FIGURE-GROUND AND AGING

THE EFFECTS OF AGING ON FIGURE-GROUND ORGANIZATION

By

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Abstract

The Effects of Aging on Figure-Ground Organization

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Little is known about how healthy aging impacts figure-ground (FG) perception, which is critical in organizing complex visual input into coherent figures. Inhibitory-suppression is thought to be critical in resolution between competing FG interpretations. Given the age-related changes to inhibitory cortical mechanisms, my thesis investigated the hypothesis that processes underlying FG organization are impaired in aging. We explored the effects of age on the convexity context effect (CCE): the tendency to perceive convex regions as figural [i.e., P(Convex=Figure)] increases with surrounding convex and concave regions. In Chapter 2, we observed that adding context by increasing region number, increased P(Convex=Figure) in younger and older observers, but this CCE was significantly reduced in older adults. Reducing competition between perceptual interpretations by heterogeneously colouring convex regions, thereby invalidating the alternative {Concave=Figure} stimulus interpretation, greatly increased P(Convex=Figure) in older observers. These results supported the notion that aging impairs FG organization, particularly in relatively high competition contexts. In Chapter 3, we explored the possibility that reduced presumption of depth in our stimuli might explain the reduced the CCE in older observers by adding texture motion to region fills consistent with depth in the stimulus. The results were inconsistent with the hypothesis, but supported the reduced inhibitory-suppression hypothesis of the age effect. In Chapter 4, we explored the neural activation associated with the processing mechanisms underlying the resolution of FG competition. The results indicated that the N250 in younger observers but not older observers is sensitive to high vs. low competition contexts. Furthermore, individual differences in this N250-competition effect were correlated with the behavioural effect of competition. Our findings are consistent with the hypothesis that the processing underlying FG organization is impaired in senescence, which may stem from reduced efficacy of the neural architecture supporting this ability. Various implications of this work are discussed.

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This PhD would have never been attainable without the camaraderie and collaboration of fellow Vision Lab members. The time spent with you all taught me so much and shifted my outlooks on the world for the better. I would especially like to thank Donna Waxman for help and support that have been inarticulable.

I would be remiss if I did not acknowledge the many great teachers and students that I've had over the years who have sparked, deepened, and expanded my curiosity. I would particularly like to acknowledge Mary Peterson for serving as a major collaborator, and from whom I have learned so much, throughout this process. A special thank you to my supervisors Allison Sekuler and Patrick Bennett, who provided me with the opportunity to develop as a scientist and thinker at the highest level. I appreciate being taken on as a student, provided with tools and environment to develop my academic skills through contributing to and engaging in the scientific community, and challenged at a level that pushed me past my own boundaries in many ways.

I would have never made it here without the constant support of my friends and family. The support from my two sisters has been matched only by the example set through their bravery in taking on the challenges of life. I also cannot overlook the two strong brothers-in-law standing behind me who served as incredible sources of strength, and two in-laws who have taken me on as their own.

There is no doubt, however, that I would have been lost many times without my wife, who was my anchor through the storms that I could not have weathered without her standing by my side every step of the way.

Finally, this thesis is dedicated to my parents, who made me the person I am. My mother nurtured my creativity and open-mindedness, and she was always there to assure me that everything would work out when I did not believe in myself. My father always challenged me to succeed on my own, but was never too far away to save me from drowning in my most challenging moments.

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List of Abbreviations

	Description
%	percent
2-AFC	two-alternative forced-choice
AD	accretion-deletion
AMD	age-related macular degeneration
ANCOVA	Analysis of Covariance
ANOVA	Analysis of Variance
BW2	2-region black and white convexity stimuli
BW8	8-region black and white convexity stimuli
CAV	concave
CavHom	8-region concave-homogeneous/convex-heterogeneous stimulus
CCE	convexity context effect
CCompE	convexity competition effect
$\mathbf{cd/m^2}$	candelas per square meter
cm	centimeters
CRT	cathode-ray tube
deg or °	degrees (of visual angle)
EEG	electroencephalography
ERP	evoked response potential
FG	figure-ground
Hz	Hertz, i.e., cycles per second
fMRI	functional magnetic resonance imaging
HET	heterogeneous
HOM	homogeneous
$\mathbf{k\Omega}$	kilo-Ohm; standard unit of electrical resistance or impedance
KCl	Potassium chloride
LGN	lateral geniculate nucleus

M	mean
MoCA	Montreal Cognitive Assessment
MMSE	Mini Mental State Exam
ms	milliseconds
μ**V**	Micro-Volt
n	number; sample size
N150	event-related potential peak at 150 ms post stimulus onset
N250	event-related potential peak at 250 ms post stimulus onset
N350	event-related potential peak at 350 ms post stimulus onset
P100	event-related potential peak at 100 ms post stimulus onset
P200	event-related potential peak at 200 ms post stimulus onset
P300	event-related potential peak at 300 ms post stimulus onset
P(VEX = Figure)	percentage of trials where convex region was reported as figure
PET	positron emission tomography
RT	reaction time
sd	standard deviation
SEM	standard error of the mean
SOA	stimulus-mask offset asynchrony
UFOV	useful field of view
V1	primary visual cortex
V2	secondary visual cortex
vs.	versus
VEX	convex

Declaration of Academic Achievement

This thesis comprises 5 chapters, including a general introduction (Chapter 1) and general discussion (Chapter 5), which were written by me, and three body chapters (Chapters 2-4) that present the main research I conducted during graduate school, which were written in collaboration with my supervisors (Allison Sekuler and Patrick Bennett) and other collaborators (Mary Peterson and Ali Hashemi). I was the primary writer for each of the body chapters, which are written in journal article format and are in preparation for submission.

Chapters 1 & 5 were written by me. Chapters 2 & 3 were written collaboratively with Allison Sekuler, Patrick Bennett, and Mary Peterson. Chapter 4 was written collaboratively with Allison Sekuler, Patrick Bennett, Mary Peterson, and Ali Hashemi. These three data chapters (Chapters 2, 3, & 4) have not yet been submitted for publication.

For all chapters, as primary author, I oversaw all aspects of the research. The generation of ideas and the development of these ideas into experimental designs was a collaborative effort between myself and the other co-authors. I was solely responsible for the experimental programming for Chapters 2 & 3, and was assisted with programming by Ali Hashemi for Chapter 4. Data collection was performed largely by research assistant Donna Waxman (Chapters 2, 3, & 4) and myself (Chapter 4), with assistance from research collaborator Ali Hashemi (Chapter 4) and several undergraduate research assistants (Chapters 3 & 4). I was primarily responsible for the data analysis for all chapters. My supervisors and other co-authors worked with me to determine appropriate analyses, and to interpret the subsequent results. I was responsible for initial drafts of all chapters; subsequent versions were collaboratively edited amongst all co-authors, and I was responsible for integrating the various comments and perspectives.

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Chapter 1

General Introduction

Science can be conceptualized as a project to create a model of the world that allows us to characterize the relationships between observable variables, organize this knowledge, and make predictions about how the real world works that can be used to control the various *understood* phenomena. The scientific method seeks to methodically improve our ability to harness nature's laws by constantly refining the falsifiable theories that place specific phenomena under the microscope (Popper, 1959). Every research project pushes the limits of knowledge and/or connects broadly spread theories as part of the effort towards forming a unified, reducible, ever expanding body that is *Science*.

Over the past five years, my research program has explored the effects of healthy aging on visual perception with specific focus on Figure-Ground (FG) perceptual organization. This work has uncovered previously unknown effects of the aging process on visual processing and explored these effects from behavioural to neural levels. The results are exciting in that they have important implications on our understanding of visual perception, the influences of aging on visual perception, and the applications by which scientific, industrial, and policy-making communities might target the challenges posed to an aging society in the coming years.

The thesis focuses on one aspect (FG perception) of a specific topic (Perception) within a specific field (Psychology, Neuroscience & Behaviour) within the broad range of science. Yet, it is important to keep the big picture in perspective in order to understand the value of this work, link it to the broader project of science, and inform the related disciplines that can contribute to, and make use of, this expanding scientific knowledge. This introduction (Chapter 1) sets the stage for the following three data chapters (Chapters 2, 3, and 4), manuscripts of scientific research exploring the effects of aging on FG perception, and the concluding discussion (Chapter 5) that ties it all together.

1.1 The study of aging in Psychology

Animal development is a phenomenon that involves the systematic change in physiology and behaviour over time. Human development entails the growth from a single cell into a complex organism that is birthed after about 40 weeks, the subsequent developmental periods from infancy through childhood through adolescence, and the later-life changes, often referred to as "senescence" or "aging" (late adulthood), that are commonly perceived as a period of declines and functional challenges (National Council on Aging, 2002). In reality, aging does involve declines in physical (Weale, 1963), sensory (Sekuler et al., 2000), and perceptual (Owsley, 2011; Andersen, 2012) domains, some of which will be discussed below. Understanding the effects of aging is important because changes to functioning of individuals potentially comes at a huge cost to society (Goldman et al., 2013), and the lives of many people can be improved by developing tools and training programs that alleviate the negative effects of senescence. This is an increasingly important issue as the population ages (Milan, 2011; Colby and Ortman, 2014). However, these effects of aging are increasingly understood to be a plastic process and people who are chronologically older are aging more slowly (Crimmins, 2015), which means that more of the population will live longer as time goes on. One goal of aging research is to understand the aging process in order to ultimately help maintain and improve the quality of life of older adults.

The study aging has been pursued from within diverse fields and perspectives, geared toward understanding the age-related changes to various functions, and informing society on ways to overcome the negative consequences associated with senescence. Many reviews exist on this topic including a well put together text reviewing the vast approaches and literature on aging in late adulthood (Lemme, 2005).

1.1.1 Aging and general sensory declines

It has long been known that aging affects the earliest parts of our sensory systems including the eyes (Weale, 1963; Kim and Mayer, 1994) and ears (Fitzgibbons and Gordon-

Salant, 1998), and that such age-related changes lower the quality of sensory information that is passed on to higher cortical centres. As would be predicted by models of sensory/perceptual processing, such front-end limitations on vision sequentially impact the rest of the visual system's ability to extract information from the environment (Geisler, 1989). However, much recent work on aging has focussed beyond the optics of the eye and explored the effects of aging on neural mechanisms that rely on a careful balance required to accurately and effectively organize the visual input. Age-related changes that deteriorate the input at various stages of processing, which indeed occur in sensory (Weale, 1963) and higher-order perceptual mechanisms (Spear, 1993; Sekuler et al., 2000; Owsley, 2011; Andersen, 2012), will be outlined in Section 1.3. Consideration of the sequential effects of aging to components of the visual processing pathway was a focus – particularly in screening measuring, experimental design, and control experiments – throughout this thesis.

1.1.2 Individual differences in aging

Recent work on aging has demonstrated that aging is a plastic process in the sense that the rate of aging varies widely across individuals and is affected greatly by environmental factors (Kuh and Wadsworth, 1993). Examining the variables that determine who ages well vs. who does not is motivated by the goals seeking to properly understand aging effects and inform policy on important health decisions. Although some abilities are compromised in the older adult population, some older *individuals* still show intact functioning in these domains (perhaps supported by compensatory neural systems, e.g., see McIntosh et al., 1999). Understanding the characteristics of high vs. low functioning subgroups yields deeper understanding of the effects of aging on the abilities that change in senescence. For example, Cabeza et al. (2002) showed that older adults are impaired on specific tasks assessing memory. However, they also observed that only a subset of the older group showed this deficit and that the brain activity associated with performing the tasks varied among subgroups. Interestingly, individuals showing significant impairments had similar patterns of cortical activity compared to the younger group, whereas those with intact memory ability were showing a different pattern with increased frontal activity. The results are consistent with the hypothesis that older observers were impaired on this particular task only if they did not adapt their underlying neural processing, whereas those who compensated with additional frontal lobe processing were able to overcome the negative impacts of aging that would otherwise have led to the memory deficit.

The findings of Cabeza et al. (2002) are but one example of how studying individual differences, and associating them with other measures and/or variables, is important. Considering individual differences not only helps researchers avoid falling into the trap of collapsing all older observers into a single group, but, in doing so, allow the identification of the key factors causing an effect (or in this case overcoming it). The work in this thesis considers individual differences in various visual abilities, controls for low level factors that might cause effects we report through impacting front-end visual inputs, and tries to relate behavioural to neural findings in attempt to more rigorously characterize the effects of aging on performance in FG perception. Not all individual differences explored, nor all the individual analyses conducted in this project, are reported in the thesis. However, the individual differences perspective was an essential aspect of our approach to studying the effects of aging. This issue comes into play with the electrophysiology results and is returned to in the general discussion (Chapter 5).

1.1.3 The challenges in studying aging & our approach

Examining the effects of aging is not as simple as comparing older and younger groups on the task of interest. Other variables, which often are difficult to control, are confounded with age and make it difficult to draw conclusions about the effects of aging *per se*. On the other hand, some such variables, like the fact that the sensory pathways undergo anatomical and physiological changes throughout the lifespan (Weale, 1963; Pinto et al., 2010), may be considered to be an intrinsic component of aging. As we understand more about such front-end factors – for example, age-related changes to optics of the eye – they can be incorporated into models of visual aging and therefore help us to identify the effects of age-related changes in other, higher level mechanisms in the processing pathway. Other variables, like the fact that different cohorts of individuals grow up in different historical, cultural, and social contexts, can seriously impact conclusions made when comparing age groups without controlling for such *cohort effects*. For example, individuals in an older cohort grew up in a society without computers whereas the lives of the younger cohort were pervaded by computers from infancy. When an experimental task assessing a visual ability requires the use of computers, it is possible that an age difference in performance might be observed that is actually caused by a cohort difference in ability to use the computer that serves as the measuring stick. Other intergenerational effects stemming from the fact that education, healthcare, technology, etc., have changed dramatically over the last century, can also confound results and make conclusions difficult to ascertain.

There were various steps taken in our research designed to grapple with this challenge. Firstly, as part of our experimental process, a battery of visual and cognitive tests were administered to all observers. The tests measured basic visual abilities including near and far visual acuity (Bailey and Lovie, 1976), contrast sensitivity (Pelli and Robson, 1988), and – in some experiments – stereo vision. Cognitive faculties were assessed using the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005) and the Mini Mental State Exam (MMSE; Folstein et al., 1975). We also measured individual characteristics like handedness, morning/eveningness, race, years of education, and first language. These data were used to both screen for anything that might influence the results and to have these demographics at our disposal for making comparisons across groups and individuals after controlling for these factors. Secondly, we are selective with our samples, recruiting participants into the lab to participate in many studies. All of the recruited individuals were comfortable with computer-based tasks. All participants also were highly motivated because they were paid, or given course credit, for participating. Thirdly, all of our experiments contained basic standardized instructions that were identical across groups and which were given by an experimenter who has experience working with both younger and older participants. This ensured that the experiments were administered without systematically biasing individuals.

Other approaches to overcoming these challenges have attempted to create complex designs that combine cross-sectional, like those used by us, and longitudinal methods in a so-called *cross-sequential design* (Schaie and Strother, 1968). This method entails comparing cohorts at different age points while also employing longitudinal re-tests that enable the examination of age effects within the same cohort. We did not use longitudinal or cross-sequential designs in the current project; however, the way that such tools could be employed to address certain challenges associated with studying aging, as well as to investigate the trajectories of age-related effects, is returned to in the general discussion of the thesis (Chapter 5).

1.2 Visual perception

The study of perception entails examining how perceptual systems process and represent information received through the sensory organs. The overarching question fuelling research on visual perception is: How does the brain process information extracted by the eyes, and relate the visual data to the information brought in through other sensory systems, to learn about and act within the world? This broad question has been approached from a variety of perspectives, focussed on addressing many specific aspects of visual perception. Answering this question has called on various approaches, techniques, and technologies that are under constant development. Many comprehensive review texts covering visual perception have been compiled, and I drew information from the following two texts, which I have found to be particularly good: Blake and Sekuler (2006) and Goldstein (2010).

Our main focus here is on the effects of aging on the segregation components of perceptual organization: How does the aging brain impact the way FG organization is accomplished? This question is inherently intertwined with other phenomena including the grouping components of perceptual organization and other visual abilities. Given the relation to the plethora of known effects of aging, it thus requires some broad brushstrokes of background on visual perception to appropriately frame our question and our approach to answering it.

1.2.1 Hierarchical models of visual processing

The eyes are the front-end of the visual system, meaning that they are the input source for visual information. The cornea focusses light of the outside world through the pupil and the interior lens focuses light further, forming an inverted pattern of light that falls onto the retina at the back of the eye (for example, see Weale, 1963). The retina is the multilayer tissue composed of photoreceptors, bipolar cells, and ganglion cells that carry the front-end signal to the brain. Photoreceptors, including rods and cones, are photosensitive cells that detect points of light by absorbing individual photons, which cause a change in photoreceptor structure leading the cell to change its output to the ganglion cell it innervates. This process of converting light energy emitted or reflected by environmental objects into action potentials (i.e., *Transduction*), allows the signal sourced to the stimulus to be coded by, propagated through, and processed by the rest of the brain.

The eye thus captures, focuses, and converts patterns of light into the language of neurons. This sensory process interfaces with the early stages of perceptual machinery in the retina, where the earliest integration of sensory signals takes place in the ganglion layers. These cells have a center-ON/surround-OFF character. The resulting signal is then carried by the optic nerve into the brain and by the optic tract to the lateral geniculate nucleus (LGN), which acts as a relay centre that breaks up and integrates signals coming from different retinal cells and eyes. The signal then spreads to cells of the occipitally localized primary visual cortex (V1). These neurons were discovered to be sensitive to bars of light (Hubel and Wiesel, 1962), and have been shown to respond to Gabor-like patterns of small receptive fields and specific orientations within the stimulus(Hubel and Wiesel, 1968). More complex receptive field tuning properties of these cells have also been discovered, including properties like *border ownership* (Zhou et al., 2000), which are thought to be important to FG organization. Theories of perceptual organization, discussed below in Section 1.2.2, work towards explaining how low-level visual properties (like colour, orientation of local/global elements, spatial frequency) are used to perceptually group and segregate stimulus elements. This visual processing organizes the low-level information and feeds it forward to high-level visual networks that are tuned to shape representation and 3D structure of stimuli (Pasupathy and Connor, 2001; Kourtzi et al., 2003), and areas extending into extra-striate that are thought to engage in complex object recognition like that of human bodies (Downing et al., 2001) and faces (Kanwisher and Yovel, 2006).

All the way up through the hierarchy of the visual system, the signal is integrated and combined as it is fed forward through the system. Within the eye itself, photoreceptors detect and code points of light, but the ganglion cells that they synapse with integrate across multiple photoreceptors resulting in becoming excited by central receptive field light and inhibited by peripheral receptive field light. This centre/surround signal coded by ganglion cells are integrated in V1, and the resulting signal is fed forward to secondary visual cortex (V2), higher levels of the visual processing hierarchy, and eventually to other brain regions that integrate visual inputs with other sensory modalities and other cognitive functions.

This hierarchical description of the visual system is a simplistic view, since we do know that there is both feedback and feedforward signals throughout the process. Yet, this conceptualization provides a powerful framework that allows us to understand how a complex and ambiguous pattern of light, detected by point-source sensory photoreceptors, can be integrated to become tuned to various macroscopic properties of the stimulus. The functions of early visual areas, like the edge-detection in V1, have been fairly well characterized, as have some of the later areas associated with processing of complex stimulus properties. However, the perceptual organization mechanisms that link low-level properties like detection of edges with high level complex pattern recognition, through grouping and segregational processes, are relatively less understood. Great advancements were made in the study of perceptual organization by the Gestaltists in the early 20th century (for example, Rubin, 1915/1958, and Wertheimer, 1923), and attempts to address the same questions has seen a recent resurgence built on the same tenets but incorporating modern approaches (see Westheimer, 1999; Wagemans et al., 2012a; Wagemans et al., 2012b). Let us now turn focus to this level in the hierarchy of visual processing, which encompasses the major topic under investigation in this thesis.

1.2.2 Perceptual organization: Grouping and figure-ground

Perceptual organization refers to the processes that are involved in grouping and segregating sensory or simple perceptual units into *Gestalten*, or *wholes*. The Gestalt psychologists classically studied perceptual organization using phenomenological approaches to demonstrate the principles of *grouping*, the processing by which elements are grouped into the perceived *whole*, and *figure-ground*, the processes that results in a segregation of regions of space into a shaped foreground lying in front of a shapeless background that falls behind it. The Gestalt approach was part of a philosophical orientation that stressed the phenomenological uniqueness of the whole and that it was different from (although not, as it is often misrepresented, “greater than”) the sum of the parts (Wagemans et al., 2012a; Westheimer, 1999).

In his famous presentation of the *Principles of Grouping*, Wertheimer (1923) identified a number of factors that, all else being equal, would determine which elements in an array would become perceptually grouped. Using simple patterns to provide compelling demonstrations of perceptual grouping phenomena, Wertheimer argued that elements are grouped by *proximity* (i.e., elements that are close together are more likely to be grouped than elements that are far apart), *similarity* (i.e., similar elements are more likely to be grouped than dissimilar elements), *common fate* (i.e., elements that move together are grouped together), *continuity* (i.e., elements that fall along “good” trajectories are grouped together), and *closure* (i.e., elements that form closed contours are more likely to be grouped to form a figure).

Similarly, Rubin (1915/1958) explored the factors that determine FG organization. His work explored the classic *configural cues*, which refer to region/contour properties that enable the determination of which region is figural, and include: *convexity*, *symme-*

try, *enclosure*, and *small area*. Regions that are convex (VEX), symmetrical, enclosed, and of relatively smaller area, are more likely to be seen as figures compared to adjacent regions of opposite properties. Yet, Rubin demonstrated in his phenomenological way, that FG perception is not stable. Consider Figure 1.1, a hand drawn image of the famous Rubin's Vase, which is copied directly from Rubin (1915/1958). Rubin constructed this face-vase image to demonstrate how the *figure* is perceived as a shaped entity that owns the border while the *ground* is perceived as a shapeless region behind the figure. Rubin's Vase also demonstrates that FG organization can be unstable, with most observers reporting that their perception alternates between seeing the vase and the faces as figure.

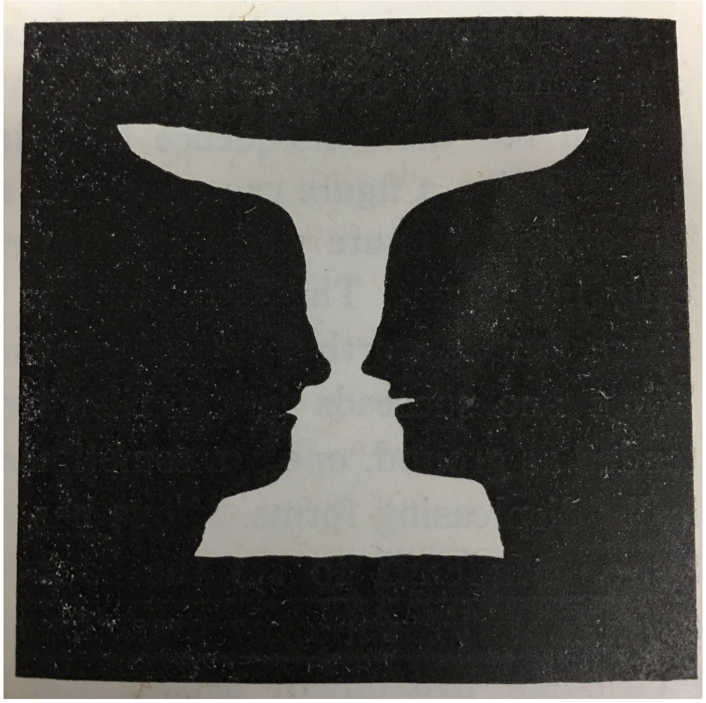

Figure 1.1: The original Rubin's Vase, taken from Rubin (1915/1958). This image has become a textbook example of how stimuli are ambiguous and how FG organization of the stimuli can alternate between perceptual interpretations. Rubin used this example to demonstrate phenomenologically the experience of FG, and how, as perception alternates, the *figure* becomes shaped while the *ground* becomes a shapeless backdrop.

Rubin and Wertheimer, along with their fellow Gestaltists, argued that configural cues and principles of grouping are used to determine how the mind resolves perceptual ambiguity in organizing stimulus elements into wholes. Many more grouping and configural factors have been discovered since the days of the classic schools of Gestalt psychology. These have subsequently been examined using modern experimental techniques applied to classical questions seeking to understand the rules by which perception is organized and the processes underlying it (e.g., Alais et al., 1998; Blake and Lee, 2000; Kandil and Fahle, 2004; Sekuler and Bennett, 2001). While certain fundamental assumptions and tenets of Gestaltism have not stood the test of time, some of the basic principles elucidated by the champions of the Berlin school of Gestalt psychology continue to guide research on perceptual organization.

It is worth noting that despite early beliefs that perceptual organization processes occur at discrete stages in a feedforward model of visual processing, research has demonstrated convincingly that perceptual organization occurs through the integration of iterative feedforward and feedback mechanisms that tune the visual system to an appropriate interpretation of the stimulus. For example, it has been shown that grouping rules can depend on stereoscopic information integrated across the eyes (Rock and Brosgole, 1964), that grouping can be determined by light constancy – which is itself determined by grouping principles – (Palmer et al., 2003), and that FG segregation can be determined by grouping of visual elements (Alais et al., 1998; Lee and Blake, 1999; Sekuler and Bennett, 2001; Guttman et al., 2005). Finding like these demonstrate that timing and order within perceptual organizational processes are in and of themselves complex multidirectional processes. Yet, there is value in drawing flowchart-like models of perceptual organization, as there is for hierarchical processing more generally, in that it allows us to understand the flow of information and link brain areas to the information processing mechanisms conceptualized. Furthermore, these models can be adapted to incorporate feedback, allowing them to handle the more complex models (Lee and Mumford, 2003) that have replaced the simpler linear views of perception and perceptual organization. Thus, even though it is now commonly accepted that grouping and FG segregation do not happen at distinct times or points along the hierarchy, we still ask "when" to investigate the flow of information along processing pathways to form conceivable models of how a stimulus becomes perceptually organized.

One of the more recent approaches attempting link stimulus properties with the cortical mechanisms processing the stimulus has explored the grouping factor of *synchrony*: synchronous change in element properties group those elements together (Alais et al., 1998; Lee and Blake, 1999). Similar to the principle of common fate, synchrony differs in that it does not require actual motion of elements but rather is invoked by the temporal change in the features (other than position), and it can therefore be conceived of as a *generalized* common fate (Sekuler and Bennett, 2001). In other words, synchronous change in characteristics of different features, such as a shifting luminance of squares that form a checkerboard pattern, can serve as cues for grouping that results in segmentation of differently grouped elements into target and background regions (Sekuler and Bennett, 2001). Furthermore, Guttman et al. (2005) showed that synchronous changes of various properties of the elements can invoke grouping that causes FG segregation. They surprisingly showed that even changes across unrelated properties can cause grouping of elements, and that figural status of these regions can be formed through generalized common fate grouping of local elements. Logically speaking, if spatial grouping that segments regions is caused by temporal structure, which is a grouping factor, then segregation, evidently, can rely on the process of grouping. This is another piece of evidence that perceptual organization results from multidirectional processing networks, which is consistent with the observed interaction between different brain regions associated with the process of grouping (Kourtzi et al., 2003) and the potentially top-down effects of familiarity on FG processing (Trujillo et al., 2010).

It thus seems that perceptual organization is the result of coordinated, interactive networks at multiple levels of the visual pathway. Yet our approach to understanding grouping and segregation remains routed in the phenomenological descriptions of Rubin (1915/1958) and Wertheimer (1923) about the experience of figure and ground, and the perception of grouped objects forming the *whole*. While the study of perceptual organization has generally become less reliant on phenomenological descriptions of the experience, there has been a resurgence in exploring the way cues are used in the process of determining grouping and FG organization of stimuli. These approaches are motivated by falsifiable theories, tested with well-controlled experimental designs, and stress performance patterns, but they still speak to the perceptual experience of the stimulus that inspired the field (Westheimer, 1999; Wagemans et al., 2012a).

1.2.3 FG competition & convexity context effects

Modern experiments have used a broad range of behavioural and neurological techniques to explore FG from a variety of perspectives. The cues for figure and ground have been explored and expanded to include: familiar configuration, top/bottom polarity, lower region, part salience, spatial frequency, fixation location, attentional focus, and volitional control (Peterson and Kimchi, 2013). Much focus has been shifted toward systematically testing the influence of stimulus properties on perceptual biases and exploring the *processing* of stimuli in FG ground tasks.

