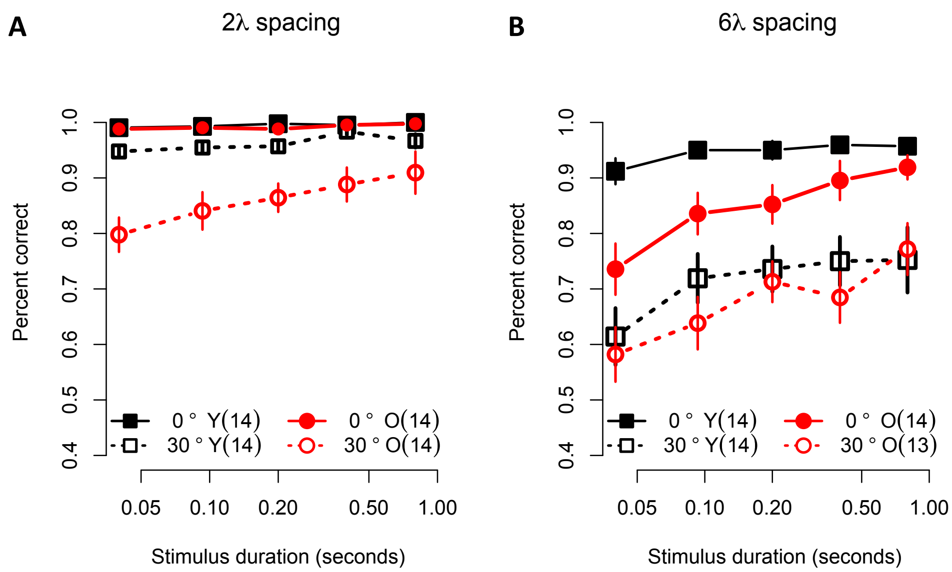


Figure 4.5: Mean contour discrimination accuracy in Experiment 2 is shown as a function of stimulus duration for younger (black squares) and older (red circles) subjects for contours with 2λ spacing and contours with 6λ spacing. Error bars represent ± 1 SEM.

Statistical analyses were performed with same software and procedures used in Experiment 1.

Figure 4.5 shows the contour discrimination accuracy of younger and older subjects as a function of stimulus duration for stimuli with small and large inter-element separations. As can be seen, accuracy generally increased with stimulus duration, but the rate of increase and the asymptotic level of performance varied as a function of age, inter-element separation, and orientation jitter. A mixed-model 2 (age)$\times$ 4 (spacing) $\times$ 5 (orientation jitter) $\times$ 5 (duration) ANOVA on arcsine-transformed accuracy values revealed significant main effects of Age ($F(1,25) = 5.78$, $p = 0.02$, $\eta_g^2 = 0.09$), Spacing ($F(1,25) = 219.9$, $p < 0.0001$, $\eta_g^2 = 0.45$), Orientation jitter ($F(1,25) = 232.1$, $p < 0.001$, $\eta_g^2 = 0.43$), and Duration ($F(4,100) = 26.4$, $\hat{\epsilon} = 0.80$, $p < 0.0001$, $\eta_g^2 = 0.10$). The effects of stimulus duration, contour spacing, and orientation jitter also interacted with each other, as revealed by significant Spacing $\times$ Orientation jitter ($F(1,25) = 9.79$, $p = 0.004$, $\eta_g^2 = 0.03$), Spacing $\times$ Duration ($F(4,100) = 4.10$, $\hat{\epsilon} = 0.76$, $p = 0.009$, $\eta_g^2 = 0.01$), and Spacing $\times$ Orientation jitter $\times$ Duration ($F(4,100) = 3.33$, $\hat{\epsilon} = 0.84$, $p = 0.02$, $\eta_g^2 = 0.009$) interactions. The Orientation jitter $\times$ Duration interaction was not significant ($F(4,100) = 1.68$, $\hat{\epsilon} = 0.87$, $p = 0.16$, $\eta_g^2 = 0.004$). The significant three-way Spacing $\times$ Orientation jitter $\times$ Duration interaction reflects the fact that the effect of spacing was greater for non-collinear contours, especially at short stimulus durations.

Consistent with Experiment 1, the effect of age did not vary with spacing or orientation jitter, as the Age $\times$ Spacing ($F(1,25) = 0.06$ $p = 0.81$, $\eta_g^2 \approx 0$), and Age $\times$ Orientation jitter ($F(1,25) = 0.64$, $p = 0.43$, $\eta_g^2 = 0.002$) interactions were not significant. Unlike what was found in Experiment 1, the Age $\times$ Spacing $\times$ Orientation jitter interaction was significant ($F(1,25) = 12.3$, $p = 0.002$, $\eta_g^2 = 0.04$). This result reflects the fact that disruption of collinearity had a greater effect in younger subjects in the 6λ compared to the 2λ condition. On the other hand, adding orientation jitter affected older subjects' accuracy approximately to the same extent in the small and large spacing conditions (compare the difference in the vertical separation of the two black curves in Figure 4.5A and B versus the same comparison in the red curves). However, it is likely that this interaction is due, at least in part, to ceiling effects in the no-jitter, 2λ conditions.

Importantly, the effect of age also varied with stimulus duration, as revealed by a significant Age $\times$ Duration interaction ($F(4,100) = 2.97$, $\hat{\epsilon} = 0.80$, $p = 0.02$, $\eta_g^2 = 0.01$). None of the three- and four-way interactions that included Age and Duration factors were significant (Age $\times$ Spacing $\times$ Duration: $F(4,100) = 0.29$, $\hat{\epsilon} = 0.76$, $p = 0.88$; Age $\times$ Orientation jitter$\times$Duration: $F(4,100) = 1.94$,$\hat{\epsilon} = 0.87$, $p = 0.11$; Age $\times$ Spacing $\times$ Orientation jitter $\times$ Duration: ($F(4,100) = 1.90$, $\hat{\epsilon} = 0.84$, $p = 0.12$, $\eta_g^2 = 0.005$).

To dissect the significant interactions, separate 2 (age) $\times$ 5 (duration) ANOVAs were conducted for each contour type. In addition, the effect of stimulus duration was analysed by computing linear trend scores of accuracy across log stimulus duration, and comparing these trend scores across age groups with one-way ANOVAs. Figure 4.5A shows the data for stimuli with a small (2λ) inter-element spacing. For collinear contours, both groups showed ceiling performance for all durations: average response accuracy in the two groups did not differ (Age: $F(1, 25) = 1.50$, $p = 0.23$, $\eta_g^2 = 0.03$), the linear trend of accuracy across duration did not reach significance ($F(1, 25) = 4.01$, $p = 0.06$), and the linear trend did not differ between age groups ($F(1, 25) = 0.03$, $p = 0.59$). When collinearity was disrupted by 30° orientation jitter, response accuracy in the two age groups differed at all stimulus durations except the longest (i.e., 0.8 s): average response accuracy was lower in older subjects ($F(1, 25) = 11.25$, $p = 0.003$, $\eta_g^2 = 0.23$), the linear trend of accuracy across duration was significant ($F(1, 25) = 44.8$, $p < 0.0001$); and, importantly, the linear trend differed between age groups ($F(1, 25) = 5.60$, $p = 0.03$), reflecting the fact that response accuracy in older subjects declined more than that of younger subjects. In summary, for contours with short inter-element spacings, the effect of aging on contour discrimination accuracy increased at shorter stimulus durations, but only for non-collinear contours.

Figure 4.5B shows the data for stimuli with a large (6λ) inter-element spacing. For collinear contours, younger subjects' accuracy improved from 91% to 95% between 0.04-0.093 s, after which it remained constant as stimulus duration increased. On the other hand, older subjects' accuracy was $\approx 73\%$ when the stimulus duration was 0.04 s, and showed an approximately linear increase until reaching younger subjects' accuracy at 0.8 s. Consistent with these observations, the main effect of age was significant ($F(1, 25) = 7.11$, $p = 0.01$, $\eta_g^2 = 0.16$), the linear trend across log duration was significant ($F(1, 25) = 39.35$, $p < 0.0001$) and the linear trend was greater in older compared to younger subjects ($F(1, 25) = 7.72$, $p = 0.01$). For non-collinear (30° jitter) contours, both groups showed similar levels of accuracy at all durations. The main effect of age was not significant ($F(1, 25) = 0.48$, $p = 0.49$, $\eta_g^2 = 0.01$). The linear trend across log duration was significant ($F(1, 25) = 20.60$, $p = 0.0001$), but it did not differ across the two age groups (linear trend $\times$ Age: $F(1, 25) = 0.32$, $p = 0.57$). In summary, for contours with 6λ spacing, the effect of aging increased with decreasing stimulus duration when contour elements were collinear, but the effect of aging remained constant for non-collinear contours.

4.3.3 Discussion

When spiral contours were composed of closely spaced collinear elements, younger and older subjects showed nearly perfect contour discrimination performance, even when stimulus duration was decreased to 0.04 s. However, contour discrimination accuracy declined with decreasing stimulus duration when contour element spacing was large and when contour element collinearity was disrupted by local orientation jitter. When both proximity and collinearity were disrupted (6λ and $30°$ jitter condition), both groups showed similar, poor performance at all durations. However, when only proximity *or* collinearity was disrupted, performance was more severely impaired in older subjects than younger subjects at short stimulus durations.

These findings are consistent with a previous study showing an age-related increase in duration thresholds for discriminating contours in clutter (Roudaia et al., 2011). Roudaia et al. demonstrated that this age difference in processing time could not be ascribed to age-related reductions in retinal illuminance (Weale, 1963), nor to delays in the processing of individual Gabor elements, and therefore argued that the age difference in contour discrimination reflected delays in the contour integration process *per se*. Similar to the current results, Roudaia et al. found that older subjects were disproportionately slower at processing less salient contours composed of elements oriented orthogonally to the contour path.

Roudaia et al. (2011) reported that older subjects required longer durations to process collinear contours than younger subjects, and that younger and older subejcts in that study required 0.05 s and 0.150 s respectively to discriminate contours with 75% accuracy. It may be surprising, therefore, that the current study found that response accuracy in both age groups was quite high at short stimulus durations. However, the difference between experiments is likely due to the fact that stimuli used by Roudaia et al. were followed by a mask, whereas those used in the current study were not. This hypothesis is supported by Hess et al. (2001), who found that successful contour detection required a stimulus duration ≥ 0.83 s when stimuli were preceded and followed by a mask, but only 0.013 s when stimuli were not masked.

The current data suggest that processing time for contour integration increases with increasing inter-element spacing. Subjects in both groups showed a steeper decrease in accuracy with decreasing stimulus duration for contours with large, compared to small, inter-element spacings. The only other study that measured contour detection as a function of stimulus duration and inter-element separation was conducted in macaque monkeys and also reported increased processing time for integrating across larger separations (Mandon and Kreiter, 2005).

Finally, consistent with Experiment 1, the effect of aging on discrimination of contours did not systematically differ as a function of contour spacing in this experiment. This result corroborates the conclusion made in Experiment 1, namely that aging does not differentially affect the ability to group contours across large distances.

4.4 Experiment 3: The effect of relative contour and distracter spacing in iso- and randomly-oriented backgrounds

In Experiments 1 and 2, the average spacing between adjacent distracter and contour elements were equal in order to minimize the number of distracters while simultaneously ensuring that the contour could not be detected on the basis of density cues. Previous studies have shown that contour detection becomes more difficult when the minimum distracter element spacing is less than the minimum contour element spacing, resulting in displays where any given contour element is closer to a distracter than to their neighbouring contour element (Braun, 1999; Li and Gilbert, 2002; Kovács et al., 1999). Del Viva and Agostini (2007) found that younger subjects are able to tolerate a greater number of distracter Gabors than older subjects when detecting circular contours, which suggests that older subjects are less efficient than younger subjects at extracting contours from dense backgrounds. However, the stimuli in that study did not equate the average spacing between elements across the display, resulting in differences in local density that may have been used to locate the contour. In this experiment, we investigated the effect of relative spacing of contour and distracter elements on contour discrimination in younger and older subjects by decreasing distracter spacing while keeping contour spacing constant. In addition, we examined whether contour integration in older subjects is differentially affected by the variability of the orientations of the background elements.

Table 4.2: Experiment 3: Mean ± 1 SD age, near and far logMAR acuity, Pelli-Robson contrast sensitivity, and Mini-Mental State Examination (MMSE).

N (M:F)	Age	Near Acuity	Far Acuity	Pelli-Robson	MMSE
12 (4:8)	20.0 ± 3.5	-0.12 ± 0.07	-0.12 ± 0.11	1.90 ± 0.07	
12 (6:6)	67.6 ± 6.5	0.03 ± 0.08	0.01 ± 0.09	1.95 ± 0	28.8 ± 1.03

4.4.1 Methods

Subjects

Twelve younger and twelve older subjects, none of whom had participated in Experiments 1 or 2, were recruited to participate in this experiment. Subjects were compensated for their time at a rate of $10/hour. Table 4.2 summarizes the demographic factors, visual acuity, contrast sensitivity, and cognitive measures for these two groups.

Apparatus

The apparatus was the same as in Experiment 1.

Stimuli

Spiral contours were sampled with Gabors ($\lambda = 0.30$ deg, $\sigma = 0.11$ deg) and positioned at equally spaced intervals of 3λ (0.9 deg) or 6λ (1.8 deg) along the path of a logarithmic spiral, as described in Experiment 1. The global spiral orientation was either clockwise or counterclockwise and was oriented in one of four directions. The spiral was centred in a 9.5 deg square region and then displaced horizontally and vertically by random amounts selected from a Normal distribution with $\sigma = 1.5$ deg. The orientations of the Gabors composing the spiral were tangential to the contour path.

Distracter elements were positioned randomly within the square stimulus area using an iterative procedure that maintained a pre-determined minimum separation between distracter elements. The iterative procedure continued until no more distracters could be placed. The 3λ contours were embedded in backgrounds with minimum distracter spacing of 2.9, 2.4, 2.0, 1.7 and 1.5 λ. The 6λ contours were embedded in backgrounds with minimum distracter spacing of 6.1, 5.0, 4.0, 3.4 and 2.9 λ. Thus, the relative spacing between contour and distracter elements were equal to 1.0, 1.2, 1.5, 1.8, or 2.1, where numbers greater than 1 indicate that contour spacing was larger than distracter spacing. The orientation of distracter elements varied in two conditions: random and iso-oriented. In the random condition, distacter orientations were sampled from a uniform distribution of angles from 0° to 360°. In the iso-oriented condition, each distracter orientation was sampled from a Gaussian normal distribution with $\sigma = 5°$ and a mean that was equal to a randomly chosen angle between 0° and 360°. The iso-oriented background was tested only for relative spacing levels of 1.0 and 2.1, and the randomly-oriented background was tested with all five levels of relative spacing. Examples of stimuli are shown in Figure 4.6.

Procedure

The task and trial sequence were similar to Experiments 1 and 2. Subjects were asked to maintain fixation on a black fixation point displayed in the middle of the screen of mean luminance throughout the trials. The fixation point flickered to indicate the start of each trial. The stimulus contained a spiral contour oriented in one of four directions, was displayed for 0.4 s and followed by a blank screen of mean luminance for 0.5 s. In a 4 alternative forced-choice procedure, subjects reported the location of the tail of the spiral by pressing one of the four arrow keys on the keyboard. Auditory feedback was provided after every trial with a high pitch tone following a correct response and a low pitch tone following an error. The subsequent trial began after a 1.5 s inter-trial interval.

Trials were blocked by contour spacing: half the subjects in each group completed all the 3λ contour trials first and the other half of the subjects completed all the 6λ contour trials first. Within each block, all relative spacing levels and background context conditions (iso- or randomly-oriented) were intermixed. There were 50 trials per condition, resulting in a total of 600 trials. Subjects were allowed to take a short break after every 125 trials and the experiment lasted approximately 50 minutes.

4.4.2 Results

Statistical analyses were performed with same software and procedures used in Experiments 1 and 2. Figure 4.7 shows contour discrimination accuracy as a function of

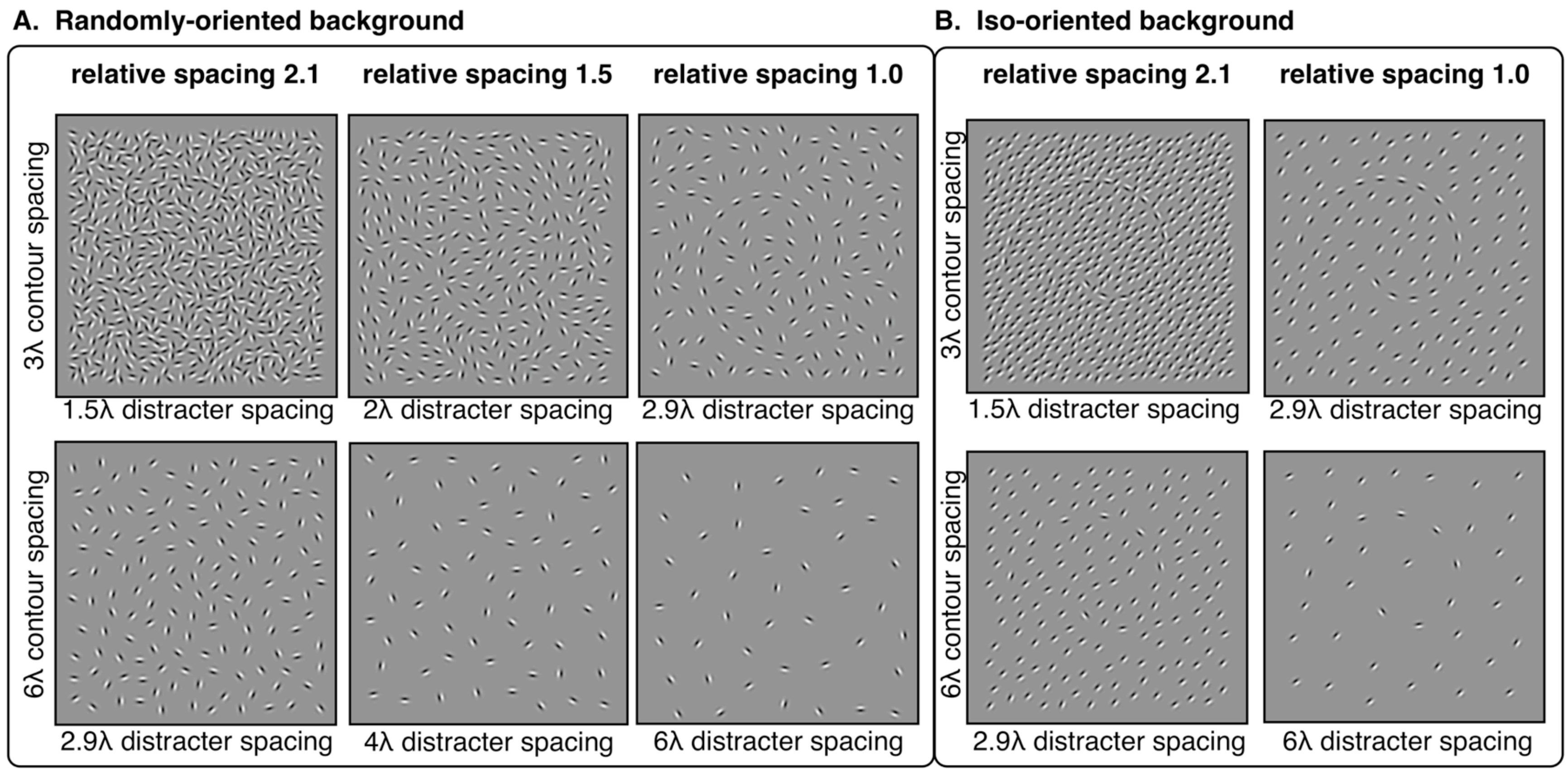


Figure 4.6: Experiment 3 stimuli: spiral contours embedded in a background of randomly-oriented (A) or iso-oriented (B) Gabors with varying inter-element spacing. Contour elements had either 3λ (top row) or 6λ (bottom row) spacing. Distracter spacing varied from 1.5λ to 6.1λ, resulting in contour-distracter relative spacing ranging from 1.0 to 2.1. Three levels of relative spacing – 1, 1.5, and 2.1 – are shown here.

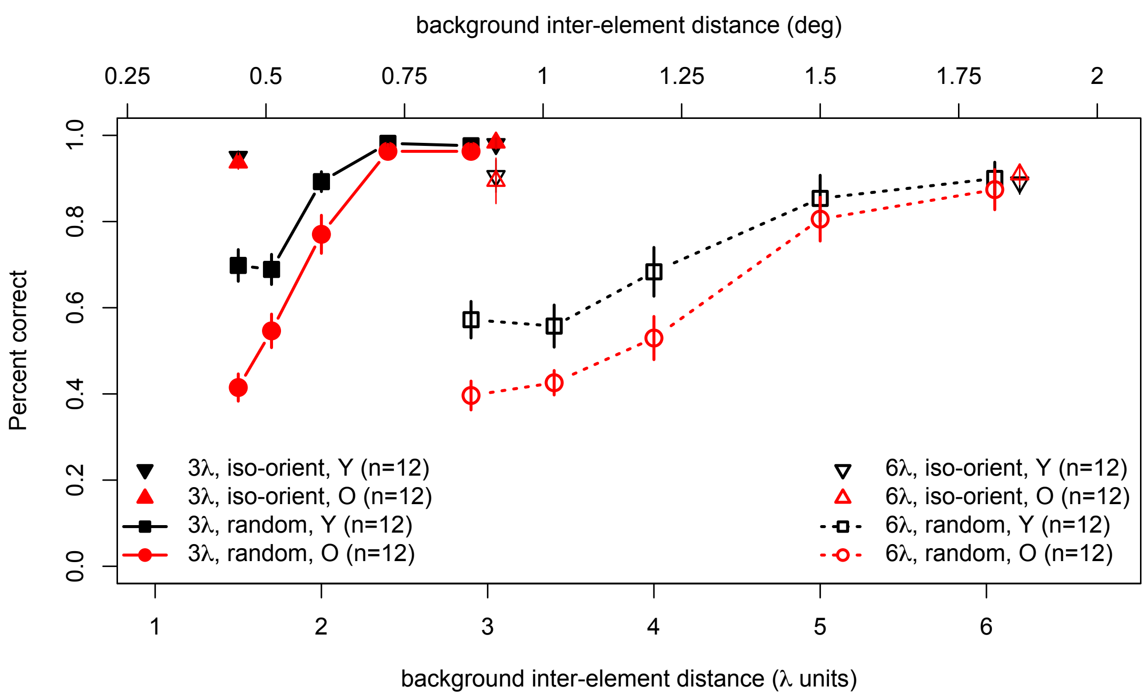


Figure 4.7: Experiment 3 results: Contour discrimination accuracy is shown as a function of background inter-element spacing for all conditions tested. Data for the iso-oriented background conditions are shown by the triangle symbols (up, black for younger subjects and down, red for older subjects). Black squares and red circles show younger and older subjects' performance in the random background condition. Solid lines and filled symbols show data for contours with 3λ spacing and dotted lines with open symbols show data for contours with 6λ spacing. Error bars represent $\pm 1 SEM$.

background element spacing and Figure 4.8 shows the same data as a function of the relative spacing of contour and background elements.

Arcsine-transformed accuracy values from the iso-oriented background (upright and inverted triangles) and random background conditions (circles and squares) were analysed separately with 2 (age) × 2 (contour spacing) × 2 (relative spacing) mixed-model ANOVAs. For the iso-oriented background, the ANOVA revealed significant main effects of contour spacing ($F(1, 22) = 14.6$, $p = 0.001$, $\eta_g^2 = 0.13$) and relative pacing ($F(1, 22) = 16.7$, $p = 0.004$, $\eta_g^2 = 0.07$), as well as a significant Contour spacing × Relative spacing interaction ($F(1, 22) = 9.58$, $p = 0.005$, $\eta_g^2 = 0.04$). Accuracy was higher for contours with 3λ spacing than 6λ spacing in both groups, but this difference was slightly diminished when relative spacing was high, as accuracy for 3λ contours decreased but that for 6λ contours remained constant. The main effect of age was not significant ($F(1, 22) = 0$, $p = 0.92$) and none of the two-way and three-way interactions with age were significant ($F \leq 1.29$ and $p \geq 0.26$ in each case). Thus, contour discrimination accuracy in the iso-oriented background condition did not differ significantly between age groups.

For the random background condition, the ANOVA revealed significant main effects of contour spacing ($F(1, 22) = 54.7$, $p < 0.001$, $\eta_g^2 = 0.25$), relative spacing ($F(4, 88) = 225.5$, $\hat{\epsilon} = 0.67$, $p < 0.001$, $\eta_g^2 = 0.67$), and age ($F(1, 22) = 7.39$, $p = 0.01$, $\eta_g^2 = 0.15$). Accuracy was higher overall for 3λ compared to 6λ contours and decreased with increasing relative spacing (Figure 4.8). The Contour spacing × Relative spacing interaction also was significant ($F(4, 88) = 8.68$, $\hat{\epsilon} = 0.61$, $p = 0.0001$, $\eta_g^2 = 0.05$), indicating that the difference in accuracy for 3λ and 6λ spacing contours depended on the relative spacing. The significant main effect of age confirmed that older subjects showed poorer accuracy than younger subjects. As in Experiments 1 and 2, the Age × Contour spacing interaction was not significant ($F(1, 22) = 0.13$, $p = 0.72$), indicating that the effect of contour spacing did not differ for the two age groups. On the other hand, the Age × Relative spacing interaction was significant ($F(4, 88) = 5.11$, $\hat{\epsilon} = 0.67$, $p = 0.004$, $\eta_g^2 = 0.04$). As can be seen in Figure 4.8, younger and older subjects showed equally good performance at a relative spacing of 1.0. However, as distracter spacing decreased, accuracy decreased more in older subjects than younger subjects. Finally, the Age × Contour spacing × Relative spacing interaction was not significant ($F(4, 88) = 1.07$, $\hat{\epsilon} = 0.61$, $p = 0.36$), indicating that the increased sensitivity to relative spacing in older subjects was not significantly different for contours with 3λ and 6λ spacing.

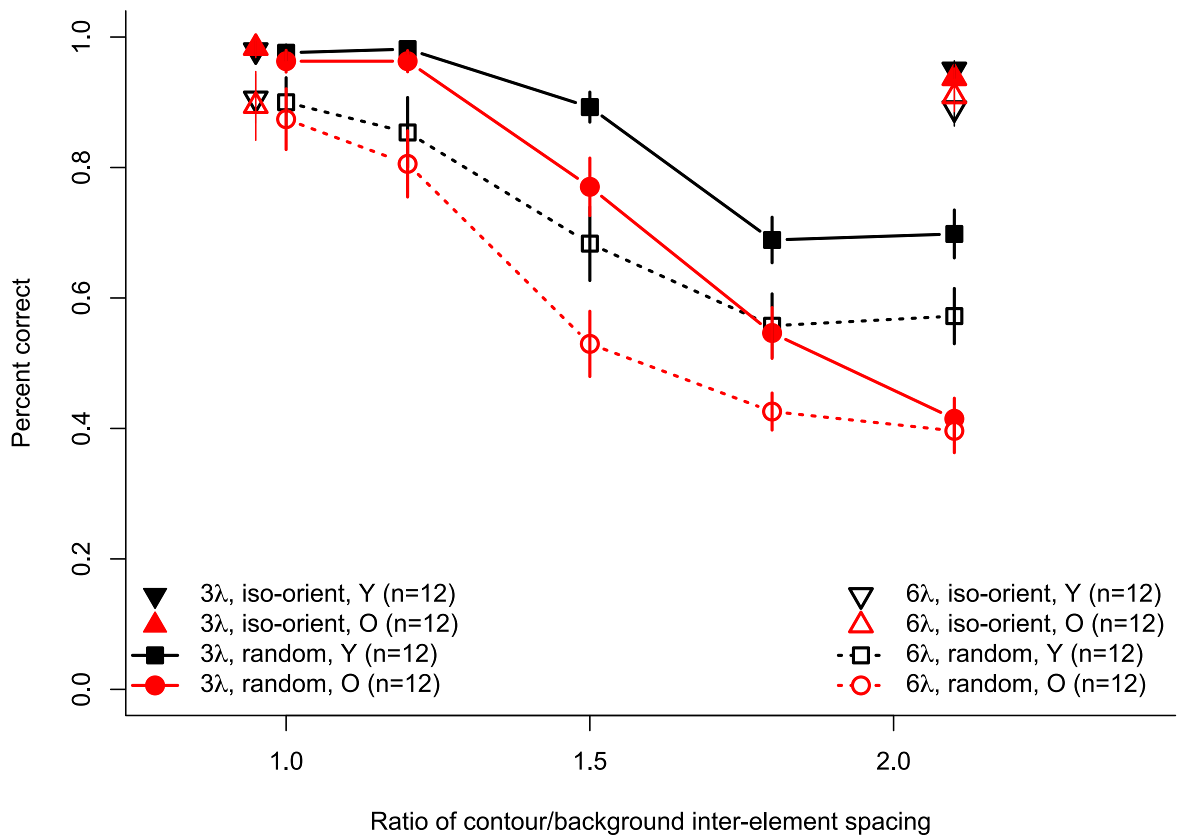


Figure 4.8: Experiment 3 results: Contour discrimination accuracy is shown as a function of relative contour and background spacing. Data for the iso-oriented background conditions are shown by the triangle symbols (up, black for younger subjects and down, red for older subjects) that are displaced horizontally to avoid overlap. Data for the random orientation condition background condition are shown with filled symbols and solid lines for the 3λ contours and with open symbols and dashed lines for the 6λ contours. Error bars represent $\pm 1 SEM$.

The effect of relative spacing was analysed further by computing the linear trend scores of accuracy across relative spacing and submitting them to a 2(age) × 2 (contour spacing) mixed-model ANOVA. The grand mean differed significantly from zero ($F(1, 22) = 476.9$, $p < 0.0001$), confirming the presence of a significant linear trend. The main effect of contour spacing ($F(1, 22) = 8.14$, $p = 0.009$) was significant, with higher linear trend scores for 3λ spacing than 6λ spacing. The main effect of Age also was significant ($F(1, 22) = 9.92$, $p = 0.005$), reflecting the increased effect of relative spacing (i.e., a greater linear trend) in older subjects. The Age × Contour spacing interaction was not significant ($F(1, 22) = 1.74$, $p = 0.20$), indicating that the age difference in the linear trend across relative spacing was similar for contours with small and large spacings.

4.4.3 Discussion

This experiment examined the effect of distracter inter-element spacing on contour discrimination for contours composed of elements with small and large spacing. We found that that the effect of aging depended critically on the variability of the orientations of the distractor elements. When the orientation of each distracter was selected randomly and independently, contour discrimination accuracy declined monotonically with increasing relative spacing (i.e., the ratio of contour- and distractor-element spacing), consistent with previous reports (Li and Gilbert, 2002; Kovács et al., 1999), but the effect of relative spacing differed between age groups. Specifically, reducing distracter spacing decreased older subjects' accuracy much more than that of younger subjects. For example, response accuracy was equal in both groups when contour and distracter elements had equal spacing, but accuracy was as much as 28% lower in older subjects when distractor spacing was reduced by half. On the other hand, when all of the distractor elements had the same, randomly selected orientation, older and younger subjects were equally accurate at discriminating the spiral contours, even when contour elements were spaced far apart and were interspersed with distracter elements.

As in Experiment 1, the effect of aging did not vary with contour element separation, and the increase in the effect of aging with relative spacing also did not differ as a function of contour element separation. Thus, older subjects are not disproportionately impaired at integrating contours across larger distances, even when relative spacing of contour and distracter elements is high.

Overall, our results are consistent with findings of Del Viva and Agostini (2007) who showed that younger subjects could tolerate more distracters than older subjects when detecting circular closed contours composed of a varying number of Gabors (i.e., with varying inter-element separations). They also reported a greater effect of age for contours with small spacing (3.2λ), suggesting that aging may have a greater effect on contour integration over short-range separations (Del Viva and Agostini, 2007). Similarly, if we examine performance at the largest relative spacing condition in our data (i.e., conditions with the maximum number of distracters for each contour spacing (see Figure 4.8, relative spacing = 2.1), the difference in average accuracy of younger and older subjects was in fact greater for contours with 3λ spacing compared to 6λ spacing. However, this differential effect was apparent only at the largest relative spacing and was not significant when examined over the full range of relative spacings.

4.5 General Discussion

Previous research has shown that older subjects are less accurate at detecting and discriminating contours embedded in noisy or cluttered backgrounds (Del Viva and Agostini, 2007; Roudaia et al., 2011; Casco et al., 2011; Hadad, 2012; McKendrick et al., 2010). The current experiments examined how the age difference in contour discrimination accuracy varies with absolute and relative spacing between contour and distracter elements, contour element collinearity, stimulus duration, and background context. In all experiments, subjects were required to report the global orientation of a spiral contour composed of Gabor elements embedded within a homogeneous field of distracter Gabors having the same contrast, spatial frequency, and phase as the contour elements. The spiral contour was either clockwise or counter-clockwise, but its overall shape and size remained constant. The position and global orientation of the spiral varied across trials. The subjects' task in all three experiments was to report the location of the tail of the spiral. Care was taken to ensure that the alignment of the orientations of the contour elements was the only cue available for grouping the contour. A preliminary experiment indicated that young subjects required half of the contour elements to be visible in order to perform this task accurately in a condition that did not include distractor elements, which suggests that the task is a reasonable measure of how well subjects perceive the shape of an extended contour.

The current experiments revealed several novel findings. First, Experiment 1 showed that the effect of aging on contour discrimination does not vary with contour element spacing, at least over the range of spacings tested here (i.e., 2-8 times the Gabor wavelength). Second, Experiment 1 also showed that younger and older subjects are equally sensitive to disruptions in contour element collinearity at all contour element spacings tested. Third, Experiment 2 revealed that younger and older subjects can discriminate salient contours (collinear contours with small spacing) at very short stimulus durations (0.04 s). For less salient contours, older subjects showed a greater decline in performance with decreasing stimulus duration than younger subjects, consistent with previous research (Roudaia et al., 2011). Fourth, Experiment 3, revealed that the age difference in contour integration depended on the relative spacing between contour and disctrater elements, rather than the absolute separation between contour elements. Lastly, both groups performed equally well when discriminating contours embedded in a dense field of iso-oriented distracters, showing that the presence of distracters *per se* is not sufficient to impair older subjects' performance.

The current study was the first to systematically examine contour discrimination for a range of contour spacings and collinearity levels in older subjects, but the current results are consistent with several previous findings. For example, Del Viva and Agostini (2007) found that the age-related reduction in sensitivity for detecting aligned contours among distracters did not vary with contour element spacing. In addition, a recent study found that the effect of aging on contour discrimination accuracy remained constant for contours with small and large inter-element spacings (Hadad, 2012). One seemingly contradictory study found that older subjects required a greater number of contour elements to correctly discriminate the shape of a sampled contour than younger subjects, leading to authors to conclude that older adults are especially impaired at integrating contours across large separations (McKendrick et al., 2010). However, their results may also be explained by a general decline in contour discrimination with aging as observed in our study. Indeed, if older subjects' accuracy is overall lower at all contour spacings, the minimum number of contour elements required to support a criterion level of performance will also be higher than that of younger subjects. Nonetheless, examining contour integration across a range of contour spacings in Experiment 1 revealed that aging affects performance equally for a range of contour spacings, not only at larger spacings. Finally, the current results also complement findings by McKendrick et al. by showing that increasing orientation jitter impairs contour shape discrimination to the same extent in younger and older subjects.

The sensitivity to collinearity in contour integration is thought to rely on orientation-tuned neurons in primary visual cortex and long-range horizontal connections between columns of similar orientation preference (Polat, 1999; Hess et al., 2003). Neurophysiological studies in older primates have revealed significant functional changes in V1 neurons, such as increased spontaneous activity, broader orientation tuning bandwidths, and decreased signal to noise ratios (Schmolesky, Wang, Pu, and Leventhal, 2000; Zhang, Wang, Wang, Fu, Liang, Ma, and Leventhal, 2008). Such changes in human visual cortex would be expected to lead to age-related changes in tolerance to orientation jitter in contour integration tasks. However, psychophysical and electrophysiological studies in humans have found no evidence for changes in orientation tuning (Delahunt, Hardy, and Werner, 2008; Govenlock, Taylor, Sekuler, and Bennett, 2009, 2010) or orientation discrimination ability with age (Betts, Sekuler, and Bennett, 2007; Delahunt et al., 2008), even for very brief stimulus durations (Roudaia et al., 2011). Thus, the finding that sensitivity to collinearity in contour integration does not change with aging is consistent with human psychophysics and electrophysiology showing preserved mechanisms for orientation encoding.

Although contour element spacing and local orientation alignment had no influence on the effect of aging on contour discrimination, older subjects were more affected by decreasing stimulus duration than younger subjects when discriminating less salient contours in Experiment 2. This change in the time needed to discriminate contours is consistent with the results of Roudaia et al. (2011), who found that older subjects needed longer stimulus durations to discriminate contours embedded in clutter. Roudaia et al. argued that the increase in duration thresholds could not be explained by age-related reductions in retinal illuminance (Weale, 1963, 1982), because reducing stimulus luminance by 90% did not increase duration thresholds in younger subjects. Moreover, Roudaia et al. found no age difference in the amount of time needed to detect individual Gabors or discriminate their orientation. Together with the current findings, these results suggest that the the longer time needed to perceive extended contours with aging results from changes in processes involved in grouping the contours and/or segregating them from the background, as opposed to processing of individual elements.