A) Familiar Silhouettes

B) Novel High Competition (Familiar Ground)

C Novel Low Competition (Non Familiar Ground)

Figure 1.2: Example stimuli used by Peterson and Skow (2008), Trujillo et al. (2010), Sanguinetti et al. (2015), and Cacciamani et al. (2015). Each stimulus was a central, symmetrical, enclosed silhouette. The stimulus set contained familiar (A) and novel (B and C) silhouettes. The procedure involved individual presentation of stimuli, and participants' task was to categorize whether a given image was a familiar or novel object. The critical manipulation was within the novel stimuli, which either contained a familiar shape on the ground side (B), or no familiar shape on the ground side of enclosing contour (C). Ground side regions had to be suppressed for the central region to be perceived as figural. Therefore, stimuli containing a familiar ground side shape were deemed *high competition*, because there were two valid alternative perceptual interpretation. Stimuli with non familiar shapes on the ground side were deemed *low competition*.

Insights from behavioural (Peterson and Skow, 2008; Peterson and Salvagio, 2008) and neural studies of FG organization (Likova and Tyler, 2008; Cacciamani et al., 2015) have supported the hypothesis that FG perception emerges through the inhibitory-suppression of ground regions. Ground-suppression increases saliency of figural regions and promotes representation of the region's shape. For example, Peterson and Skow (2008) used a cleverly constructed set of stimuli that were all enclosed, shaped silhouettes that either depicted *familiar* or *novel* figures (see Figure 1.2 for examples of their stimuli). Each of the silhouettes was biased to be perceived as figure by the configural properties of the central shape, which included symmetrical and enclosed structure, and by task instructions, which involved classifying the silhouette as “familiar” or “novel”. A critical property of the novel stimuli was that half contained shapes of familiar objects on the background side of the silhouette contour (Figure 1.2B), and half did not (Figure 1.2C). For all of these stimuli, the region on the ground side of the silhouette outline had to be suppressed in order for the central region to be perceived as the figure. However, for the familiar-ground subset of the stimuli, a familiar shape had to be suppressed, which was hypothesized to require increased inhibitory processing that entails resolving competition between two valid perceptual alternatives of these stimuli. Familiar-ground silhouettes can thus be considered, and in subsequent studies have been considered, *high competition* stimuli. Participants were unaware of this property but nevertheless showed relatively delayed responses to words associated with the shapes that had been suppressed.

Electrophysiological observations extended these behavioural findings, and it was observed that the familiar ground-side shapes that participants were unaware of can be indexed by early neural signals $\approx 100\,\text{ms}$ post stimulus onset (Trujillo et al., 2010). This finding is consistent with the theory that the competitive processes underlying the suppression of the ground side shapes specifically, and that ground-suppression underlying FG organization more generally, is reflected in the neural processing pattern. Follow up studies found support for the hypothesis that the neural signal $\approx 100\,\text{ms}$ after stimulus onset reflects suppression involved in resolving varying degrees of FG competition across the high competition (Figure 1.2B) vs. low competition (Figure 1.2C) silhouettes (Sanguinetti et al., 2015). Recent functional Magnetic Resonance Imaging (fMRI) work also has supported the notion that cortical regions associated with visual processing of spatial locations that are perceived to be in the background, are suppressed in a *competition-mediated* manner. It was observed that early visual areas (V1 and V2) representing ground locations were inhibited, relative to voxels representing figure spatial locations when a figure was present. However, the higher competition stimuli (with ground side shapes) resulted in greater suppression of the activity of ground-voxels compared to the low competition stimuli (no ground side shapes) (Cacciamani et al., 2015).

Other studies have explored the effects of context on FG perception and revealed that FG relations are determined by grouping of other contextual elements with the border of interest. Peterson and Salvagio (2008) explored the effects of context in combination with convexity, one of the classical configural cues (Rubin,1915/1958; Kanizsa and Gerbino, 1976), on FG organization. Peterson and Salvagio replicated the well documented findings of a tendency to perceive VEX regions as figures using 2-region displays with a single border separating one VEX and one concave (CAV) region. However, they also observed that the probability of perceiving the convex region as figure, or P(VEX = Figure), increased as the number of alternating VEX and CAV regions in the stimulus increased (see Figure 1.3). By demonstrating that this convexity context effect (CCE)[1] requires homogeneous CAV regions but not homogeneous VEX regions, the results were consistent with the interpretation that CCEs were facilitated through the spread of inhibitory suppression of the grouped CAV ground regions. More recent work has shown that the CCE is abolished by backwards masking within 100 ms of stimulus presentation for black and white stimuli (Salvagio and Peterson, 2010). However, the effect of context is still exhibited with backwards masking if VEX regions are heterogeneous (Salvagio and Peterson, 2012). These findings are consistent with the hypothesis that resolving stimuli with homogeneous VEX regions requires greater inhibitory processing to suppress the {CAV = Figure} interpretation when compared to stimuli with heterogeneous VEX regions, which is inconsistent with the {CAV = Figure} interpretation (Goldreich and Peterson, 2012). In other words, the homogeneity cues in the black and white stimulus have increased ambiguity relative to when CAV regions are homogeneous and VEX regions are heterogeneous, which results in increased competition for figural status. As with the silhouette stimuli used by Peterson and Skow (2008), observers can resolve the higher competition convexity stimuli used by Peterson and Salvagio (2008), but it takes longer to do so compared to the lower competition convexity stimuli (Salvagio and Peterson, 2010, 2012).

The observed interaction between context and convexity, and the implications this relationship has to competition resolution processing underlying FG organization, are particularly interesting. The CCE can be used to study the combination of grouping and configural cue aspects of perceptual organization. The context effects, and related competition effects, thus provide an interesting tool for examining the effects of aging on the processing underlying FG perception.

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[1] Throughout the chapters presented, I refer to CCE as the difference in P(VEX = Figure) between black and white 8- and 2-region conditions, as defined in Equation 4.1. The phrase *convexity effects* encompasses a broader range of effects including the bias to perceive convex regions as figure Rubin (1915/1958), and differences in performance across conditions though to reflect levels of FG competition (e.g., see Equation 4.2).

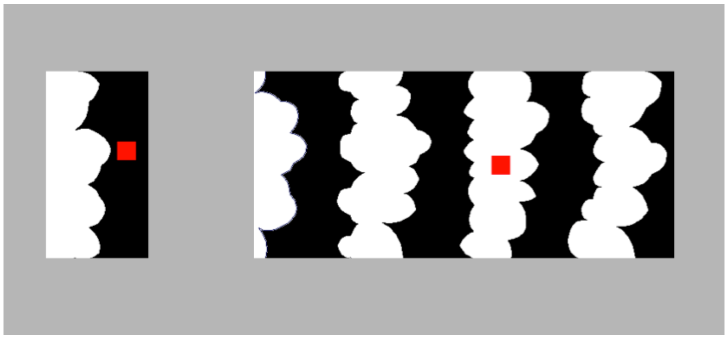

Figure 1.3: Example convexity stimuli used by Peterson and Salvagio (2008). This diagram depicts one example 2-region and one example 8-region black and white convexity stimulus. The 2-region stimuli were composed of a single VEX and single CAV region and 8-region stimuli were composed of alternating VEX and CAV regions. The red probe was used for the task of indicating the figure, which specifically was to indicate after each stimulus presented: "Was the red square probe ON or OFF the region that appeared to be the figure?". In these examples, the probe is on the black CAV region in the 2-region stimulus, and on a white VEX region in the 8-region stimulus. During all experiments that used this task, the side, colour, and region type (CAV vs. VEX) that the probe was placed on was balanced across the stimulus set. The background surrounding the stimuli was grey that was equal luminance steps between the brightness of black and white regions.

1.3 Aging & visual perception

Healthy aging is associated with a variety of anatomical and physiological changes in the visual pathway (Owsley, 2011; Andersen, 2012). Here, I review the effects of aging on the visual system and on performance of visual tasks to set the stage for our examination of FG perception in healthy aging.

1.3.1 Age-related changes in the eye

Aging affects multiple components of the eye (Weale, 1963). Age-related changes to the optics of the eye include presbyopia, reduced ability to accommodate due to hardening of the lens and weakening of the ciliary muscles (Sekuler and Sekuler, 2000a). The transparency of the crystalline lens also becomes reduced in aging, leading to increased absorption and therefore decreased passing of light through to the photoreceptors at the back of the retina. Cataracts, opacities in the lens, can also form, blocking and causing increased scatter to light entering the pupil. There is also evidence of reduced rod density at the level of the retina, in peri-foveal regions, that would impact ability to detect light with the same acuity as a more densely packed photoreceptor lattice (Weale, 1963; Sekuler and Sekuler, 2000a; Werner et al., 2010). Additionally, at the level of the retina, age-related macular degeneration (AMD) is the degradation of the macula, which is the part of the retina where fixated objects are focussed; it contains the fovea at its most central zone. AMD blurs the macular image, which can obstruct central vision and develop into blind spots. It is the leading cause of vision loss for people aged 60 and older (National Eye Institue, 2015).

1.3.2 Effects of aging on visual processing

Aging is associated with deficits in several aspects of visual function. These include reductions to contrast sensitivity (Owsley et al., 1983), acuity, glare sensitivity, (Rubin et al., 1997), stereoacuity (Laframboise et al., 2006), visual field extent (Rubin et al., 1997), luminance sensitivity, spatial orientation sensitivity, motion perception, (Sekuler and Sekuler, 2000b; Owsley, 2011; Andersen, 2012), motion direction selectivity tuning (Tsotsos, 2012), surround-suppression for static gratings (Betts et al., 2005) but with conflicting results with respect to moving/drifting gratings (Farber et al., 2010, found no age difference whereas Karas and McKendrick, 2012; 2015, demonstrated an age effect), and stereopsis (Bell et al., 1995). Deficits associated with aging also have been demonstrated for higher level processes, for example, in a face identification task (Rousselet et al., 2009) and reduced ability to judge faces from different viewpoints (Habak et al., 2008).

Some of the work examining the effects of aging on visual perception has been motivated by the aging-inhibition hypothesis. According to this hypothesis, changes to perceptual processing in aging arise from changes in inhibitory cortical mechanisms, which have been shown to be compromised in a study of postmortem human tissue (Pinto et al., 2010). This result has been demonstrated in a variety of animal studies. For example, reduced GABAergic mechanisms have been shown to be related to increased random firing and higher excitability of V1 neurons, as well as being associated with age-related declines in orientation and directional selectivity of those cells (Schmolesky et al., 2000). In another demonstration of this link, Leventhal et al. (2003) demonstrated that administration of GABA antagonists caused neural tuning functions of younger monkeys to resemble properties of older monkeys. These authors also observed that administration of GABA agonists in older monkeys caused neural responses to resemble that of younger monkeys and improve direction and orientation selectivity of the treated neurons.

The aging-inhibition hypothesis suggests that aspects of perceptual processing involving inhibitory processing might be impaired in aging. Indeed, some findings have supported this notion (Betts et al., 2005, 2009, 2012; Habak et al., 2008; Wilson et al., 2011; Tsotsos, 2012), although other results have not (Govenlock et al., 2009, 2010; Rosen et al., 2013; Karas and McKendrick, 2012; Karas and Mckendrick, 2015). The idea that inhibitory processing mechanisms might be impaired in aging continues to stimulate aging research. Given the evidence that inhibitory processing mechanisms underly FG organization, as reflected at behavioural (Peterson and Skow, 2008; Peterson and Salvagio, 2008) and neural (Likova and Tyler, 2008; Sanguinetti et al., 2015) levels, the work comprising this thesis was motivated by the possibility that reduced cortical inhibition might impair processes underlying FG organization in older humans. I will return to this key idea in the final sections of this chapter and the argument will be developed throughout the thesis. However, the wide range of behavioural studies in humans that have demonstrated various impairments to visual perception, by inhibition or otherwise, beg the question of what consequences these age-related changes produce.

1.3.3 Consequences of aging on visual perception

The visual system is impacted by aging at sensory and perceptual levels, as discussed in the previous section. However, an important question at the applied level is how the deficits to various visual functions affect performance on real world tasks, everyday functioning, and common functional deficits affecting older adults. For example, one of the major problems negatively affecting older people is the high incidence of falls, which negatively impacts quality of life and has been linked to mortality rates across individuals (Wild et al., 1981; Dunn et al., 1992). Indeed, it is difficult to precisely quantify the consequences of falls in aging due to the snowballing effects that injury from falls has on the ability to function autonomously and engage in activities linked with successful aging, for example exercise (Niemann et al., 2014) and social interaction (Seeman and Crimmins, 2001). Falls result from multiple factors. The high incidence of falls in the older population likely involves the interplay between changing perceptual systems (including balance, proprioception, and vision) and physical impairments (including weakened muscles and reduced ability to react to fall inducers like missteps). Given the strong link between falls and visual impairment (Källstrand-Ericson and Hildingh, 2009), the role of different aspects of visual processing on trips and falls is an ongoing topic of aging research.

Similarly, the impacts of aging on tasks like driving (Wood, 2002) have wide ranging impacts on those who have compromised driving ability, as well as those who interact with them. Understanding the factors that impact and predict driving performance is critical in overcoming this societal challenge. Some of the results presented in this thesis indicate particular age-related impairments under conditions when noisy or conflicting stimulus cues lead to perceptual ambiguity; similar findings have been shown in other aspects of perception, for example, age-related changes to contour integration are particularly impaired in conditions of high clutter (Roudaia et al., 2013). As is discussed in the thesis, these findings suggest that driving could be particularly challenging for older observers under conditions of low light, in which ability of younger observers is compromised (Wood et al., 2005). The hypothesis is that low light, rain, other conditions that increase external noise or perceptual ambiguity about the correct interpretation of a stimulus, might impair important perceptual processes like FG organization or contour integration, that are critical in performing multiple simultaneous judgements and tasks involved in driving safely. There are major projects underway exploring the factors affecting driving in older adults (Langford et al., 2013; Marshall et al., 2013), and knowledge about the visual processing mechanisms that are affected by aging may be of great consequence to such efforts.

From one perspective, the purpose of my research is to explore how visual processing changes during senescence in quantifiable ways that can be applied to understand, and develop means for enhancing, visual function in the quotidian tasks that are impaired by aging. The project has focussed particularly on the effects of aging to perceptual processing underlying FG perception. Even though the research explored in this thesis is a form of *basic science*, which is concerned with characterizing and understanding the perceptual phenomena and processing mechanisms supporting them, it is important to consider how these findings might translate to more applied sciences. Yet, although it may be easy to imagine how changes to FG organization discovered in this thesis might relate to falls or driving ability, drawing this link is a project that requires focussed attention. This proposition is discussed in Chapter 5, with hopes that research programs tackling these issues might include the findings of my thesis work in studying some of the challenges burdening older adults.

1.3.4 Aging & perceptual organization

Relatively little is known about how perceptual organization is affected by aging. Some studies have reported impairments to perceptual organization in Alzheimers (Kurylo et al., 1994, 2003), but the few studies on healthy aging have shown mixed results. It seems that some aspects of perceptual organization, including grouping by line orientation and flicker, but not colour or motion, are impaired in older observers (Kurylo, 2006). These results indicate that different aspects of processes that combine low-level stimulus features across space and time into grouped units are differentially affected by aging. Work on contour integration also has found mixed results with no significant effects of age on extraction/integration of orientation and location information under normal viewing conditions(Roudaia et al., 2010), however, older adults are significantly impaired under conditions of low contrast and visual clutter (Roudaia et al., 2013). Impairments to grouping through common fate have also been observed (Pilz et al., 2010), which might be important in understanding age-related deficits to higher order functions like detection of emotion in point light walkers, a task on which older adults are impaired (Spencer et al., 2010). In a study examining the effects of aging on perceptual organization by temporal structure, Blake et al. (2008) observed that older observers were impaired at integrating the temporal grouping signal in determining FG structure, a result that might be related to older adults' reduced flicker sensitivity (Kurylo, 2006). In contrast to the age-related deficit using temporal structure, older observers had no deficit in FG organization that relied on luminance differences (Blake et al., 2008).

The results from work examining the effects of aging on perceptual organization suggest that performance on some tasks is impaired in healthy aging, whereas performance on others is retained. It also seems that the aging visual system may be selectively impaired at grouping based on integration of temporal structure, which is a theoretical substrate of the grouping mechanism that can be represented in neural circuit firing patterns. However, the question of how aging impacts FG processing remains largely unexplored. This is an important topic with regards to linking low-level visual mechanisms with visual performance on higher order tasks, and linking behavioural performance and associated neural processing patterns to real-world functional deficits impacting the older adults. One recent study, using the high vs. low competition silhouettes described earlier (see Peterson and Skow, 2008), found evidence that FG organization is impaired in aging (Anderson et al., 2016). It was the purpose of the work composing this dissertation to address the issue of the effect of aging on FG perception. The sets of studies run within attempted to explore the processing mechanisms underlying FG in at behavioural and neural levels in younger and older observers.

1.4 Thesis overview

This thesis examined the effects of aging on FG organization, particularly focussing on the competitive processes underlying FG perception. The experiments manipulated several stimulus properties affecting the interaction between convexity and contextual influences on FG organization and measured behavioural and electrophysiological responses in a figure assignment task like the one used by Peterson and Salvagio (2008). Our results provide insight into the processing underlying FG organization and the way this processing is affected by healthy aging.

This dissertation is composed of five chapters. The first chapter is the one you have just read, which has explained the purpose of the research program and laid the ground work for the next three chapters. Chapters 2, 3, and 4 each explore a different question related to the effects of aging on FG organization. The final chapter (Chapter 5) ties it all together and focuses on the implications and future directions that follow from our findings.

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Chapter 2

Effects of aging on figure-ground perception: Convexity context effects and competition resolution

Abstract

We examined age-related changes to figure-ground perception by exploring the effect of age on Convexity Context Effects (CCE; Peterson & Salvagio, *J Vision*, 8(16):1-13, 2008). Experiment 2.1, using Peterson and Salvagio's procedure and black and white stimuli consisting of 2 to 8 alternating concave and convex regions, established that older adults exhibited reduced CCEs compared to younger adults. Experiments 2.2 and 2.3 demonstrated that this age difference was found at various stimulus durations and sizes. Experiment 2.4 compared CCEs obtained with achromatic stimuli, in which the alternating convex and concave regions were each all black or all white, and chromatic stimuli in which the concave regions were HOM in colour but the convex regions varied in colour. We found that the difference between CCEs measured with achromatic and coloured stimuli was larger in older than younger adults. Our results are consistent with the hypothesis that the senescent visual system is less able to resolve the competition among various perceptual interpretations of the figure-ground relations among stimulus regions.

Introduction

Figure-ground (FG) perception is one possible outcome of perceptual organization processes operating on a border between two regions in the visual input. FG processes enable us to assign contours to objects, which are perceived as figures lying in front of a background, and is a critical component of perception in naturalistic contexts. Given the importance of the phenomenon, it has been studied for nearly a century; yet, many questions remain about the mechanisms underlying FG organization.

The convexity of a border between adjacent regions is one of the classic configural cues involved in FG perception first discussed by Rubin (1915/1958). Specifically, the region on the convex (VEX) side of a border (i.e., the *VEX region*) is more likely than the region on the concave (CAV) side of the border (i.e., the *CAV region*) to be perceived as a shaped entity, or figure, lying in front of a shapeless background (Kanizsa and Gerbino, 1976). Some authors, including Rubin (1915/1958), have held convexity to be a weak cue while others, including Kanizsa and Gerbino (1976), have argued that it is a relatively strong cue. The reality appears to be that the probability of perceiving VEX regions as figures actually depends on the context of the border of interest.

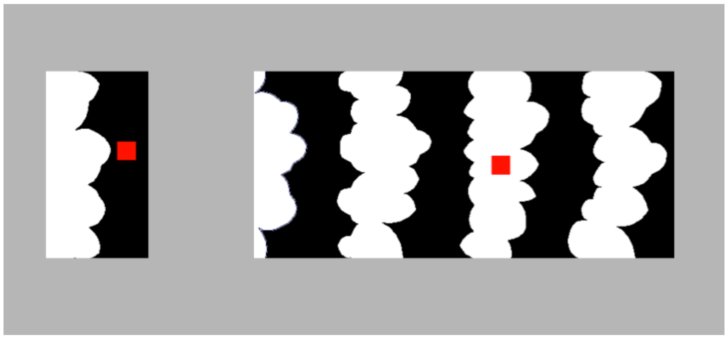

Figure 2.1: Convexity stimuli used by Peterson and Salvagio (2008). This figure contains 2- and 8-region black and white (BW) stimuli, composed of alternating VEX and CAV regions. The red probe is on the black CAV region in the 2-region stimulus, and on a white VEX region in the 8-region example. The side, colour, and region type that the probe was placed on was balanced across the stimulus set. The background surrounding the stimuli was grey that was equal luminance steps between the black and white luminances.

Peterson and Salvagio (2008) developed a novel method to examine the influence of convexity on FG perception and how this influence is affected by the context of surrounding regions. Their stimuli, illustrated in Figure 2.1, contained 2, 4, 6, or 8 alternating black and white regions with VEX/CAV borders. A red probe was located on one of the regions adjacent to the central border and occurred equally on each side, region type (VEX vs. CAV), and polarity (black vs. white). Participants viewed each stimulus for 100 ms, and indicated whether the probe was on or off the region they perceived as figure. Peterson and Salvagio found that when the stimulus contained only two regions separated by a VEX/CAV border (left panel, Figure 2.1), participants indicated that they perceived the VEX region as figure on 57% of the trials. In other words, VEX regions were perceived as figure significantly more than CAV regions, confirming that convexity is a figural cue, but its influence was not strong; even young subjects don't always perceive the VEX regions as figures in 2-region displays. Interestingly, the probability that participants perceived the central VEX region as the figure increased as the number of regions surrounding the central border increased from 2 to 8. Hence, the context surrounding the region of interest affected the proportion of trials where the VEX region was perceived as figure, such that in 8-region displays (right panel, Figure 2.1) observers perceived the VEX region as the figure on nearly 90% of the trials. This context effect was later replicated with the configural cue symmetry (Mojica and Peterson, 2014).

This so-called convexity context effect (CCE) persists when the VEX regions are heterogeneous (HET) in colour, but is abolished when the CAV regions vary in colour (Peterson and Salvagio, 2008). This indicates that homogeneity across potential background segments is required for the increase in P(VEX=Figure) observed with increased region number, so long as there are VEX regions that signal foreground. This suggests that heterogeneity across spatially separated CAV regions is inconsistent with the interpretation of those regions being parts of unified background. The CCE also is abolished when a mask is presented 0-50 ms after the stimulus offset, and re-emerges with increased stimulus-mask asynchrony (Salvagio and Peterson, 2010). Peterson and Salvagio (2008) interpreted their results as showing that figure-ground perception results from inhibitory competition between alternative perceptual interpretations of the display, which takes time and is mediated by context, including the number of regions and the homogeneity of colour across regions. This inhibitory-competition model of FG perception has been supported by behavioural findings indicating suppression of object representations falling on the perceived grounds (Peterson and Skow, 2008), functional imaging results demonstrating suppression of voxels representing spatial locations of ground-side image regions (Likova and Tyler, 2008; Cacciamani et al., 2015), and electrophysiological evidence consistent with processing mechanisms involving online inhibitory suppression in response to differing degrees of FG competition (Sanguinetti et al., 2015).

The suggestion that figure-ground perception is based on inhibitory competition raises the possibility that figure-ground perception may change during healthy aging. Evidence from anatomical, physiological, and psychophysical studies suggests that aging may affect the balance of excitatory and inhibitory mechanisms in visual cortex. For example, a study of human visual cortex from older adults found that there were changes in several pre- and post-synaptic GABAergic markers (Pinto et al., 2010), consistent with an aging-related reduction in the efficacy of the GABAergic system. A reduction in the efficacy of inhibitory mechanisms is thought to contribute to the age-related decline in orientation and directional selectivity of V1 neurons (Leventhal et al., 2003; Schmolesky et al., 2000), and perhaps the reduction in selectivity of speed and directional MT neurons (Liang et al., 2010; Yang et al., 2009) in older monkeys. A decrease in the density of GABA-immunoreactive neurons also has been associated with neurophysiological changes in visual neurons in cat striate cortex (Hua et al., 2008) consistent with an age-related decline in inhibitory function. Finally, the results of several psychophysical studies are consistent with the hypothesis that inhibitory cortical neural circuits are diminished by aging. For example, motion detection and discrimination thresholds are consistent with models of aging that incorporate broader directional tuning and increased internal noise (Bennett et al., 2007), similar to the changes found in neurophysiological studies. Age-related changes in the ability to recognize faces across different viewpoints (Habak et al., 2008) also are consistent with neural models that incorporate a reduction of inhibition with aging (Wilson et al., 2011). As well, spatial suppression in a motion discrimination task is significantly lower in older adults compared to younger adults (Betts et al., 2009, 2005), a result consistent with the idea that aging alters the balance between excitatory and inhibitory mechanisms that encode motion direction (Betts et al. 2012; but see Govenlock et al., 2009, 2010; Rosen et al., 2013; Karas and McKendrick, 2012; Karas and Mckendrick, 2015, for examples of tasks in which aging does not appear to be linked to decreased inhibition).

Hence, a variety of studies suggest that healthy aging may be associated with a change in the balance between excitation and inhibition, with decreased efficacy of inhibitory mechanisms. If inhibitory competition is important for figure-ground perception, one might expect to find both reduced likelihood of seeing convex regions as figures overall (because FG requires competition resolution) and reduced CCEs. The current experiments tested that prediction.

2.1 Experiment 2.1

Experiment 2.1 used the method described by Peterson and Salvagio (2008) to measure the CCE in younger and older adults using 2- and 8-region displays.

2.1.1 Methods

Participants

Two groups of observers participated in this study: The younger group consisted of 25 participants ($M = 22.6$ years, $sd = 4.1$ years) and the older group consisted of 24 participants ($M = 70.0$ years, $sd = 5.9$ years). All of the older participants were compensated $10 per hour for participating, whereas younger participants received partial course credit.

Every observer participated in two experimental conditions, and the order of the conditions was counter-balanced. The study took approximately 30 minutes to complete.

Stimuli and apparatus

Stimuli were presented on an NEC MultiSync FE992 CRT with a resolution of 1280 × 1024 pixels and a frame rate of 85 Hz. The experiment was controlled with an Apple Power Mac G5 computer using MATLAB (version 7.4.0.287) and the Video and Psychophysics toolboxes (Brainard, 1997; Pelli, 1997).

This study used the 2- and 8-region convexity stimuli from Peterson and Salvagio (2008). Each stimulus consisted of 2 or 8 alternating black and white sections with complex curved borders (Figure 2.1). Black and white regions were always equal in area. The left and right sides of each black/white section were bounded by convex (VEX) or concave (CAV) borders, making for *regions* that were either VEX or CAV. For example, the 8-region stimulus in Figure 2.1 is composed of alternating white VEX regions and black CAV regions. The tops and bottoms of each stimulus were separated from the background by horizontal edges and the left and rightmost regions of each display met the background at vertical edges. The stimulus set was balanced such that the leftmost (and rightmost) region in each pattern was black 50% of the time and VEX 50% of the time (see Mojica and Peterson, 2014, for evidence that the shape of display edges matters). Each stimulus also had a red square probe that was always on one of the two regions adjacent to the pattern's central border. The probe's placement was balanced across trials such that it was on VEX and CAV regions equally often, located to the left and right of the central border equally often and placed on black and white regions equally often. Each curved edge in every stimulus was created by creating 3-15 points that corresponded to minima of curvature. These points were distributed randomly along a virtual vertical contour with slight horizontal jitter, and then smooth curves were drawn upwards and downwards from each point until adjacent arcs intersected to form a curved bump. There were a total of 64 stimuli in each of the 2- and 8-region conditions.

Each stimulus was presented in the center of a uniform display that subtended 22.9° (width) × 17.2° (height) from the viewing distance of 90 cm. The stimuli were 5.4° in height; the mean widths of the 2- and 8-region displays were 2.5° and 11.5°, respectively. The luminance was 53.5 cd/m^2 for the background, 0.6 cd/m^2 for the black regions, and 96.4 cd/m^2 for the white regions. Viewing was binocular, and a head/chin rest was used to stabilize viewing position. The experiment took place in a dark and quiet room with the experimental monitor serving as the only light source.

Procedure & task

Every participant completed two blocks of 64 trials: one with 2-region stimuli, and another with 8-region stimuli. Block order was randomly determined, and stimulus presentation order was randomized within each block. No stimuli were repeated. Each block began with five practice trials.

The task was to indicate whether a red probe square appearing on one of the two central regions was ON or OFF the region perceived as figure. Before the experiment began, the experimenter introduced the participant to the concept of FG perception, explaining that figures appear to have a definite shape and appear closer than the adjacent region(s) that are seen as shapeless background. The experimenter stayed in the room while instructions were presented on the screen and participants completed five practice trials of the first condition. After the first block of trials was completed, there was a short break before instructions for the second block were presented on-screen. There were five practice trials and participants completed the second block.

Each trial began with a central fixation point that flickered on the screen for 800 ms,

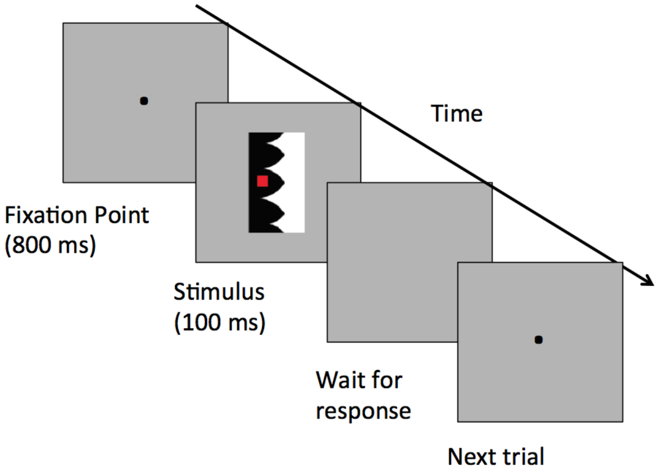

Figure 2.2: A schematic of the progression of a single trial. Each trial began with a flickering fixation point and after 800 ms the stimulus was displayed for 100 ms (for Experiment 2.1, although the stimulus duration was manipulated in later experiments). After stimulus offset, the screen was left with a background grey fill until the participant responded by indicating whether the red probe was ON or OFF the region perceived to be the figure.

followed directly by the presentation of an FG stimulus for 100 ms (see Figure 2.2). The entire screen was filled with background grey 100 ms after the stimulus onset. After stimulus offset, participants indicated which of the two central regions they perceived to be the figure by pressing the ON or OFF button to signal whether the red probe was on or off the perceived *figure*. They were told that there were no wrong answers, and that they should answer based on their first impression while maintaining accuracy. The next trial began immediately after participants made their response.

2.1.2 Results

All statistical analyses were performed using the R statistical computing environment (R Core Team, 2016).

Figure 2.3 depicts the proportion of stimuli for which the VEX region was perceived as the figure for each condition and each age group. As expected from previous work demonstrating the influence of convexity on FG perception, both age groups indicated the VEX region as figure significantly more than 50% of the time; however, P(VEX=Figure) was higher in younger adults, particularly in the 8-region condition. The CCE is defined as the change in the proportion of VEX responses as the number of regions increases, and therefore the results shown in Figure 2.3 suggest that the CCE was stronger in younger observers. Here we calculated the CCE as follows:

$$\text{CCE} = P(\text{VEX} = \mathit{figure})_{8-Region} - P(\text{VEX} = \mathit{figure})_{2-Region} \tag{2.1}$$

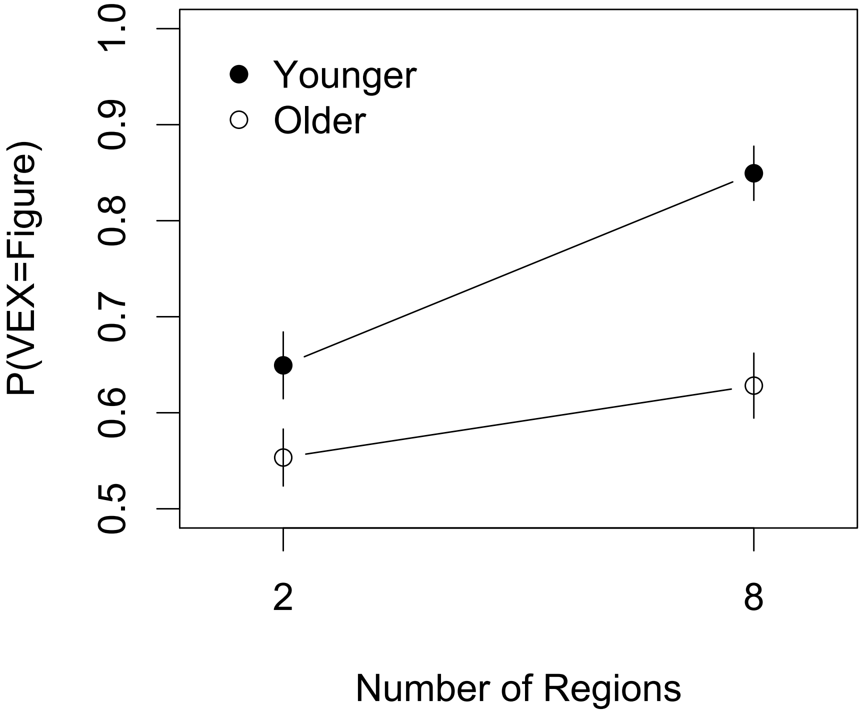

Figure 2.3: Behavioural performance in Experiment 2.1. The figure shows the mean proportion of trials on which the convex region was perceived as figure for younger (filled circles) and older (open circles) observers in the 2- and 8-region displays. Error bars represent ±1 SEM. In 2-region displays, VEX regions were reported as figure more often than chance for both younger, $t(24) = 4.29, p < .0001$, and older adults, $t(23) = 1.80, p = .021$ (one-tailed).

To quantify these effects, data in Figure 2.3 were analyzed with a 2 (age group) × 2 (region number) × 2 (condition order) split plot Analysis of Variance (ANOVA).

Previous studies examining CCEs used a between observers design, and therefore we included condition order in our analysis to determine if the probability of perceiving the VEX region as figure differed between groups who saw the 2- or 8-region stimuli first. The results of the ANOVA are presented in Table 2.1. The main effects of Age Group, Region Number, and Order were significant. Importantly, the Age Group × Region Number interaction was significant, indicating that the CCE differed between age groups, and the interaction did not depend on the order of the conditions. Although the interaction shows that the extent of the CCE was greater for younger observers than older observers, follow-up analyses indicated that effect of region number was significant in both younger ($t(24) = 4.62$, $p = 0.0012$) and older groups ($t(23) = 2.14$, $p = .043$). With respect to the main effect of order, observers tended to report VEX region as figure more often when the 8-region condition was conducted first ($M = .72$) compared to when the 2-region condition was first ($M = .62$).

	df	Sum Sq	Mean Sq	F	Pr(>F)
Age Group	1	0.58	0.58	18.19	0.001
Regions	1	0.37	0.37	25.23	< 0.001
Order	1	0.20	0.20	6.34	0.015
Age Group × Regions	1	0.11	0.11	7.53	0.009
Age Group × Order	1	0.002	0.002	0.05	0.83
Regions × Order	1	0.02	0.02	1.39	0.24
Age Group × Regions × Order	1	0.003	0.003	0.19	0.66
Residuals (Within/Mixed)	44	0.64	0.014		
Residuals (Between)	44	1.41	0.032		

Table 2.1: Analysis of Variance results for Experiment 2.1.

2.1.3 Discussion

The current experiment had two main results. First, we replicated the CCE in young adults that was observed by Peterson and Salvagio (2008). Second, our key finding is the interaction between region number and age group. This interaction indicates that, although region number affected the probability of perceiving VEX regions as figure in both age groups, the CCE was significantly lower in older adults compared to younger adults (Figure 2.3).

Peterson and colleagues (Peterson and Salvagio, 2008; Salvagio and Peterson, 2012) have suggested that the CCE is a manifestation of an inhibitory competition between regions on opposite sides of a contour that leads to one region being perceived as a figure and the other as the background. Within this framework, our results suggest that the competitive FG process is less effective in older adults, perhaps due to age-related changes in inhibitory processing. However, other potential causes need to be considered. One possibility is that FG processing is simply slower in older adults. This idea is examined in Experiments 2.2 and 2.3. Alternatively, older adults may be less able to spatially integrate information across the large, 8-region stimuli used in the current task. If this is correct, then older adults should also be less sensitive to the effects of region homogeneity reported by Peterson and Salvagio (2008). This hypothesis is examined in Experiment 2.4.

2.2 Experiment 2.2

Some age-related changes in perception and cognition may reflect a generalized slowing of perceptual and cognitive processing rather than a qualitative change in processing (Salthouse, 1996). Hence, it is plausible to suggest that the age differences in CCEs found in Experiment 2.1 were simply the result of slower FG processing in older adults. Might younger observers show reduced CCEs, similar to those observed in older participants, if stimuli were presented for shorter durations? Experiment 2.2 addressed this question by measuring CCEs in younger observers using shorter stimulus durations.

2.2.1 Methods

Participants

Twenty-four younger observers participated in this experiment ($M = 21.5, sd = 2.9$ years). Nine of the participants received partial course credit for completing the experiment, whereas the other 15 were compensated $10 per hour after completing the study.

Procedure

The same methods were used as in Experiment 2.1, except that two shorter durations (50 ms and 25 ms) were included along with the original stimulus duration of 100 ms. Two- and 8-region stimuli were each shown at three stimulus durations (25, 50, & 100 ms), yielding a total of six experimental conditions. Each condition included 64 trials; stimuli were not repeated within conditions but were repeated across conditions. The presentation orders for region number and stimulus duration were counterbalanced across participants using a Latin square with 4 subjects per order.

Stimuli were the same as those used in Experiment 2.1: From the viewing distance of 96 cm, they subtended 5.1 ° in height and had a mean width of 2.3 ° for 2-region and 10.8 ° for 8-region stimuli. All stimuli were presented in each stimulus duration condition.

2.2.2 Results

The results are displayed in Figure 2.4, which shows that there was no obvious effect of stimulus duration on the magnitude of CCEs in younger observers. These observations were supported by a two-way (stimulus duration × region number) within-subjects ANOVA: the main effect of region number was significant, $F(1, 23) = 22.27$, $p < .0001$, but the main effect of stimulus duration, $F(2, 46) = 0.12, p = .89$, and the stimulus duration × region number interaction, $F(2, 46) = 2.00$, $p = .15$ were not.

2.2.3 Discussion

The results of this experiment demonstrated that reducing stimulus duration from 100 ms to 25 ms did not significantly alter the CCE measured in younger observers. Overall, the pattern of results is inconsistent with the hypothesis that reducing stimulus presentation durations by a factor of 2 and 4 in younger observers would shift CCEs towards those observed in older observers. Hence, the results of the current experiment suggest that the age difference observed in Experiment 2.1 was not caused by simple differences in ability to organize briefly exposed stimuli. To further investigate this issue, Experiment 2.3 examined if increasing stimulus duration would increase CCEs in older observers. Experiment 2.3 also examined whether the magnitude of the CCE in seniors is constrained by their difficulty in quickly processing large stimuli.

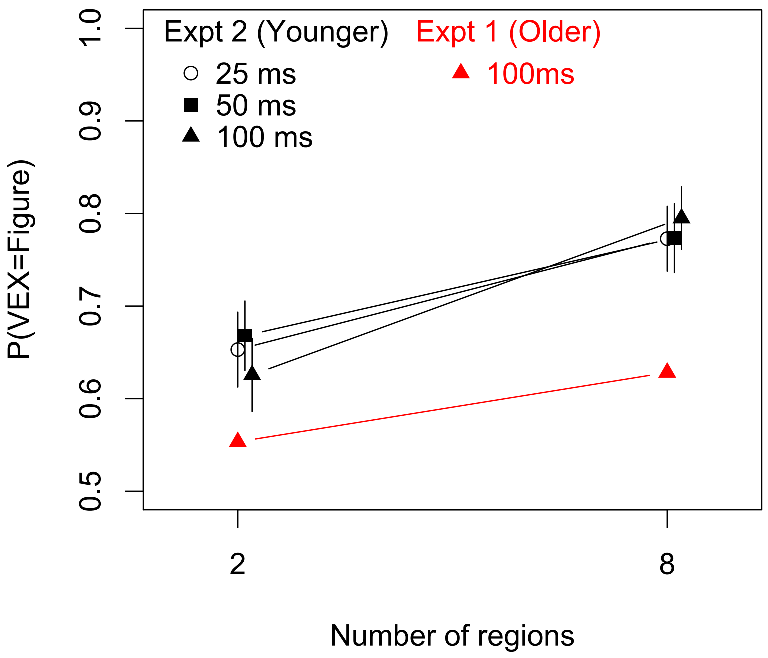

Figure 2.4: Performance for younger observers with reduced stimulus durations. *M* ±1 SEM proportion of figures where VEX region was seen as figure –P(VEX=Figure)– for younger observers in 2- and 8-region displays across the different stimulus duration conditions. The data points for the older group are included in red to allow for direct comparison of CCEs across groups even under such time-constrained conditions. This figure also allows for comparison of the slopes between age groups and demonstrates that even compared to the shallowest CCE slope from experiment 2 the older group has a reduced effect of region number.

2.3 Experiment 2.3

Our interpretation of the effects of decreasing stimulus presentation time for younger observers may be limited by the fact that, due to age-related differences in visual masking (Kline and Birren, 1975; Farber et al., 2010), we did not include a mask following stimulus presentation. Thus, it is possible that although younger people viewed short-duration stimuli visual processing may have continued for longer periods of time after stimulus offset. To more directly assess the effect of processing time on age-related changes in the CCE, it is important also to examine performance under conditions of increased stimulus duration. To that end, the current experiment presented stimuli at both our original presentation duration (100 ms) as well as at a longer duration (250 ms). We did not extend presentation durations beyond that to avoid introducing complications from age-related changes in eye-movements (Sharpe and Zackon, 1987; Munoz et al., 1998; Peltsch et al., 2011). If seniors' CCE was constrained by the relatively short duration in Experiment 2.1, we would expect that increasing stimulus duration from 100 to 250 ms would increase the CCE obtained in older observers.

Because older observers are known to have different spatial integration limits and reduced effective useful fields of view compared to younger observers (Andersen and Ni, 2008; Del Viva and Agostini, 2007; Richards et al., 2006; Sekuler et al., 2000), Experiment 2.3 also manipulated the spatial scale of the stimuli.

2.3.1 Methods

Participants

For Experiment 2.3, the sample consisted of 8 older ($M = 71.5$ years, $sd = 6.5$ years) and 8 younger ($M = 23.0$ years, $sd = 2.7$ years) participants. All of the participants were paid \$10 for participating, except for two observers from the younger group, who were naive volunteers working on other projects in McMaster's Vision and Cognitive Neuroscience lab. The experiment took 30 minutes to complete.

Procedure

The same methods and task used in Experiment 2.1 were employed in the current experiment, with the following changes. The current experiment used two stimulus size conditions (i.e., *large* and *small*). Large stimuli were the same size used in Experiment 2.1 and subtended 5.4° in height with a mean width of 2.5° and 11.5° for 2- and 8-region stimuli, respectively. Small stimuli subtended 3.3° in height with a mean width of 1.5° and 7.0° for 2- and 8-region stimuli, respectively.

The experiment employed a 2 (stimulus size: large vs. small) × 2 (stimulus duration: 100 vs 250 ms) × 2 (region number: 2 vs. 8) × 2 (age group: older vs. younger) design. This design allowed us to examine whether the age × CCE interaction depends on the effects of stimulus size, stimulus duration, and the interaction between size and duration.

Eight different orders were created by dividing each factor, duration, size, and region number, into two sub-orders, namely: 100 ms or 250 ms first; large or small first; and 2- or 8-region first. The sub-orders were then crossed, resulting in eight conditions in which sequential blocks always alternated between the 2- and 8-region conditions. Each participant within an age group completed the task according to a different order, with all 8 orders completed across all participants within each age group. Each condition involved 64 trials; stimuli were not repeated within conditions but were repeated across conditions.

2.3.2 Results

The results are plotted in Figure 2.5. An ANOVA revealed significant main effects of age group, $F(1,14) = 57.78, p < .0001$, and region number, $F(1,14) = 14.03, p = .0022$. The interaction between age group and region number, $F(1,14) = 18.80, p = .00068$, was significant. Follow-up tests indicated that the effect of region number was significant in younger $F(1,7) = 20.30, p < .01$, but not in older observers, $F(1,7) = 0.44, p = .53$. There was no evidence of a main effect of exposure duration, $F(1,14) = 1.44, p = .25$, or an effect of stimulus size, $F(1,14) = 1.70, p = .21$. The overall ANOVA also revealed a significant interaction between age group and stimulus size $F(1,14) = 5.00, p = .042$. Subsequent tests found no simple main effect of stimulus size in older observers, $F(1,7) = 1.10, p = .33$, but a marginally significant effect of stimulus size in younger observers, $F(1,7) = 3.90, p = .089$, with higher P(VEX=Figure) for smaller stimuli. Younger observers reported perceiving VEX regions as figure greater than chance for all 2-region, all ps $< .017$, and 8-region conditions, all ps $< .0001$. However, older observers did not report perceiving VEX regions as figures greater than chance for either 2-region, all ps $> .16$, or 8-region stimuli, all ps $> .2$.

In summary, we found strong CCEs in younger but not older adults in all conditions, and the results did not support the hypothesis that age differences in CCEs was caused by a change in spatial integration or reduced ability to encode brief stimuli.

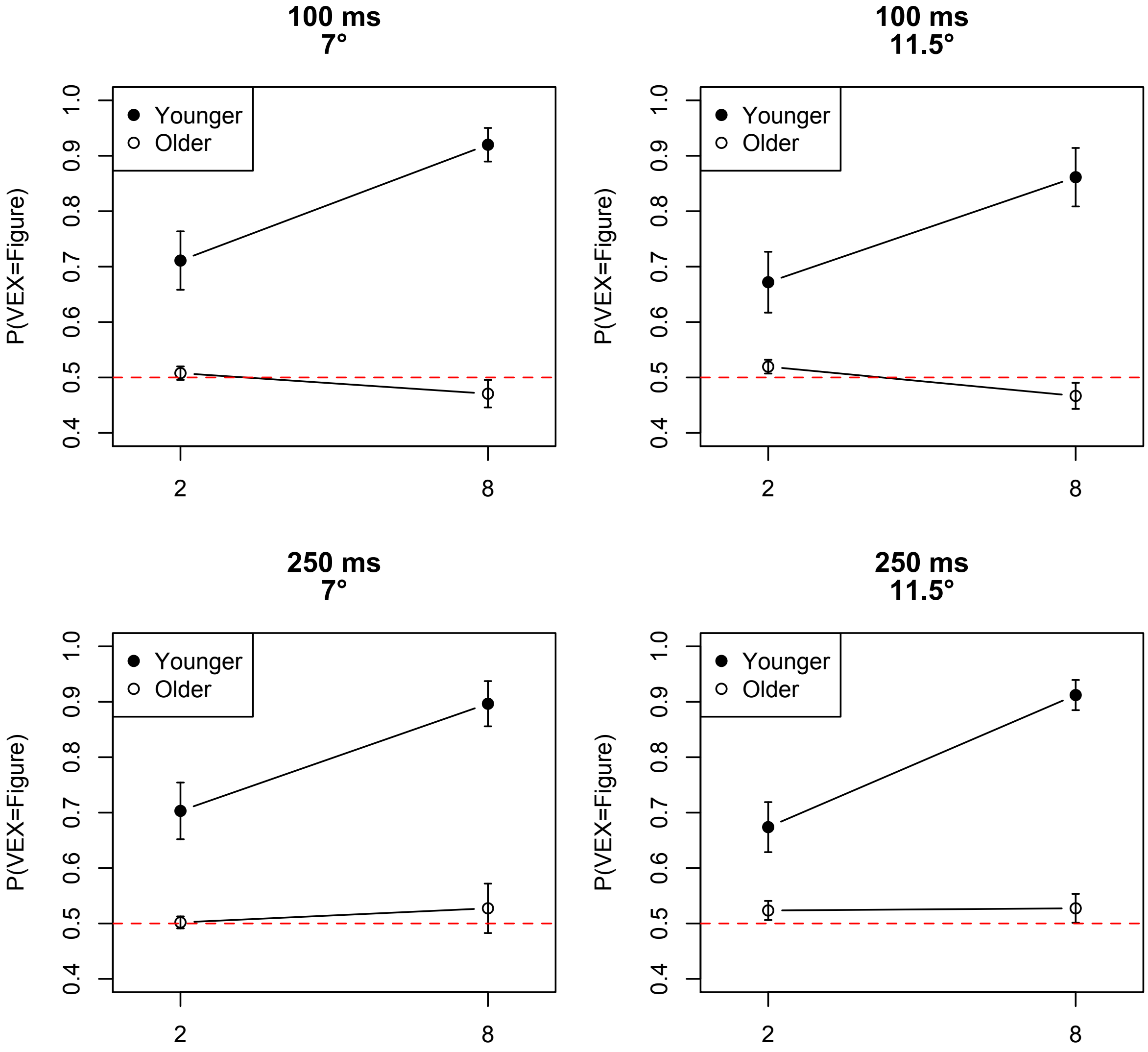

Figure 2.5: The results of Experiment 3 shown for each age group and each combination of stimulus duration and size. Each graph plots the mean proportion of trials on which VEX regions were perceived to be the figure in the 2- and 8-region stimuli. In all conditions, younger observers exhibited strong CCEs whereas older observers exhibited very small or zero CCEs. Error bars represent ±1SEM.

2.3.3 Discussion

As in Experiment 2.1, younger observers perceived the VEX regions as figure more often than the CAV regions in both 2- and 8-region stimuli, whereas older observers did not. We observed CCEs for younger observers but not for older observers. Contrary to the duration and size hypothesis, the CCE observed in seniors was not influenced by stimulus duration or stimulus size. In particular, we found no evidence that increasing stimulus duration, or decreasing stimulus size, increased the CCE in older observers. It is important to note that in this experiment, contrary to our observation in Experiment 2.1, the older group did not report seeing VEX regions as figure more than chance in any of the conditions, and the group did not show a significant CCE. However, given that a large proportion of the older group in Experiment 2.1 (16/24 or 66%) performed near chance, and considering that the older group showed weak CCEs, it is not surprising that 7/8 observers in this experiment demonstrated this behavioural pattern. Such sample-to sample variation might be expected due to random variation, especially for small effects being assessed with small sample size. Importantly, if spatial integration or stimulus duration contributed largely to the reduced CCE in older observers, we would expect to see a strong increase in P(VEX=Figure) and significantly *reduced* proportions of observers lacking CCEs, a pattern clearly not supported by these data.

These results demonstrate that neither the inclusion of stimuli that require less spatial integration (smaller visual angle), nor increased stimulus presentation time, nor the combination of the two, was enough result in the emergence of a CCE in older observers. The results strengthen the suggestion that age-related differences are not limited by encoding differences of low-level visual processes, but what then might cause this FG impairment in aging. Does the convexity bias/prior decline with age? This would be odd given that people are continuing to experience environmental regularities where the VEX side of a border is more likely to be the near side (Burge et al., 2010). Or is the absence of effects of convexity in older observers due to a failure to resolve the competition in BW displays? This seems like a reasonable possibility given the suppressive mechanisms underlying FG resolution (Peterson and Skow, 2008; Likova and Tyler, 2008; Sanguinetti et al., 2015; Cacciamani et al., 2015), the evidence that CCEs result from spreading of inhibition across HOM CAV regions (Peterson and Salvagio, 2008), the observation that increased competition requires more processing to resolve (Salvagio and Peterson, 2010, 2012), and the findings of deteriorated cortical inhibition in aging (Pinto et al., 2010) that is thought to underlie some inhibitory perceptual processes impaired in aging (Betts et al., 2005; Bennett et al., 2007; Wilson et al., 2011; Anderson et al., 2016). The next experiment explores this hypothesis by investigating whether older observers perceive VEX regions as figure more often when the competition in 8-region displays is reduced.

2.4 Experiment 2.4

The results from Experiments 2.2 and 2.3 are inconsistent with the idea that the age-related difference in the CCE identified in Experiment 2.1 are due to age differences in spatial or temporal integrations, and therefore raise the possibility that aging alters the competitive processes that are thought to be important for FG perception. Salvagio and Peterson (2012) suggested that suppression of competing, alternative interpretations of visual input is critical for successful FG resolution. If the efficacy of these suppressive processes is reduced by aging, then providing additional cues to reduce FG competition may increase the CCE in older observers. Experiment 2.4 examined this hypothesis by measuring CCEs with stimuli that consisted of regions that were coloured in a way that aided FG organization by making it more plausible to perceive some regions as figures and others as ground.

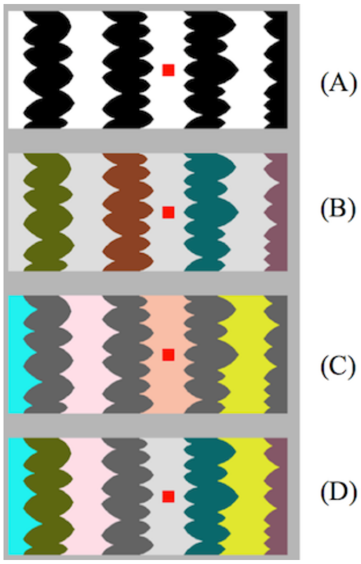

Figure 2.6: Four types of stimuli used in Experiment 2.4. A) *Black and white* (BW), which were also used in experiments 1-3. b) *CAV-HOM/VEX-HET* (CavHom), which have HOM concave but HET convex regions. C) *VEX-HOM/CAV-HET* (VexHom), which have HOM convex and HET concave regions, the reverse of CavHom stimuli. D) Multicoloured displays, where both CAV and VEX regions are heterogeneously coloured thereby resulting in stimuli where each region is a different colour.

Using stimuli like those illustrated in Figure 2.6, Peterson and Salvagio (2008) demonstrated that the heterogeneity or homogeneity of CAV region colour modulates the CCE. They found that only when CAV regions were homogeneously coloured, as in Figures

2.6A and B, did the CCE remain intact, presumably because HOM CAV regions are more likely than HET CAV regions to be a single surface, and this is therefore a requirement for perceiving CAV regions as a unified background (Goldreich and Peterson, 2012). However, whereas the CCE for BW stimuli could be abolished by backwards masking, requiring a stimulus-mask onset asynchrony (SOA) of 200 ms (Salvagio and Peterson, 2010), the CCE was maintained for CavHom coloured stimuli even with SOAs as low as 100 ms (Salvagio and Peterson, 2012). These findings suggest that the HET colour of VEX regions helped speed and/or strengthen resolution of alternative perceptual interpretations, enabling a more stable FG percept, because with HET VEX regions the alternative CAV=figure interpretation of the display is invalid (i.e., the colour cue is inconsistent with a VEX=background scene). Hence, competition is reduced with CavHom stimuli (Figure 2.6B). Importantly, when VEX regions were homogeneously coloured, as in Figure 2.6C, there was no reverse CCE effect (Peterson and Salvagio, 2008; Salvagio and Peterson, 2012; Peterson and Salvagio, 2013). This suggests that the colouring of regions is not itself a FG background cue but rather that the visual system integrates convexity and colour cues when resolving perceptual ambiguity in FG stimuli.

Here we examine whether the age-related decline in the CCE is related to seniors' inability to resolve an ambiguous percept through inhibitory processing that suppresses representation of regions likely to be ground. If age-related changes to this type of processing underlie the age × CCE interaction, adding an additional colour cue to reduce the competition may support a CCE in older observers. Specifically, we hypothesized that using CavHom stimuli, which require less competition resolution, would enable the emergence of a a strong region number effect in seniors.

2.4.1 Methods

Participants

Sixteen older (M = 72.1 years, sd = 7.3 years) and 16 younger (M = 20.9 years, sd = 2.5 years) observers participated in this experiment. All of the participants were compensated $10 for participating in the study, which took approximately 30 minutes to complete.

Stimuli and task

The same task used in Experiments 2.1-2.3 was used here. However, for this study, all conditions used only 8-region stimuli. Stimulus size was the same as the small size from Experiment 2.3 (i.e., mean height of 3.1 °, and mean width 6.6 ° at the viewing distance of 96 cm). The stimulus duration was 250 ms. The experiment used four classes of stimuli that varied in terms of *region type* (i.e., the homogeneity of both VEX and CAV regions): black and white (BW), CAV-HOM/VEX-HET (CavHom), VEX-HOM/CAV-HET (VexHom), and multicoloured (see Figure 2.6). As in Salvagio and Peterson (2012), coloured stimuli consisted of several colours including high and low luminance tones of yellow, cyan, magenta, and grey. The luminance was HOM across CAV regions and across VEX regions, and luminance between CAV versus VEX were equal steps from the background grey. The average luminance of high luminance fills was 81.5 cd/m^2, and the average of low luminance fills was 24.5 cd/m^2.