The stimulus duration required to detect or discriminate a contour among distracters varies with the characteristics of the contour and background elements, the nature of the task (detection or discrimination), the presentation of a mask, as well as subjects' previous experience with the task (Braun, 1999; Dakin and Baruch, 2009; Hess et al., 2001; Mandon and Kreiter, 2005; Mathes, Trenner, and Fahle, 2006; May and Hess, 2007). Contour detection can be very rapid, especially when stimuli are not masked (Hess et al., 2001). Mandon and Kreiter (2005) reported that monkeys can detect and discriminate contours after a masked presentation of only 0.03 s. Fast contour integration in some cases may result from the involvement of linear filters that may be used to detect contours that are composed of collinear elements with constant contrast phase (Hess et al., 2003). Such linear detectors may have been involved in the discrimination of the collinear contours in the 2λ spacing condition in the current experiments, and may explain the exceptionally good performance at short durations in that condition. The fact that older subjects showed no decline in performance in that condition is consistent with our previous study that indicated that the efficiency of linear filters for contour discrimination does not change with aging (Roudaia et al., 2011). On the other hand, using phase-alternating contours, where linear filters cannot contribute to detection, Hess et al. (2001) found that subjects required stimulus durations of ≈ 0.1 s to detect straight contours and up to ≈ 0.5 s for curved contours in stimuli that were preceded and followed by masks consisting of randomly oriented Gabors. Similarly, the earliest contour-specific neural correlate appears ≈ 0.15 s after stimulus onset for collinear contours and its latency is significantly delayed for less detectable contours (Mathes et al., 2006; Tanskanen et al., 2008). The current experiments showed that processing time for grouping contours increases with aging, especially for less detectable contours, which is consistent with the generalized slowing hypothesis with aging (Salthouse, 2000). However, reducing stimulus duration does not increase the effects of aging on shape discrimination (Habak, Wilkinson, and Wilson, 2009) or detection of motion (Bennett, Sekuler, and Sekuler, 2007). Furthermore, older subjects required shorter stimulus durations than younger subjects to discriminate the direction of large, high-contrast drifting gratings (Betts, Taylor, Sekuler, and Bennett, 2005; Betts, Sekuler, and Bennett, 2009). Therefore, increases in processing time are not ubiquitous in aging and the nature of age-related slowing of the dynamics of contour integration poses an interesting question for future research.

In addition to requiring longer stimulus durations to discriminate contours, older subjects showed lower accuracy when the relative spacing of contour and distracter elements was high (i.e., when contour elements were sparser than distracter elements). By varying relative spacing for contours with small and large spacing in Experiment 3, we found that the effect of aging does not depend on the absolute number or density of distracters, but rather on the relative spacing of contour and distracter elements. Previous studies have shown that contour detection is limited by the relative spacing of contour and background elements (Braun, 1999; Kovács, 1996; Kovács et al., 1999). When contour element spacing is smaller than distracter spacing, proximity and density cues may be used to locate and group the contour elements. However, when the average distracter spacing is smaller than the contour spacing, density or proximity cues are no longer available.

In that situation, contour integration is more difficult because i) the greater proximity of distracters to contour elements increases the likelihood that contour elements will be grouped with distracters instead of the neighbouring contour elements; and ii) the greater proximity of distracters to each other increases the likelihood that a chain of distractors will group together to form false-positive contours that will compete with the target contour. Thus, successful detection of the target contour depends on the grouping strength among contour elements, the grouping strength among distracters, and on the ability to select the apppropriate contour among competing alternatives. Results from Experiment 1 suggest that, even if the grouping strength among contour elements may be weaker in older subjects, the relative grouping strength between elements at different separations and orientation alignments remains unchanged. Therefore, the greater effect of relative spacing on contour integration in older subjects is likely caused by a reduced ability to segregate the contour from a cluttered background containing many competing contours.

Several investigators (e.g., Roudaia et al., 2008, 2011; Casco et al., 2011) have suggested that age-related reductions in the efficacy of inhibitory interactions in the visual cortex (Leventhal, Wang, Pu, Zhou, and Ma, 2003) may contribute to age differences in contour integration. Contour integration mechanisms are thought to be mediated by both excitatory and inhibitory interactions (Polat, 1999; Hess et al., 2003). However, the exact role of inhibition in contour integration is not well understood and future studies are needed to establish a direct link between age-related changes in inhibition and contour integration deficits.

Other possible explanations of age differences may involve changes in top-down processes that have been shown to affect contour integration (Ciaramelli et al., 2007; Li et al., 2006, 2008; Sassi et al., 2010; Nygaard, Looy, and Wagemans, 2009; Verghese, 2009). For example, Verghese (2009) provided evidence that aligned contour elements act as attentional cues for other elements with a similar orientation located on the linear extension of the contour path. Verghese suggested that this type of self-cueing mechanism can help to eliminate competing distracters in the context of a cluttered noisy background. Although the neural underpinnings of this proposed mechanism are not known, a reduction in the efficiency of such a self-cueing mechanism might explain the observed declines in contour integration with aging. In addition, other research has suggested that aging may be associated with a delay in deploying top-down suppression (Gazzaley, Clapp, Kelley, McEvoy, Knight, and D'Esposito, 2008). In the context of contour integration, a delay in top-down suppression may result in greater processing of spurious contour segments formed by distracters, which may help explain the increase in processing time needed to extract the target contour, as well as the reduced efficiency at discriminating contours in the presence of a large number of false-positive contours.

Finally, it is important to consider whether differences in cognitive strategy may have contributed to age-related differences in performance in the current experiments. For example, in the current task, subjects may be able to accurately determine the location of the tail of the spiral even on trials where they perceived only a part of the spiral if they were able to correctly extrapolate the rest of the spiral's shape. To what extent does the use of such cognitive strategies contribute to the effects of age observed in the current experiments? It can be argued that the small effect of age observed in Experiment 1 across all contour spacing conditions and orientation jitter levels may be due to differences in cognitive strategies or top-down effects. However, differences in cognitive strategies can not easily account for the increase in the effect of aging at short durations in Experiment 2, or the greater effect of relative spacing in older subjects in Experiment 3. In sum, although differences in the use of cognitive strategies may contribute to the effects of age observed in the current experiments, they are not sufficient to explain the full pattern of results.

4.6 Conclusion

The current study replicated previous findings of impaired contour integration with aging and revealed that the effect of aging does not vary with contour element spacing or with the local orientation alignment of contour elements. Instead, the effect of aging on contour integration increased with decreasing stimulus durations and when the relative spacing of contour and distracter elements was increased.

Bibliography

Altmann, C. F., Bülthoff, H. H., Kourtzi, Z., 2003. Perceptual organization of local elements into global shapes in the human visual cortex. Current Biology 13 (4), 342–349.

Amir, Y., Harel, M., Malach, R., 1993. Cortical hierarchy reflected in the organization of intrinsic connections in macaque monkey visual cortex. Journal of Comparative Neurology 334 (1), 19–46.

Bakeman, R., 2005. Recommended effect size statistics for repeated measures designs. Behavior research methods 37 (3), 379–84.

Beaudot, W. H., Mullen, K. T., 2001. Processing time of contour integration: the role of colour, contrast, and curvature. Perception 30 (7), 833–53.

Beaudot, W. H. a., Mullen, K. T., 2003. How long range is contour integration in human color vision? Visual neuroscience 20 (1), 51–64.

Bennett, P. J., Sekuler, R., Sekuler, A. B., 2007. The effects of aging on motion detection and direction identification. Vision Research 47 (6), 799–809.

Betts, L. R., Sekuler, A. B., Bennett, P. J., 2007. The effects of aging on orientation discrimination. Vision Research 47 (13), 1769–80.

Betts, L. R., Sekuler, A. B., Bennett, P. J., 2009. Spatial characteristics of center-surround antagonism in younger and older adults. Journal of Vision 9 (1), 25.1–15.

Betts, L. R., Taylor, C. P., Sekuler, A. B., Bennett, P. J., 2005. Aging reduces center-surround antagonism in visual motion processing. Neuron 45 (3), 361–366.

Brainard, D. H., 1997. The psychophysics toolbox. Spatial Vision 10 (4), 433–436.

Braun, J., 1999. On the detection of salient contours. Spatial Vision 12 (2), 211–25.

Casco, C., Robol, V., Barollo, M., Cansino, S., 2011. Effects of aging on visual contour integration and segmentation. Investigative ophthalmology & visual science 52 (7), 3955–61.

Cass, J. R., Spehar, B., 2005. Dynamics of collinear contrast facilitation are consistent with long-range horizontal striate transmission. Vision Research 45 (21), 2728–39.

Ciaramelli, E., Leo, F., Del Viva, M. M., Burr, D. C., Ladavas, E., 2007. The contribution of prefrontal cortex to global perception. Experimental brain research. Experimentelle Hirnforschung. Expérimentation cérébrale 181 (3), 427–34.

Dakin, S. C., Baruch, N. J., 2009. Context influences contour integration. Journal of Vision 9 (2), 13.1–13.

Dakin, S. C., Hess, R. F., 1998. Spatial-frequency tuning of visual contour integration. Journal of the Optical Society of America. A, Optics, image science, and vision 15 (6), 1486–99.

Del Viva, M. M., Agostini, R., 2007. Visual spatial integration in the elderly. Investigative Ophthalmology & Visual Science 48 (6), 2940–2946.

Delahunt, P. B., Hardy, J. L., Werner, J. S., 2008. The effect of senescence on orientation discrimination and mechanism tuning. Journal of Vision 8 (3), 1–9.

Dumoulin, S. O., Hess, R. F., 2007. Cortical specialization for concentric shape processing. Vision Research 47 (12), 1608–13.

Elder, J. H., Goldberg, R. M., 2002. Ecological statistics of Gestalt laws for the perceptual organization of contours. Journal of Vision 2 (4), 324–53.

Elliott, D. B., Sanderson, K., Conkey, A., 1990. The reliability of the pelli-robson contrast sensitivity chart. Ophthalmic & Physiological Optics 10 (1), 21–24.

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 (2), 173–193.

Folstein, M. F., Folstein, S. E., McHugh, P. R., 1975. ”Mini-mental state”. a practical method for grading the cognitive state of patients for the clinician. Journal of Psychiatric Research 12 (3), 189–198.

Gazzaley, A., Clapp, W., Kelley, J., McEvoy, K., Knight, R. T., D'Esposito, M., 2008. Age-related top-down suppression deficit in the early stages of cortical visual memory processing. Proceedings of the National Academy of Sciences of the United States of America 105 (35), 13122–6.

Geisler, W. S., Perry, J. S., 2009. Contour statistics in natural images: grouping across occlusions. Visual Neuroscience 26 (1), 109–21.

Geisler, W. S., Perry, J. S., Super, B. J., Gallogly, D. P., 2001. Edge co-occurrence in natural images predicts contour grouping performance. Vision Research 41 (6), 711–24.

Gilbert, C., Ito, M., Kapadia, M., Westheimer, G., 2000. Interactions between attention, context and learning in primary visual cortex. Vision Research 40 (10-12), 1217–26.

Gilbert, C. D., Wiesel, T. N., 1989. Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. The Journal of Neuroscience 9 (7), 2432–2442.

Govenlock, S. W., Taylor, C. P., Sekuler, A. B., Bennett, P. J., 2009. The effect of aging on the orientational selectivity of the human visual system. Vision Research 49 (1), 164–172.

Govenlock, S. W., Taylor, C. P., Sekuler, A. B., Bennett, P. J., 2010. The effect of aging on the spatial frequency selectivity of the human visual system. Vision Research 50 (17), 1712–9.

Habak, C., Wilkinson, F., Wilson, H. R., 2009. Preservation of shape discrimination in aging. Journal of Vision 9 (12), 18.1–8.

Hadad, B., Maurer, D., Lewis, T. L., 2010. The effects of spatial proximity and collinearity on contour integration in adults and children. Vision Research 50 (8), 772–8.

Hadad, B.-S., 2012. Sensitivity of spatial integration to perceptual cues is preserved in healthy aging. Vision Research 60, 1–6.

Hess, R. F., Beaudot, W. H., Mullen, K. T., 2001. Dynamics of contour integration. Vision Research 41 (8), 1023–1037.

Hess, R. F., Dakin, S. C., 1997. Absence of contour linking in peripheral vision. Nature 390 (6660), 602–604.

Hess, R. F., Hayes, A., Field, D. J., 2003. Contour integration and cortical processing. Journal of Physiology – Paris 97 (2-3), 105–119.

Kapadia, M. K., Ito, M., Gilbert, C. D., Westheimer, G., 1995. Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in v1 of alert monkeys. Neuron 15 (4), 843–56.

Kourtzi, Z., Huberle, E., 2005. Spatiotemporal characteristics of form analysis in the human visual cortex revealed by rapid event-related fmri adaptation. Neuroimage 28 (2), 440–52.

Kourtzi, Z., Tolias, A. S., Altmann, C. F., Augath, M., Logothetis, N. K., 2003. Integration of local features into global shapes: monkey and human fmri studies. Neuron 37 (2), 333–46.

Kovács, I., 1996. Gestalten of today: early processing of visual contours and surfaces. Behavioural Brain Research 82 (1), 1–11.

Kovács, I., Julesz, B., 1993. A closed curve is much more than an incomplete one: effect of closure in figure-ground segmentation. Proceedings of the National Academy of Sciences of the United States of America 90 (16), 7495–7497.

Kovács, I., Kozma, P., Fehér, Ákos, A., Benedek, G., 1999. Late maturation of visual spatial integration in humans. Proceedings of the National Academy of Sciences of the United States of America 96 (21), 12204–9.

Kuai, S.-G., Yu, C., 2006. Constant contour integration in peripheral vision for stimuli with good Gestalt properties. Journal of Vision 6 (12), 1412–20.

Lawrence, M. A., 2011. ez: Easy analysis and visualization of factorial experiments. R package version 3.0-0.

Ledgeway, T., Hess, R. F., Geisler, W. S., 2005. Grouping local orientation and direction signals to extract spatial contours: empirical tests of "association field" models of contour integration. Vision Research 45 (19), 2511–2522.

Leventhal, A. G., Wang, Y. C., Pu, M. L., Zhou, Y. F., Ma, Y. Y., 2003. GABA and its agonists improved visual cortical function in senescent monkeys. Science 300 (5620), 812–815.

Li, W., Gilbert, C. D., 2002. Global contour saliency and local colinear interactions. Journal of Neurophysiology 88 (5), 2846–56.

Li, W., Piëch, V., Gilbert, C. D., 2006. Contour saliency in primary visual cortex. Neuron 50 (6), 951–62.

Li, W., Piëch, V., Gilbert, C. D., 2008. Learning to link visual contours. Neuron 57 (3), 442–51.

Li, Z., 1998. A neural model of contour integration in the primary visual cortex. Neural computation 10 (4), 903–40.

Machilsen, B., Novitskiy, N., Vancleef, K., Wagemans, J., 2011. Context modulates the erp signature of contour integration. PLoS One 6 (9), e25151.

Malach, R., Amir, Y., Harel, M., Grinvald, A., 1993. Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primate striate cortex. Proceedings of the National Academy of Sciences of the United States of America 90 (22), 10469–10473.

Mandon, S., Kreiter, A. K., 2005. Rapid contour integration in macaque monkeys. Vision Research 45 (3), 291–300.

Mäntyjärvi, M., Laitinen, T., 2001. Normal values for the Pelli-Robson contrast sensitivity test. Journal of Cataract and Refractive Surgery 27 (2), 261–266.

Mathes, B., Fahle, M., 2007. Closure facilitates contour integration. Vision Research 47 (6), 818–827.

Mathes, B., Trenner, D., Fahle, M., 2006. The electrophysiological correlate of contour integration is modulated by task demands. Brain Research 1114 (1), 98–112.

Maxwell, S. E., Delaney, H. D., 2004. Designing experiments and analyzing data: a model comparison perspective, 2nd Edition. Lawrence Erlbaum Associates, Mahwah, N.J.

May, K. A., Hess, R. F., 2007. Dynamics of snakes and ladders. Journal of Vision 7 (12), 13.1–9.

McKendrick, A. M., Weymouth, A. E., Battista, J., 2010. The effect of normal aging on closed contour shape discrimination. Journal of Vision 10 (2).

Nikolaev, A. R., van Leeuwen, C., 2007. Collinearity, curvature interpolation, and the power of perceptual integration. Psychological Research 71 (4), 427–437.

Nygaard, G. E., Looy, T. V., Wagemans, J., 2009. The influence of orientation jitter and motion on contour saliency and object identification. Vision Research 49 (20), 2475–84.

Nygaard, G. E., Sassi, M., Wagemans, J., 2011. The influence of orientation and contrast flicker on contour saliency of outlines of everyday objects. Vision Research 51 (1), 65–73.

Olejnik, S., Algina, J., 2003. Generalized eta and omega squared statistics: measures of effect size for some common research designs. Psychological methods 8 (4), 434–47.

Pelli, D., Robson, J., Wilkins, A., 1988. The design of a new chart for measuring contrast sensitivity. Clinical Vision Science 2 (3), 187–199.

Pelli, D. G., 1997. The videotoolbox software for visual psychophysics: transforming numbers into movies. Spatial Vision 10 (4), 437–442.

Polat, U., 1999. Functional architecture of long-range perceptual interactions. Spatial Vision 12 (2), 143–162.

Polat, U., Sagi, D., 1993. Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. Vision Research 33 (7), 993–9.

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (http://www.R-project.org).

Rockland, K. S., Lund, J. S., 1983. Intrinsic laminar lattice connections in primate visual cortex. Journal of Comparative Neurology 216 (3), 303–18.

Roudaia, E., Bennett, P. J., Sekuler, A. B., 2008. The effect of aging on contour integration. Vision Research 48 (28), 2767–2774.

Roudaia, E., Farber, L. E., Bennett, P. J., Sekuler, A. B., 2011. The effects of aging on contour discrimination in clutter. Vision Research 51 (9), 1022–1032.

Saarinen, J., Levi, D. M., 2001. Integration of local features into a global shape. Vision Research 41 (14), 1785–1790.

Salthouse, T. A., 2000. Aging and measures of processing speed. Biological Psychology 54 (1-3), 35–54.

Sassi, M., Vancleef, K., Machilsen, B., Panis, S., Wagemans, J., 2010. Identification of everyday objects on the basis of gaborized outline versions. i-Perception 1 (3), 121–142.

Schmolesky, M. T., Wang, Y., Pu, M., Leventhal, A. G., 2000. Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. Nature Neuroscience 3 (4), 384–390.

Schumacher, J. F., Quinn, C. F., Olman, C. A., 2011. An exploration of the spatial scale over which orientation-dependent surround effects affect contour detection. Journal of Vision 11 (8), 12.

Sigman, M., Cecchi, G. A., Gilbert, C. D., Magnasco, M. O., 2001. On a common circle: natural scenes and gestalt rules. Proceedings of the National Academy of Sciences of the United States of America 98 (4), 1935–40.