Procedure

The task was the same as in the previous experiments and there were six practice trials with novel multicoloured stimuli before experimental trials. Stimuli were blocked by condition and condition order was determined quasi-randomly: each participant was assigned to one of four groups that varied in terms of which condition was presented first, and the order of the three remaining conditions was randomized for each observer.

2.4.2 Results

One older observer had a P(VEX=Figure) score of 0.03 in the CavHom condition, which was more than 3 sd below the mean, meeting the exclusion criteria for experiments presented here. This observer was removed from the sample and not included in subsequent analyses.

Younger observers reported perceiving VEX regions as figure significantly more than chance with BW ($t(15) = 10.9, p < .0001$), CavHom ($t(15) = 13.5, p < .0001$), VexHom ($t(15) = 4.8, p = .00012$), and multicoloured displays ($t(15) = 6.5, p < .0001$). Within the older group, P(VEX=Figure) was greater than chance in the BW ($t(14) = 1.77, p = .049$) and CavHom ($t(14) = 4.4, p < .0003$) conditions, but not in the VexHom ($t(14) =$

$-0.21, p = .58$) or multicoloured conditions ($t(14) = 1.4, p = .09$).

We analyzed the effects of adding colour by conducting two planned linear contrasts. To assess the effect of reducing competition required to resolve displays, we first computed the difference between P(VEX=Figure) in the CavHom and BW conditions. This effect of reducing competition differed between age groups ($t(29) = 2.25$, $p = .032$, two-tailed).The difference score was significantly greater than zero in older observers ($M = 0.17$, $t(14) = 2.69$, $p = 0.018$, two-tailed) but no different from zero in younger observers ($M = 0.033$, $t(15) = 1.66$, $p = 0.12$, two-tailed) These analyses indicate that FG judgements made by older observers were more affected by the addition of colour than were judgements by younger observers. Older observers showed a strong increase in P(VEX=Figure) when competition was reduced.

To assess the effect of CAV-region homogeneity, we compared P(VEX=Figure) judgments in conditions in which the CAV regions were HOM (CavHom + BW) to conditions in which they were HET (VexHom + multicoloured). We found that P(VEX=Figure) was higher in with HOM CAV regions ($t(29) = 4.73$, $p < .0001$), but that the effect of homogeneity did not differ between age groups ($t(29) = 1.21$, $p = 0.54$). These results suggest that both younger and older observers have a higher P(VEX=Figure) for HOM colour grouping of CAV regions, compared to heterogenous colours among CAV regions, replicating the requirement of homogeneity of colour across CAV regions in emergence of the CCE (Peterson and Salvagio, 2008; Goldreich and Peterson, 2012).

These analyses are illustrated by Figure 2.7, which plots P(VEX=Figure) for each each group and condition. In older observers, P(VEX=Figure) is significantly larger in the CavHom condition than the BW condition, and the difference between those two conditions is much larger in older than younger observers. However, the difference between P(VEX=Figure) in the HOM and HET conditions is approximately the same in both age groups.

2.4.3 Discussion

The results from our younger observers follow the same pattern as Peterson and Salvagio (2008): P(VEX=Figure) was greater for 8-region displays when the CAV regions were HOM (BW and CavHom) compared to when they were HET (VexHom and multicoloured) in younger and older observers. Critically, we also found that older ob-

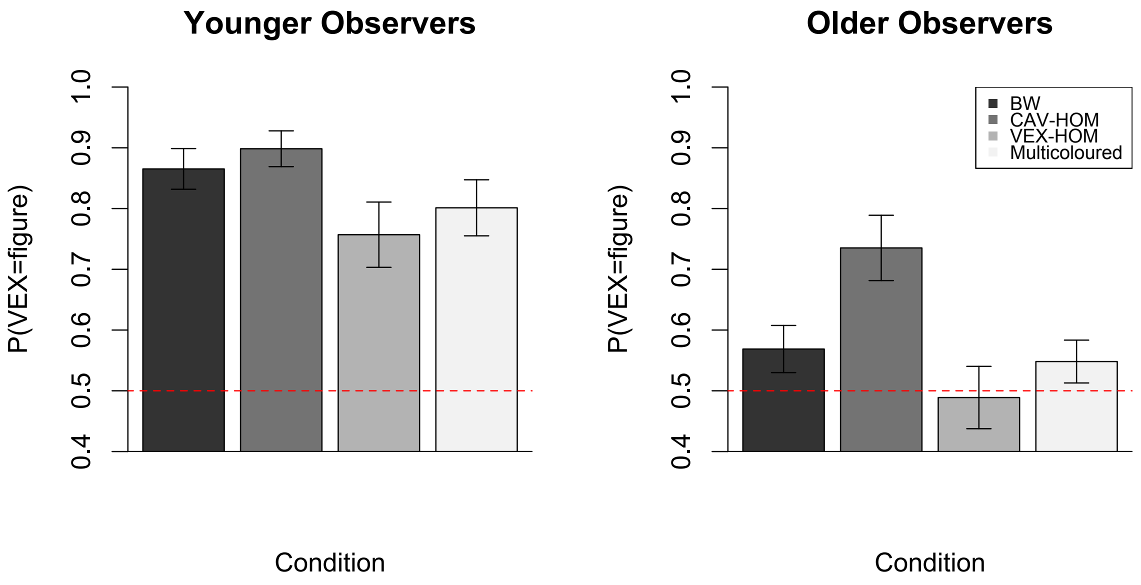

Figure 2.7: Proportion of stimuli where convex regions were perceived as figure for 8-region coloured stimuli used in Experiment 2.4. Each bar shows the mean proportion of trials on which the VEX region was perceived as figure (i.e., P(VEX=Figure)). Red dotted line represents chance performance. Error bars represent ±1SEM.

servers reported seeing VEX regions as figure on a large percentage of trials, showing high P(VEX=Figure) with the addition of HET colour cues to VEX regions while CAV regions were HOM, whereas this manipulation did not have significant effects in younger adults. This result supports the idea that when competition amongst alternate percepts is reduced, perception in older observers is indeed influenced by convexity. Importantly, the lack of a lower than chance P(VEX=Figure) with VexHom stimuli indicated that this strong convexity effect is not simply an effect of colour. These results support the idea that age-related differences in CCEs for BW displays is, at least in part, the result of differential processing in that older observers have a reduced ability to complete FG resolution for high competition displays.

2.5 General Discussion

2.5.1 Main Findings

Younger observers show strong CCEs in the perceptual resolution of FG: the tendency to perceive VEX regions as figures increases with number of regions surrounding the border of interest (Peterson and Salvagio, 2008); see Figure 2.1 and 2.1. We found that CCEs are significantly reduced in older observers. Furthermore, we found that age differences in CCEs are not affected significantly by manipulations of stimulus duration or size (Experiments 2.2 and 2.3). However, we did find that older observers do exhibit robust convexity effects in conditions that reduced competition among different FG percepts (Experiment 2.4).

Our findings support the hypothesis that age differences in CCEs were due to perceptual organization processing differences across age groups, as opposed to being the result of basic visual differences in ability to encode briefly presented images or to spatially integrate information across large displays. More specifically, the finding that P(VEX=Figure) increases in older observers when CAV regions are HOM and VEX regions are HET supports the idea that the age differences observed with BW stimuli in Experiments 2.1 and 2.3 were the result of age differences in ability to resolve the competition between alternative FG interpretations of those stimuli. The previous finding that younger participants perform at chance in all conditions, with no clear CCE, when post-stimulus processing time is cut short by masking for BW displays, but not for CavHom displays (Salvagio and Peterson, 2012), demonstrates that resolution of competing perceptual interpretations entails more competition when alternative interpretations of the display (i.e, the CAV=Figure interpretation) are more valid. Specifically, competition between alternative perceptual interpretations of a stimulus is reduced when likelihood of VEX regions composing a unified surface is eliminated by using HET fills across VEX regions. However, the increased competition between BW alternative interpretations compared to CavHom stimuli that takes longer to resolve in younger adults cannot be resolved by older adults even with excess processing time (i.e., without masking). Yet, the reduced CCE in aging is largely overcome when competition is relatively reduced using HET VEX regions. Effectively, the removal of the conflicting VEX-HOM cue increases the ability of seniors to determine which regions most clearly align with figure or ground, so they can inhibit the ground regions.

The results reported here are extend previous findings of impaired FG organization in older observers observed in a temporal structure paradigm (Blake et al., 2008). Our results demonstrate age-related FG impairments using static stimuli, consistent with a recent report by Anderson et al. (2016) using different FG displays and showing impaired inhibitory competition in older adults. These findings are consistent with other age-related inhibitory perceptual effects (Betts et al., 2005, 2009) and, overall, support the notion that changes to inhibitory processing in aging affect FG perceptual organization.

2.5.2 Questions and Future Direction

Having found an age difference in FG perception and demonstrating that age differences in the ability to resolve competition among alternative percepts accounts for much of the age effect, a number of questions remain.

First, is there a neural correlate associated with FG segregation that can explain individual differences in behaviour within and across age groups to further our understanding of the way aging affects FG processing? At the cellular level, border ownership cells in V1, V2, and V4 depend on FG organization of a contour passing through the receptive field of the cell (Zhou et al., 2000). Therefore, we would expect the firing rates of older monkeys to be noisier and to less reliably encode the implied FG organization. We would also expect that, through manipulation of cortical GABA levels, reducing inhibition in younger monkeys to cause cell responses to resemble the pattern seen in older monkeys and that enhancing inhibition in older monkeys might cause cells to respond more similarly to those in younger monkeys. An examination of event-related potentials (ERPs) associated with presentation of convexity stimuli would yield insight into the temporal dynamics of FG processing and how these dynamics are affected by healthy aging in humans. Using stimuli that manipulated presence of a familiar shape on the ground-side of stimuli, Trujillo et al. (2010) showed that the influence of this undetected cue was reflected in the P1 of the ERP. We might therefore expect the amplitude of the the occipital ERP in the same time window to correlate with behavioural CCEs across individuals, age groups, and the contrast of high competition BW to lower competition CavHom stimuli. Another framework has linked alpha oscillations to suppression of perceptual input (Klimesch et al. (2007); see Payne and Sekuler (2014)) and recently indicated alpha power as an index of competitive FG processes (Sanguinetti et al., 2015). Given that alpha band power is reduced in healthy aging (Hong et al., 2015), evoked alpha associated with CCEs is another potential neural correlate that might yield insight into the inhibitory processing underlying the CCE, its reduction in healthy aging, and the effects of reducing competition using CavHom displays. We are exploring these possibilities in ongoing research.

Second, how does aging affect the processing of other configural cues and the combination of multiple cues? As noted since the time of Rubin (1915/1958), convexity is just one cue among many that influence FG organization. Comparing the way that different cues (for example enclosure, symmetry, and size), are affected by aging would further our knowledge of where impairments are cause for concern and where perception remains intact as a function of aging. Exploring the effects of combining multiple FG cues to modulate competition and ambiguity would yield further insight into FG segmentation of real-world stimuli. How could cues be combined to produce strong segregation in all the older observers? Are some older adults impaired in even highly unambiguous contexts? Are there specific cue-combinations or competition patterns that cause particular difficulties for older observers? A recent study (Froyen et al., 2013) demonstrated that the combination of convexity, motion, and accretion-deletion, results in a novel percept of depth where VEX regions are perceived as rotating columns. Stimuli were similar in shape to those used in the current study with random-dot texture-filled VEX and CAV regions that drifted horizontally at equal speed but in opposite direction to each other. Accretion/deletion occurred at all region boundaries where the textures filling regions were terminating or being generated. This combination of configural, structure-from-motion, and background cues increases evidence that adjacent regions are separated in depth. Using such multi-cue stimuli would allow us to explore the question of whether the reduced CCE in aging reported here results in part from decreased presumption of three-dimensional character in the older group, which would reduce the CCE according to the Goldreich and Peterson (2012) Bayesian model of CCEs Peterson and Salvagio (2008). We are currently investigating this possibility.

Finally, from a more general perspective, it is important to ask: how do age-related changes in the ability to resolve FG assignment relate to real-world functioning? Although reduced competition resolution clearly has a significant impact on resolving convexity stimuli, how does this relate to segregating contours of real objects? And how does the overall pattern of FG age differences relate to individuals' ability to function in the real world? On one hand, it may be easy to imagine how the slowing of the processing that resolves a multi-region stimulus into an object that is occluding the adjacent background region could impact important functional activities like navigation and locomotion. For example, impaired FG organization could contribute to tasks that commonly affect older observers like compromised driving ability (Wood, 2002; Wood et al., 2005), which requires rapid estimation of depth relations of multiple objects, and increased incidence of falls (Källstrand-Ericson and Hildingh, 2009), which could result from responding non optimally to slowly segmented objects, or from miss-assigning the depth order of a stair, curb, or convex obstacle. Recent findings that perceived depth in displays with binocular disparity are biased by border convexity (Burge et al., 2010) suggest that these are real possibilities. However, such real world implications of FG processing in aging remain an open question and one that is important in the study of how aging effects perception and how this relationship effects the lives of real individuals.

2.5.3 Summary and conclusion

The studies presented above demonstrate reduced ability to use convexity for FG segregation in healthy aging. The effect is unlikely to be explained solely by lower-level issues related to visual encoding, and deficits remain even for stimulus durations of 250 ms (with no mask) and for stimuli within seniors' integration area (Sekuler et al., 2000). Rather, the data presented here support the idea that the deficit in seniors is related to higher order processes that suppress irrelevant information, that lead to more plausible inferences in determining perceptual organization of ambiguous visual input.

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Chapter 3

Reduced convexity context effects in older adults not attributable to reduced presumption of depth

Abstract

Border convexity influences perceptual organizational processes that resolve competing figure-ground (FG) interpretations of a stimulus. The probability of perceiving convex (VEX) regions as figures increases as the number of alternating VEX and homogeneously filled concave (CAV) regions in the surround increases (Peterson & Salvagio, 2008). This so-called Convexity Context Effect (CCE) is reduced in healthy aging (Lass, et al., 2012; 2013), and this result has been interpreted as evidence for reduced inhibitory processing in seniors. However, CCEs may be based, in part, on an *a priori* assumption that the stimulus contains depth (Goldreich & Peterson, 2012), so age-related reductions in the CCE may be caused by a change in the assumed depth in the stimulus. If so, then adding depth cues to the 8-region stimuli used by Peterson and Salvagio should increase the CCE in older adults. We tested this hypothesis by conducting four experiments with younger and older adults using a method that induces perception of depth in younger adults (Froyen, et al., 2013): We filled alternating regions of 8-region displays with light or dark texture, and added horizontal motion that produced texture accretion/deletion at the bounding edges of the CAV and/or VEX regions. Stimuli were presented for 100 ms or 250 ms, and observers reported whether the light or dark region(s) appeared

to be in the foreground. We predicted that the addition of opposing motion to both region types simultaneously would increase the CCE in older adults. In both age groups, moving regions were more likely to be perceived as background: relative to the baseline static condition, P(VEX = Figure) increased when motion was added to CAV regions and decreased when added to VEX regions. Critically, the addition of motion to both CAV and VEX regions simultaneously did not increase the CCE in either age group despite this condition increasing evidence that the stimulus contains depth. These results are inconsistent with the hypothesis that the reduced CCE in older adults result from reduced presumption of depth in these stimuli.

Introduction

Perceptual organization, which involves the grouping and segregation of low level stimulus properties into perceptual units, is crucial to perception. Yet, little is known about how the aging visual system organizes information that can be deteriorated from the front-end sensory inputs (Weale, 1963) through to neural processing networks (Spear, 1993; Andersen, 2012). As the aging population lives ever longer and increasingly maintains function in later life (Milan, 2011), the question of how senescence affects perceptual organization is an important project. Grappling with this question can bridge the gap in understanding between low and high level processes, yielding insights into the processing mechanisms underlying perceptual organization and the effects that aging has on these processes. This effort will be important in uncovering which aspects of visual perception are maintained and which aspects are impaired in aging, which is crucial in understanding how age-related changes to visual processing impact daily living. Age-related impairment to the processes underlying perceptual organization could conceivably impact performance in tasks involving quick and accurate perceptual inferences about the environment, like driving (Wood, 2002; Wood et al., 2005), and ability to avoid visual mistakes leading to trips and falls (Källstrand-Ericson and Hildingh, 2009). On the other hand, understanding how aging affects perceptual mechanisms can also uncover tasks for which the aging visual system is actually superior to that of younger adults, for example that observed by Betts et al. (2005).

Normal healthy aging is associated with changes in many parts of the visual pathway, including the crystalline lens, the outer layers of the retina (Weale, 1963), and visual neurons in several cortical areas (Sekuler and Sekuler, 2000; Owsley, 2011). Research on animal physiology of the aging visual system has found that inhibitory cortical mechanisms deteriorate in aging (Schmolesky et al., 2000; Leventhal et al., 2003; Yang et al., 2009; Liang et al., 2010), and disrupted excitatory-inhibitory balance has been observed in older adult human cortical tissue (Pinto et al., 2010). These findings have lead to speculation that human performance on psychophysical tasks involving inhibitory processing might be compromised in the late adulthood. Some evidence has supported this hypothesis including reduced spatial/surround suppression (Betts et al., 2005, 2009) and impaired motion detection and discrimination performance consistent with broadened direction tuning through internal noise (Bennett et al., 2007; Tsotsos, 2012). Age-effects consistent with this aging-inhibition hypothesis have also been observed in various psychophysical tasks (e.g., Pilz et al., 2010; Roudaia et al., 2013a; Wilson et al., 2011; Spencer et al., 2016), as well as at multisensory levels of processing (Roudaia et al., 2013b). However, other studies have failed to find psychophysical effects consistent with this hypothesis (e.g., see Govenlock et al., 2009, 2010; Rosen et al., 2013; Karas and McKendrick, 2012; Karas and Mckendrick, 2015). As we will explain below, our prior work on aging and FG perception has demonstrated that aging also influences aspects of perceptual processing underlying perceptual organization.

Figure-ground (FG) segmentation and grouping are two aspects of perceptual organization that have been studied in the Gestalt tradition (Rubin, 1915/1958, Wertheimer, 1923). FG organization is thought to involve the competition between competing perceptual interpretations of a stimulus, which is resolved through inhibition of interpretations that do not reach awareness (Peterson and Skow, 2008; Sanguinetti et al., 2015). Neuroimaging studies have supported the notion that suppression from higher visual areas mediates FG organization and that activity within neural voxels linked to representation of *background* spatial locations is inhibited (Likova and Tyler, 2008; Cacciamani et al., 2015).

Convexity is one of the classical configural cues that influences perception by signalling which region is likely the figure. Convex (VEX) regions are more likely to be perceived as figures than concave (CAV) regions on the adjacent side of the bounding contour. Although convexity can be a potent cue (Kanizsa and Gerbino, 1976), the probability with which VEX regions are perceived as figural, i.e., P(VEX = Figure), depends on the context in which the VEX edge appears. For example, Peterson and Salvagio (2008) demonstrated that P(VEX = Figure) increases as the number of alternating VEX and homogeneously coloured CAV regions in the display were increased from 2 to 8 regions. This convexity context effect (CCE) demonstrates that the way the FG cue influences perception depends on context, in this case the correspondence of properties of regions separated across the visual field. An example 8-region convexity stimulus, composed of alternating CAV and VEX regions, is depicted in Figure 3.1a, which is similar to the black and white displays used by Peterson and Salvagio (2008) except with light and dark texture fills instead of solid black or white fills. Follow up studies on these context effects demonstrated that stimuli with heterogeneous VEX regions but homogeneous (HOM) CAV regions (i.e., *CavHom* stimuli) are processed more rapidly in younger observers than black and white stimuli (Salvagio and Peterson, 2010, 2012). These findings have been understood within a model of FG perception that conceptualizes FG organization resulting from a competition between alternative interpretations of the stimulus (Peterson and Skow, 2008). In theory, the competition is resolved by integrating grouping and segregation cues to infer which regions should be inhibited as background in order to represent the most plausible FG representation of the stimulus (Peterson and Skow, 2008; Goldreich and Peterson, 2012). Through the manipulation of homogeneity across CAV vs. VEX regions, and demonstrating that colouring alone does not cause FG context effects, Peterson and Salvagio (2008) presented compelling evidence that spreading of inhibitory suppression of ground regions underlies the CCE.

In a study that compared CCE effects in younger and older observers using the same task and achromatic stimuli as Peterson and Salvagio (2008), we observed significant CCEs in both age groups, but found that the CCE was significantly reduced in older adults (Lass et al., 2012). We subsequently found that CCEs significantly increased within the older group with the CavHom stimuli compared to black and white stimuli. This finding suggests that the age-related reduction in the CCE obtained is due to an age-related impairment in the ability to resolve the high competition among several plausible FG interpretations of black and white stimuli (Lass et al., 2013).

Goldreich and Peterson (2012) derived a Bayesian model of FG processing that can account for these CCEs. The model proposes that, for a convexity stimulus, the posterior probability of each FG interpretation is inferred from the joint probability of the stimulus being three-dimensional (versus two-dimensional), and the likelihood of each set of regions (i.e., VEX vs. CAV) being in the foreground given that the stimulus is 3D and given the geometrical structure of the regions (i.e., the convexity). This is summarized by Equation 3.1, which is Equation (1) from Goldreich and Peterson (2012):

$$P(\text{VEX} = \mathit{Figure}|I) = P(\text{VEX} = \mathit{Figure}|3D, I)P(3D|I) + (1/2)P(2D|I) \tag{3.1}$$

The probability of the stimulus being three dimensional given the stimulus properties,

$P(3D|I)$, is influenced by the probability that a given set of regions could constitute a background, which is a function of region homogeneity in the stimuli used by Peterson and Salvagio (2008). Thus, the model predicts that decreasing the probability that the stimulus represents a three-dimensional object or scene should decrease the magnitude of the CCE. Within the context of this model, one explanation for reduced CCE in older compared to younger observers would be a difference in presumed probability that stimuli used in our tasks are three dimensional. In other words, it may be possible that older observers are more likely than younger observers to assume the convexity stimuli are flat, which would reduce the CCE in aging. Following on this reasoning, we predict that providing stronger evidence that the stimuli contain depth should increase CCEs in older observers, and perhaps in younger observers as well.

Lass et al. (2013) demonstrated reduced CCEs in older observers for high competition black and white stimuli but observed strong convexity effects in older adults only with the reduced competition CavHom stimuli. However it is also possible that the older group simply had a strong assumption that the stimuli were flat. For black and white displays, Equation 3.1 predicts that this presumption should shift weight to the 2D interpretation, resulting in ambiguous – or lack of – interpretation of FG structure, which would reduce the CCE relative to younger observers. For the CavHom stimuli, which are more consistent with a 3D scene (Goldreich and Peterson, 2012), the model might predict that increased CCEs in the older group are due to the increased evidence of depth in the stimuli. Younger observers would not show this effect of VEX-fill heterogeneity since that they already strongly infer depth in black and white displays, as indicated by the strong CCEs driven by high P(VEX = Figure) in the 8-region condition.

This brings an interesting prediction: increasing the evidence of depth in the convexity stimuli should increase CCEs in older observers, if the reduced CCE in aging is partially due to reduced presumption of depth. Froyen et al. (2013) created convexity stimuli that were similar to the ones used by Peterson and Salvagio (2008), but which contained additional properties. Specifically, Froyen et al. added alternating light and dark random dot texture to each CAV and VEX region and, during presentation, the textures within CAV and VEX drifted horizontally in opposite directions. The motion produced texture accretion/deletion (AD) at each leading and lagging bounding edge, respectively (see Figure 3.1b for a static depiction of the stimuli). Traditionally, texture AD has been applied to *one* region adjacent to an edge, and serves as a cue that the region containing the moving texture is behind an occluding figure (Kaplan, 1969). However, Froyen et al. applied AD to adjacent regions in an alternating pattern at the same time, resulting in dual AD at every edge as regions drifted towards/away from each other (see Tanrikulu et al., 2015, for a comparison of this unique motion-AD and traditional AD). It was observed that this combination of convexity, motion, and AD resulted in a strong novel depth percept where observers perceived the VEX regions as rotating columns in front of a background composed of the CAV regions.

Froyen et al. (2013) reasoned that the unique AD occurring at both sides of an edge causes the visual system to presume depth and infer the depth order of CAV vs. VEX regions using the FG cue. The motion is consistent with spatially separated regions that are perceptually grouped as a unified ground, and the strong Gestalt convexity cue is used to resolve the stimulus in favour of the VEX regions being in the foreground and CAV regions in the background. Given strong evidence that the stimulus contains depth and presence of AD within VEX regions, the most reasonable way to resolve the motion is that the VEX figures must be rotating. In the absence of a configural cue, i.e., when the stimulus is composed of alternating light and dark rectangular or unbiased sinusoidally modulated regions, both of the FG interpretations (light or dark rotating figures) are equally valid and bistable perception occurs; however, the addition of cues signalling FG structure produce a bias to perceive the regions containing the configural cue to be rotating in the foreground. Froyen et al. demonstrated this relationship for convexity, symmetry, and parallelism, and showed that modulation of the configural cue of small area also predictably modulated the strength of the depth percept. This evidence supported the notion that the addition of motion and AD increased evidence of depth, and that depth order was resolved in favour of FG cues, the strongest of which was convexity (consistent with demonstrations by Kanizsa and Gerbino, 1976).

The goal of the present set of studies was to test the possibility that the reduced CCE in aging is partially due to reduced presumption of depth in our static black and white stimuli. The hypothesis was that, if reduced CCEs in older adults are caused by decreased depth presumption, increasing evidence of depth should increase the CCE in seniors and possibly in younger observers. We predicted that adding the unbiased motion used by Froyen et al. (2013) to texture fills should increase the CCE in seniors (see Figure 3.1b).

General methods & stimuli

The methods and stimuli described in this section were used in all of the following experiments, except for the specific changes that are described when relevant.

3.0.1 Apparatus

The only light in the testing room was produced by the experimental display, which was a NEC MultiSync FE992 CRT. The resolution was set to 1280 × 1024 pixels with an 85 Hz refresh rate. The display was viewed binocularly from a distance of 96 cm and subtended 21.5° (width) × 16.1° (height). Viewing position was stabilized with a forehead/chin rest. The experiment was run using an Apple Power Mac G5 computer controlled by in-house scripts run with MATLAB R2010a (version 7.10.0.499) that used the Video and Psychophysics toolboxes (Brainard, 1997; Pelli, 1997).

3.0.2 Stimuli

The stimuli used in this study were adapted convexity stimuli from Peterson and Salvagio (2008). These stimuli have been used in a number of studies examining CCEs (Peterson and Salvagio, 2008; Salvagio and Peterson, 2010, 2012; Lass et al., 2014), including those that have explored the question of age-related changes to FG processing (Lass et al., 2012, 2013).

In the original stimulus set, stimuli were composed of alternating vertical VEX and CAV regions. Each contour separating adjacent regions was produced by combining VEX arcs and orienting them such that every odd region was VEX on both sides and even regions were CAV on both sides, or vice versa. The distance between contours was determined by equalizing the area of each region. For this study, we applied the motion manipulation used by Froyen et al. (2013) to the Peterson and Salvagio (2008) stimuli. The resulting stimuli consisted of 2 or 8 alternating light ($60.5\,\mathrm{cd/m^2}$) and dark ($5.4\,\mathrm{cd/m^2}$) texture-defined VEX/CAV regions presented against a uniform grey ($32.1\,\mathrm{cd/m^2}$) background. The stimuli were 3.3 ° in height with a mean width of 1.4 ° for 2-region and 6.6 ° for 8-region stimuli. Stimuli could be presented as a static image, or the texture fills of CAV and VEX regions would slide in opposite directions at a rate of 2.3 °/s for the stimulus duration (see Figure 3.1a and b for examples of *static* and

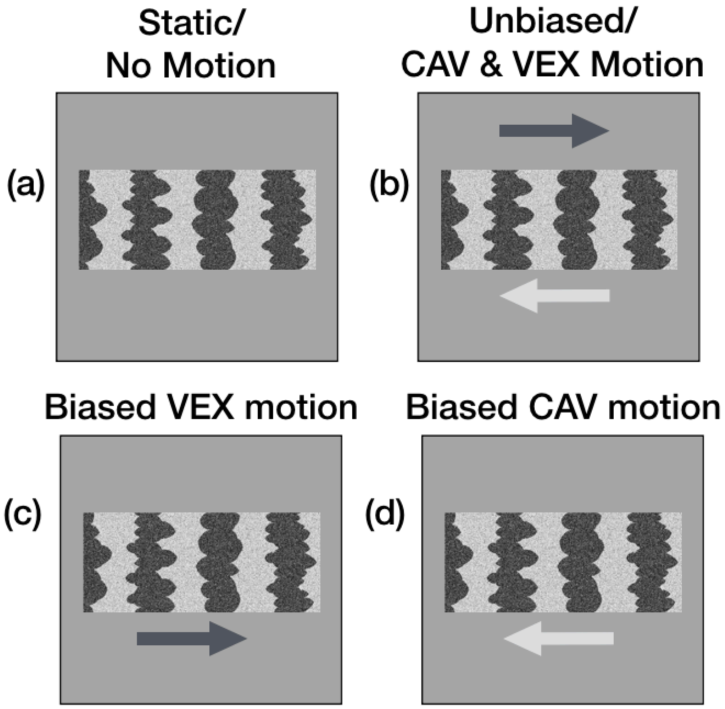

Figure 3.1: Static depiction of an 8-region stimulus under the four conditions used in the experiments below. For each of (a) to (d) the screen area is depicted by the box that filled with uniform grey, and an example stimulus, which is composed of alternating light/dark random dot texture fills, is presented centrally. The light/dark arrows symbolize the direction of movement of light/dark texture within the stimulus that accreted/deleted at region boundaries. The *static* condition involved no motion in either region type (a). The *unbiased motion* condition involved simultaneous motion in both CAV and VEX regions simultaneously but in opposite directions (b). The *biased VEX motion* (c) and *biased CAV motion* (d) conditions involved motion in only VEX or CAV regions, respectively, resulting in biased motion and accretion/deletion cues. Experiments 3.1, 3.2, and 3.3 involved static (a) and unbiased motion condition (b) conditions, and included both 2-region and 8-region conditions within each motion condition. Experiment 3.4 involved all four motion conditions but only used 8-region stimuli.

unbiased motion stimuli).

Each stimulus was created by transforming one of the original Peterson and Salvagio (2008) stimuli. First, a black and white filled 2- or 8-region stimulus was loaded and the red square probe was removed. Next, with the aid of a motion toolbox developed by Vicky Froyen, each region of the stimulus was converted to a dark or light random dot texture corresponding to whether the region was black or white, respectively. The motion was then incorporated by creating a sequence of images where the luminance value of every pixel making up VEX regions shifted by one pixel per image/frame while all luminance values for each pixel in CAV regions shifted in the opposite direction. This was accomplished by creating light and dark textures that were many pixels longer than the width of the stimulus with the same height as the stimulus. One texture sheet was aligned with the left/right edge of the stimulus and the other texture was aligned with the opposite edge. Each pixel location of the displayed stimulus was labeled as belonging to either a VEX or CAV region. The first image was created by setting the pixel values of *VEX pixels* – those at stimulus locations within the VEX regions – to the values of the texture sheet aligned with the left/right edge of the stimulus and *CAV pixels* were set to luminance values of corresponding pixels of the second texture sheet. Each subsequent image in the series was created by sliding texture sheets in the direction of the edge they were originally aligned with by a single pixel and re-setting each CAV and VEX pixel luminance value to the luminance of the pixel in that location from the corresponding texture sheet. Textures drifted horizontally at a speed of 2.3°/s.

Experiment 3.4 contained two additional motion conditions in which motion was applied for all CAV *or* all VEX regions separately (i.e., only the CAV or VEX regions contained motion; see Figure 3.1c and d). This manipulation created biased motion, which serves as background cue (Tanrikulu et al., 2016), that determined whether the motion opposed convexity (i.e., *VEX motion*; Figure 3.1c) or was consistent with the FG cue (i.e., *CAV motion*; Figure 3.1d).

In Experiments 3.1 and 3.2, stimulus durations of 100 ms (i.e., 8 display frames) were used. In Experiment 3.3, both 100 ms and 250 ms (i.e., 21 display frames) stimulus durations were used. In Experiment 3.4 only 250 ms stimulus durations were used.

3.0.3 Procedure & task

Participants were brought into the lab and given a letter of information. After signing the consent form, a battery of visual screening tests was conducted to measure various demographics and visual abilities including visual acuity, contrast sensitivity, and stereo-acuity.

The progression of a trial and a depiction of the stimuli is shown in Figure 3.2. The task was to indicate which of the two central regions appeared to be in the foreground by responding whether the darker or lighter region was perceived as being closer to the observer by pressing a key on a computer keyboard labeled “DARKER” or “LIGHTER”. This task differed from the one used previously to examine the age-related changes in the CCE, in which observers indicated if a centrally-located red probe was located on or off the region that was seen as figure. The new procedure was used because the stimuli used here did not contain a red probe, and because the instructions (which were identical in all of the experiments in this chapter) contained a statement that the figure was the region that “has a definite shape and appears *closer* to you than the background region”, and therefore the task of indicating “was the lighter or darker region closer?” seemed more intuitive and appropriate.

Experimental trials were always blocked by condition, with 64 trials per block and randomize order of stimulus presentation within blocks. There were short breaks between blocks. Before the experimental trials, participants viewed eight practice trials consisting of equal numbers of randomly intermixed static and unbiased motion stimuli presented for 100 ms (Figure 3.1a & b). The experimenter stayed in the room for practice trials to ensure each participant understood the task.

3.1 Experiment 3.1

3.1.1 Methods

Participants

The younger group consisted of 15 participants ($M = 21.2, sd = 3.5$ years old) and the older group had 16 participants ($M = 66.1, sd = 4.1$ years old). All of the older participants were compensated $10 for participating while subjects in the younger group received credit for an undergraduate course.

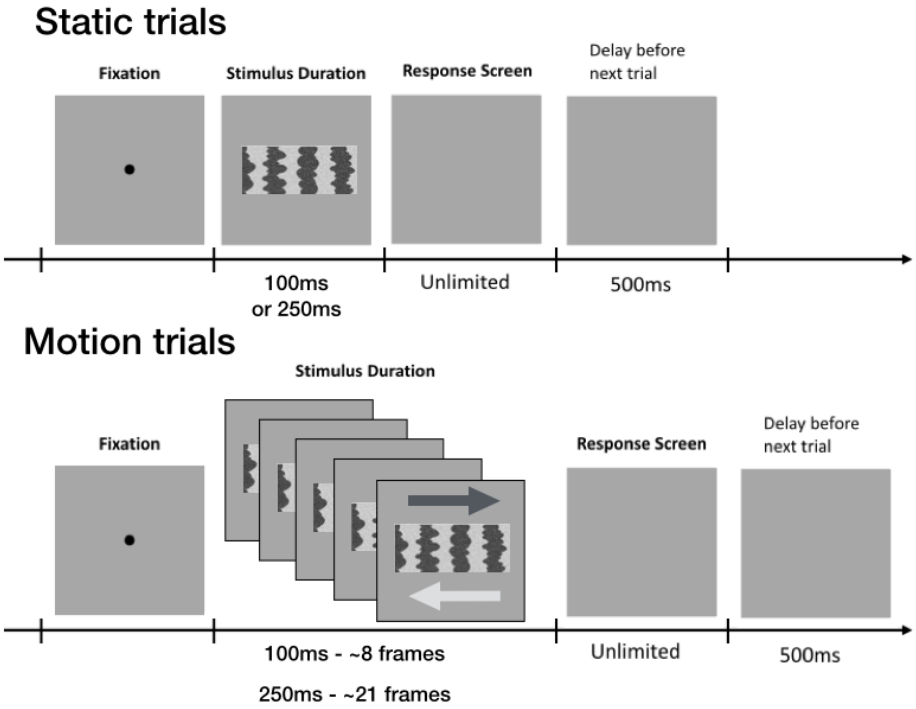

Figure 3.2: This schematic shows what the progression of a single trial was like for the static and motion conditions. All trials began with a fixation point that flickered briefly. The stimulus was then presented for 100 ms in Experiments 3.1 and 3.2, 100 ms or 250 ms in Experiment 3.3, and 250 ms in Experiment 3.4. As shown in the top panel, static trials involved the brief presentation of the 2- or 8-region textured convexity stimulus followed by an unlimited grey response screen. The bottom panel shows the procedure for motion stimuli, which was similar to that for static stimuli except that stimulus presentation entailed displaying a series of frames where the texture fills of "moving" regions were displaced to the right or left by one pixel from frame to frame.

Procedure

The experiment was run in two orders: 2- then 8-region sub-blocks were embedded within static and motion blocks, and the order of which was presented first (static or motion) was balanced across participants. Initially the study was run in a single order, with static blocks always occurring first. This was done to minimize order effects because the sensitive CCEs could be influenced by performing multiple conditions. However, after running 8 younger and 8 older observers, the remaining participants completed blocks in reversed order. Thus, the control for order in this study was limited in that there was no random assignment to order groups. The entire experiment took under 30 minutes to complete.

3.1.2 Results

All statistical analyses were carried out using the R statistical software (R Core Team, 2016).

The data were analyzed using a three-way mixed Analysis of Variance (ANOVA) with age as a between-groups factor, and region number and motion as within-subjects factors. The age × region number × motion interaction was not significant, $F(1, 29) = 0.22, p = .64$. There was no evidence of a two way interaction between motion and age, $F(1, 29) = 1.68, p = .21$, or motion and region number, $F(1, 29) = 1.39, p = .25$. Finally, there was also no main effect of motion, $F(1, 29) = 1.94, p = .17$. Thus, the current experiment failed to find any effect significant effect of motion.

There was, however, strong evidence for an age × region number interaction, $F(1, 29) = 8.20, p = .0034$ (one-tailed), a replication of reduced CCEs in older observers (Lass et al., 2012). This relationship is depicted in Figure 3.3, which shows that for both motion conditions younger observers show a large increase in P(VEX = Figure) in 8-region compared to 2-region displays whereas this effect of region number is highly reduced in the older group. Post-hoc tests found a significant region number effect in the younger group, $F(1, 14) = 23.1., p < .0001$, but no significant CCE in the older group, $F(1, 14) = 1.32, p = .14$ (both one-tailed). The figure also illustrates that in all conditions and in both age groups, P(VEX = Figure) was significantly greater than chance, i.e., P(VEX = Figure) = 0.5, all $ts > 3.6, p < .003$.

3.1.3 Discussion

The results observed here replicate previous experiments that found large CCEs in younger observers (Peterson and Salvagio, 2008; Salvagio and Peterson, 2010, 2012). The non significant CCE in the older group was trending in the correct direction but was not significant here; this was not unexpected given that the CCE strength is weak, making it difficult to detect (Lass et al., 2012, 2013, e.g., see combined results of Experiment 3.1 and 3.2 below). Hence, the results serve to validate the new task used in the current

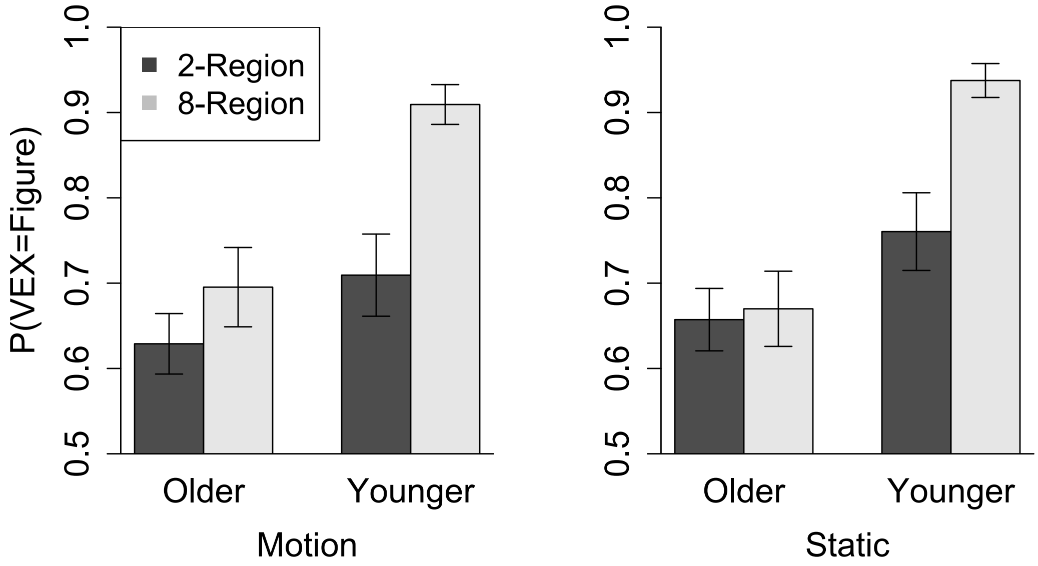

Figure 3.3: Experiment 3.1 results for each group and condition. Bars represent group mean ±1 SEM P(VEX = Figure) for 2- vs 8-region stimuli (dark vs. light grey bars, respectively) in the older vs. younger groups for motion (left panel) vs. static (right panel) displays. The age x region number interaction is apparent for both conditions, with the younger group showing a larger effect of region number than the older group in both motion conditions.

experiment. However, the current experiments found no evidence that adding unbiased motion affected FG perception in either age group. Thus these results failed to support the hypothesis that adding motion to convexity stimuli, a cue that produces depth perception in young adults viewing similar stimuli (Froyen et al., 2013), increased CCEs in older observers.

To increase our evidence of lack of motion effects, Experiment 3.2 was conducted to replicate the results obtained in the first experiment. Also, Experiment 3.2 used a better experimental design by randomly assigning subjects to two static-motion stimulus orders. All other aspects of the methods for Experiment 3.2 were identical to those used in Experiment 3.1.

3.2 Experiment 3.2

3.2.1 Methods

Participants

For this experiment, 16 younger observers ($M = 20.3, sd = 4.3$ years old) and 16 older observers ($M = 70.8, sd = 5.6$ years old) completed the study. Older participants were compensated $10 for their time and the younger participants were either compensated partial course credit or $10 for completing the study.

Procedure

The procedure was the same as that used in Experiment 1, except that participants were randomly assigned to one of two static-motion stimulus orders.

3.2.2 Results

One younger participant was excluded from the analysis after indicating that this individual reversed the response buttons on many experimental trials.

The characteristic age × region number interaction can again be seen in Figure 3.4: younger observers exhibited larger CCEs than older observers with both the static and motion conditions. It might be argued that Figure 3.4 suggests that in older adults (but not younger adults) the CCE is larger in the motion than the static condition, however, the larger region number effect observed is due to an relatively low P(VEX = Figure) with 2-region stimuli rather than a increased P(VEX = Figure) with 8-region stimuli. This pattern is not consistent with the hypothesis that motion would strengthen CCEs.

These data were analyzed using a three-way mixed ANOVA, which showed a significant age × region number interaction, indicating that the effect of region number was larger in younger than older participants, $F(1, 29) = 3.01, p = .047$ (one tailed). The region number effect was significant in the younger group, $F(1, 14) = 10.7, p = .0028$ (one tailed), but was not significant in the older group, $F(1, 15) = 1.45, p = .12$ (one tailed). No other effects or interactions were significant. There was also no evidence of

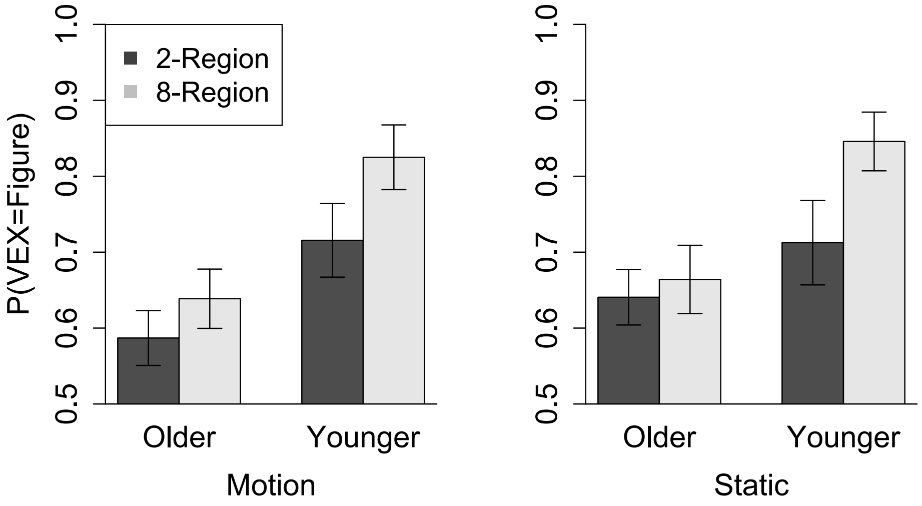

Figure 3.4: Mean ±1 SEM P(VEX = Figure) for each age group and condition in Experiment 3.2. The region number effect, i.e., CCE, is strong in the younger group and not significant in the older group, and this can be seen for both motion (left panel) and static (right panel) conditions.

an effect of motion, $F(1, 29) = 1.6622, p = .2$.

Additionally, P(VEX = Figure) was significantly higher than chance in all conditions and in both age groups, all $ts > 2.4, ps < .03$ (one tailed).

Experiments 1 & 2 combined: Combined results & discussion

In this section we analyzed the data combined across Experiments 1 and 2 to increase the sample size and statistical power.

The combined data were analyzed using a mixed ANOVA that included region number, motion, age group, order, and experiment. The ANOVA yielded a significant interaction between age × region number, $F(1, 58) = 10.75, p = .00088$, corresponding to the larger CCE in the younger group compared to the older group. This interaction can be seen in data from both Experiments 3.1 and 3.2, shown in Figures 3.3 and 3.4, for both motion and static stimuli (the left and right panels). Younger adults show the same increase in P(VEX = Figure) for the 8-region compared to 2-

region displays, $F(1,28) = 32.9, p < .0001$, whereas the older group shows a weak CCE, $F(1,30) = 2.75, p = .05$ (one-tailed). There were also main effects of age and region number, both ps $< .0001$, but no other interactions nor an effect of experiment were observed, all ps $> .15$. Interestingly, the ANOVA also revealed a marginally significant effect of motion, $F(1,58) = 3.51, p = 0.066$. However, the direction of this effect was opposite to the one predicted by our hypothesis: specifically, across the two experiments P(VEX = Figure) was marginally greater in the static condition than the motion condition.

Overall, combining the data from Experiments 3.1 and 3.2 demonstrated that the CCE is robust in young adults, is smaller in older adults, and that CCEs in both age groups are not affected greatly by the addition of unbiased motion. Importantly, whereas the CCE, i.e., the region number effect, could not be significantly detected in older observers in previous experiments alone, with results trending in the right direction, the result was marginally significant when the data were combined. It is important to keep in mind when exploring this very weak CCE in older observers that replication of the pattern across experiments is the true test of its existence, and not the statistical significance of the effect in any single experiment. It is also worth noting that the lack of any significant effect or interactions involving the *experiment* factor indicated that results did not depend on experiment, which therefore justifies the combination of these data to make the statistic inferences presented above.

3.3 Experiment 3.3

Experiment 3.3 included a longer (i.e., 250 ms) stimulus duration, to ensure that our failure to find effects of motion was not due to an inability of older observers to perceive the motion in briefly presented stimuli.

3.3.1 Methods

Participants

Seventeen younger ($M = 22.4, sd = 4.6$ years old) and 18 older ($M = 70.9, sd = 7.2$ years old) observers participated in this experiment. All of the older participants were compensated \$10 per hour for their time, and younger participants were either given course credit or compensated at the $10 per hour rate.

Procedure

The procedure for Experiment 3.3 was similar to that of Experiments 3.1 and 3.2, except that stimulus durations of 100 and 250 ms were used. Thus, the experiment used a 2 (age) × 2 (motion) × 2 (duration) × 2 (region number) design. The experiment took approximately one hour to complete.

There were 16 different conditions in this experiment and many potential orders. We thus controlled for order by assigning individuals to 1 of 4 groups that controlled the first condition presented, which always used 2-region stimuli crossed with motion type (static vs. motion) and stimulus duration (100 vs. 250 ms) followed by an 8-region block with the same motion and duration. The remaining blocks alternated between 2-region then 8-region conditions, and presentation order for each remaining motion × duration combination was randomized. Given that order did not significantly affect the results from the previous experiments, we believe that this was a reasonable control that would allow for examination of the 2- vs. 8-region conditions within each motion × duration combination in isolation without any possible contamination from the order of the other blocks/conditions.

3.3.2 Results

The results from one younger and one older observer were discarded and replaced after they reported having visual abnormalities/eye disease in pre-experiment questioning. Two more older observers were excluded from the analysis due to low Montreal Cognitive Assessment (MoCA) scores that did not meet our inclusion criterion. The final sample consisted of 16 younger adults and 16 older adults.

The data are illustrated graphically in Figure 3.5 and the ANOVA results are presented below. Figure 3.5 plots P(VEX = Figure) for 100 ms (left panels) and 250 ms (right panels) durations, motion and static conditions (left and right panels within each stimulus duration), older and younger groups (left and right pairs of bars within each duration × motion combination), and 2- vs. 8-region region number conditions (dark vs. light grey bars). In every condition, the CCE (i.e., the difference between P(VEX = Figure) measured with 2- and 8-region stimuli) was larger in younger than older participants. With

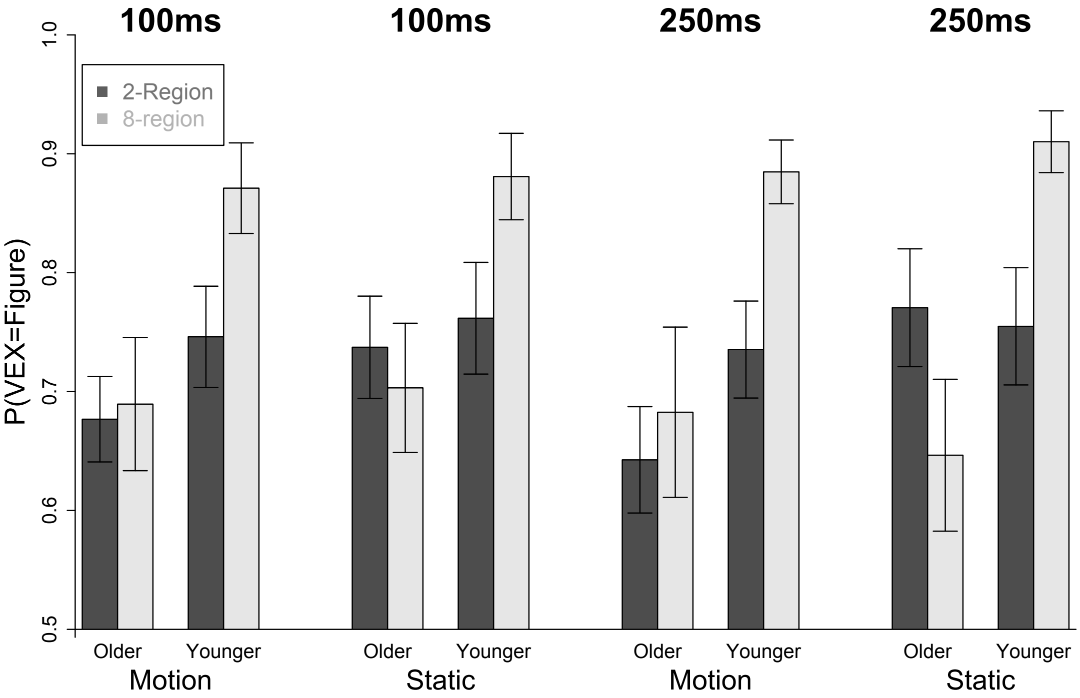

Figure 3.5: Mean ±1 SEM of P(VEX = Figure) for 2- vs 8-region conditions for each age group, motion condition, and stimulus duration condition. The age x region interaction is apparent for each combination of motion and duration, in that younger observers show a consistent and strong region number effect whereas older observers show inconsistent region number effects. This is driven by the younger observers always showing a relatively high P(VEX = Figure) for 8-region stimuli, whereas the older observers do not.

100 ms stimuli (two left panels), the CCEs from both age groups are not noticably affected by stimulus motion. With 250 ms stimuli (two right panels), CCEs in younger adults were similar in the static and motion conditions, but in older adults the CCE appears greater in the motion condition than the static condition. This difference in P(VEX = Figure) in older participants reflects the fact that, in the static 250 ms condition, P(VEX = Figure) with 2-region was particularly high, and P(VEX = Figure) with 8-region stimuli was particularly low. Note that this result is not consistent with the idea that the CCE is enhanced by unbiased motion cues. The ANOVA revealed a marginally significant four-way age × region × motion × duration interaction, $F(1,30) = 4.01, p = .054$, and therefore we analyzed data obtained with the two stimulus durations with separate 2 (age) × 2 (region number) × 2 (motion) ANOVAs. For the 100 ms condition, only the age × region interaction, $F(1,30) = 6.42, p = .0084$ (one tailed), was significant, repli-

cating previous results showing that the effect of region number was smaller in older than younger adults. For the 250 ms condition, there was a three-way simple interaction between age, region number, and motion, $F(1, 30) = 8.0, p = .0081$. Post-hoc analyses of this simple interaction revealed the age difference in the CCE was in the correct direction but not statistically significant in the motion condition $F(1, 30) = 2.42, p = .065$ (one-tailed), but was statistically significant in the static condition $F(1, 30) = 18.10, p < .0001$ (one-tailed). In other words, the four way interaction observed here appears to be driven by a relatively high P(VEX = Figure) in older observers in the static 250 ms 2-region condition, which caused the age × region number simple simple interaction be be smaller in the motion compared to static condition. This pattern of results does not support the hypothesis.

Decomposing the complex interaction in another way, we ran separate 2 (stimulus duration) x 2 (age) ANOVAs on data from the motion and static conditions. These analysis showed no effect of stimulus duration in either motion or static conditions, both Fs $< 1, p$s $> .65$, nor an age x duration interactions at either level of motion, both Fs $< 1, p$s $> .41$. However, there was a significant effect of age in the motion condition, $F(1, 30) = 6.57, p = .016$, and marginal effect of age in static condition, $F(1, 30) = 3.87, p = .058$. The lack of effects of stimulus duration indicate that increasing duration does not strengthen the effect of motion, as the hypothesis of this experiment predicted.

3.3.3 Discussion

The results of Experiment 3.3 found no evidence of the hypothesized effects of motion on CCEs in the older or younger group at stimulus exposures of 250 ms. These results replicate previous demonstrations of the strong region number effect in younger observers, with the addition of unbiased motion to both CAV and VEX regions, and inconsistent patterns of CCEs in healthy aging (Lass et al., 2012).

3.4 Experiment 3.4

Experiment 3.4 was run to test whether the motion used influences FG perception by applying it in a biased manner to only one set of regions (CAV or VEX) at a time.

With motion present within CAV and VEX regions separately (Figure 3.1d and c, repsectively), the AD at region edges indicates background in an unambiguous, biased direction (i.e., moving regions are more likely to be occluded by the static regions). We therefore predicted that motion would shift FG perception towards an interpretation in which the moving regions are perceived as background and the static regions are perceived as figures: adding motion only to CAV or VEX regions should increase and decrease P(VEX = Figure), respectively, relative to static displays. Given the results of our previous experiments, we predicted no effect of unbiased motion (i.e., motion added to both CAV and VEX regions simultaneously; Figure 3.1b). This result would replicate the null effect observed in previous experiments and further refute the hypothesis that unbiased motion increases the strengthen of the CCE in the older observers. Additionally, demonstrating that biased motion does have an effect is an important control in validating the assumption that the motion with texture AD at region boundaries does influence FG perception, as has been established previously (Kaplan, 1969; Tanrikulu et al., 2015, 2016). This is an important consideration making conclusions about the null effects of the unbiased motion, which we assume cues depth without adding any information about depth order. Usefully, combining the biased motion cue (signalling background) with convexity (signalling foreground) results in situations where the two cues are either consistent or conflicting with each other. This allowed us to examine the hypothesis supported in our previous work (Lass et al., 2013) that high competition between perceptual interpretations is what impairs FG perception in the older adults: if the CAV-motion signals CAV regions in the back, then the {VEX=figure} interpretation becomes more plausible and the {CAV=figure} interpretation less plausible, effectively reducing competition between the alternative interpretations of the CAV-motion stimuli compared to static stimuli. On the other hand, biased VEX motion stimuli pits convexity against the motion cue, creating more competition. Thus, by varying whether VEX, CAV, or both sets of regions are filled with moving texture fill, Experiment 3.4 sought to demonstrate that the motion manipulation affects FG perception, and that it is the high competition that impairs older adults in this perceptual organization task.

3.4.1 Methods

Participants

The two groups for this experiment comprised 24 younger ($M = 20.0$, $sd = 1.7$ years old) and 25 older ($M = 71.8$, $sd = 6.1$ years old) observers. The older group included an extra observer because one participant had poor visual acuity (20/40 = decimal acuity of 0.48, which was 2.7 sd below the mean and 1.7 sd lower than the next lowest acuity in the older group).