Stettler, D. D., Das, A., Bennett, J., Gilbert, C. D., 2002. Lateral connectivity and contextual interactions in macaque primary visual cortex. Neuron 36 (4), 739–50.

Tanskanen, T., Saarinen, J., Parkkonen, L., Hari, R., 2008. From local to global: Cortical dynamics of contour integration. Journal of Vision 8 (7), 15.1–12.

Verghese, P., 2009. Contours in noise: a role for self-cuing? Journal of Vision 9 (13), 2.1–16.

Watt, R., Ledgeway, T., Dakin, S. C., 2008. Families of models for gabor paths demonstrate the importance of spatial adjacency. Journal of Vision 8 (7), 23.1–19.

Weale, R. A., 1963. The Aging Eye. Lewis, London.

Weale, R. A., 1982. Senile ocular changes, cell death, and vision. In: Sekuler, R., Kline, D., Dismukes, K. (Eds.), Aging and visual function. Liss, New York, pp. 161–171.

Yen, S. C., Finkel, L. H., 1998. Extraction of perceptually salient contours by striate cortical networks. Vision Research 38 (5), 719–41.

Zhang, J., Wang, X., Wang, Y., Fu, Y., Liang, Z., Ma, Y., Leventhal, A. G., 2008. Spatial and temporal sensitivity degradation of primary visual cortical cells in senescent rhesus monkeys. European Journal of Neuroscience 28 (1), 201–7.

Chapter 5

The role of orientation and position in shape perception in younger and older adults

Abstract

The perception of contour shapes is an important processing step in object recognition. Although shape perception mechanisms remain relatively unimpaired with healthy aging, older adults are less able to process orientation information across space (Wang, 2001; Roudaia, Bennett, and Sekuler, 2008). The perceived shape of a sampled contour results from a weighted combination of local element positions and orientations (Day and Loffler, 2009). Here, we examined whether younger (mean age: 24 years) and o lder (mean age: 66 years) subjects combine orientation and position information in the same way to extract the shape of sampled contours. 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 reported whether the conflicting contour (target) or a radial frequency contour (test) looked more circular. The amplitude of the test contour was varied to estimate the perceived shape of the target contour. The relative amount of position and orientation information in the target was manipulated by varying the number of Gabors comprising the target contour. Results showed that orientation information dominated the percept for contours sampled with 15–40 elements, 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 were required to discriminate between five contours: two conflicting contours, a circle, and two radial frequency patterns with different amplitudes. Consistent with Experiment 1, sensitivity (d') for discriminating between the conflicting contours and their perceptually equivalent radial frequency pattern was poor in both groups. However, older subjects showed overall poorer d' than younger subjects for all shapes, including suprathreshold radial frequency patterns. In sum, the integration of orientation and position information in shape perception of sampled contours is robust to the effects of aging. However, probing shape discrimination of sampled contour shapes revealed a small decline in sensitivity to shape differences with aging.

5.1 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 Spear, 1993; Sekuler and Sekuler, 2000; Faubert, 2002). Neurophysiological studies in senescent 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, and Leventhal, 2000; Wang, Zhou, Ma, and Leventhal, 2005; Yu, Wang, Li, Zhou, and Leventhal, 2006). Although these neurophysiological changes would be expected to produce noticeable declines in pattern vision with aging, behavioural studies in older humans have found no evidence of broader orientation or spatial frequency tuning with aging (Delahunt, Hardy, and Werner, 2008; Govenlock, Taylor, Sekuler, and Bennett, 2009, 2010), and no evidence for decreased orientation and spatial frequency discrimination ability for single gratings (Bennett, Sekuler, McIntosh, and Della-Maggiore, 2001; Betts, Sekuler, and Bennett, 2007; Delahunt et al., 2008). On the other hand, several recent studies have found age-related changes in processes that require precise integration of information across space, such as contour integration. 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 the performance of younger subjects (Saarinen and Levi, 2001), but not older subjects (Roudaia et al., 2008). Del Viva and Agostini (2007) found that older subjects show reduced sensitivity for detecting circular sampled contours embedded in a field of distractor elements. Moreover, Roudaia, Farber, Bennett, and Sekuler (2011) found that older subjects required longer stimulus exposure for detecting and discriminating high-contrast, open contours in clutter. Finally, older subjects also showed less sensitivity for detecting a displaced contour element in sampled contours embedded in clutter, and in isolated contours consisting of mixed aligned and orthogonal orientations (Casco, Robol, Barollo, and Cansino, 2011). Besides contour integration, age-related changes in curvature discrimination, bilateral symmetry detection, perceptual grouping, and perceptual completion have been reported (Legault, Allard, and Faubert, 2007; Herbert, Overbury, Singh, and Faubert, 2002; Kurylo, 2006; Richards, Bennett, and Sekuler, 2006; Salthouse and Prill, 1988).

Interestingly, the ability to discriminate closed contour *shapes* appears to be unimpaired in older age. Wang (2001) measured the minimum detectable deformation of a continuous, luminance-defined circle and found that thresholds for low-frequency radial modulations remained unchanged with aging. Habak, Wilkinson, and Wilson (2009) replicated these results and found equivalent thresholds in younger and older subjects even for very brief stimulus presentations; lateral shape interactions also had the same effect in both age groups. Habak et al. (2009) suggested that the robust nature of shape perception mechanisms may be the reason for its immunity to the effects of aging.

In a study that combined certain aspects of contour integration and shape discrimination tasks, McKendrick, Weymouth, and Battista (2010) presented subjects with sampled circles or ellipses and measured the minimum aspect ratio of the ellipse required to discriminate it from a circle. The minimum aspect ratios differed only slightly between age groups, with older subjects requiring one or two more elements than younger subjects to discriminate the global shape of the contours. At the same time, shape discrimination performance was not differentially affected in the two groups by the addition of orientation noise to the contour elements, or the addition of background cluttering elements (McKendrick et al., 2010). In sum, it appears that once elements are integrated into a closed contour, the ability to discriminate its shape remains unchanged in older age.

Recently, Day and Loffler (2009) showed that shape perception of sampled contours is based on a weighted combination of local element positions and orientations. 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.

The current study examined the effects of aging on shape perception by first examining whether orientation and position information are combined in a similar way in younger and older subjects and second, by measuring shape discrimination performance for contours differing either in orientation information, position information, or both.

5.2 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 5.1). 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.

5.2.1 Methods

Subjects

Twelve younger ($M = 25$ years; range: $19 - 32$; 6 males) and twelve older subjects ($M = 68$ years; range: $62 - 75$; 6 males) participated in Experiment 1. Subjects were compensated for their time at a rate of \$10/hour. All subjects had normal or corrected-to-normal visual acuity as assessed by the SLOAN Two Sided ETDRS Near Point Test and the 4 Meter 2000 Series Revised ETDRS charts (Precision Vision, LaSalle, Illinois, USA). Contrast sensitivity was estimated using the Pelli-Robson Contrast Sensitivity Test and all subjects showed normal contrast sensitivity for their age group (Elliott, Sanderson, and Conkey, 1990; Mäntyjärvi and Laitinen, 2001; Pelli, Robson, and Wilkins, 1988). Subjects wore their usual optical correction during vision testing and during the experiment. A general health questionnaire was also administered to screen for visual problems such as cataracts or glaucoma. None of the subjects reported any visual 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. Table 5.1 summarizes the demographic information for all subjects.

Table 5.1: Mean(SD) age,near and far Snellen decimal acuity, Pelli-Robson contrast sensitivity, and Mini-Mental State Examination (MMSE). Standard deviations are shown in parentheses.

Group	Age	Near Acuity	Far Acuity	Pelli-Robson	MMSE
Younger	25.17 (4.51)	1.36 (.24)	1.47 (.27)	1.95 (0.06)	
Older	68.25 (4.29)	1.01 (.22)	1.10 (.23)	1.94 (0.05)	29.33 (1.15)

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 in a dark room on a 21-in. Sony Trinitron monitor with 1280 × 1024 resolution (pixel size = 0.014 deg) and a refresh rate of 75 Hz. The full display subtended 18.1 × 14.5 deg visual angle at a viewing distance of 114 cm. The mean luminance of the display was 65 cd/m^2. The display was the only light source in the room. Head position and viewing distance were stabilized using a forehead/chin rest. A standard QWERTY Macintosh keyboard was used to collect subjects' responses.

Stimuli

Stimuli consisted of closed sampled contours presented against a uniform grey 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, Wilson, and Habak, 1998).

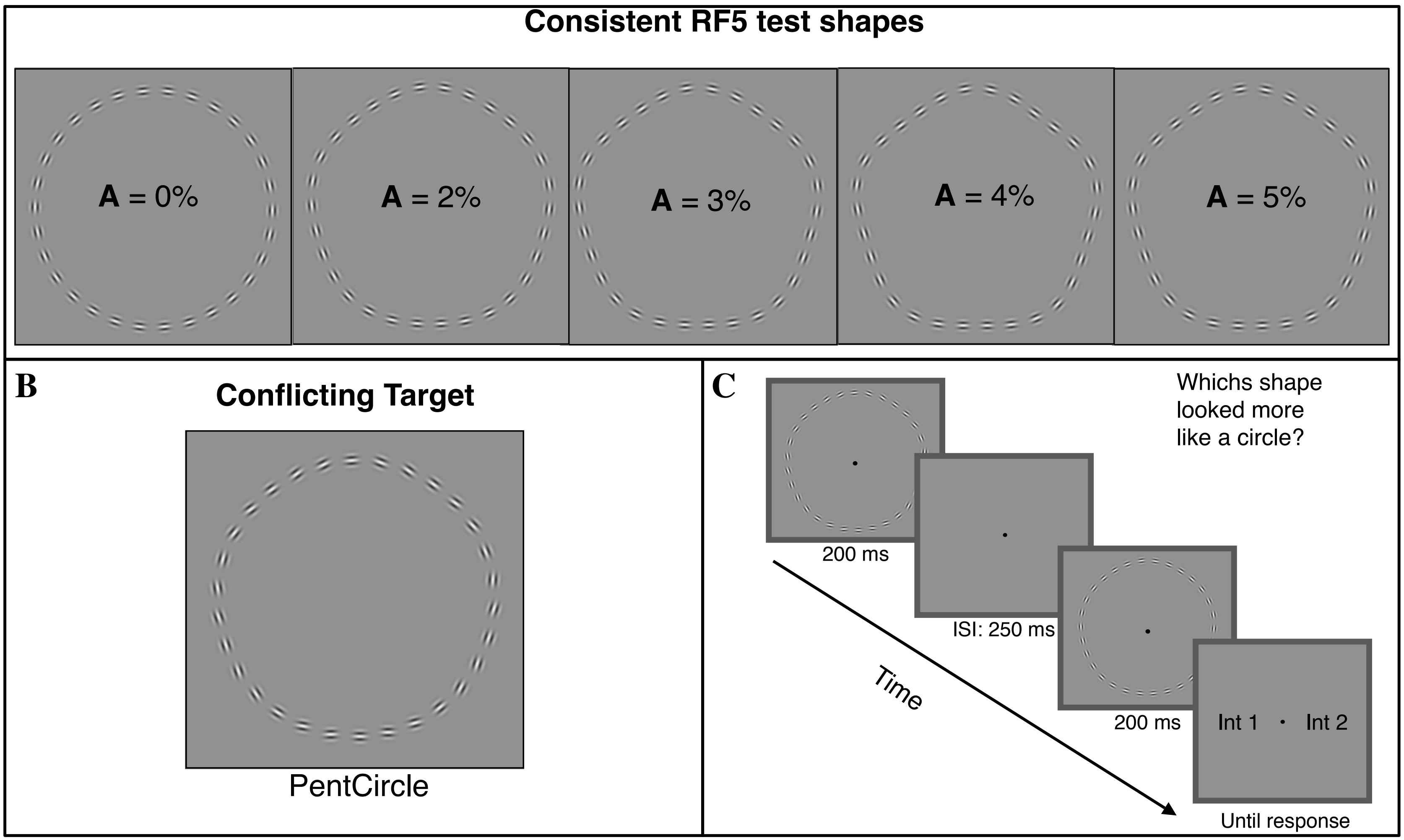
The radius of each shape can be described by the formula

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

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 *5% pentagon* or a *5% RF5 pattern*. The overall orientation of the shape was kept constant by setting the phase parameter to π. 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 5.1). 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 5.1). Thus, the positions of this contour describe a circle, but the orientations come from a 5% RF5 shape.

Figure 5.1: 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.



Procedure

The McMaster University Research Ethics Board approved the experimental protocol and written informed consent was obtained from all subjects prior to their participation.

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 inter-stimulus interval (ISI) of 250 ms (Figure 5.1). The (non-flickering) 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. The amplitude of the sampled RF5 contour that produced a shape that was perceptually equivalent to the conflicting target shape was estimated by calculating the mean of the last four reversal points of the 1-up/1-down staircase. A second estimate was obtained by estimating the 50% point on psychometric functions that were fit to the combined data from all three staircases. In most cases, the two estimates were nearly identical. However, the two estimates differed in some cases where the lower asymptote of the psychometric function fit was above 50%. This occurred when subjects judged the conflicting target to look more circular than a RF5 contour with $A = 0$ (i.e. a true circle) on a majority of the trials. This result suggests that subjects developed a response bias in those conditions, perhaps as a result of judging the RF5 patterns as less circular throughout the block. This bias was seen in 7 younger and 8 older subjects and occurred in the random orientation condition (in 4 younger and 8 older subjects) and in the 60 Gabor condition (in 7 younger and 4 older subjects). Two of the older subjects also showed this result in the 15 Gabor condition. Nevertheless, in all these cases, the 1-up/1-down staircase yielded ≥ 4 reversals. The plots and statistical analyses in the next section are based on the average of the 1-up/1-down staircase reversals, but the main results do not change if the 50% point from the psychometric function fits are used.

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

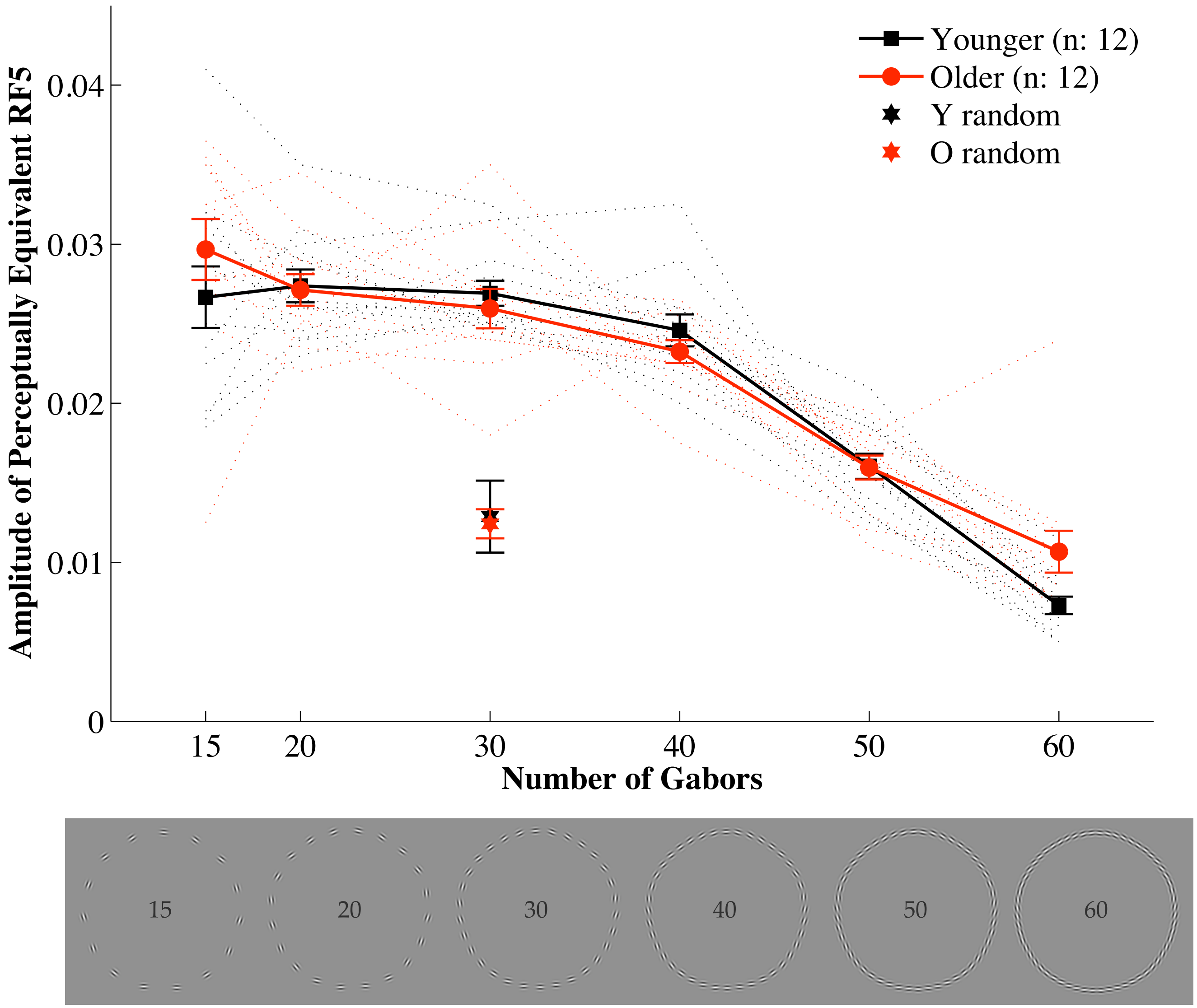


Figure 5.2: Mean amplitudes of the perceptually equivalent pentagon are shown as a function of the number of Gabors comprising the conflicting PentCircle contour for younger subjects (black, solid line) and older subjects (red, solid line). Error bars represent ±1 standard error of the mean. Dotted lines show individual subjects' performance.

5.2.2 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 as circular as the PentCircle 50% of the time. Figure 5.2 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 5.2, the illusion was present for contours sampled with 15 - 40 Gabors and disappeared 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 Age × Number of elements ANOVA revealed a significant main effect of Number of elements ($F(5, 110) = 91.9$, $\hat{\epsilon} = 0.50$, $p < 0.0001$, $\eta_g^2 = 0.77$), 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 Age × Number of elements interaction ($F(5, 110) = 1.62$, $\hat{\epsilon} = 0.50$, $p = 0.20$, $\eta_g^2 = 0.05$) 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. PEP amplitudes in the 15G, 20G, 30G, and 40G conditions differed significantly from the random condition ($p_{adj} < 0.02$ in each case) and did not differ from each other ($p_{adj} > 0.07$) for both younger and older groups. This result confirms the presence of a shape illusion in these condition and indicates that the illusion strength is comparable across these conditions. On the other hand, PEP amplitudes were significantly higher in the 40G compared to the 50G condition ($ps_{adj} < 0.004$), and in the 50G compared to the 60G condition ($ps_{adj} < 0.01$), and neither of these conditions differed from the random condition ($ps_{adj} > 0.07$) for both age groups. This result indicates that orientation information did not affect 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, unlike the current results, Day and Loffler found the strongest illusion in the 30 Gabor condition, with a weaker illusion in the 15 and 40 Gabor conditions. This difference between studies may be due to individual differences in performance. Examining individual subjects' data (Figure

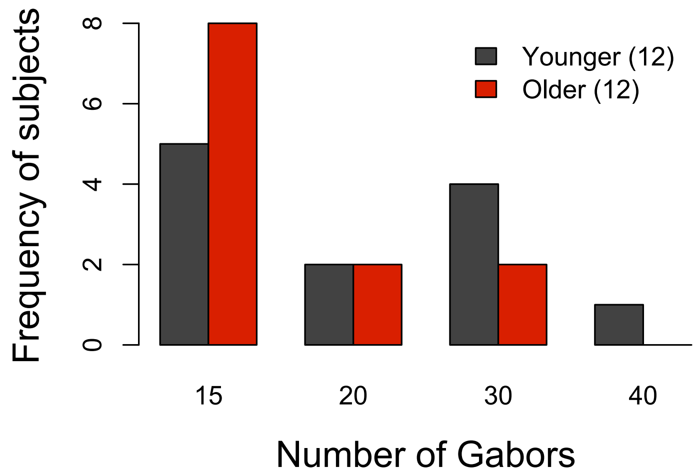


Figure 5.3: Histogram showing the number of subjects in each group who showed the largest illusion at each number of elements condition

5.2, dotted lines) reveals that the number of elements in the contour associated with the maximum illusion varies substantially across subjects. Figure 5.3 shows a histogram depicting the number of subjects who showed the strongest illusion for each condition. As can be seen, the number of Gabors composing the contour that was associated with the strongest illusion varied across subjects between 15 and 40. 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 ($\chi^2(3) = 2.36$, $p = 0.50$). Moreover, the maximum PEP amplitudes of younger subjects ($\mu = 3.05\%$) and older subjects ($\mu = 3.21\%$) also did not differ from each other ($F(1, 22) = 1.00, p = 0.33$, $\eta_g^2 = 0.043$).

5.3 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 $\approx 2.6\%$. However, it is not clear to what extent the two contours are perceptually similar on other

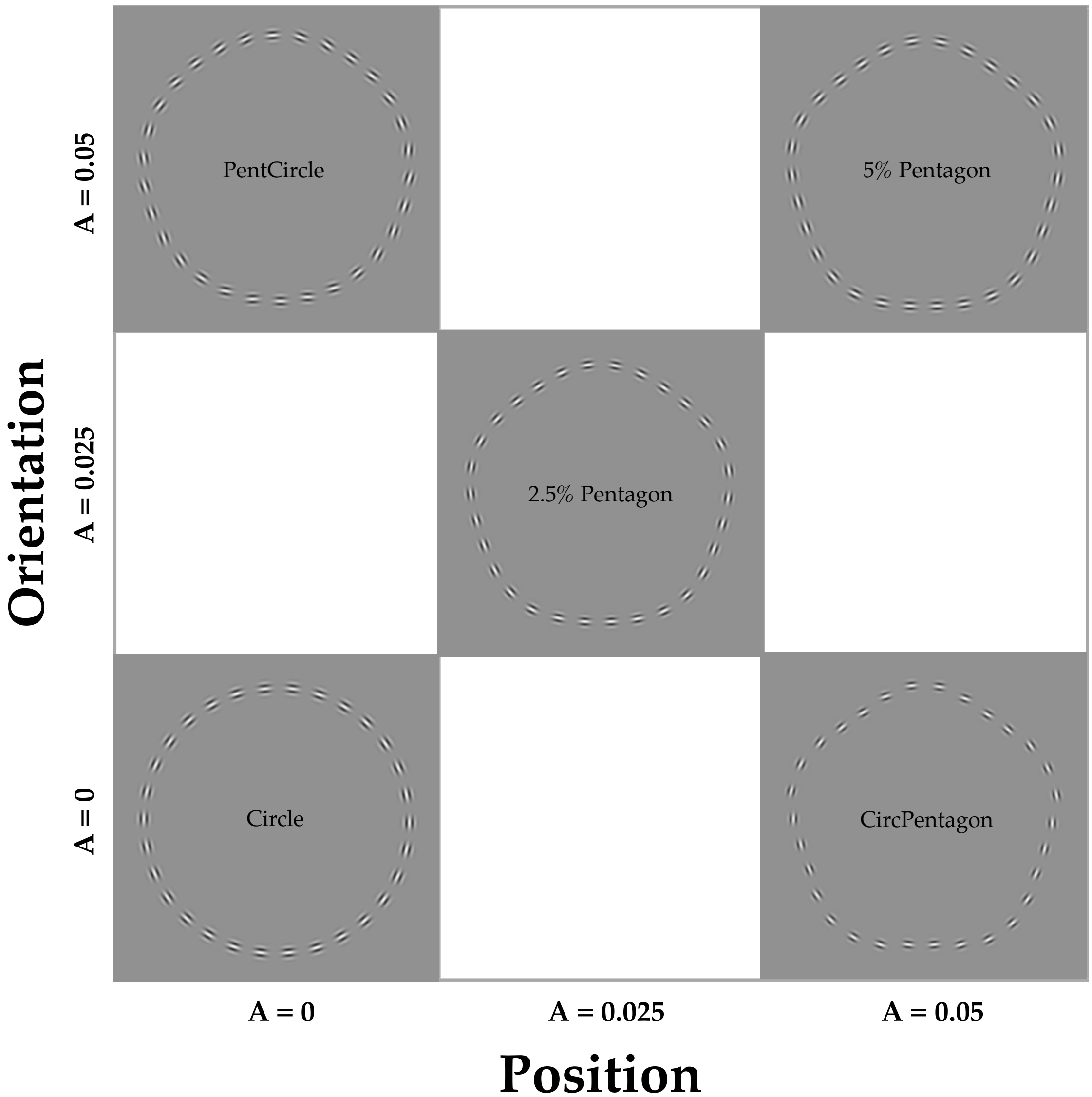


Figure 5.4: This figure shows the five patterns used in Experiment 2. Shapes on the same row but in different columns only differ by the positions of the Gabors. Shapes in the same column but in different rows only differ by the orientations of the Gabors. The amplitude of the RF5 used to generate the positions and orientations of the shapes is indicated beside each row and column.

dimensions.

The current experiment attempted to better quantify the illusion by measuring subjects' ability to discriminate between the conflicting target and its perceptually equivalent consistent contour. 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, the contours should be easily discriminable and sensitivity (i.e. d') should be high. Conversely, if the illusion is very strong, then the 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, orientations, or both positions and orientations (see Figure 5.4).

5.3.1 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 (i.e., a 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 5.4). 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 $\times$ 5 contours) and 300 different trials (30 trials $\times$ 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 judgements on local changes occurring at particular locations on the screen.

Analysis

d' was calculated using the differencing strategy for same-different tasks (Kaplan, Macmillan, and Creelman, 1978; Macmillan and Creelman, 1991, p.151). Hit rate was defined as P("different" | different trial) and False Alarm rate was defined as P("different" | same trial).

5.3.2 Results

Figure 5.5A plots mean d' values for discriminating shapes with consistent, or collinear, contours: the Circle, the 2.5% pentagon, and the 5% pentagon. Subjects in both age groups showed very good discrimination performance for these shapes. This result was expected, as the 2.5% difference in radial modulation amplitude between the shapes is several times greater than the threshold for detecting radial modulations (Wilkinson et al., 1998). There was no effect of age on d' for the circle and 5% pentagon pair ($F(1, 18) = 0.76$, $p = 0.40$, $\eta_g^2 = 0.04$) and circle and 2.5% pentagon pair ($F(1, 18) = 4.07$, $p = 0.06$, $\eta_g^2 = 0.18$), consistent with previous research showing no increase in shape discrimination thresholds with age for low radial frequency patterns (Wang, 2001; Habak et al., 2009). Interestingly, older subjects showed significantly lower d' than younger subjects for the 2.5% and 5% pentagon pair ($F(1, 18) = 12.72$, $p = 0.002$, $\eta_g^2 = 0.41$). Thus, shape discrimination between two supra-threshold radial frequency contours may be affected in older age.

Figure 5.5B shows the 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 ($F(1, 18) = 451.7$, $p < 0.0001$). The relatively poor discrimination of these contours indicates that the perceived shapes of these contours were similar. Thus, consistent with Experiment 1 and the study by Day and Loffler (2009), the orientations of the PentCircle shifted the perception of the contour shape from a circle to a rounded pentagon. Similarly, the orientations in the CircPentagon influenced the appearance of its shape and made it seem more rounded. As a result, discrimination of the PentCircle and the CircPentagon was

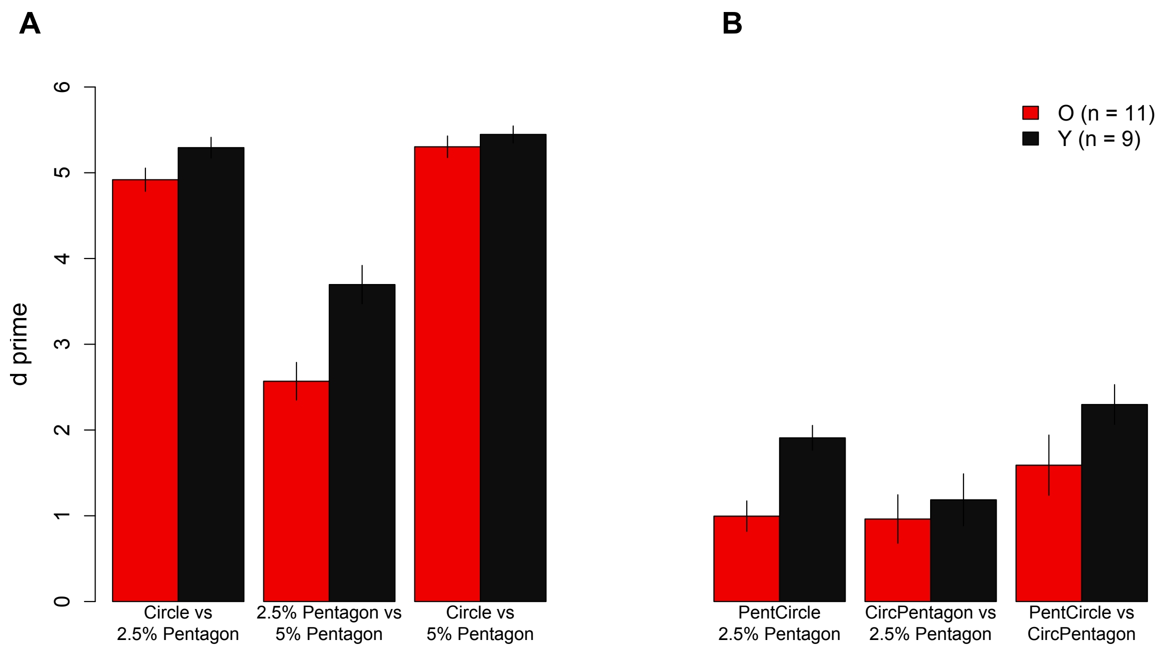


Figure 5.5: A) Mean sensitivity, d', for discriminating consistent shapes: Circle, 2.5% Pentagon and 5% Pentagon) for younger (black bars) and older (red bars) subjects. B) Mean sensitivity, d', for discriminating the 2.5% Pentagon and two conflicting shapes: the PentCircle and CircPentagon for younger (black bars) and older (red bars) subjects. Error bars represent ±1 standard error of the mean. See Figure 5.4 for shape examples.

also very poor (younger: $d' = 2.30$, older: $d' = 1.59$), especially considering the high discriminability of the corresponding consistent shapes, the Circle and 5% pentagon. Older subjects had lower d' than younger subjects for the PentCircle and 2.5% pentagon pair ($F(1, 18) = 14.9$, $p = 0.001$, $\eta_g^2 = 0.45$), but there was no significant effect of age on discrimination of the CircPentagon and 2.5% pentagon ($F(1, 18) = 0.29$, $p = 0.60$, $\eta_g^2 = 0.02$) or the PentCircle versus the CircPentagon pair ($F(1, 18) = 2.56, p = 0.13$, $\eta_g^2 = 0.12$).

Figure 5.6 compares the effect of a change in element positions versus a change in element orientations on shape discrimination. The left side of the graph shows the mean d' for two pairs of contours whose Gabor positions are the same, but whose orientations are different. The right side of the graph shows mean d' for two pairs of contours that differ by their Gabor positions, but not their orientations. A change in orientations only resulted in slightly better discrimination than a change in positions only ($F(1, 18) = 7.61$, $p = 0.01$), and this effect did not interact with Age ($F(1, 18) = 0.38$, $p = 0.55$, $\eta_g^2 = 0.02$). This result suggests that a change in orientation information was more conspicuous in this situation than a change in position information only. A greater influence of orientation compared to position on shape discrimination was also previously reported by Wang and Hess (2005).

Finally, the current results also demonstrate that performance is best for pairs containing a true circle: a focused comparison of four pairs that contained a circle versus the remaining six pairs was significant ($F(1, 18) = 402.7$, $p < 0.0001$) and this was true for both younger and older subjects ($F(1, 18) = 1.07$, $p = 0.31$).

Older subjects showed overall lower sensitivity for shape discrimination in Experiment 2, although the magnitude of the effect varied across different shape pairs. One possible explanation for decreased sensitivity may be that older subjects have a higher probability of making "finger errors". How would having a higher "finger error" rate, or lapse rate, affect d' values in this task? To answer this question, 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.

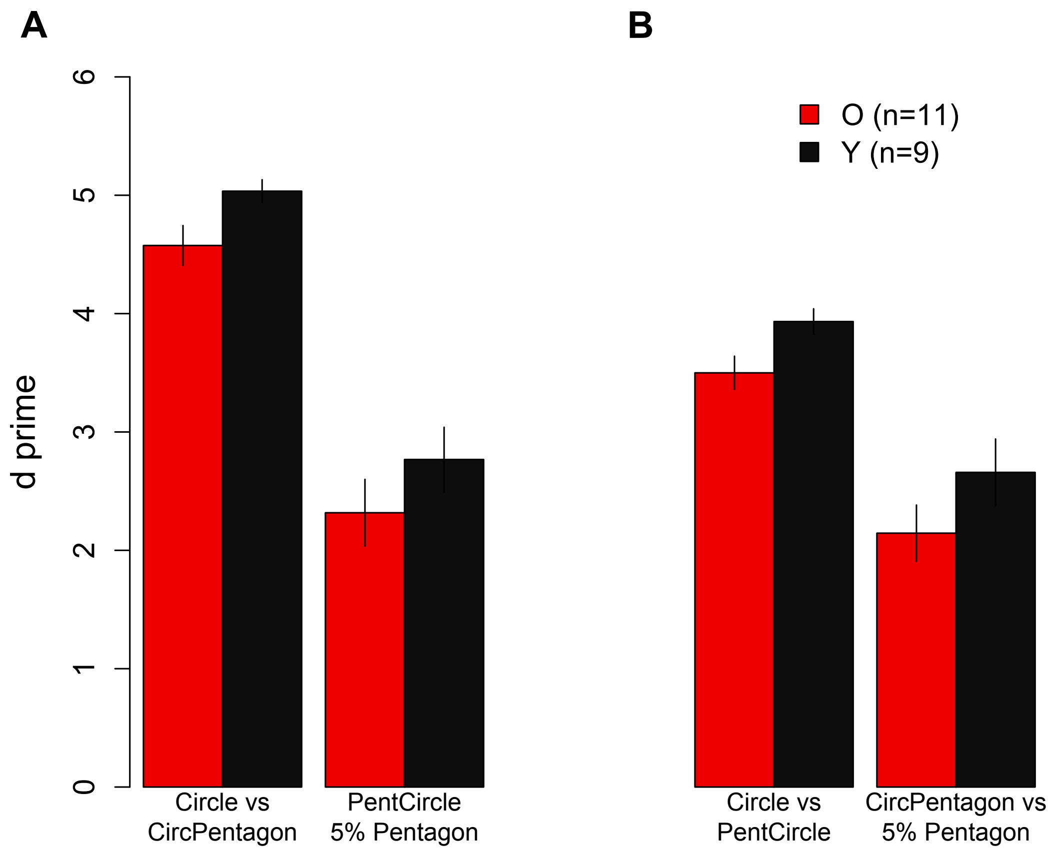


Figure 5.6: Mean sensitivity, d', for discriminating contours that differ by their Gabor positions only (A), or by their Gabor orientations only (B), for younger (black bars) and older (red bars) subjects. Error bars represent ±1 standard error of the mean.

5.4 Discussion

Experiment 1 used a shape illusion discovered by Day and Loffler (2009) to examine the roles of orientation and position information in shape perception in younger and older subjects. Consistent with Day and Loffler's findings, Experiment 1 showed that a contour whose elements were positioned on a circle, but whose orientations were consistent with a pentagon (PentCircle) appeared as a rounded pentagon. The extent to which local orientations influenced the percept depended on number (or spacing) 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 sparsely, the element orientations influenced the percept and generated the illusion of a pentagon shape. Experiment 2 demonstrated that this method can also be used to make a rounded pentagonal contour appear more circular (CircPentagon). Thus, the perceived shape of sampled contours is not uniquely determined by combining the position of elements defining the contour, but also is heavily influenced by the orientation of these elements (Day and Loffler, 2009). 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 substantially across subjects, and, on average, the average strength of the illusion was comparable for contours composed of 15 - 40 Gabors. Importantly, Experiment 1 revealed that the strength of the illusion was the same in older and younger subjects and that the effect of contour element number (or spacing) on the strength of the illusion did not differ with aging. These findings indicate that the way orientation and position information are combined in shape perception is not affected in aging.

To obtain a quantitative assessment of the illusion, Experiment 2 measured the discriminability of shapes described by conflicting and consistent contours using a same-different shape discrimination task. We found that both conflicting contours (PentCircle and CircPentagon) and the 2.5% pentagon contour appeared similar to each other, as discrimination performance was poorest for these three pairs. Older subjects showed lower d' than younger subjects when discriminating between the PentCircle and 2.5% pentagon, but showed similar sensitivity for discriminating the CircPentagon from the 2.5% pentagon pair, as well as the PentCircle from the CircPentagon. Interestingly, discrimination performance for all three pairs 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". 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 revealed that two contours that differed only in their element orientations were more discriminable than two contours that differed only in their element positions. This result is consistent with a previous study that examined the contribution of orientation and position information to shape discrimination (Wang and Hess, 2005). Radial frequency contours were sampled with Gabors such that either their positions or their orientations differentiated the contour from a true circle. Discrimination thresholds for patterns defined by element orientations were found to be lower than discrimination thresholds for patterns defined by element positions. Nevertheless, thresholds in either case were higher than those obtained when both orientation and position information were available, suggesting that both cues are used in shape discrimination. The current experiment 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 effect did not interact with age, further indicating that the influence of local orientation on shape perception is preserved with aging.