Procedure

The methods were identical to those described in the General Methods section, except for the following changes.

If the predicted effects interacted with stimulus duration, then we might not observe them in the older group if we used a stimulus duration of 100 ms. Therefore, all stimuli were presented for 250 ms, maximizing the likelihood of observing the predicted effects. Observers participated in four motion conditions: 1) static stimuli (no motion; Figure 3.1a); 2) unbiased motion (i.e., motion added to CAV *and* VEX regions; Figure 3.1b); 3) biased VEX motion (Figure 3.1c); and 4) biased CAV motion (Figure 3.1d). The static and unbiased motion conditions were the same 8-region conditions used in the prior experiments (Figures 3.1a & 3.1b). The biased VEX motion and CAV motion conditions (Figures 3.1c & 3.1d) were new conditions that contained motion in *either* the VEX or CAV regions, and therefore provided strong, biased FG cues. In these latter conditions, AD was also limited to the moving set alone, providing unambiguous evidence that the moving regions are in the back, occluded by the static regions. The movement when only CAV regions contained motion was consistent with the {VEX=figures} interpretations, since motion signalled CAV regions being in back, thereby reducing competition between perceptual interpretations. Conversely, when only VEX regions were moving, the motion acted in opposition to convexity, thereby increasing the likelihood of CAV regions being figures (thereby increasing competition).

This experiment used only 8-region stimuli because multiple CAV and VEX regions tend to be grouped across space into distinct coherent units, making these stimuli appropriate for comparing the effects of motion that group spatially separated regions into a unified background. As observed in Experiments 3.1, 3.2, and 3.3, CCEs were larger for younger compared to older observers for both static displays and displays with opposite motion on CAV and VEX regions. The age effect was larger for 8-region compared to 2-region stimuli, meaning that age-related reductions to P(VEX = Figure) are strongest in these multi-region stimuli. It is in 8-region conditions that younger observers have increased tendency to perceive VEX regions as figures, granted that this interpretation is validated by HOM coloured CAV regions (Peterson and Salvagio, 2008), and where older observers showed strong convexity effects with reduced competition (CavHom) stimuli (Lass et al., 2013).

Stimuli were blocked by condition. Each observer was assigned randomly to one of four groups that controlled for which condition was participated in first, and the order of the remaining three conditions was selected randomly. This method controlled which stimuli were experienced first, leaving the possibility of examining performance in all conditions using a between-groups ANOVA performed on the first block.

Additionally, a motion detection task was performed after the four experimental blocks were completed. Stimuli in the motion detection task were presented exactly as in the main experimental task; however, after each trial, observers indicated “Was there motion?” by responding YES or NO using a computer keyboard. This task consisted of a single block of 60 intermixed trials: half of the trials contained motion (split evenly among the three motion conditions) and half were static displays.

3.4.2 Results

Two younger observers were excluded from the analysis because P(VEX = Figure) for these observers was more than 3 sd below the group mean on multiple conditions. One older observer was excluded from the analysis because the observer exhibited a strong *concavity bias* ($.14 < P(VEX = Figure) < .29$) in all conditions, suggesting that the task may not have been performed correctly. Upon inspection of the data, the older observer with poor acuity (20/40) was not removed because response accuracy on the motion detection task (93% correct) was higher than the older group mean ($M = 81\%$), indicating that visual acuity did not constrain this individual’s ability to detect the motion in our stimuli.

The data were analyzed using split plot ANOVAs that analyzed the effects of age group × focussed contrasts that assessed each motion effect. The proportion of trials on which VEX regions were seen as figure, i.e., P(VEX = Figure), is illustrated for each condition and age group in Figure 3.6. The effects of motion, indexed by the difference between P(VEX = Figure) in each motion condition minus P(VEX=Figure) in the static condition, which correspond to the focussed contrasts, are depicted in Figure 3.7. The effect of motion was significant in the CAV motion condition, $F(1,44) = 6.5$, $p = .007$ (one tailed), but the effect of motion did not differ between age groups, $F(1,44) = 0.59$, $p = .45$. There also was a significant effect of motion in the VEX motion condition, $F(1,44) = 10.6$, $p = .001$ (one-tailed), which also did not interact with age group, $F(1,44) = 2.0$, $p = .16$ (two-tailed). These results are consistent with the predictions that adding motion to the CAV and VEX regions should increase and decrease P(VEX = Figure), respectively, but they provide no evidence that biased motion had a different effect on P(VEX = Figure) in younger and older participants. Finally, adding unbiased motion (i.e., adding motion to CAV and VEX regions simultaneously) did not affect P(VEX = Figure) significantly, $F(1,44) = 0.346$, $p = .56$, and the effect of unbiased motion did not differ between age groups, $F(1,44) = 0.008$, $p = .93$.

Motion detection

Data from the motion detection task are shown in Figure 3.8. The median response accuracy was higher in younger than older participants, and the data in the older group exhibited a pronounced negative skew. Hence, it appears that sensitivity to motion was greater in younger participants, a conclusion that was supported by a Welch t-test with unequal variance assumed (Bartlett's $K^2(1) = 40.40, p < .0001$), which found that the means of the two groups differed significantly, $t(24.93) = 4.03$, $p = 0.00045$.

To examine if age differences in motion detection influenced FG judgements, we reanalyzed the effects of motion on FG perception using an analysis of covariance (ANCOVA) that included accuracy in the motion detection task as a covariate. For the effects of unbiased (CAV and VEX) motion and VEX motion, the addition of the covariate did not alter the main results described above, suggesting that group differences in motion sensitivity did not account for, or hide, age differences in the effects of unbiased or VEX motion on FG perception. However, in the CAV motion condition, the ANCOVA found the effect of motion on P(VEX = Figure) significantly differed between age groups, $F(1,43) = 4.24, p = .041$, indicating that the effect of CAV motion differed between younger and older observers after accounting for individual differences in motion

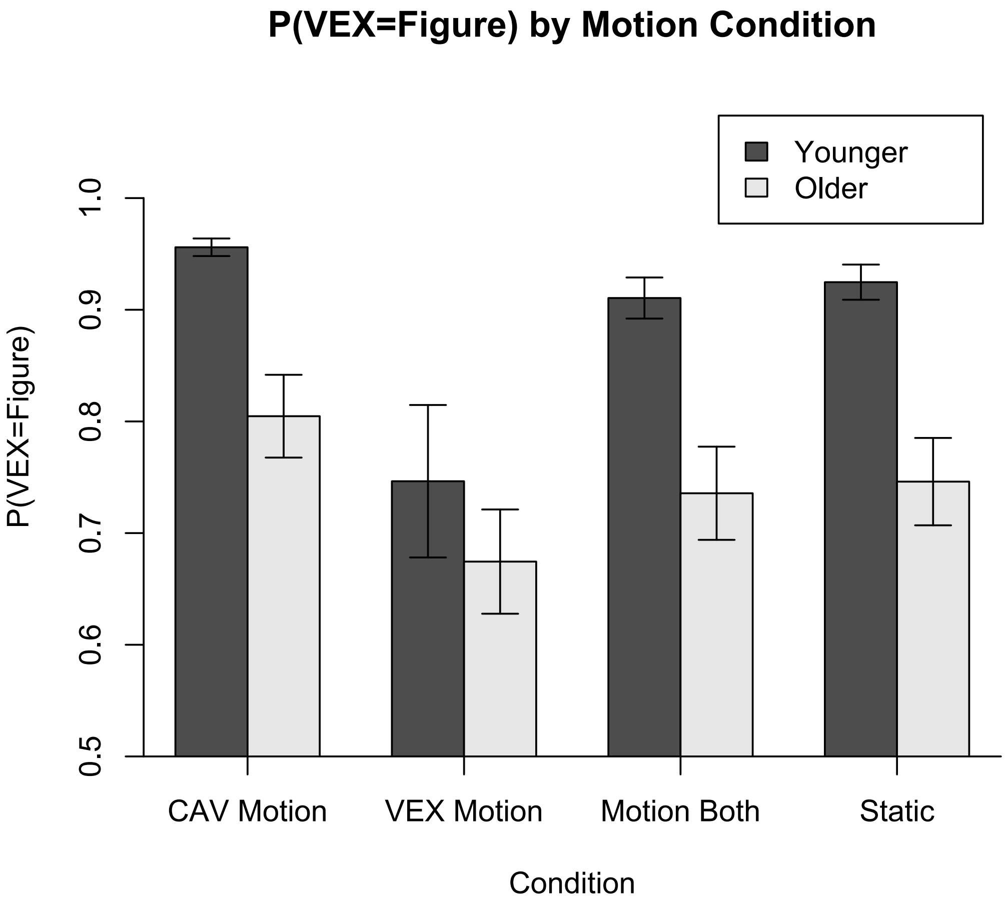

Figure 3.6: Likelihood of perceiving VEX regions as the figure across conditions and groups in Experiment 3.4. The height of each bar indicates P(VEX = Figure) for 8-region convexity stimuli for a given motion condition and age group. Error bars represent ±1 SEM.

detection accuracy. Figure 3.9 plots CCE distributions for younger observers, and older observers split by whether or not motion detection accuracy was *high*, i.e., higher than than 75%. The box plots show that the effect of CAV motion was slightly stronger in the older observers if they had high motion detection accuracy compared to the younger observers ($t(18.6) = 1.62, p = .061$, one-tailed; equal variance was not assumed, Bartlett's $K^2(1) = 13.6, p = .0002$). The 75% accuracy threshold was chosen because it fell between performance of two sub groups of older observers indicated using a hierarchical clustering algorithm with a two-mean constraint. Although, this high vs. low detection accuracy criterion was also varied between 65% and 90%, and t-values for tests comparing CAV

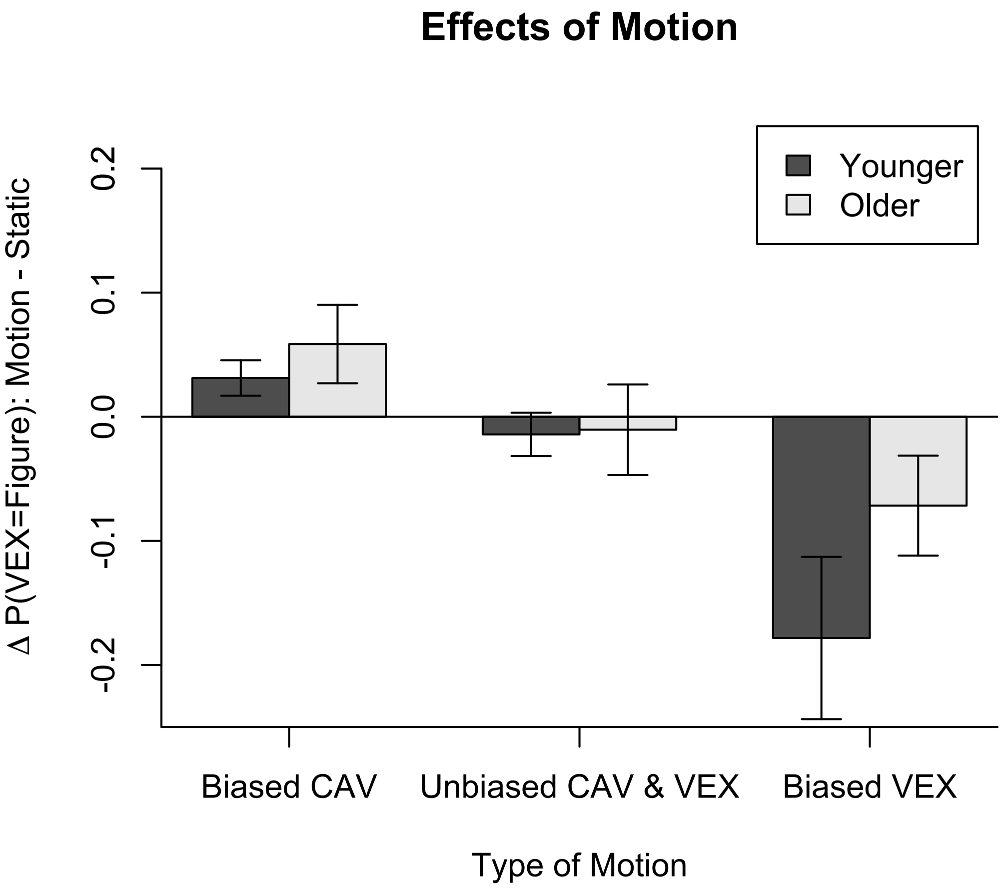

Figure 3.7: Effects of various motion manipulations on likelihood of perceiving VEX regions as the figure. Each bar represents the difference in P(VEX = Figure) between a given motion condition and the static condition. Error bars represent 1 SEM. Positive scores indicate that VEX regions were more often perceived as figures in the motion condition of interest compared to in the static condition, negative scores indicate the opposite, and scores of zero indicate no behavioural effect of motion. The plot shows that motion affects P(VEX = Figure): motion added to either VEX or CAV regions alone increased likelihood of moving regions being perceived as the ground compared to perception in the static condition. However, the unbiased motion condition, where motion was added to both CAV and VEX regions simultaneously, did not have a significant effect on P(VEX = Figure).

motion effects in younger to high accuracy older observers ranged from 1.40 to 1.98, with *p*-values ranging from .088 to .035, indicating that the choice of 75% was not critical to

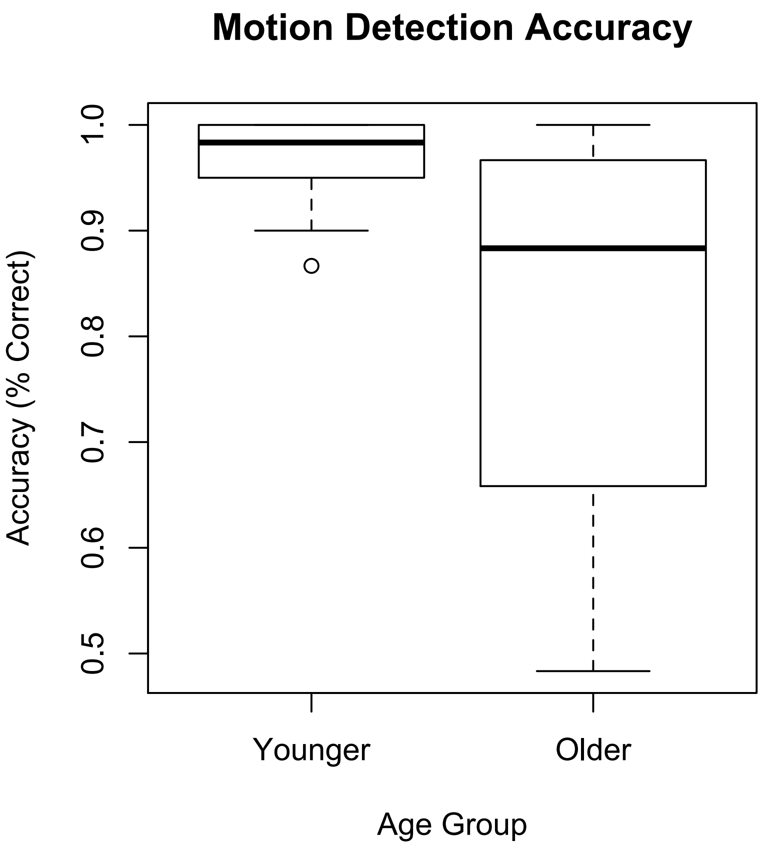

Figure 3.8: Accuracy (% correct) in the control task of Experiment 3.4 for each age group. Distributions of group accuracy scores are depicted as boxplots, which illustrate worse performance in the older observers, with more variability and greater negative skew, compared to the younger observers.

this result.

3.4.3 Discussion

In this experiment, we demonstrated that motion does have an effect on FG perception: specifically, moving regions were more likely to be perceived as background. Hence, relative to a baseline static condition, adding motion only to CAV regions increased P(VEX = Figure), adding motion only to VEX regions decreased P(VEX = Figure), and adding motion to both regions had no effect on theP(VEX = Figure). These results

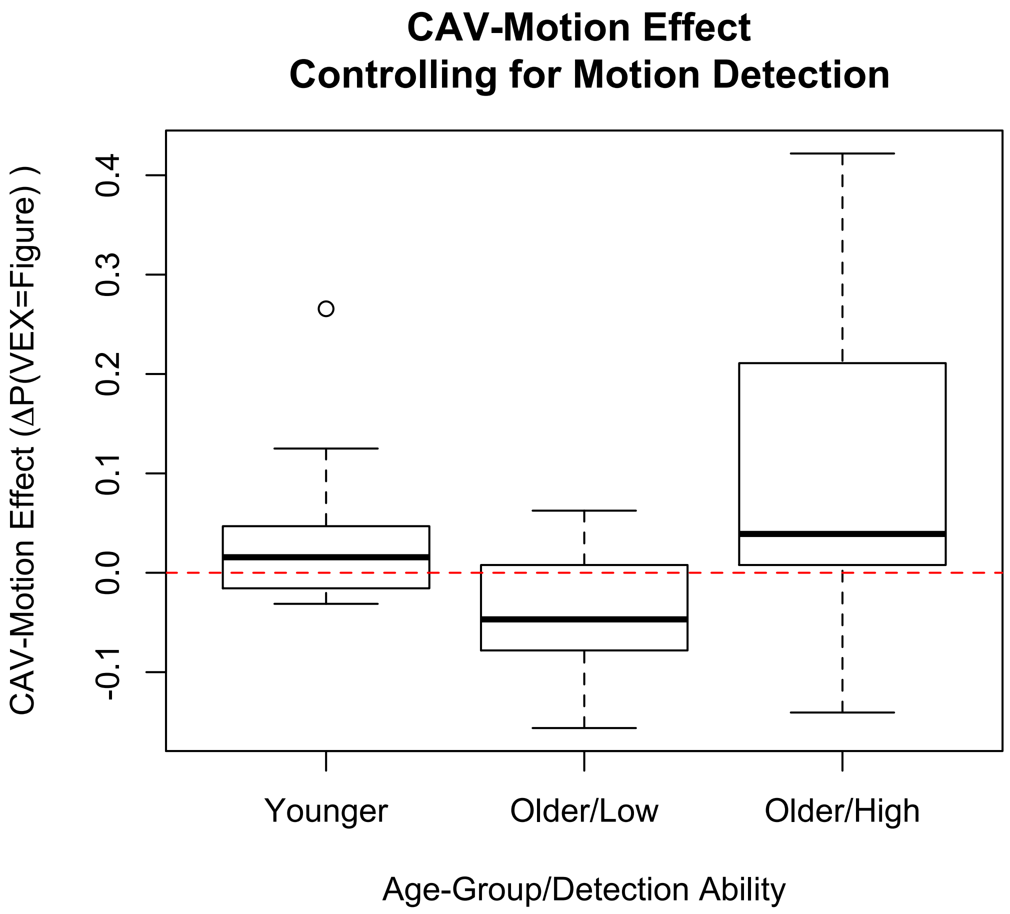

Figure 3.9: Box plots of the effects of adding CAV motion for the younger observers and older observers split by motion detection sensitivity. Each box represents the distribution of CAV motion effects (performance on CAV-motion contrasted to performance in static condition) and this is shown for the younger group, older observers who had low ($<$ .75%) accuracy on the motion detection task, and older observers who had high motion detection accuracy ($>$ .75%). The plots of the distributions show that the effect of CAV motion was greater in older observers who could accurately perceive the motion compared to younger observers, Welch $t(18.6) = 1.62, p = .061$.

generally are consistent with the results from Experiments 3.1, 3.2, and 3.3, and provide evidence against the hypothesis that reduced depth presumption in older observers accounts for the reduced CCE in aging. The observed effects of biased motion further validate the findings of the previous experiments by demonstrating that biased motion can instantiate a shift in perceived depth order.

We also conducted a motion detection control task, which indicated that the older group had reduced sensitivity to motion compared to the younger group. After accounting for these effects by using motion detection performance as a covariate, we found that adding biased CAV-only motion had a greater effect on P(VEX = Figure) in older than younger participants, whereas the effects of VEX-motion and unbiased motion still did not differ between age groups. The results of the ANCOVAs rule out the possibility that our failure to find age differences in the effect of unbiased motion was due to an inability of older adults to detect the motion.

As was found in the previous experiments, the current experiment found that unbiased motion does not increase the CCE in either age group. In addition, the current results demonstrate that biased motion affected FG assignment in the expected way. Finally, we found that adding motion only to CAV regions had a greater effect on convexity effects in older subjects compared to younger subjects, when age differences in motion sensitivity were taken into account. Thus, these results do not support the hypothesis that the reduced CCEs in older adults can be attributed to reduced presumption of depth in the stimuli. However, the findings are consistent with the hypothesis that the reduced CCE reflects a reduced ability to resolve competition among several plausible FG organizations of ambiguous stimuli.

3.5 General discussion

3.5.1 Summary of main findings

Our findings support the idea that texture motion with AD at region boundaries affects FG organization in both younger and older observers. However, the results not support the notion that reduced CCEs in older observers reflect a lower presumption of depth in the stimuli used in our task. Addition of unambiguous, biased HOM horizontal motion, which produces texture AD at region boundaries, to CAV or VEX region fills promotes perception of those regions as being in the background (consistent with previous findings, see Tanrikulu et al., 2016). However, addition of unbiased, ambiguous motion with AD that occurs at both regions adjacent to an edge simultaneously, which indicates the presence of depth but not depth order (Froyen et al., 2013), does not alter FG perception in either older or younger observers. If older observers presumed less depth in our stimuli, which would reduce the CCE by decreasing the ability to infer depth order or by decreasing confidence in response selection that regressed performance to chance, addition of this unbiased motion, which increases evidence of depth, should increase convexity effects in the older group. The lack of evidence for this relationship is inconsistent with the hypothesis that reduced CCEs in older observers result from reduced presumption of depth in the convexity stimuli. Rather, the observation that the subset of older observers who perceived the motion showed a strong increase in P(VEX = Figure) in response to the reduced competition (convexity/motion-congruent) CAV-motion stimuli, suggests that the relatively higher competition in the static and unbiased motion conditions underly the age-CCE interaction. These findings thus strengthen the proposal that healthy aging alters perceptual organization processes (Lass et al., 2013) that segregate figure and ground through the combination of the configural cue convexity, and the spreading of inhibition between regions grouped across space through context (Peterson and Salvagio, 2008). Our interpretation of these results is that compromised inhibitory processing in aging (Pinto et al., 2010) affects the ability to successfully resolve high competition for FG structure (Salvagio and Peterson, 2010, 2012) that is achieved in younger adults through efficient inhibitory FG processes (Peterson and Salvagio, 2008; Peterson and Skow, 2008; Likova and Tyler, 2008; Sanguinetti et al., 2015; Cacciamani et al., 2015).

3.5.2 Aging and motion perception

Our results also demonstrate that motion perception is impaired in aging: a subset of the older group had highly impaired ability to perceive the motion used, whereas the younger group had highly accurate ability to detect it. These results are consistent with previous studies showing that older observers are less sensitive to motion (Bennett et al., 2007; Andersen and Atchley, 1995; Roudaia et al., 2010), specifically showing a deficit in spatial integration of motion signals (Andersen and Ni, 2008). However it has also been shown that older observers can extract depth and shape information from differential motion (Norman et al., 2000) and motion parallax (Norman et al., 2004). Like these studies, we found evidence that older observers were impaired compared to younger observers in motion perception, but we also showed that motion could be used to influence perception in older observers when it was perceived accurately. Importantly, we controlled for individual differences motion sensitivity by running a task where observers indicated whether or not they perceived motion using the same stimuli as the experiment. The age differences in motion perception did not account for the FG effects reported here except for in the reduced competition (by motion/convexity cue-congruency) CAV motion condition. This observation indicates that older observers who can perceive the motion show a significantly larger effect of CAV motion compared to younger observers. Thus, the evidence reported here supports the proposal by Lass et al. (2013) that, after accounting for reduced motion sensitivity in older observers, it is the ability to resolve high conflict between perceptual interpretations that is impaired in aging.

3.5.3 Aging and structure from temporal synchrony

A broader question surrounding the phenomena explored here is: how does aging impact perceptual organization determined from temporal structure? Common fate has long been studied as a cue by which stimulus components are grouped (Wertheimer, 1923). The notion that "objects that move together, group together", however, has been extended to conceptualize a more *generalized common fate*, indicating that stimulus properties (beyond spatial location) that change together promote grouping (Sekuler and Bennett, 2001). These kinds of signals have been proposed as important in studying the phenomenon of grouping in that they correspond to a framework where neural coding can transmit grouping signals through synchrony of firing between neurons and networks coding the to-be-grouped stimulus properties (Lee and Blake, 1999; Kandil and Fahle, 2004; Blake and Lee, 2005). Interestingly, it has been demonstrated that temporal structure, used to group elements in determination of FG structure, can even be integrated across different stimulus properties: whether it is changes to/across contrast, spatial frequency, orientation, or phase of stimulus components, it is the timing of the change of these *mixed-messengers* acting as the signal detected and utilized in perceptual organization (Guttman et al., 2005, 2007).

Blake et al. (2008) demonstrated age-related deficits in the ability to determine FG organization through temporal structure of component stimulus elements, indicating that this aspect of perceptual organization is impaired in aging. We showed impaired ability to detect highly coherent motion signals in older observers, but intact ability to extract information from that motion when perceived. Extending our work to explore FG structure invoked by temporal structure of stimulus elements might provide a nice avenue for future exploration of FG perception in aging. The techniques used in studying perceptual organization from temporal structure provide an objective task (with true correct/incorrect answers), with multiple cues that can be combined to manipulate competition (through cue combination/congruency and correlation of generalized common fate signals within/between figure and ground regions), which incorporates both FG and grouping processes in the determination of perceptual organization. Results indicating that the extraction of information from motion is impaired by aging at low- (Roudaia et al., 2010) and high-levels (Spencer et al., 2016) of visual processing, urge further study of age-related changes to perceptual organization through temporal structure, to close the gap in understanding of how senescence affects encoding of stimulus properties at various stages of perceptual processing. The application of more controlled temporal structure of region fills in our stimuli – i.e., by manipulating correlation between change in direction, luminance, and speed of fill elements within and between regions – could thus be a useful tool. Such a paradigm could help address the question of how classic configural cues (like region convexity), and contextual factors that interact with them (like homogeneity properties of disparate regions), are encoded from within a more information-processing based framework.

3.5.4 Aging and depth perception

We found evidence against the possibility that the age-CCE interaction is the result of reduced depth presumption by the aging visual system. A related but important future research direction will be to directly relate the effects of aging on FG to depth perception. The suggestion that configural cues can actually influence perceived depth signalled through binocular disparity (Burge et al., 2005) is one interesting avenue into this question. Bertamini and Lawson (2008) demonstrated that congruence between depth order suggested by binocular disparity and convexity speeds performance in indicating depth compared to when disparity signals that the VEX region is in the back. The authors suggested that this arises from cue conflict, whereby incongruence between the configural and disparity cues require more processing to resolve, which slows responses. However, an integration account would conceptualize depth perception as arising from the appropriate weighting of both sources in making a perceptual inference. In line with this idea, Burge et al. (2010) measured the natural scene statistics of real world depth maps and examined how VEX figures in the scenes relate to actual depth separating VEX/CAV foregrounds from backgrounds. In a psychophysical experiment, Burge et al. showed that convexity of a contour is integrated with stereoscopic depth information such that perceived depth is biased by convexity: when disparity indicates a particular depth, perceived depth is overestimated when the foreground is VEX and underestimated when the foreground is CAV. These results motivate an interesting question about how the age reduction to CCEs observed in our lab relate to real-world depth perception, as depth perception is influenced by convexity. Does the effect of convexity on perceived depth (as integrated with stereoscopic depth cues) also diminish in healthy aging? We might expect that, given the reduced CCEs in aging, older observers would show reduced reliance on convexity in estimating depth.

Considering this integrative depth perception mechanism presumably increases accuracy or speed in inferring depth in many scenarios, hypothesized reduction to the weighing of convexity in aging might impair performance on tasks involving estimation of depth when convexity is a salient cue. When navigating the world, it is critical to quickly and accurately infer depth of, relative depth between, and changes in depth amongst, various curved objects in order to ensure stable and effective reaction to the environment. Compromised depth inference could negatively impact driving performance (requiring tracking depth of curved vehicles and pedestrians) and lead to increased falls (caused by decreased ability to infer depth of a curb, stair, or curved protrusion in the ground ahead). Both of these activities have been shown to be impacted in healthy aging (Wood, 2002; Källstrand-Ericson and Hildingh, 2009). As far as we are aware, the role of convexity in these deficits is yet to be explored but seems like an important direction given the results of our research program. Interestingly, however, if aging does reduce the influence of convexity on depth perception, we would also paradoxically expect *more* accurate depth judgements in older observers, specifically under conditions where convexity is not consistent with true depth.