Subjects in both groups showed very high sensitivity for discriminating the true circle relative to any other contour, consistent with many previous studies showing that human vision is highly sensitive to circular shape (e.g., Achtman, Hess, and Wang, 2003; Kurki and Saarinen, 2004; Levi and Klein, 2000; Dumoulin and Hess, 2007; Wilkinson, James, Wilson, Gati, Menon, and Goodale, 2000). Previous studies examining shape perception in aging have always used shape discrimination tasks to measure the minimum radial modulation required to discriminate an ellipse, rounded square (RF4), or rounded pentagon (RF5) from a perfect circle (McKendrick et al., 2010; Habak et al., 2009; Wang, 2001). These studies have consistently found very little or no impairments in shape discrimination thresholds with age, leading to the conclusion that shape discrimination remains unimpaired in older age. Consistent with these findings, younger and older subjects showed similar sensitivity for discriminating the circle from all non-circular contours in Experiment 2.

However, older subjects were less sensitive than younger subjects at discriminating the 2.5% pentagon and 5% pentagon contours. This result is consistent with a very recent study where older subjects showed higher minimum radial modulation thresholds than younger subjects when discriminating between RF3 and RF4 radial frequency contours (Weymouth and McKendrick, 2012). Thus, it appears that the ability to discriminate between a circle and a non-circular contour remains unimpaired, whereas the ability to make fine discriminations between non-circular shapes declines with aging.

What type of mechanisms underlie shape perception of sampled contours? Day and Loffler (2009) argued the shape illusion results from the integration of orientation and position information by a global pooling mechanism, as opposed to local inter-element interactions. This conclusion was supported by experiments showing that the illusion was not affected by randomizing the contour elements' spatial scale, phase, or contrast polarity, and the fact that the strength of the illusion greatly decreased for linear contours. However, it is also possible that the shape illusion was caused by intermediate-stage mechanisms that combine orientation and position information into more complex features, such as curvature and inflection points, and these intermediate features were then pooled by the global shape mechanism (e.g., Bell, Gheorghiu, Hess, and Kingdom, 2011; Bell, Hancock, Kingdom, and Peirce, 2010). Previous research found that curvature discrimination was impaired in older subjects for two of three types of curvature tested, suggesting that aging affects the pooling of orientation signals for curvature perception (Legault et al., 2007). These changes may be related to declines in shape discrimination observed in Experiment 2.

Neurophysiological studies have shown broader tuning for orientation and direction in V1 neurons in older monkeys and cats (Schmolesky et al., 2000; Leventhal, Wang, Pu, Zhou, and Ma, 2003; Hua, Li, He, Zhou, Wang, and Leventhal, 2006). This detuning of orientation selectivity was even more pronounced in V2 (Yu et al., 2006). Moreover, older macaque neurons also showed delays in response latencies within and between V1 and V2 (Wang et al., 2005). Neurophysiological recordings in primate area V4 have shown that neurons in this area are sensitive to different curves and angles, as well as complex combinations of curves (Pasupathy and Connor, 1999, 2001; Pasupathy, 2006). Moreover, it has been shown that a population of neurons with these properties is sufficient to encode complete shapes using a population code (Pasupathy, 2006; Cadieu, Kouh, Pasupathy, Connor, Riesenhuber, and Poggio, 2007). Given that shape selective neurons in area V4 receive their inputs from these early areas V1 and V2, it would be interesting to examine the effect of aging on the shape selective neurons in area V4.

In sum, the current experiments showed that magnitude of a shape illusion generated by conflicting orientation and position information does not change with aging. Moreover, whereas sensitivity to circular shape appears unimpaired in older age, the ability to make fine shape discriminations between non-circular contours declines with aging. Future research is needed to explain these disparate findings in shape discrimination.

Bibliography

Achtman, R. L., Hess, R. F., Wang, Y.-Z., 2003. Sensitivity for global shape detection. Journal of Vision 3 (10), 616–624.

Bakeman, R., 2005. Recommended effect size statistics for repeated measures designs. Behavior research methods 37 (3), 379–84.

Bell, J., Gheorghiu, E., Hess, R. F., Kingdom, F. A. A., 2011. Global shape processing involves a hierarchy of integration stages. Vision Research.

Bell, J., Hancock, S., Kingdom, F. A. A., Peirce, J. W., 2010. Global shape processing: which parts form the whole? Journal of Vision 10 (6), 16.

Bennett, P. J., Sekuler, A. B., McIntosh, A. R., Della-Maggiore, V., 2001. The effects of aging on visual memory: evidence for functional reorganization of cortical networks. Acta Psychologica 107 (1-3), 249–273.

Betts, L. R., Sekuler, A. B., Bennett, P. J., 2007. The effects of aging on orientation discrimination. Vision Research 47 (13), 1769–80.

Brainard, D. H., 1997. The psychophysics toolbox. Spatial Vision 10 (4), 433–436.

Cadieu, C., Kouh, M., Pasupathy, A., Connor, C. E., Riesenhuber, M., Poggio, T., 2007.

A model of v4 shape selectivity and invariance. Journal of Neurophysiology 98 (3), 1733–50.

Casco, C., Robol, V., Barollo, M., Cansino, S., 2011. Effects of aging on visual contour integration and segmentation. Investigative ophthalmology & visual science 52 (7), 3955–61.

Day, M., Loffler, G., 2009. The role of orientation and position in shape perception. Journal of Vision 9, 1–17.

Del Viva, M. M., Agostini, R., 2007. Visual spatial integration in the elderly. Investigative Ophthalmology & Visual Science 48 (6), 2940–2946.

Delahunt, P. B., Hardy, J. L., Werner, J. S., 2008. The effect of senescence on orientation discrimination and mechanism tuning. Journal of Vision 8 (3), 1–9.

Dumoulin, S. O., Hess, R. F., 2007. Cortical specialization for concentric shape processing. Vision Research 47 (12), 1608–13.

Elliott, D. B., Sanderson, K., Conkey, A., 1990. The reliability of the pelli-robson contrast sensitivity chart. Ophthalmic & Physiological Optics 10 (1), 21–24.

Faubert, J., 2002. Visual perception and aging. Canadian Journal of Experimental Psychology 56 (3), 164–176.

Govenlock, S. W., Taylor, C. P., Sekuler, A. B., Bennett, P. J., 2009. The effect of aging on the orientational selectivity of the human visual system. Vision Research 49 (1), 164–172.

Govenlock, S. W., Taylor, C. P., Sekuler, A. B., Bennett, P. J., 2010. The effect of aging on the spatial frequency selectivity of the human visual system. Vision Research 50 (17), 1712–9.

Habak, C., Wilkinson, F., Wilson, H. R., 2009. Preservation of shape discrimination in aging. Journal of Vision 9 (12), 18.1–8.

Herbert, A. M., Overbury, O., Singh, J., Faubert, J., 2002. Aging and bilateral symmetry detection. The Journals Of Gerontology Series B Psychological Sciences And Social Sciences 57 (3), P241–P245.

Hua, T., Li, X., He, L., Zhou, Y., Wang, Y., Leventhal, A. G., 2006. Functional degradation of visual cortical cells in old cats. Neurobiology of Aging 27 (1), 155–162.

Kaplan, H. L., Macmillan, N. A., Creelman, C. D., 1978. Tables of d ' for variable-standard discrimination paradigms. Behavior Research Methods & Instrumentation 10 (6), 796–813.

Kurki, I., Saarinen, J., 2004. Shape perception in human vision: specialized detectors for concentric spatial structures? Neuroscience Letters 360 (1-2), 100–2.

Kurylo, D. D., 2006. Effects of aging on perceptual organization: efficacy of stimulus features. Experimental Aging Research 32 (2), 137–152.

Legault, I., Allard, R., Faubert, J., 2007. Normal aging and the perception of curvature shapes. Optometry and vision science : official publication of the American Academy of Optometry 84 (12), 1087–92.

Leventhal, A. G., Wang, Y. C., Pu, M. L., Zhou, Y. F., Ma, Y. Y., 2003. GABA and its agonists improved visual cortical function in senescent monkeys. Science 300 (5620), 812–815.

Levi, D. M., Klein, S. a., 2000. Seeing circles: what limits shape perception? Vision Research 40 (17), 2329–39.

Macmillan, N. A., Creelman, C. D., 1991. Detection theory: a user's guide. Cambridge University Press, Cambridge.

Mäntyjärvi, M., Laitinen, T., 2001. Normal values for the Pelli-Robson contrast sensitivity test. Journal of Cataract and Refractive Surgery 27 (2), 261–266.

Maxwell, S. E., Delaney, H. D., 2004. Designing experiments and analyzing data: a model comparison perspective, 2nd Edition. Lawrence Erlbaum Associates, Mahwah, N.J.

McKendrick, A. M., Weymouth, A. E., Battista, J., 2010. The effect of normal aging on closed contour shape discrimination. Journal of Vision 10 (2).

Olejnik, S., Algina, J., 2003. Generalized eta and omega squared statistics: measures of effect size for some common research designs. Psychological methods 8 (4), 434–47.

Pasupathy, A., 2006. Neural basis of shape representation in the primate brain. Progress in Brain Research 154, 293–313.

Pasupathy, A., Connor, C. E., 1999. Responses to contour features in macaque area v4. Journal of Neurophysiology 82 (5), 2490–502.

Pasupathy, A., Connor, C. E., 2001. Shape representation in area v4: position-specific tuning for boundary conformation. Journal of Neurophysiology 86 (5), 2505–19.

Pelli, D., Robson, J., Wilkins, A., 1988. The design of a new chart for measuring contrast sensitivity. Clinical Vision Science 2 (3), 187–199.

Pelli, D. G., 1997. The videotoolbox software for visual psychophysics: transforming numbers into movies. Spatial Vision 10 (4), 437–442.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0.

Richards, E. D., Bennett, P. J., Sekuler, A. B., 2006. The effects of task switching on age-related differences in shape perception. Journal of Vision 6 (6), 325–325.

Roudaia, E., Bennett, P. J., Sekuler, A. B., 2008. The effect of aging on contour integration. Vision Research 48 (28), 2767–2774.

Roudaia, E., Farber, L. E., Bennett, P. J., Sekuler, A. B., 2011. The effects of aging on contour discrimination in clutter. Vision Research 51 (9), 1022–1032.

Saarinen, J., Levi, D. M., 2001. Integration of local features into a global shape. Vision Research 41 (14), 1785–1790.

Salthouse, T. A., Prill, K. A., 1988. Effects of aging on perceptual closure. The American Journal of Psychology 101 (2), 217–238.

Schmolesky, M. T., Wang, Y., Pu, M., Leventhal, A. G., 2000. Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. Nature Neuroscience 3 (4), 384–390.

Sekuler, R., Sekuler, A. B., 2000. Visual perception and cognition. In: Evans, J., Williams, T., Beattie, B., Michel, J.-P., Wilcock, G. (Eds.), Oxford Textbook of Geriatric Medicine, 2nd Edition. Oxford University Press, New York, pp. 753–756.

Spear, P. D., 1993. Neural bases of visual deficits during aging. Vision Research 33 (18), 2589–2609.

Wang, Y., Zhou, Y., Ma, Y., Leventhal, A. G., 2005. Degradation of signal timing in cortical areas v1 and v2 of senescent monkeys. Cerebral Cortex 15 (4), 403–8.

Wang, Y. Z., 2001. Effects of aging on shape discrimination. Optometry and vision science : official publication of the American Academy of Optometry 78 (6), 447–54.

Wang, Y.-Z., Hess, R. F., 2005. Contributions of local orientation and position features to shape integration. Vision Research 45 (11), 1375–83.

Weymouth, A. E., McKendrick, A. M., 2012. Shape perception is altered by normal aging. Investigative Ophthalmology & Visual Science 53 (6), 3226–33.

Wilkinson, F., James, T. W., Wilson, H. R., Gati, J. S., Menon, R. S., Goodale, M. A., 2000. An fmri study of the selective activation of human extrastriate form vision areas by radial and concentric gratings. Current Biology 10 (22), 1455–8.

Wilkinson, F., Wilson, H. R., Habak, C., 1998. Detection and recognition of radial frequency patterns. Vision Research 38 (22), 3555–68.

Yu, S., Wang, Y., Li, X., Zhou, Y., Leventhal, A. G., 2006. Functional degradation of extrastriate visual cortex in senescent rhesus monkeys. Neuroscience 140 (3), 1023–1029.

Chapter 6

General Discussion

This dissertation investigated the effects of healthy aging on perceptual organization, in particular, the integration of local orientation information across space to form elongated contours and shapes. The ability to quickly and effortlessly group separate elements of the visual scene to form extended contours is an important step in the process of translating the patterns of light falling on the retina into meaningful objects and shapes. Some of the ways in which information can be combined across space include single first-order linear filters that average the information falling within their receptive field (Hess and Dakin, 1997), local non-linear interactions between adjacent linear filters (e.g., Field, Hayes, and Hess, 1993; Polat and Sagi, 1993), and global non-linear interactions by that pool orientation information from neighbouring and distant locations (e.g., Achtman, Hess, and Wang, 2003; Wilkinson, Wilson, and Habak, 1998; Gheorghiu and Kingdom, 2009). The research presented in the previous chapters suggests that aging affects some, but not all aspects of the above mechanisms. In this chapter, I will outline the main findings and conclusions from this research, identify some remaining open questions, and provide suggestions for future research.

6.1 Contour and shape perception in the absence of clutter

6.1.1 Local interactions

In Chapter 2, we evaluated contour grouping using stimuli that did not contain any visual noise or clutter (e.g., Sekuler and Ball, 1986). Contour grouping was assessed by comparing the contrast threshold required to locate the gap in a Landolt-C contour composed of Gabor elements whose orientations were aligned, orthogonal, or mixed (i.e., alternating aligned and orthogonal) with the “C” shape. Younger, but not older, subjects showed evidence of contour grouping, as their thresholds for contours composed of aligned Gabors were significantly lower than thresholds for contours composed of orthogonal or mixed Gabors. Greater sensitivity to aligned contours is thought to be a result of local interactions among neighbouring orientation-tuned filters whose receptive fields are co-axial with their orientation preference (Bonneh and Sagi, 1998; Saarinen and Levi, 2001). Thus, the absence of contrast facilitation for aligned contours in older subjects is consistent with the hypothesis that local interactions between orientation-tuned filters change with aging (Roudaia, Bennett, and Sekuler, 2008).

Lateral interactions between orientation-tuned filters also have been proposed to underlie *collinear facilitation* (Polat and Sagi, 1994), an effect characterized by a reduction in contrast detection threshold for a target Gabor when it is positioned in-between two high-contrast Gabors, so that the three Gabors form a collinear configuration (Polat and Sagi, 1993). Contrast facilitation is greatest when target and flankers are separated by $\approx$3-4 cycles and declines for larger distances, or when flankers are non-collinear with the target (Polat and Sagi, 1993). Some researchers have argued that the lateral interactions underlying collinear facilitation are the same interactions that allow the integration of high-contrast contours embedded in a field of distracter elements as in the path paradigm (Polat, 1999; Li and Gilbert, 2002; Polat and Bonneh, 2000; Sterkin, Sterkin, and Polat, 2008). However, this view has proven to be controversial because, unlike collinear facilitation, contour integration operates across depth, can link elements with alternating contrast polarity, and is not associated with perceptual contrast enhancement of contour elements (Hess, Dakin, and Field, 1998; Huang, Hess, and Dakin, 2006; Williams and Hess, 1998). In light of the latter position, some researchers have suggested that the deficits in contour grouping that we reported in Chapter 2 (Roudaia et al., 2008) may reflect age differences in collinear facilitation (Casco, Robol, Barollo, and Cansino, 2011) rather than contour integration at high contrast (McKendrick, Weymouth, and Battista, 2010).

If the reduced contrast thresholds for aligned contours seen in Chapter 2 are mediated by collinear facilitation, then the absence of contrast facilitation in the aligned condition in older adults would predict significantly weaker, or even absent, collinear facilitation in older adults. Alternatively, older adults may show collinear facilitation that is very broadly tuned for flanker orientation, resulting in similar contrast enhancement in orthogonal and aligned conditions. To verify these possibilities, we recently conducted two additional experiments to measure collinear facilitation as a function of target-flanker separation and target-flanker orientation alignment in younger ($n = 10$; mean age: 23.5 years) and older subjects ($n = 10$; mean age: 68.4 years) using the methods described by Polat and Sagi (1993). In Experiment 1, we estimated contrast detection thresholds for a small, vertical Gabor placed between two high-contrast collinear Gabors at targer-flanker distances ranging from $0.75 - 6\lambda$ in two spatial frequency conditions (Gabor $\lambda = 0.3$ and $0.15\,\text{deg}$; $\sigma = \lambda/2$; flanker contrast $= 0.4$; stimulus duration $= 0.06\,\text{s}$). We found significant contrast facilitation for flankers at 3 and $6\,\lambda$ for both spatial frequency conditions. Importantly, the magnitude of facilitation did not differ between the two age groups. In Experiment 2, we measured contrast detection thresholds for a vertical Gabor in the presence of two high-contrast flankers placed $3\,\lambda$ above and below the target and oriented at $0°$, $15°$, $30°$, $45°$, or $90°$ counter-clockwise of vertical. Here again, both groups showed significant contrast facilitation when the flankers were collinear. This effect declined with increasing flanker orientation offset, but the rate of decline did not differ between age groups.

Chan, Battista, and McKendrick (2012) also examined collinear facilitation in younger and older subjects in two very similar experiments with slightly different stimulus parameters (Gabor $\lambda = 0.33\,\text{deg}$, $\sigma = \lambda$, stimulus duration $= 0.1\,\text{s}$, flanker contrast $= 0.6$, target-flanker separations = 2-6 λ). Similar to our findings, both groups showed evidence of facilitation for separations of 3.5-6 λ, with peak facilitation occurring at $\approx 4\lambda$. Furthermore, the tuning of contour facilitation to flanker orientation also did not differ between age groups. On the other hand, contrary to our findings, Chan et al. found that older subjects showed slightly weaker facilitation than younger subjects. This difference between experiments may be due to differences in stimulus parameters.

Together, these two studies revealed that collinear contrast facilitation peaks at a similar target-flanker distance and shows a similar tuning for flanker orientation in older and younger subjects. The strength of contrast facilitation appears to be either the same (our experiment), or slightly weaker (Chan et al., 2012), in older subjects. In contrast, subjects with schizophrenia, who also show deficits in contour integration, showed no evidence of collinear facilitation at any target-flanker distance (Kéri, Kelemen, Benedek, and Janka, 2005). Thus, it is unlikely that the absence of contrast enhancement for discriminating aligned contours observed in older subjects (Roudaia et al., 2008) was caused by deficits in collinear facilitation.

6.1.2 Global interactions

As suggested by Saarinen and Levi (2001), contrast enhancement for aligned contours could be mediated by higher-order neurons in areas V2 and V4 that are tuned to global stimulus features, such as curvature or circularity (Gallant, Connor, Rakshit, Lewis, and Van Essen, 1996; Hegdé and Van Essen, 2000; Pasupathy and Connor, 1999). Contours with aligned local orientations may be more effective at activating these global mechanisms than contours with orthogonal or mixed local orientations, resulting in lower contrast thresholds for aligned contours. There is increasing evidence that activity of early visual neurons to stimuli within their receptive fields is modulated not only by information falling in neighbouring locations outside the receptive field, as in collinear facilitation (Polat and Sagi, 1994), but also by the global stimulus context. The influence of global context was demonstrated convincingly by Joo, Boynton, and Murray (2012) who found that the neural response (assessed psychophysically, electrophysiologically, and via BOLD response) to a central vertical Gabor was greater when the target deviated from its global context, compared to when it was consistent with its global context, even though its immediately adjacent context was identical. These findings reveal that neural activity in early visual areas is a non-linear function of both its local and global context, indicating that feedback from higher-order areas tuned to global shapes may influence local interactions very early in processing. Thus, the absence of contrast enhancement for aligned contours in older subjects in Chapter 2 may have been caused by changes in the sensitivity of neurons tuned to global circular shape, to delays in their feedback inputs, or to changes in the interaction between lateral and feedback connections.

In Chapter 5, we examined how the orientations of elements in a sampled, closed contour influence the perception of the contour's shape in younger and older subjects. Our results confirmed the findings of Day and Loffler (2009) by showing that contour shape

– defined by the smooth path connecting the centroids of its constituent elements – is influenced by local orientations, unless the contour is sampled very densely. Interestingly, the effect of orientation on shape perception was identical in younger and older subjects. These results showed that the integration of local orientation information across space in shape perception does not change with aging.

Previous studies have assessed the effect of aging on global shape mechanisms by measuring shape discrimination thresholds for radial frequency patterns (Wang, 2001; Habak, Wilkinson, and Wilson, 2009; McKendrick et al., 2010). These studies found that the minimum radial modulation required to discriminate a deformed circular contour from a perfect circle did not change with aging, even when lateral shape probes were used to modulate the magnitude of shape discrimination thresholds, or when stimulus exposure duration was varied (Habak et al., 2009). There results were interpreted as evidence that global shape mechanisms are not affected in aging. However, it is still not clear whether shape discrimination thresholds in radial frequency patterns reflect the activity of global shape mechanisms (Wilkinson et al., 1998) or whether local contour mechanisms may be sufficient to account for performance (Mullen, Beaudot, and Ivanov, 2011).

When we measured subjects' sensitivity to differences in contour shape (Chapter 5, Figure 5.5A, middle bars), older subjects were less able to discriminate two rounded pentagons that differed in the amplitude of their radial modulation by 2.5% - an amplitude much larger than the radial modulation thresholds found by Habak et al. (2009). On the other hand, consistent with previous findings, sensitivity did not differ between age groups when subjects discriminated a circular contour from other shapes (see Chapter 5, Figure 5.5A and 5.6). Another recent study also found that thresholds for discriminating between two different radial frequencies were higher in older subjects Weymouth and McKendrick (2012). Thus, aging appears to affect the ability to discriminate two non-circular shapes, but not the ability to discriminate between a circle and a non-circle. However, this conclusion is based on a comparison across different studies and subject groups. Further research is needed to confirm this differential effect by testing the same group of subjects and with similar stimuli and tasks.

6.2 Contour and shape perception in the presence of clutter

6.2.1 Effects of contour parameters

In Chapters 3 and 4, we examined effects of aging on the ability to extract contours embedded in a cluttered field of distracters. In all experiments that required detecting a contour or discriminating its global orientation, older subjects showed poorer performance than younger subjects, either by showing overall poorer accuracy (Chapter 4), or requiring longer stimulus durations to achieve a certain level of accuracy (Chapter 3). These results are similar to previous reports that older subjects are more sensitive to the presence of distracters when detecting (Del Viva and Agostini, 2007) or discriminating (Hadad, 2012) closed contours embedded in noise.

The perception of contours embedded in clutter is thought to rely on local interactions between adjacent elements, as it would be computationally inefficient for the visual system to have developed global mechanisms tuned to every possible elongated contour shape (Field et al., 1993). Two of the main characteristics of these local interactions are that they are highly sensitive to the co-alignment of local orientation with the contour path (i.e., collinearity), and that they operate over a limited spatial range (for review, see Hess, Hayes, and Field, 2003). The spatial phase of contour elements also influences performance: although contour detection accuracy is still very high for contours composed of elements with alternating contrast polarity, contour detection accuracy is significantly higher for contours comprising elements with the same spatial phase. Thus, the detection of contours in clutter can be based on phase-selective or phase-insensitive processes (Field, Hayes, and Hess, 2000).

Experiments in Chapter 3 examined whether aging affects the phase-sensitive process on contour integration by comparing stimulus duration thresholds for detecting and discriminating collinear contours having either the same spatial phase (aligned condition) or spatial phase that alternated by 180 deg (phase condition). The results showed that the improvement in performance in the aligned condition compared to the phase condition was similar in both age groups, suggesting that the phase-sensitive process underlying contour grouping in not impaired in older age. Seeing that collinear facilitation is also phase-selective, Field et al. (2000) suggested that the phase-selective process involved in contour integration may be the same process that underlies collinear facilitation. If so, then it is perhaps not a coincidence that we find no age differences in collinear facilitation and also no age differences in the contribution of the phase-sensitive process to contour integration in clutter.

We examined whether aging affects the sensitivity of lateral interactions to collinearity and proximity in Chapter 4 by parametrically varying orientation alignment and contour element spacing, while controlling for the other stimulus parameters known to affect younger and older subjects differently (i.e., relative noise density and stimulus duration), and found that the effects of contour element collinearity and proximity did not differ between age groups. In other words, the deficit in contour integration does not depend on the distance over which contour elements must be integrated, or on the level of co-alignment of contour element orientations. These findings are consistent with two other studies, where disruption of contour element collinearity had a similar detrimental effect on younger and older subjects' performance in a shape discrimination task (McKendrick et al., 2010) and for discriminating contours with small and large element spacings (Hadad, 2012).

In sum, converging evidence from several studies using different stimuli and tasks suggests that age-related deficits in the perception of contours in noise are not caused by deficits in the *integration* mechanism (Casco et al., 2011; McKendrick et al., 2010; Roudaia, Farber, Bennett, and Sekuler, 2011; Hadad, 2012). In contrast, changes in the integration mechanism have been linked to changes in contour perception that have been observed in several other populations. For example, adults with dyslexia consistently show lower tolerance for disruptions in contour element collinearity for stimuli with low and high levels of background density (Simmers and Bex, 2001). Persons with schizophrenia also show lower tolerance for disruptions in collinearity, which is accompanied by poorer processing of local orientation of isolated contour elements (Butler, Silverstein, and Dakin, 2008; Robol, Anderson, Tibber, Bobin, Carlin, Shergill, and Dakin, 2012a). On the other hand, similar to what we found with older subjects, the spatial range of contour integration is not affected in adults with schizophrenia (Keane, Silverstein, Barch, Carter, Gold, Kovács, Macdonald, Ragland, and Strauss, 2012). Only children have shown poorer grouping ability across larger distances (Kovács, Kozma, Fehér, and Benedek, 1999; Hadad, Maurer, and Lewis, 2010), with suggests that once the long-range cooperative interactions are set up in development, they remain in place in adulthood into older age.

6.2.2 Effects of background noise

Perceiving contours embedded in a field of distractors requires not only the ability to group contour elements together, but also the ability to segregate the contour from the background. Integration of contour elements and segregation of the contour from the background have often been discussed as two separate processes (e.g., Casco et al., 2011) and some researchers have suggested that age-differences in performance in contour perception tasks are caused by an inability to segregate the contour from noise or to suppress irrelevant local orientations (Hadad, 2012; Casco et al., 2011). However, even if integration and segregation constitute separate mechanisms, the two processes must be interdependent and their dynamics must overlap, making it difficult for any given paradigm to unambiguously distinguish the contributions of these two processes to performance in different age groups.

In Chapter 4, we approached this question by parametrically varying contour and background stimulus parameters separately and examining their effects on contour discrimination performance in younger and older subjects. Instead of comparing absolute age-differences in performance in different conditions, we examined the pattern of effects of contour and background parameters on performance in the two groups. Our results revealed that the age-difference in contour discrimination performance is not systematically related to the absolute number or absolute density of distractors, or the mere presence of distractors. Instead, we showed that older subjects are disproportionately affected by change in the relative spacing between contour elements and randomly-oriented background elements. In contrast, varying the relative spacing of contour and background elements does not have a differential effect on contour discrimination in adults with dyslexia (Simmers and Bex, 2001) or adults with schizophrenia (Keane et al., 2012). What kind of mechanism can account for this increased sensitivity to the relative spacing of contour and background elements in older age? Some potential causes that were discussed in the General Discussion in Chapter 4 include reduced efficiency at segregating the target contour from competing false-positives, changes in attentional self-cueing (Verghese, 2009), or deficits in top-down processes (Gazzaley, Clapp, Kelley, McEvoy, Knight, and D'Esposito, 2008).

Another potential cause underlying the increased sensitivity to the influence of distractors in aging may be related to crowding, as recent studies have proposed that crowding and contour integration may be related (Chakravarthi and Pelli, 2011; May and Hess, 2007; Robol, Casco, and Dakin, 2012b). Crowding refers to the phenomenon where discrimination, but not detection, of a particular target feature is disrupted by the presence of adjacent flankers (Levi, 2008). Robol et al. (2012b) measured orientation discrimination of a single target Gabor in the context of two flankers that were randomly oriented, or oriented parallel or orthogonal relative to the target and found that the variation in crowding strength produced by these types of flankers could account for the differential effects of parallel, orthogonal and randomly-oriented background contexts in a contour localization task. Robol et al. suggested therefore that the effect of background context on contour integration is mediated by crowding: background elements crowd contour elements and consequently increase the orientation uncertainty of contour elements, making it more difficult to group contour elements into a perceptual unit. This model accounts well for the effect of relative contour and distracter element spacing on contour integration performance, because crowding is known to increase with proximity of flankers to the target.

If crowding strength at any given target-flanker distance increases with aging, then flankers would start crowding contour elements at smaller target-flanker distances, thereby affecting contour discrimination at lower contour-distracter relative spacings. Thus, changes in crowding strength with aging could explain age-related deficits in contour integration. Unfortunately, the effect of aging on crowding has not been examined extensively. The only published study measured crowding by comparing acuity of a Landolt C at two eccentricities with and without lateral flankers (Scialfa, Cordazzo, Bubric, and Lyon, 2012). Although the absolute increase in logMAR acuity due to crowding was greater in older subjects subjects, the ratio of acuity with and without flankers did not change with aging. Another study from our lab examined crowding by comparing orientation discrimination of a target Gabor with and without the presence of eight surrounding Gabors. Preliminary results showed that older subjects experienced stronger crowding than younger subjects (Govenlock, 2010, p. 119). Future studies should measure crowding and contour integration using similar stimuli in the same subjects to determine if there is a direct relationship between the effect of aging on contour integration and crowding. Finally, it's important to note that the mechanisms underlying crowding are still poorly understood (Levi, 2008). Therefore, if the deficit in contour integration with aging is found to be caused by crowding, this result would link two concepts together, but would not explain the mechanism itself.

6.2.3 Inhibition

Phillips and Silverstein (2003) proposed that contour integration deficits in schizophrenia are manifestations of a general reduction in cognitive coordination caused by reduced activation of NMDA receptors and associated reductions in the activity of GABAergic inhibitory interneurons (see Silverstein and Keane, 2011). Neurophysiological studies in the visual cortex of older cats and primates have suggested that aging is also associated with reduced efficiency of GABAergic inhibitory function (Schmolesky, Wang, Pu, and Leventhal, 2000; Leventhal, Wang, Pu, Zhou, and Ma, 2003; Hua, Kao, Sun, Li, and Zhou, 2008). Older adults and subjects with schizophrenia show evidence of reduced surround suppresion in motion direction-discrimination (Betts, Taylor, Sekuler, and Bennett, 2005; Tadin, Kim, Doop, Gibson, Lappin, Blake, and Park, 2006). Thus it is possible that inhibitory deficits may be the cause of contour integration declines in aging and in schizophrenia. However, given that the role of inhibition in contour integration is not well understood, these suppositions are necessarily speculative.

6.3 Further research

6.3.1 Perceptual learning

Practice in a perceptual task improves performance in younger and older subjects and can, in some circumstances, reduce or eliminate age-related differences in performance (e.g., Ball and Sekuler, 1986; Sekuler and Ball, 1986; Richards, Bennett, and Sekuler, 2006; Legault and Faubert, 2012). Although training benefits in some studies were specific to the trained stimulus and task (e.g., Ball and Sekuler, 1986), other studies found that training benefits transfered to different, untrained stimuli (Neider, Boot, and Kramer, 2010), or even to entirely different tasks (Legault and Faubert, 2012).

Previous studies with children, young adults, and adult monkeys have shown that contour integration performance can be improved with practice, but the training benefits appear to be stimulus-specific (Kovács et al., 1999; Schwarzkopf and Kourtzi, 2008; Li, Piëch, and Gilbert, 2008). Li et al. (2008) trained two adult monkeys to detect contours composed of line segments embedded among randomly-oriented lines. Both monkeys successfully learned to detect the contours after ten sessions and this behavioural improvement was accompanied by the emergence of a contour-related neural response in

V1 neurons. However, when the stimuli were presented in an untrained location, contour detection accuracy and the contour-related V1 response were not different from pre-training levels. Kovács et al. (1999) trained 5-6 year old children and young adults to detect closed contours embedded in a field of distracters of varying density. Subjects were trained to detect contours that were defined either by a local orientation cue or by a colour similarity cue. All subjects showed improvements in performance after only three training sessions, but those who trained on orientation-defined contours did not improve on the colour-defined contours, and vice-versa. Finally, Schwarzkopf and Kourtzi (2008) trained subjects to detect contours composed of orthogonally-oriented Gabors embedded in a field of randomly-oriented Gabors. Contour salience was manipulated by adding local orientation jitter to contour elements. Training dramaticaly improved contour detection accuracy and orientation jitter thresholds for orthogonal contours, however, the training benefits did not transfer to detection of contours composed of collinear or oblique orientations, suggesting that learning specifically improved grouping of orthogonal contours, as opposed to improving a general ability to extract patterns from a noisy background.

Nevertheless, a growing number of studies are showing successful transfer of perceptual learning to untrained stimuli and tasks, especially in situations where the training and transfer tasks engage similar cortical mechanisms. For example, McGovern, Webb, and Peirce (2012) trained three groups of subjects on either an orientation discrimination task, a curvature discrimination task, or a global shape coherence task and tested for improvements in performance in the other two tasks. Training on orientation discrimination improved curvature discrimination and vice versa, and training on the global coherence task improved performance on curvature discrimination. The success of learning transfer can be attributed to a few factors. First, the stimuli in all three tasks consisted of arrays of randomly positioned Gabor elements of the same size and spatial frequency, increasing the likelihood that the same neuronal populations were active in all tasks. Second, all three tasks required the integration of local orientation information across space. Thus, training may have improved the overall efficiency of integrative processes, for example, by increasing the weighting on inputs arriving from he most informative or reliable orientation filters (McGovern et al., 2012).

It is likely that practicing to detect or discriminate contours in clutter can improve performance in older adults. It is less clear whether the benefits of training will extend to other stimuli and tasks, ultimately improving perceptual function in real life contexts. Results in Chapters 3 and 4 demonstrate that age-differences in performance are greatest when distracter elements are very close to contour elements, and when stimulus durations are very short. Thus, it would be useful to improve contour discrimination in dense backgrounds. For example, subjects could practice discriminating the global orientation of a collinear spiral contour (as in Chapter 4) with increasing levels of relative contour-distracter spacing. Although we would expect to see improvements in overall accuracy at discriminating the spiral contour in dense backgrounds, it would be important to test for transfer to different contour shapes and to non-collinear contours. Moreover, if the training paradigm presented stimuli for a long stimulus duration, would an improvement in accuracy at long stimulus durations necessarily result in a decrease in duration thresholds for contour discrimination? Finally, if cortical mechanisms underlying crowding and contour integration are the same (Chakravarthi and Pelli, 2011; May and Hess, 2007; Robol et al., 2012b), improving contour integration performance may reduce crowding and vice versa. Recently, a perceptual learning paradigm successfully reduced crowding in amblyopes and in the periphery in healthy young adults (Hussain, Webb, Astle, and McGraw, 2012), suggesting that cortical mechanisms underlying crowding are flexible and can be modified through experience in adulthood. Thus, training crowding may be another potential approach to reducing contour integration deficits in aging.

6.3.2 Electrophysiological correlates of contour integration

Although behavioural measures can provide a lot of information on age-related changes in visual processing, they have limitations. In particular, behavioural measures do not provide direct information on the brain areas or networks that are used to complete the task. This lack of information is important because previous studies have shown that equivalent behavioural performance in younger and older subjects can be associated with activity in different brain areas and neural networks across the two groups (Della-Maggiore, Sekuler, Grady, Bennett, Sekuler, and McIntosh, 2000; McIntosh, Sekuler, Penpeci, Rajah, Grady, Sekuler, and Bennett, 1999; Bennett, Sekuler, McIntosh, and Della-Maggiore, 2001). In one study, older subjects who showed high performance in a face-matching task engaged a network of brain areas that was not activated in younger adults or low-performing older adults (Lee, Grady, Habak, Wilson, and Moscovitch, 2011), suggesting that good performance in face-matching relies on the engagement of compensatory mechanisms in older age. Compensatory mechanisms may also be involved in perceptual organization. One study used positron emission tomography (PET) to examine the regional cerebral blood flow (rCBF) in younger and older subjects while they viewed two types of patterns: one type was composed of black and white rectangular patches with a random arrangement and the other type contained black and white patches that were arranged to form extended vertical or horizontal structure (Levine, Beason-Held, Aronchick, Optican, Alexander, Horwitz, Rapoport, and Schapiro, 2000). The results showed that the brain regions that showed differential rCBF to the two types of patterns differed across the two groups: whereas occipital and temporal regions were primarily involved in younger subjects, occipital and frontal regions were involved in older subjects. Although it is possible that older subjects activated frontal regions to compensate for deficits in occipito-temporal regions, it is impossible to make that conclusion without verifying the relationship between the frontal activity and perceptual organization.