3.5.5 Conclusion

In this paper, we examined whether reduced CCEs in aging result from decreased presumption of depth in the convexity stimuli. We found that increasing evidence of depth in the stimulus, without giving any information about depth order, did not increase CCEs in the older or younger adults, evidence inconsistent with the hypothesis. We did show that the motion manipulation applied in biased ways does shift FG perception towards moving being perceived as background in both age groups. However, the reduced competition CAV motion caused a larger increase in P(VEX = Figure) for older observers who could accurately detect the motion compared to younger observers. These findings are consistent with our previous work showing that reduced competition through cue combination accounts for a portion of the reduced CCE in healthy aging Lass et al. (2013). The observations reported here thus support the interpretation that the inhibitory processing underlying FG organization, which are required to resolve high competition between perceptual interpretations of an ambiguous stimulus, is impaired in healthy aging.

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Chapter 4

Neural signatures of convexity context and competition effects: An electroencephalographic investigation of the effects of aging on the processing underlying figure-ground organization

Abstract

We explored the age-related impairments to the processing underlying figure-ground (FG) organization by relating neural signatures associated with FG competition resolution to behavioural performance. Older and younger observers participated in a figure assignment task while viewing displays composed of two or eight alternating convex and concave regions. The critical comparison was between performance with the 8-region displays that had regions that alternated between black and white (BW8) vs. other displays had multiple colours filling convex regions and uniform fills across concave regions (CavHom). Properties of CavHom stimuli are consistent with the dominant {convex = Figure} interpretation of the displays, which has been shown to reduce competition between competing perceptual interpretations of the stimuli (Salvagio and Peterson, 2012).

Our results supported the hypothesis that the evoked response potential (ERP) associated with processing these stimuli is sensitive to the competition between perceptual interpretations of these different displays. The younger group showed a significant ERP difference between high and low competition conditions (BW8 vs. CavHom) around 250 ms post stimulus onset, but older observers did not. Furthermore, individual differences in this neural response to the varying competition were inversely correlated to differences in behavioural performance across conditions: observers who showed similar performance across conditions showed a large ERP effect whereas those who showed a large behavioural performance difference across conditions showed weak ERP effects. These results are consistent with the notion that individuals who are able to resolve higher competition stimuli do so by appropriately adjusting the processing mechanisms underlying FG competition resolution in response to higher levels of competition. On the other hand, those less able to resolve the higher competition stimuli, as indexed by a large effect of condition on behavioural performance, did not show the same index of altered processing. The results suggest that younger observers tend be to able to resolve the high competition between competing FG interpretations of a stimulus by adjusting processing mechanisms to overcome high competition whereas older observers may tend to be unable to resolve the higher competition stimuli because they cannot invoke the processing resources required to overcome the high conflict. The implications into our understanding of FG organization, and the way that processing underlying FG is affected by aging, are discussed.

General Introduction

Convexity is an important cue to figure-ground (FG) organization, which confers figural status to the convex (VEX) side adjacent to a curved contour (Rubin, 1915/1958; Kanizsa and Gerbino, 1976). However, the probability with which VEX regions are perceived as figure [i.e., P(VEX = Figure)] depends on context: specifically, P(VEX = figure) increases with the number of alternating VEX and homogeneously filled concave (CAV) regions in a stimulus (Peterson and Salvagio, 2008). Figure 4.1 depicts example stimuli used by Peterson and Salvagio (2008) and the current study: 4.1(A) shows an example 2-region (BW2) stimulus; 4.1(B) depicts a black and white 8-region (BW8) stimulus where both CAV and VEX regions are homogeneous (HOM); and 4.1(C) depicts a stimulus where VEX regions are heterogeneously coloured and CAV regions are HOM in colour (i.e., a CavHom stimulus).

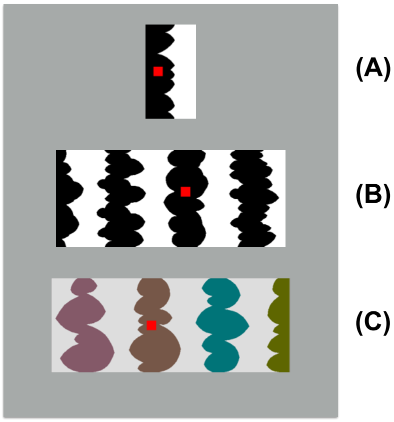

Figure 4.1: Convexity stimuli used in the current experiments, originally created by Peterson and Salvagio (2008). Stimuli were composed of alternating VEX and CAV regions, and were either black and white or composed of multiple colours. (A) shows an example *BW2* 2-region stimulus, (B) depicts a *BW8* black and white 8-region stimulus, in which both CAV and VEX regions have the property of homogeneous fill, and (C) depicts a *CavHom* stimulus with heterogeneously coloured VEX regions and homogeneously coloured CAV regions. A red square probe appeared on one of the two central regions of each stimulus as part of the experimental task, which was to indicate "Was the red square probe ON or OFF the region perceived to be the figure?". Placement of the red square probe was balanced between VEX vs. CAV, black vs. white, and left vs. white regions, within each stimulus set.

This effect of region number, i.e, the so-called convexity context effect (CCE), requires that CAV regions are homogenous (HOM) in colour (Peterson and Salvagio, 2008), which supports the possibility that spatially separated CAV regions make up a unified background (Goldreich and Peterson, 2012). In other words, behavioural data and Bayesian modelling support the notion that the the visual system favours a FG organization in which HOM regions are seen as a unified background occluded by non-HOM regions that are less likely to be parts of a unified ground. When both CAV and VEX sets of regions are homogeneously coloured, the HOM cue is ambiguous (i.e., supports both {VEX = Figure} and {CAV = Figure} interpretations of the stimulus). Therefore, the context underlying the CCE is present in BW8 stimuli, but the contextual cues also validate the alternative interpretation, which would in theory require stronger inhibition to suppress the perceptual alternative and resolve the stimulus. In contrast, when only VEX regions are HOM, the heterogeneity across CAV regions is inconsistent with convexity in cuing FG organization, which prevents the contextual property underlying the CCE from taking effect (Peterson and Salvagio, 2008; Goldreich and Peterson, 2012). However, when only CAV regions are homogeneously coloured (i.e., CavHom stimuli), both the convexity and homogeneity cues are consistent with the interpretation that the VEX regions are figures. This consistency among cues presumably reduces the conflict between the alternative perceptual interpretations of the stimulus compared to when VEX region are also HOM, which is the proposed explanation for why younger observers can resolve CavHom stimuli more quickly than BW8 stimuli (Salvagio and Peterson, 2010, 2012). The pattern of convexity and context effects is consistent with the hypothesis that FG organization involves a process of inhibitory competition among multiple interpretations of ambiguous stimuli (Peterson and Salvagio, 2008; Peterson and Skow, 2008) and among regions within a stimulus (Likova and Tyler, 2008; Cacciamani et al., 2015).

Our previous work has explored the hypothesis that decreased inhibitory control of cortical networks in late adulthood (Pinto et al., 2010; Leventhal et al., 2003; Schmolesky et al., 2000; Hua et al., 2008) might cause decreased inhibitory processing in various psychophysical tasks. This aging-inhibition hypothesis has been supported by performance patterns on some tasks (Betts et al., 2005, 2009; Bennett et al., 2007; Wilson et al., 2011), and we predicted that older observers might show impaired FG organization, which involves inhibitory competition resolution (Likova and Tyler, 2008; Peterson and Skow, 2008; Peterson and Salvagio, 2008; Cacciamani et al., 2015). As expected, the CCE is reduced in older observers, suggesting that inhibitory competition underlying the CCE is impaired in aging (Lass et al., 2012). In conditions with ambiguous stimuli (e.g., BW8 stimuli), which presumably result in relatively higher competition in the determination of FG organization, older observers showed greatly reduced CCEs, indicating the difficulty for the aging visual system in resolving high competition (Lass et al., 2012). However the significantly increased P(VEX = Figure) observed in older adults when using less ambiguous stimuli (i.e., the CavHom stimuli, where both homogeneity and convexity are consistent with the $\{\text{VEX} = \text{Figure}\}$ interpretation; see Figure 4.1C), demonstrates that older observers do integrate convexity and context in resolving FG competition (Lass et al., 2013). Taken together, these observations are consistent with the hypothesis that reduced inhibitory processing in aging might impact FG organization, and support the idea that high conflict stimuli pose a particular challenge for the aging visual system in resolving FG competition.

Are age-related changes to the processing underlying FG perception represented at the cortical level? We explored this question by examining task-related evoked cortical responses associated with FG organization. Recent studies assessing the electrophysiology of competition underlying FG organization used a paradigm in which observers classified silhouettes from a cleverly designed stimulus set as either "novel" or "familiar". The stimuli were all symmetrical enclosed silhouettes that included a set of familiar shapes (like an apple, bell, telephone, etc.,) and novel shapes (Trujillo et al., 2010; Sanguinetti et al., 2015; Cacciamani et al., 2015). Some of the novel silhouettes were enclosed by a contour composed of the shape of familiar object on the two vertical ground side edges (i.e., *high competition* stimuli) similar to Rubin's vase (Rubin, 1915/1958). In other words, for these high competition stimuli, the regions perceived as the background during the task had shapes of familiar objects. The remaining novel figures contained a FG organization that did not contain a familiar shape on the ground (i.e., *low competition* stimuli). It has been shown that resolving FG structure of the high competition stimuli involves inhibitory processing. Specifically, classification of objects related to the suppressed ground side shape was slower for high competition stimuli compared to objects unrelated to the suppressed shapes (Peterson and Skow, 2008).

Trujillo et al. (2010) examined neural activity of observers who the authors were highly certain did not perceive the ground side figures. It was observed that presence of a familiar object on the ground affected the amplitude of the evoked electrical brain response as early as 100 ms after stimulus onset. These results demonstrated the influence of past experience, operationalized as the presence of the shape of a familiar object on the ground, on the processes underlying FG perception. Theoretically, the presence of a familiar shape on the ground side competes with the interpretation of the central region as a figure, which was primed as figure by other configural cues of enclosure and small area, as well as task instructions to classify the symmetrical central figure. It is argued that the suppression of the familiar-shaped ground in the high competition condition, leading it to be perceived as the shapeless background, requires increased inhibitory processing mechanisms underlying resolution of the FG conflict, relative to low competition silhouettes. It was interesting that this effect of familiar shape configuration was shown by Trujillo et al. (2010) to impact processing signatures on a temporal scale thought to reflect the early stages of FG organization (Caputo and Casco, 1999).

In line with the inhibitory-suppression hypothesis of FG processing, the higher competition stimuli (with suppressed ground side familiar objects) were also shown to evoke greater power in the $\alpha-$band compared to the lower competition stimuli during the similar/novel categorization task (Sanguinetti et al., 2015). The literature linking evoked α response to attentional suppression (Klimesch et al., 2007) supports the interpretation that the evoked response potential (ERP) and evoked α oscillations around 100 ms post stimulus onset reflect mediated inhibitory processing mechanisms underlying the resolution FG competition. A recent functional magnetic resonance imaging (fMRI) study explored the ground region suppression reflected in V1 and V2 activation (e.g., Likova and Tyler, 2008) using the same silhouette stimuli but different task than Peterson and Skow and Trujillo et al.. It was observed that voxels with activation associated with receptive fields falling on background regions of the silhouettes, showed greater suppression of neural activity in response to the high competition compared to low competition stimuli (Cacciamani et al., 2015). These results demonstrate that the degree of competition involved in processing the figures mediates the invoked suppression of the ground regions. This supports the theory that varying degrees of FG competition are resolved through *competition-mediated* suppression of networks representing ground regions.

Interestingly, and of particular importance to our research focus, a recent reaction time (RT) study quantified the inhibitory FG effects in the high/low competition silhouettes in an exploration of the effects of aging on FG perception. Anderson et al. (2016) observed that for younger adults, RTs were faster when classifying high compared to low competition silhouettes, a finding consistent with the idea that resolving higher competition requires increased inhibitory processing that speeds performance. However, older adults showed the opposite pattern, that responses were slower for the high competition stimuli compared to low competition stimuli. This result was consistent with the hypothesis that older adults have reduced ability to recruit the needed inhibitory processing, that underlies the suppression of irrelevant familiar ground side shapes, which therefore caused the resolution of high competition stimuli to be more difficult and take longer. These findings support the hypothesis of impaired FG processing in healthy aging using stimuli that have been linked to competition-mediated suppression (Cacciamani et al., 2015), which further motivates exploration of the effects of aging on the processing mechanisms underlying the CCE in the context of inhibitory processing mechanisms.

Our previous study examining the electroencephalography (EEG) of processing signatures underlying the CCE found that the different perceptual interpretations of black and white stimuli are reflected in the time-locked ERP (Lass et al., 2014). The difference between mean amplitude of {VEX = Figure} vs. {CAV = Figure} ERPs at around 170 ms post stimulus onset indicates when the neural response is sensitive to the way that the stimulus is organized. However, another particularly interesting question about the neural circuitry underlying the CCE, especially as it pertains to the question of age-related changes to FG perception, is whether the neural signals reflect the competition involved in organizing the sensory data during the figure assignment task. Lass et al. found that the effects of perceptual interpretation were weak and inconsistent. However, it was observed that, relative to the ERP for BW8 stimuli, the ERP for BW2 stimuli was delayed between the P100 and N150, and there was a large amplitude difference at P200. There two effects can be seen in Figure 4.2, which plots the ERP for each condition and perceptual interpretation: black traces are delayed compared to red traces at between 100-150 ms, and the amplitude for the red traces are much larger than the amplitude for black traces around 200 ms.

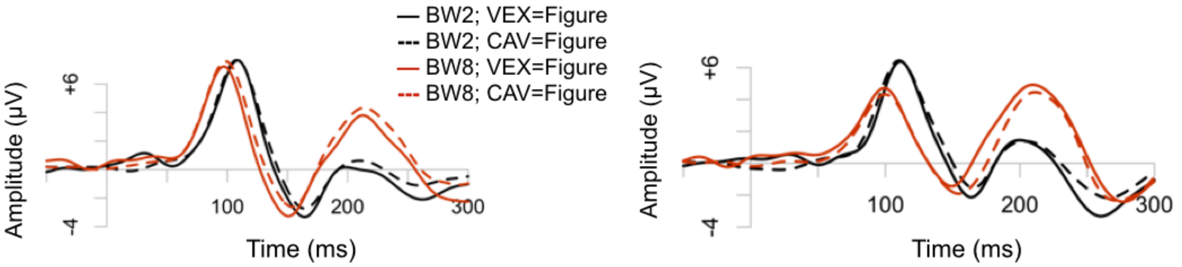

Figure 4.2: Event-related Potentials (ERPs) from Lass et al. (2014). Shown here are ERPs in left and right parietal/occipital electrodes. The red lines are ERPs for the 8-region stimuli (BW8 condition) and black lines are for 2-region stimuli (BW2 condition); dashed lines indicate ERPs for {CAV = Figure} response whereas solid lines show ERPs for {VEX = Figure} response. The effects of perceptual interpretation (i.e., response: {VEX = Figure} vs. {CAV = Figure}) were weak (difference between solid and dashed lines) but there were noticeable effects of region number in the delayed P100 and reduced amplitude P200 in 2- compared to 8-region conditions.

The current experiments examine the processing of FG competition underlying the CCE by comparing ERPs associated with BW8 stimuli to ERPs associated wtih CavHom stimuli. The results of Trujillo et al. (2010) and Sanguinetti et al. (2015) are consistent with the hypothesis that the competition evoked by suppression of the ground in their stimuli increases ERP amplitude around 100 ms post stimulus onset. Therefore, we expected to find an increased amplitude around 100 ms for relatively higher competition BW8 stimuli, which would be consistent with the idea that the homogeneity of CAV regions mediates the degree of FG competition. However, Lass et al. (2014) observed higher amplitude in the ERP response to BW2 compared to BW8 stimuli at 100-150 ms, reflecting a delayed N150 and to some degree P100, and that the P200 amplitude was higher in the 8- compared to 2-region conditions (see Figure 4.2) Thus, finding ERP activity that is delayed in response to BW8 relative to CavHom stimuli, as reflected in mean amplitude from 100-150 ms, or finding increased mean amplitude at P200 in response to CavHom compared to BW8 stimuli, would support the idea that the processing of CavHom differs from processing of BW8 stimuli in that same way that processing BW8 differs from BW2 stimuli.

Yet, there is also evidence that different cues impact processing underlying perceptual organizational on different temporal timescales (Kurylo, 1997; Han et al., 1999a,b). Thus, it is reasonable to expect that competition in our task might be associated with different ERP effects than the competition observed by Trujillo et al. (2010) 100 ms post stimulus onset, considering they used a different stimulus and task. Whereas Trujillo et al. used a stimulus in which shapes of local contours/regions were the critical factor influencing FG competition, and a task in which instructions were important to determining FG organization, the CCE depends on spatial context of the regions of interest and the task involves reporting FG assignment. Unlike local FG competition at edges surrounding a single figure/region, the mechanism of the CCE is proposed to involve the spreading of inhibitory processing (Peterson and Salvagio, 2008), and it has been shown that processing time varies with contextual influences on FG completion (Guttman et al., 2003). It is thus conceivable that CCEs might rely on more *global segmentation processes*, which have reported to be reflected later in the ERP (200-260 ms) for simple textured stimuli (Caputo and Casco, 1999). It was therefore also important for us to explore later ERP components in examining competition involves in CCEs at the neural level.

Experiment 4.1 tested the following hypotheses: First, the competition mediated by homogeneity of VEX regions in 8-region displays is similar to that observed by Trujillo et al. (2010); and second, that the effect of context between BW2 and BW8 stimuli is similar to the competition mediated by homogeneity of VEX regions. Experiment 4.1 was also used to explore the data *post hoc* for other relationships at different timescales. Experiment 4.2 replicated the the effects obtained in Experiment 4.1, and examined how aging affects the ERP responses with a well-informed set of *a priori* hypotheses. The resulting ERP findings were used to provide insight into the observed behavioural reduction to the CCE in older adults.

4.1 Experiment 4.1

Previous research showing an ERP sensitive to cross border competition at around 100 ms post-stimulus onset (Trujillo et al., 2010) suggests that the difference in competition between CavHom vs. BW8 stimuli should elicit a detectable effect on the ERP around this time window in the right parietal hemisphere, which might then be used as an index of competition resolution in the processing of these stimuli. Experiment 4.1 tested the hypothesis that decreased competition between the {VEX = Figure} perceptual interpretations of CavHom compared to BW8 stimuli, reduces the amplitude of the ERP approximately 100 ms post stimulus onset. We also compared the effects of competition (CavHom vs. BW8 stimuli) to the effects of context (BW2 vs. BW8 stimuli: shifted P100-N150, and decreased P200 amplitude), to test the hypothesis that these manipulations similarly impact the processing underlying FG competition resolution.

4.1.1 Methods

We measured EEG in observers participating in a figure assignment task with convexity stimuli (see Peterson and Salvagio, 2008; Lass et al., 2012). The procedure was similar to that used in our previous experiments (Lass et al., 2012, 2013, 2014) except that participants pressed a space bar on a computer keyboard to initiate each trial, which was similar to foot pedal used in the experimental setup used by Peterson and Salvagio (e.g., Peterson and Salvagio, 2008; Salvagio and Peterson, 2010, 2012). This change to the procedure from our previous experiments testing older observers allowed us to measure reaction time while maintaining a pause between trials. A schematic illustration of an experimental trial is shown in Figure 4.3.

Participants

Nineteen younger observers ($M = 19.72$ years, $sd = 2.1$ years) participated in this experiment. Participants were compensated $10 per hour or compensate with a course credit for participating. One observer was replaced because of an equipment malfunction that occurred during testing.

Stimuli and apparatus

This experiment used the stimuli from Peterson and Salvagio (2008). Each stimulus was composed of 2- or 8-regions that alternated in convexity. The 2-region stimuli (i.e., BW2) contained only a single VEX edge separating adjacent black and white regions. The 8-region black and white stimuli (i.e., BW8) were composed of 8 alternating regions that alternated in polarity and the direction of the convexity of the bounding contours. The CavHom stimuli contained eight regions and were similar to the BW8 stimuli, except that the VEX regions were always heterogeneously filled with different colours that were either all high or low in luminance on a given display. Similar to CAV regions in BW8 stimuli, the CAV regions in CavHom stimuli were always filled uniformly, but with a high or low luminance grey that was equal luminance steps away from the background grey as were VEX regions but in opposite direction. For all stimuli, a red square probe appeared on one of the two central regions; placement of the probe was balanced across each stimulus set such that it appeared equally often on regions that were: black vs. white, CAV vs. VEX, and left vs. right of central border. The BW2 and BW8 stimulus sets each consisted of 64 images, whereas the CavHom set contained 72 images.

Stimuli were presented in the centre of a uniform display that subtended 22.9° (width) × 17.2° (height) from the viewing distance of 96 cm. All stimuli were 3.3° in height with mean widths of 1.5° for 2-region displays, 7° for BW8 displays, and 7° for the 8-region CavHom stimuli. The luminance was $53.5\,\mathrm{cd/m^2}$ for the background, $0.6\,\mathrm{cd/m^2}$ for the black regions, and $96.4\,\mathrm{cd/m^2}$ for the white regions. For the CavHom stimuli, the luminance was $81.4\,\mathrm{cd/m^2}$ for high luminance regions, and $21.6\,\mathrm{cd/m^2}$ for low luminance regions. Viewing was binocular, and a head/chin rest was used to stabilize viewing position. The experiment took place in a dark anechoic room with the the experimental monitor serving as the only light source.

Presentation of experimental stimuli and EEG recordings were conducted using two

Power Mac G5 computers (2 × 2GHz PowerPc 970 CPUs each; one ATi R350 GPU each) running Mac OSX 10.5.8. One computer controlled the experiment and stimuli using MATLAB R2007b (version 7.5.0.338) while the second computer recorded EEG data using NetStation (version 4.3.1) simultaneously. The computers were linked through a TCP/IP link on the internal network for passing labels and synchronizing timestamps between the computers. Stimuli were presented on an NEC MultiSync FE992 CRT with resolution set to 1280 × 1024 pixels and frame rate set to 85 Hz.

EEG acquisition and processing

EEG data were recorded with a 256-channel HydroCel Sensor Net (Electrical Geodesics Inc., Eugene, Oregon, Tucker, 1993). During recording, the analog electrode signals were amplified by a factor of 1000 and converted to a digital signal sampled at 500 Hz that was bandpass filtered between 0.1-200 Hz. EEG data were referenced to electrode Cz online, synced with a recording computer using NetStation, and time-locked to the stimulus onset controlled by MATLAB on the experimental computer through the TCP/IP link established between NetStation and MATLAB on the separate computers. After data collection, continuous EEG data were filtered using a 1Hz highpass and 43Hz lowpass finite impulse response filter. The filtered recordings were then segmented from -500 to 500 ms around each stimulus presentation time marker. Resulting epochs were sorted by FG response ({CAV = Figure} vs. {VEX = Figure} trials) and region number condition using built in NetStation waveform tools. Using EEGLAB (Delorme and Makeig, 2004), we employed artifact rejection that involved removing trials with amplitudes $> 100\mu V$. Bad Channels were identified by visual inspection during recording and were estimated using EEGLAB's built-in spherical interpolation procedure. The remainder of the analyses were conducted with in house scripts that used functions from EEGLAB (Delorme and Makeig, 2004), LIMO (Pernet et al., 2011) for EEGLAB, and built-in MATLAB commands.

For this experiment, we tested the hypothesis that there would be a greater mean amplitude around 100 ms in BW8 compared to CavHom stimuli. For each of our left and right set of electrodes separately, we therefore calculated the mean amplitude for each condition and observer from 75-125 ms post stimulus onset as our measure. The average ERP traces, averaged across observers for each condition, are shown in Figure 4.6. To test the hypotheses of delayed P100-N150 and reduced amplitude at P200 for BW2 relative to BW8, we conducted similar mean amplitude measures in the 100-150 ms and 225-275 ms time windows using the appropriate condition contrasts.

Procedure and task

Upon arrival, participants read and signed the consent form followed by a short battery of visual tests that measured near and far acuity, contrast sensitivity, and stereoacuity. EEG cap size was selected based on the participant's circumference from the lower forehead to occipital bump. The cap was soaked in a solution of KCl and a drop of baby shampoo dissolved in water for at least 5 minutes. The cap was placed over the observer's head and fit to the eyeholes with middle reference set approximately to center of head (measured as intersection between the midpoint from tragus to tragus and midpoint bisecting eyebrows and occipital bump). NetStation's net impedance tool was used to identify electrodes with poor impedance, i.e., resistance above 50 kΩ, which were manipulated to have better contact with the scalp and hydrated with KCl solution using a pipette. This adjustment procedure was carried out until impedance threshold was achieved for as many recording electrodes as possible.

Prior to test, each participant received instructions which provided an explanation of what was meant by "figure" and "ground". Example stimuli were shown and the task was explained: after a briefly presented stimulus, participants had to indicate whether the red probe was ON or OFF the region that was perceived as the figure. After each trial and response, the participant pressed a space bar to initiate the next trial. Figure 4.3 illustrates the progression of a trial. There were 64 trials for BW2 and BW8 conditions, and 72 trials for the CavHom condition. Trials were blocked by condition with short breaker between blocks. Stimuli were presented in randomized order within each block. The experimenter stayed in the room for five practice trials to ensure the participant understood the task.

4.1.2 Results

Behavioural results

EEG analyses were performed with EEGLAB (Delorme and Makeig, 2004) and all statistical analyses were carried out using the R statistical software (R Core Team, 2013).

The convexity context effect (CCE) was defined as the difference between the proba-

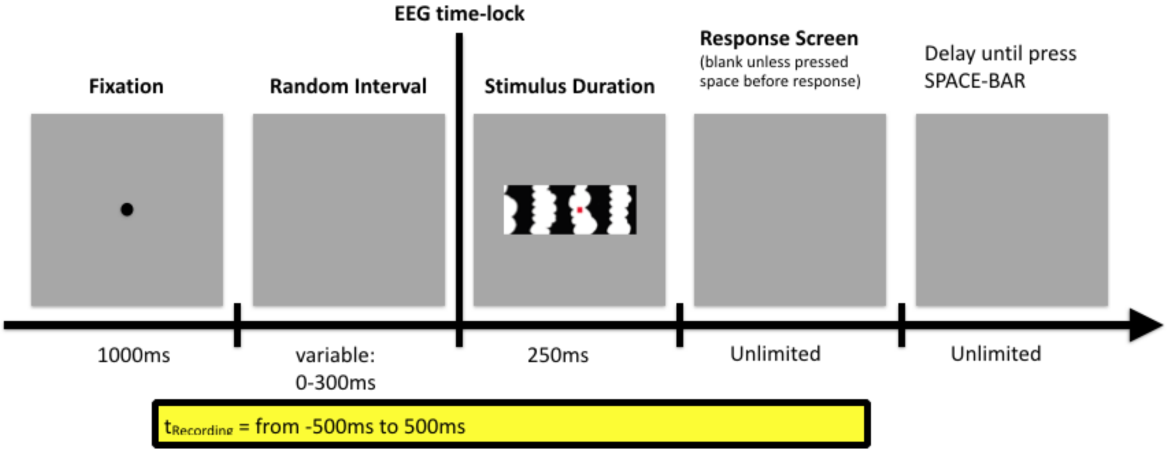

Figure 4.3: Schematic depicting the progression of a trial. Each trial began with a fixation dot that was presented for 1000 ms, followed by blank grey screen of jittered duration between 0-300 ms, after which the stimulus was presented for 250 ms against the grey background. The response screen was a blank grey screen where observers were instructed to indicate whether the red probe was ON or OFF the figure, and then press the space bar to initiate the next trial. Response screen was left on until the space bar was pressed, which caused the next trial to initiate immediately.

bility of designating the VEX region as figure in the BW8 and BW2 conditions:

$$\mathrm{CCE} = P(\mathrm{VEX} = \mathit{Figure})_{\mathrm{BW8}} - P(\mathrm{VEX} = \mathit{Figure})_{\mathrm{BW2}} \tag{4.1}$$

The convexity competition effect (CCompE) was defined as the difference between selecting the VEX region as figure in the CavHom and BW8 conditions:

$$\mathrm{CCompE} = P(\mathrm{VEX} = \mathit{Figure})_{\mathrm{CavHom}} - P(\mathrm{VEX} = \mathit{Figure})_{\mathrm{BW8}} \tag{4.2}$$

One participant had a CCE score that was more than 3 *sd* below the group mean, and therefore that observer was deemed an outlier and excluded from subsequent analyses.