Are there age-related changed in the neural processes associated with contour integration? To what extent do compensatory mechanisms contribute to the older subjects' performance? Examining the electrophysiological correlates of contour integration can reveal age-differences in the timecourse of activity related to perception of contours as well as any global differences in brain areas recruited for the task. Previous studies have identified an occipital negativity around 130 ms post stimulus onset that was related to the presence of a contour, whose amplitude and latency is modulated by the salience of the contour (Mathes, Trenner, and Fahle, 2006) and the background context (Machilsen, Novitskiy, Vancleef, and Wagemans, 2011). In addition, a frontal selection positivity was also observed when contour stimuli were preceded by a mask, suggesting that top-down attentional resources are specifically engaged when task conditions are difficult (Mathes et al., 2006).

Given that performance in contour integration tasks depends on many stimulus parameters whose effects interact with age, comparing performance across groups using traditional ERP methods may be problematic (Rousselet and Pernet, 2011). On the other hand, using single trial analysis combined with a parametric manipulation of several stimulus parameters can be a powerful tool for examining the influence of image structure and task requirements on the EEG signal. This approach was used in two recent studies to demonstrate an age-related delay in the sensitivity to noise in a face-discrimination task (Rousselet, Gaspar, Pernet, Husk, Bennett, and Sekuler, 2010; Rousselet, Husk, Pernet, Gaspar, Bennett, and Sekuler, 2009). Using a similar parametric approach and single trial analysis, future studies can examine the effects of different stimulus parameters such as contour and background elements spacing, orienation collinearity, spatial phase, and stimulus duration, and background element orientations on the EEG signal in younger and older subjects. What's more, comparing the neural correlates of contour discrimination before and after perceptual training with a contour integration task can provide important insights on the mechanism of learning.

6.3.3 Prior knowledge

In all existing studies of contour and shape perception in aging, subjects were informed of the contour shape they were asked to detect or to discriminate, allowing the possibility to employ top-down processes to guide the detection and discrimination for those contours. However, in the real world we are often faced with interpreting visual scenes without prior knowledge of what it contains. To what extent did prior knowledge of the target contour contribute to detection or discrimination performance in younger and older subjects? If prior knowledge played no role in contour grouping, then age-differences in contour discrimination that we observed reflect true differences in bottom-up perceptual grouping. On the other hand, if older adults, but not younger adults, used top-down feedback to compensate for grouping deficits, then the age-differences we observed underestimate the true differences in grouping ability. Finally, if younger subjects used top-down feedback for contour discrimination, but these top-down mechanisms are impaired (or delayed) with aging, then the age-differences observed in our experiments overestimate true differences in bottom-up grouping and rather reflect age-differences in top-down feedback.

A recently developed stimulus set of contour outlines of everyday objects provides a good opportunity to examine the role of prior knowledge on contour integration (Panis, De Winter, Vandekerckhove, and Wagemans, 2008). Nearly two hundred outlines of different objects have been sampled with Gabors and the resulting contours have been characterized by several parameters known to influence contour grouping (e.g., average path angle, number of interior segments, extent of "good continuation", etc). In addition, identifiability norms for these object outlines have been obtained for six different contour-background context combinations (Sassi, Vancleef, Machilsen, Panis, and Wagemans, 2010).

From this dataset of contours, we can choose a large subset of object outlines with similar levels of identifiability (e.g., 90%), but different levels of low-level contour salience. The salience of the contours can be further manipulated with different levels of orientation jitter in contour elements. To assess the effect of prior knowledge on contour integration, we can compare detection accuracy with and without prior knowledge of the contour identity. On every trial, two patterns will be displayed in random order: one pattern containing the contour in noise, the other pattern containing only noise Gabors. In the no-knowledge condition, subjects will be asked to report which interval contained a contour and to identify the contour (e.g., type in the name). In the prior-knowledge condition, the contour identity will be displayed at the beginning of every trial (e.g., the word "sock" for a sock contour) and subjects will be asked to report the interval containing the contour. Outlines of two different sets of objects will be used for the two prior-knowledge conditions (conterbalanced across subjects) in order to control for effects of prior exposure. If top-down feedback benefits contour grouping, we would expect to find a main effect of prior knowledge on contour detection accuracy. However, this effect should be modulated by the low-level saliency of the contours, whereby low salience contours would show greater benefit from prior knowledge than high saliency contours. If older subjects rely more on top-down feedback for contour grouping, older subjects may show a benefit of prior knowledge for contours of higher salience than younger subjects. Finally, if a significant effect of prior knowledge is found, it may be interesting to examine whether the effect of prior knowledge varies with stimulus duration. In particular, very brief stimulus exposure durations may not be sufficient to allow for top-down feedback to play a role in grouping. More importantly, in light of evidence that top-down feedback is delayed in older age (Gazzaley et al., 2008), longer stimulus durations may be required to reveal an effect of prior knowledge in older subjects compared to younger subjects.

6.4 Conclusion

Visual perception is important for everything from navigating and interacting with the environment to communication and social interaction. Integrating local orientation information across space to extract contours and encode shapes is a crucial step in translating visual sensory input into a meaningful representation. Research in this dissertation revealed age-related changes in contour grouping at low-contrast, and in integrating contours embedded in dense, cluttered backgrounds. On a positive note, the sensitivity of contour integration to contour element proximity, collinearity, and spatial-phase alignment are preserved in older age. Similarly, the integration of orientation information in shape perception is also unchanged. This research contributes to the growing body of evidence testifying to the heterogeneity of age-related changes in visual cortical function. Future research should aim to determine the nature of age-related cortical changes responsible for the observed declines in perceptual organization and to determine the usefulness of perceptual training in remediating perceptual function in older age.

Bibliography

Achtman, R. L., Hess, R. F., Wang, Y.-Z., 2003. Sensitivity for global shape detection. Journal of Vision 3 (10), 616–624.

Ball, K., Sekuler, R., 1986. Improving visual perception in older observers. Journal of Gerontology 41 (2), 176–82.

Bennett, P. J., Sekuler, A. B., McIntosh, A. R., Della-Maggiore, V., 2001. The effects of aging on visual memory: evidence for functional reorganization of cortical networks. Acta Psychologica 107 (1-3), 249–273.

Betts, L. R., Taylor, C. P., Sekuler, A. B., Bennett, P. J., 2005. Aging reduces center-surround antagonism in visual motion processing. Neuron 45 (3), 361–366.

Bonneh, Y., Sagi, D., 1998. Effects of spatial configuration on contrast detection. Vision Research 38 (22), 3541–3553.

Butler, P. D., Silverstein, S. M., Dakin, S. C., 2008. Visual perception and its impairment in schizophrenia. Biological Psychiatry 64 (1), 40–7.

Casco, C., Robol, V., Barollo, M., Cansino, S., 2011. Effects of aging on visual contour integration and segmentation. Investigative ophthalmology & visual science 52 (7), 3955–61.

Chakravarthi, R., Pelli, D. G., 2011. The same binding in contour integration and crowding. Journal of Vision 11 (8).

Chan, Y. M., Battista, J., McKendrick, A. M., 2012. Aging effects on collinear facilitation. Journal of Vision 12 (6).

Day, M., Loffler, G., 2009. The role of orientation and position in shape perception. Journal of Vision 9, 1–17.

Del Viva, M. M., Agostini, R., 2007. Visual spatial integration in the elderly. Investigative Ophthalmology & Visual Science 48 (6), 2940–2946.

Della-Maggiore, V., Sekuler, A. B., Grady, C. L., Bennett, P. J., Sekuler, R., McIntosh, A. R., 2000. Corticolimbic interactions associated with performance on a short-term memory task are modified by age. The Journal of Neuroscience 20 (22), 8410–8416.

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 (2), 173–193.

Field, D. J., Hayes, A., Hess, R. F., 2000. The roles of polarity and symmetry in the perceptual grouping of contour fragments. Spatial Vision 13 (1), 51–66.

Gallant, J. L., Connor, C. E., Rakshit, S., Lewis, J. W., Van Essen, D. C., 1996. Neural responses to polar, hyperbolic, and cartesian gratings in area v4 of the macaque monkey. Journal of Neurophysiology 76 (4), 2718–39.

Gazzaley, A., Clapp, W., Kelley, J., McEvoy, K., Knight, R. T., D'Esposito, M., 2008. Age-related top-down suppression deficit in the early stages of cortical visual memory processing. Proceedings of the National Academy of Sciences of the United States of America 105 (35), 13122–6.

Gheorghiu, E., Kingdom, F. A. A., 2009. Multiplication in curvature processing. Journal of Vision 9, 1–17.

Govenlock, S. W., 2010. The effect of aging on visual orientation and spatial frequency channels. Ph.D. thesis, McMaster University.

Habak, C., Wilkinson, F., Wilson, H. R., 2009. Preservation of shape discrimination in aging. Journal of Vision 9 (12), 18.1–8.

Hadad, B., Maurer, D., Lewis, T. L., 2010. The effects of spatial proximity and collinearity on contour integration in adults and children. Vision Research 50 (8), 772–8.

Hadad, B.-S., 2012. Sensitivity of spatial integration to perceptual cues is preserved in healthy aging. Vision Research 60, 1–6.

Hegdé, J., Van Essen, D. C., 2000. Selectivity for complex shapes in primate visual area v2. The Journal of Neuroscience 20 (5), RC61.

Hess, R. F., Dakin, S. C., 1997. Absence of contour linking in peripheral vision. Nature 390 (6660), 602–604.

Hess, R. F., Dakin, S. C., Field, D. J., 1998. The role of "contrast enhancement" in the detection and appearance of visual contours. Vision Research 38 (6), 783–787.

Hess, R. F., Hayes, A., Field, D. J., 2003. Contour integration and cortical processing. Journal of Physiology – Paris 97 (2-3), 105–119.

Hua, T., Kao, C., Sun, Q., Li, X., Zhou, Y., 2008. Decreased proportion of gaba neurons accompanies age-related degradation of neuronal function in cat striate cortex. Brain Research Bulletin 75 (1), 119–125.

Huang, P.-C., Hess, R. F., Dakin, S. C., 2006. Flank facilitation and contour integration: different sites. Vision Research 46 (21), 3699–706.

Hussain, Z., Webb, B. S., Astle, A. T., McGraw, P. V., 2012. Perceptual learning reduces crowding in amblyopia and in the normal periphery. The Journal of Neuroscience 32 (2), 474–80.

Joo, S. J., Boynton, G. M., Murray, S. O., 2012. Long-range, pattern-dependent contextual effects in early human visual cortex. Current Biology 22 (9), 781–6.

Keane, B. P., Silverstein, S. M., Barch, D. M., Carter, C. S., Gold, J. M., Kovács, I., Macdonald, 3rd, A. W., Ragland, J. D., Strauss, M. E., 2012. The spatial range of contour integration deficits in schizophrenia. Experimental Brain Research.

Kéri, S., Kelemen, O., Benedek, G., Janka, Z., 2005. Lateral interactions in the visual cortex of patients with schizophrenia and bipolar disorder. Psychological Medicine 35 (7), 1043–51.

Kovács, I., Kozma, P., Fehér, Ákos, A., Benedek, G., 1999. Late maturation of visual spatial integration in humans. Proceedings of the National Academy of Sciences of the United States of America 96 (21), 12204–9.

Lee, Y., Grady, C. L., Habak, C., Wilson, H. R., Moscovitch, M., 2011. Face processing changes in normal aging revealed by fmri adaptation. Journal of Cognitive Neuroscience 23 (11), 3433–47.

Legault, I., Faubert, J., 2012. Perceptual-cognitive training improves biological motion perception: evidence for transferability of training in healthy aging. Neuroreport 23 (8), 469–73.

Leventhal, A. G., Wang, Y. C., Pu, M. L., Zhou, Y. F., Ma, Y. Y., 2003. GABA and its agonists improved visual cortical function in senescent monkeys. Science 300 (5620), 812–815.

Levi, D. M., 2008. Crowding–an essential bottleneck for object recognition: a mini-review. Vision Research 48 (5), 635–54.

Levine, B., Beason-Held, K., Aronchick, D., Optican, L., Alexander, G., Horwitz, B., Rapoport, S., Schapiro, M., 2000. Age-related differences in visual perception: a pet study. Neurobiology of Aging 21, 577–584.

Li, W., Gilbert, C. D., 2002. Global contour saliency and local colinear interactions. Journal of Neurophysiology 88 (5), 2846–56.

Li, W., Piëch, V., Gilbert, C. D., 2008. Learning to link visual contours. Neuron 57 (3), 442–51.

Machilsen, B., Novitskiy, N., Vancleef, K., Wagemans, J., 2011. Context modulates the erp signature of contour integration. PLoS One 6 (9), e25151.

Mathes, B., Trenner, D., Fahle, M., 2006. The electrophysiological correlate of contour integration is modulated by task demands. Brain Research 1114 (1), 98–112.

May, K. A., Hess, R. F., 2007. Ladder contours are undetectable in the periphery: a crowding effect? Journal of Vision 7 (13), 9.1–15.

McGovern, D. P., Webb, B. S., Peirce, J. W., 2012. Transfer of perceptual learning between different visual tasks. Journal of Vision 12 (11).

McIntosh, A. R., Sekuler, A. B., Penpeci, C., Rajah, M. N., Grady, C. L., Sekuler, R., Bennett, P. J., 1999. Recruitment of unique neural systems to support visual memory in normal aging. Current Biology 9 (21), 1275–1278.

McKendrick, A. M., Weymouth, A. E., Battista, J., 2010. The effect of normal aging on closed contour shape discrimination. Journal of Vision 10 (2).

Mullen, K. T., Beaudot, W. H. A., Ivanov, I. V., 2011. Evidence that global processing does not limit thresholds for rf shape discrimination. Journal of Vision 11 (3).

Neider, M. B., Boot, W. R., Kramer, A. F., 2010. Visual search for real world targets under conditions of high target-background similarity: Exploring training and transfer in younger and older adults. Acta Psychologica 134 (1), 29–39.

Panis, S., De Winter, J., Vandekerckhove, J., Wagemans, J., 2008. Identification of everyday objects on the basis of fragmented outline versions. Perception 37 (2), 271–89.

Pasupathy, A., Connor, C. E., 1999. Responses to contour features in macaque area v4. Journal of Neurophysiology 82 (5), 2490–502.

Phillips, W. A., Silverstein, S. M., 2003. Convergence of biological and psychological perspectives on cognitive coordination in schizophrenia. The Behavioral and Brain Sciences 26 (1), 65–82; discussion 82–137.

Polat, U., 1999. Functional architecture of long-range perceptual interactions. Spatial Vision 12 (2), 143–162.

Polat, U., Bonneh, Y., 2000. Collinear interactions and contour integration. Spatial Vision 13 (4), 393–401.

Polat, U., Sagi, D., 1993. Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. Vision Research 33 (7), 993–9.

Polat, U., Sagi, D., 1994. Spatial interactions in human vision: from near to far via experience-dependent cascades of connections. Proceedings of the National Academy of Sciences of the United States of America 91 (4), 1206–9.

Richards, E., Bennett, P. J., Sekuler, A. B., 2006. Age related differences in learning with the useful field of view. Vision Research 46 (25), 4217–4231.

Robol, V., Anderson, E. J., Tibber, M. S., Bobin, T., Carlin, P., Shergill, S., Dakin, S. C., 2012a. Reduced crowding and poor contour detection in schizophrenia are consistent with weak surround inhibition. Journal of Vision 12 (9), 889.

Robol, V., Casco, C., Dakin, S. C., 2012b. The role of crowding in contextual influences on contour integration. Journal of Vision 12 (7), 3.

Roudaia, E., Bennett, P. J., Sekuler, A. B., 2008. The effect of aging on contour integration. Vision Research 48 (28), 2767–2774.

Roudaia, E., Farber, L. E., Bennett, P. J., Sekuler, A. B., 2011. The effects of aging on contour discrimination in clutter. Vision Research 51 (9), 1022–1032.

Rousselet, G. A., Gaspar, C. M., Pernet, C. R., Husk, J. S., Bennett, P. J., Sekuler, A. B., 2010. Healthy aging delays scalp eeg sensitivity to noise in a face discrimination task. Frontiers in Psychology 1, 19.

Rousselet, G. A., Husk, J. S., Pernet, C. R., Gaspar, C. M., Bennett, P. J., Sekuler, A. B., 2009. Age-related delay in information accrual for faces: evidence from a parametric, single-trial eeg approach. BMC Neuroscience 10, 114.

Rousselet, G. A., Pernet, C. R., 2011. Quantifying the time course of visual object processing using erps: It's time to up the game. Frontiers in Psychologyl 2, 107.

Saarinen, J., Levi, D. M., 2001. Integration of local features into a global shape. Vision Research 41 (14), 1785–1790.

Sassi, M., Vancleef, K., Machilsen, B., Panis, S., Wagemans, J., 2010. Identification of everyday objects on the basis of gaborized outline versions. i-Perception 1 (3), 121–142.

Schmolesky, M. T., Wang, Y., Pu, M., Leventhal, A. G., 2000. Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. Nature Neuroscience 3 (4), 384–390.

Schwarzkopf, D. S., Kourtzi, Z., 2008. Experience shapes the utility of natural statistics for perceptual contour integration. Current Biology 18 (15), 1162–1167.

Scialfa, C. T., Cordazzo, S., Bubric, K., Lyon, J., 2012. Aging and visual crowding. Journal of Gerontology B. Psychological Sciences and Social Sciences.

Sekuler, R., Ball, K., 1986. Visual localization: age and practice. Journal of the Optical Society of America. A 3 (6), 864–7.

Silverstein, S. M., Keane, B. P., 2011. Perceptual organization impairment in schizophrenia and associated brain mechanisms: review of research from 2005 to 2010. Schizophrenia Bulletin 37 (4), 690–9.

Simmers, a. J., Bex, P. J., 2001. Deficit of visual contour integration in dyslexia. Investigative Ophthalmology & Visual Science 42 (11), 2737–42.

Sterkin, A., Sterkin, A., Polat, U., 2008. Response similarity as a basis for perceptual binding. Journal of Vision 8 (7), 17.1–12.

Tadin, D., Kim, J., Doop, M. L., Gibson, C., Lappin, J. S., Blake, R., Park, S., 2006. Weakened center-surround interactions in visual motion processing in schizophrenia. The Journal of Neuroscience 26 (44), 11403–12.

Verghese, P., 2009. Contours in noise: a role for self-cuing? Journal of Vision 9 (13), 2.1–16.

Wang, Y. Z., 2001. Effects of aging on shape discrimination. Optometry and vision science : official publication of the American Academy of Optometry 78 (6), 447–54.

Weymouth, A. E., McKendrick, A. M., 2012. Shape perception is altered by normal aging. Investigative Ophthalmology & Visual Science 53 (6), 3226–33.

Wilkinson, F., Wilson, H. R., Habak, C., 1998. Detection and recognition of radial frequency patterns. Vision Research 38 (22), 3555–68.

Williams, C. B., Hess, R. F., 1998. Relationship between facilitation at threshold and suprathreshold contour integration. Journal of the Optical Society of America. A, Optics, image science, and vision 15 (8), 2046–51.