The behavioural results are plotted in Figure 4.4, which shows the distribution of P(VEX = Figure) scores within each condition. Contrasting the BW2 and BW8, it can be seen that the medians are starkly different but that much of the negatively skewed BW8 distribution overlaps with performance in the BW2 condition. The CavHom and BW8 medians are closer to each other, however, the bulk of the relatively narrow CavHom distribution is above the BW8 median. The distributions of the CCE and CCompE are plotted in Figure 4.5.

Based on previous studies that measured CCEs in younger observers, we expected the CCE to be greater than zero. Therefore, we evaluated the CCE with a one-tailed *t*-test to increase statistical power. As expected, the CCE was significantly greater than zero, $t(17) = 1.9, p = .034$ (one-tailed). Previous evidence regarding the size and direction of the CCompE is equivocal, and therefore we evaluated that effect with a two-tailed *t*-test. We found that the CCompE differed significantly from zero $t(17) = 3.4, p = .0036$ (two-tailed). The positive CCE and CCompE can be seen in Figure 4.5, which shows that the distribution of both of these convexity effects are above the zero-effect red dotted line. Finally, these data replicated the tendency to perceive the VEX side of a contour as figure: P(VEX = Figure) was significantly higher than chance in the BW2 condition, $t(18) = 3.5, p = .0014$ (one tailed).

EEG results

In order to analyze the EEG data, the mean amplitude of the ERP signals were calculated on individual subject data in electrodes and time ranges of interest. The resulting scores were compared across conditions using focussed contrasts representing the CCE (BW8 vs. BW2) and CCompE (CavHom vs. BW8), which were then compared to zero (to test for the presence of these convexity effects) or to each other (to compare the convexity effects to each other). Data from three additional observers could not be analyzed due to very low signal to noise ratio resulting in the inability to pull out an ERP signal with any structured pattern; the exclusion criterion was the lack of a detectable P1 as indicated by visual inspection. Additionally, for all comparisons and plots, only trials with the {VEX = Figure} interpretation were used. This restriction allowed a direct comparison of trials where the FG competition had been resolved in favour of convexity and, even though our previous work indicated that the effect of perceptual interpretation ({VEX = Figure} vs. {CAV=figure}) was weak and inconsistent at best (Lass et al., 2014), it is possible that this difference could impact the results given that there are different relative proportions of trials of each interpretation across conditions and observers. It has been argued that this response-separated type of analysis might miss important neural activation properties contained in the different responses (VanRullen, 2011); however, we believe that this methodology, which is still commonly accepted and practiced in the field (e.g., Trujillo et al., 2010), is most appropriate for the comparison

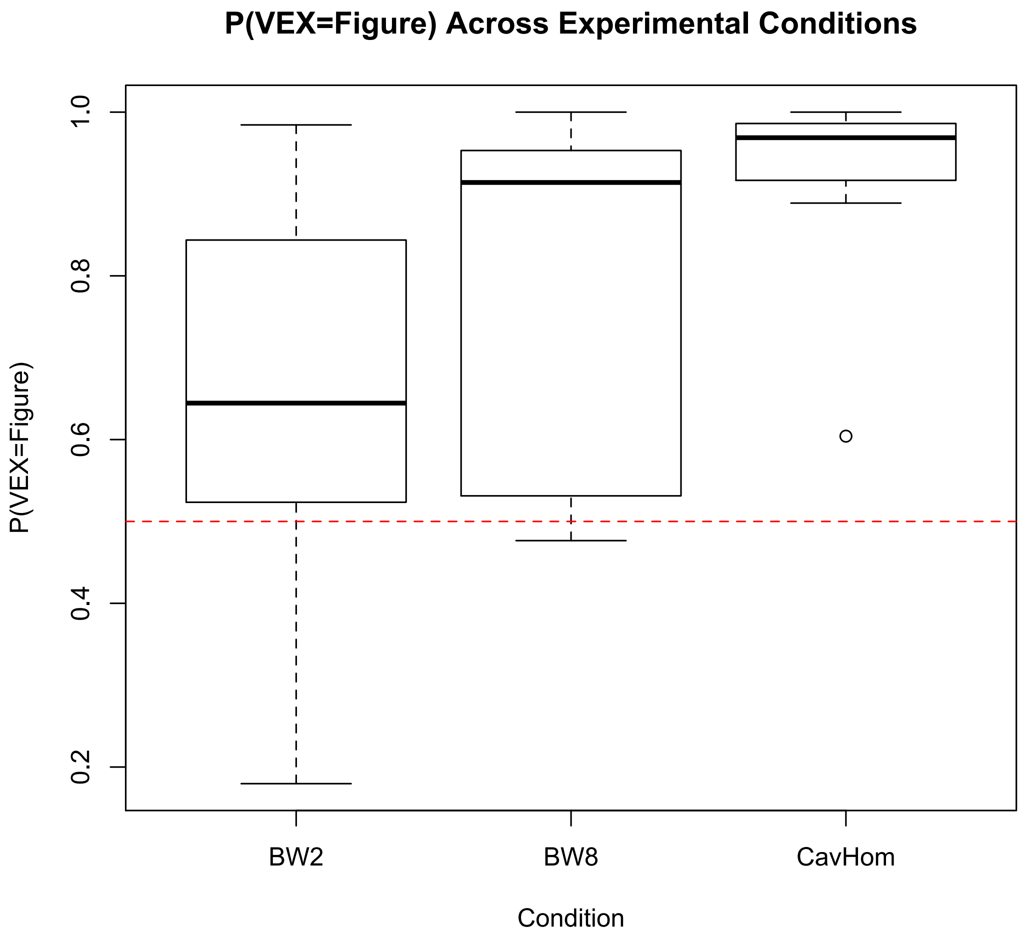

Figure 4.4: Behavioural performance in the three conditions of this experiment. Each box depicts the distribution of scores within a condition, indicating the median (solid line), interquartile range (box), and 1.5 x interquartile range, i.e., tails of distribution (whiskers). The red dotted line depicts chance performance, i.e., no behavioural bias in that condition.

we explored.

To test the hypothesis that the difference between competition induced by CavHom and BW8 stimuli is correlated with a difference in the ERP (i.e., the CCompE$_{ERP}$) of occipital-parietal regions as early as 100 ms post stimulus onset, we compared the mean ERP amplitudes measured in those conditions in a subset of parietal-occipital electrodes in the 76-124 ms time window. The results can be seen in Figure 4.6 by comparing the ERP profiles for the CavHom and BW8 conditions. It can be seen that these curves are

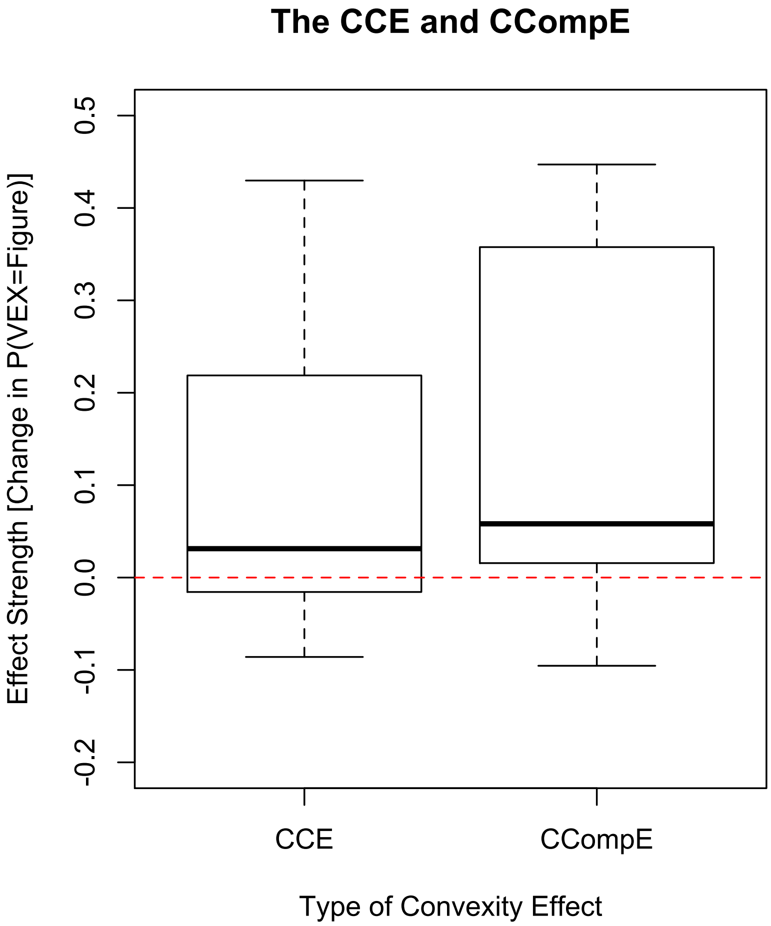

Figure 4.5: Distributions of the CCE and CCompE for Experiment 4.1. The CCE is the difference in P(VEX = Figure) between BW8 and BW2 conditions (see Equation 4.1), and the CCompE is the difference in P(VEX = Figure) between CavHom and BW8 conditions (see Equation 4.2). Each box depicts the distribution of difference score across conditions, indicating the median (solid line), interquartile range (box), and 1.5 x interquartile range, i.e., tails of distribution (whiskers). The red dotted line depicts an effect of zero, i.e., no difference in performance between conditions contrasted in the CCE or CCompE.

similar around 100 ms. The mean P100 amplitudes were compared using an ANOVA that included the within-subjects factors of stimulus condition (CavHom vs. BW8) and hemisphere (left vs. right). The effect of stimulus condition was not significant, $F(1, 13) = 1.4, p = .26$, nor was the effect of hemisphere, $F(1, 13) = .0002, p = .99$, or the condition × hemisphere interaction, $F(1, 13) = 0.48, p = .50$.

Hypothetically, the colours in CavHom stimuli should make some FG interpretations more plausible than others (Goldreich and Peterson, 2012; Salvagio and Peterson, 2012), and therefore evoke less competition among alternative FG organizations than BW8 stimuli. Since convexity cues interact with context, increasing P(VEX = Figure) in BW8 compared to BW2 conditions, competition among alternative FG interpretations might be reduced for BW8 than BW2 stimuli. In other words, differences between CavHom and BW8 stimuli on the one hand, and BW8 and BW2 on the other, might both reflect reductions in the competition among alternative FG stimulus interpretations. To examine this hypothesis, we compared average differences in ERPs in the P200 time window (i.e., 176-224 ms) between these manipulations of stimulus colour (i.e., CavHom vs. BW8) and region number (i.e., BW8 vs. BW2) to test whether they have similar effects on neural activity. The P200 time window was selected because previous work in our lab had linked P200 amplitude with the CCE conditions (Lass et al., 2014). The results are depicted in Figure 4.6, which shows a large amplitude difference between P200 ERPs associated with BW8 vs. BW2 conditions, whereas amplitudes associated with CavHom and BW8 conditions are nearly identical. A 2 (colour vs. region number) × 2 (left vs. right hemisphere) within-subjects ANOVA revealed a significant effect of manipulation, $F(1, 13) = 6.7, p = .023$. The main effect of hemisphere was not significant, $F(1, 13) = 1.45, p = .25$, nor was the manipulation × hemisphere interaction, $F(1, 13) = 0.065, p = .8$. In order to decompose the effect of manipulation, separate ANOVAs testing the effects of each manipulation separately were conducted. These analyses indicated a significant CCE, $F(1, 13) = 8.0, p = .014$, but no significant CCompE was observed, $F(1, 13) = 0.0035, p = .95$.

With respect to the hypothesis that the region number manipulation has similar effects on processing as the VEX region colour manipulation, we also explored whether the BW8 ERP showed the delay compared to the CavHom ERP, as has been observed in the BW2 relative to the BW8 ERP from P100 to N150 (Lass et al., 2014). We found no evidence of the same delay for the CCompE. Examination of Figure 4.6 makes clear that the ERP associated with the CavHom condition was shifted relative to BW8 ERP in the opposite direction as the shift in BW8 ERP relative to BW2 ERPs, whereas the hypothesis predicts that the ERP associated with the BW8 condition to be delayed relative to CavHom. The difference between the CCE and CCompE on ERPs can also clearly be illustrated in Figure 4.7, which plots the difference waves representing the CCE and CCompE. The difference profiles corresponding to the two convexity effects

(CCE vs. CCompE) are vastly different, corresponding to the different effects of the two condition contrasts on amplitude and latency. The effect of the CCE on P200 amplitude is reflected in the high CCE (solid) trace peaking around 200 ms whereas the CCompE (dashed) trace shows no corresponding effect. The delayed P100-N150 in BW2 relative to BW8 is reflected in the wave pattern in the CCE trace that has a positive peak before 100 ms and negative trough before 150 ms; this pattern is not evident in the CCompE trace.

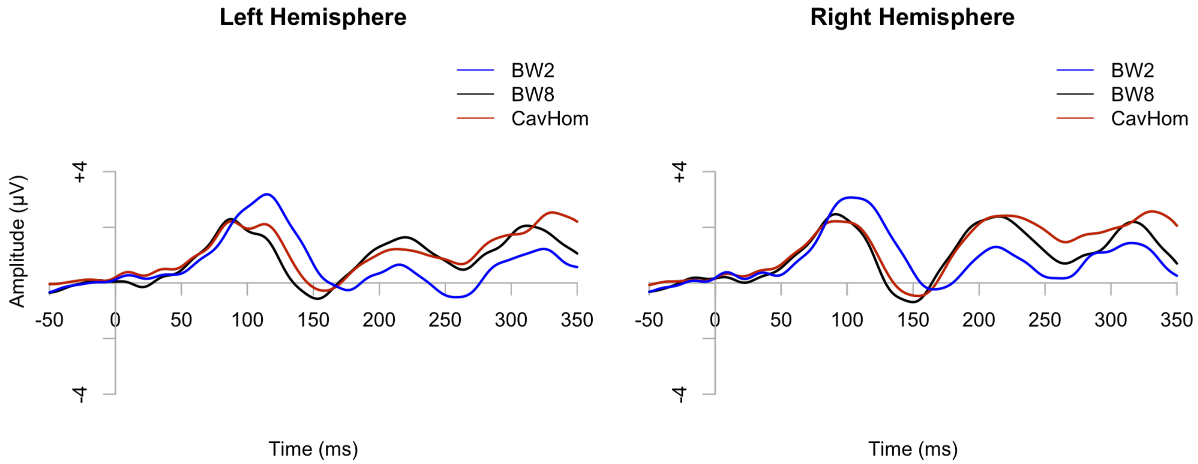

Figure 4.6: Event Related Potentials (ERPs) for Experiment 4.1. The average ERP across observers is plotted for each of the three experimental conditions for the left and right hemispheres in clusters of electrodes indicated as showing large differences between conditions in topographic plots (Figure 4.8).

EEG exploratory analyses

The analyses presented above found no evidence that the CCompE is similar to the early neural effect of competition observed by Trujillo et al. (2010) and Sanguinetti et al. (2015), and allowed us to reject the hypothesis that the effects are the same as those associated with the CCE observed by Lass et al. (2014). However, these findings do not rule out the possibility of these hypotheses being true for older observers, especially considering that the behavioural CCE and CCompE do vary by age group. However, before going on to test that directly in Experiment 4.2, we examined the data further to see if the CCompE was correlated with some other aspect of the ERP. This *post hoc* examination of the ERP in younger observers was used to produce hypotheses that

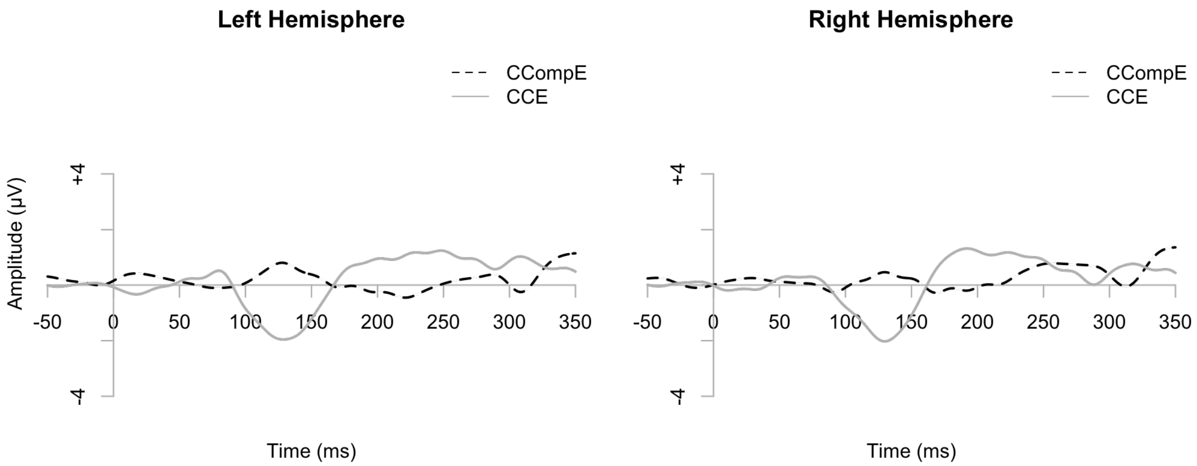

Figure 4.7: ERP difference waves representing CCompEs ($ERP_{CavHom} - ERP_{BW8}$) and CCEs ($ERP_{BW8} - ERP_{BW2}$) for younger in Experiment 4.1 observers for left (left panes) and right (right panes) hemisphere electrodes indicated as showing large effects in the topographic plots (Figure 4.8).

could be tested in a new sample of observers and compared across ages in the effort to understand the effects of aging to CCEs and CCompEs.

First, we created topographic plots of the scalp that mapped the CCompE at various time points corresponding to the major ERP peaks. For each observer, ERPs from each electrode were averaged across trials within each condition separately. Then a t-statistic was computed on mean amplitude difference between BW8 and CavHom conditions for each time window of interest. Specifically this procedure was applied to 20 ms time windows surrounding each of the following time-points post stimulus onset: 100, 150, 200, 250, 300, and 350 ms. Twenty millisecond time windows were used in order to increase power, account for variations in latency of ERP component across observers, and cancel out the random fluctuations that would increase noise of the measure.

The resulting topographic plots are shown in Figure 4.8. The topographic maps indicate a few things worthy of note. First, within the same electrode cluster we were looking at in Figure 4.6 at ≈ 100 ms post stimulus onset, there was a significant, spatially localized effect in the left hemisphere (indicated by the red dot in the figure), indicating higher mean amplitude in the CavHom relative to BW8 condition. In approximately the same location of the right hemisphere, a much weaker opposite effect is observed as indicated by the blue dots which represents lower mean amplitude in the CavHom relative to BW8 condition. These effects are captured in Figure 4.6, where the CavHom line is slightly delayed starting at 100 ms in the left hemisphere and where the BW8 line is slightly elevated just before 100 ms in the right hemisphere. The left hemisphere ERP difference is maintained until after N150, and is correspondingly visible as a red dot in the topographic plot at 150 ms, but the traces for the two conditions gradually align with each other leading to P200; correspondingly, the red dot does not appear in that location in the P200 topographic plot. Second, a difference can be seen in the right hemisphere at 250 ms and 300 ms post stimulus onset within a set of electrodes that encompasses and extends occipitally beyond the electrode cluster we examined in Figure 4.6. These differences are reflected in the ERP plot (Figure 4.6) for the right hemisphere at the N250 ERP, where the trough for the BW8 trace extends below the trough for the CavHom trace; since mean amplitude is higher in the CavHom condition, i.e., less extreme negative peak, the difference and t-value are positive. Third, the topographic plot shows widespread activation differences appearing at 350 ms post stimulus onset. The topographic map at 300 ms shows large positive difference in the left and the midline right electrode clusters corresponding to the higher amplitude for CavHom relative to BW8 that is observable in the left Figure 4.6, and there is also a great deal of opposite activation differences in the more temporal right electrodes. The later differences might reflect part of the response selection or related visuo-motor coordination, and actually overlaps in time with responses of some of the observers, and was not replicated in Experiment 4.2.

We next explored our data for possible brain-behaviour correlations. Does competition reflected behaviourally, i.e., CCompE$_{Beh}$, relate to competition reflected in the ERP signal, i.e., CCompE$_{ERP}$? This was tested using correlational analyses relating differences in activation between conditions to differences in behavioural performance across conditions, and was visualized by plotting the CCompE$_{ERP}$ for the various ERP components as a function of the CCompE$_{Beh}$ across individuals. No relationships were found, except for a moderate-strong correlation between CCompE$_{N250}$ and CCompE$_{Beh}$, $r(12) = -.58, p = .032$, which is illustrated in Figure 4.9. The scatter plot shows that the CCompE reflected at the neural level, which showed up as a significant difference at 250 ms in the right parietal-occipital region that can be seen in the topographic plot (Figure 4.8) and in the N250 component of the right ERP plot (Figure 4.6), was found to be negatively correlated with the behavioural difference in P(VEX = Figure) between CavHom and BW8 conditions. Specifically, individuals showing little difference behaviourally, i.e., a weak/near-zero CCompE$_{Beh}$, exhibited a high difference in activation across conditions, i.e., a high CCompE$_{N250}$, whereas those showing a strong behavioural

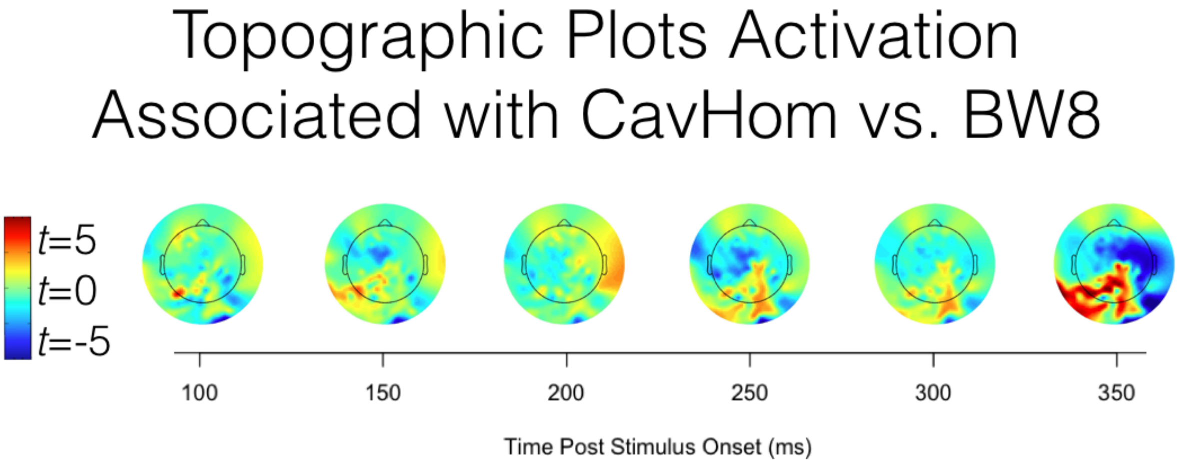

Figure 4.8: Topographic heat maps of the CCompE, indicated by t-values comparing activation associated with the lower competition CavHom condition and higher competition BW8 condition. For each topographic plot in the figure, mean amplitude was calculated for the time window ±10 ms around the time indicated and compared between conditions with a t-test at each electrode. Red values indicate higher amplitude in response to the CavHom condition and blue values indicate higher amplitude in the BW8 condition.

effect exhibited little difference in activation across competition conditions.

4.1.3 Discussion

The current findings replicated the behavioural CCE (Peterson and Salvagio, 2008). We also found a significant behavioural CCompE, which was not observed by Peterson and Salvagio (2008) but a trend in this direction was observed in our previous work (Lass et al., 2013, $p = .12$, two-tailed), where a within-subjects design similar to current experiment was used). The strong CCompE observed appears to be due to the relatively low P(VEX = Figure) in the BW8 condition, $M = .78$ observed here. Comparing distributions for BW8 and CavHom conditions in Figure 4.4, it seems as though there is a large negative skew in the BW8 distribution compared to the CavHom condition, but that the medians for the two are similar. Compare this observation to those for BW8 stimuli of $M = .89$ in Peterson and Salvagio (2008) and $M \approx .85$ across experiments in Lass et al. (2012, 2013), although some conditions low as $M = .8$, and compared to

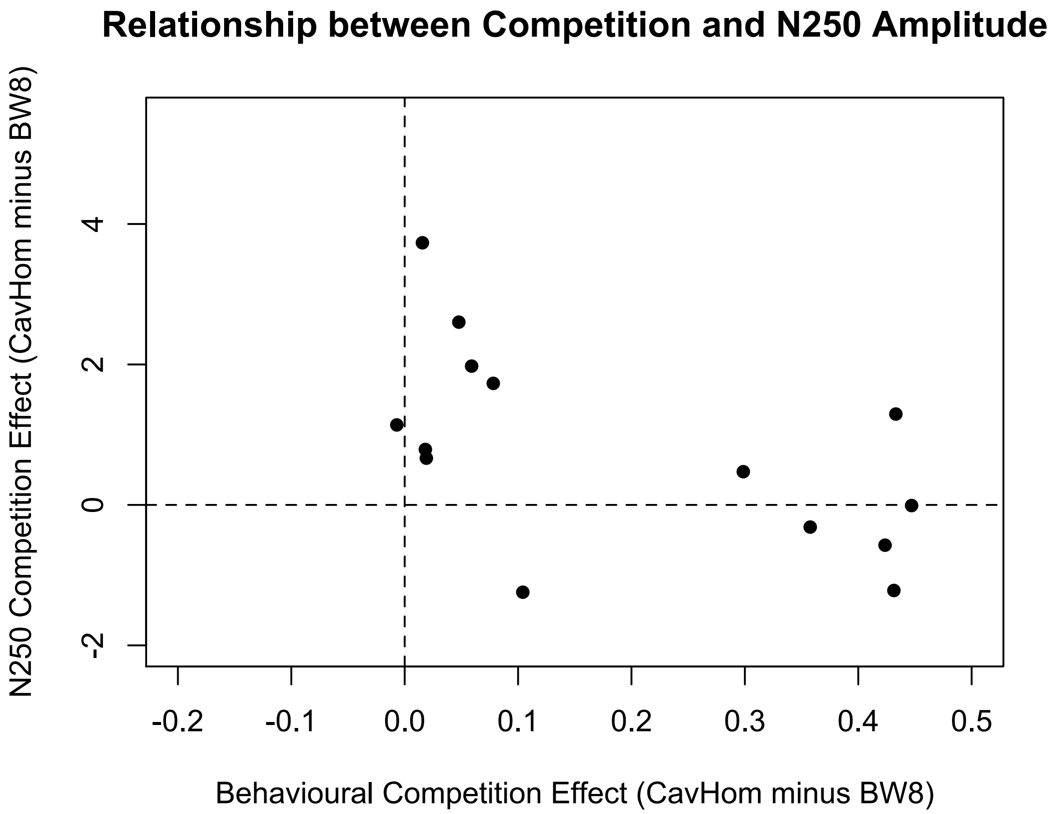

Figure 4.9: Scatter plot of individual CCompE$_{N250}$ as a function CCompE$_{Beh}$ scores: Individual's activation differences between CavHom and BW8 conditions are plotted as a function of differences in P(VEX = Figure) between the two conditions. A Pearson correlation indicated a significant relationship between behavioural and N250 amplitude, $r(12) = -.58, p = .032$: Individuals showing high activation differences between conditions around N250 showed low behavioural differences whereas those showing weak/no activation differences showed a strong behavioural CCompE. Because the N250 is a negative peak (see Figure 4.6), higher CCompE$_{N250}$ scores indicate larger troughs in response to BW8 stimuli compared to CavHom stimuli. Therefore, higher y-axis scores reflect a larger N250 for the higher competition BW8 condition compared lower competition CavHom.

$M_{Range} = .85 - .9$ in Lass et al. (2015). Additionally, the pattern of a positive CCompE is consistent with that predicted by the Bayesian model of performance on this task (Goldreich and Peterson, 2012). In any event, the significant CCompE observed here is useful in that it allowed us to use this wider variance in CCompE across observers, which would not have been observed were performance closer to ceiling in the BW8 condition as it tends to be in most samples, to compare behavioural to EEG responses at the individual level.

At the neural level, we found no evidence that the CCompE is similar to the effect of competition observed for inhibition of familiar shape representations observed by Trujillo et al. (2010) and Sanguinetti et al. (2015). We also found no evidence supporting the hypothesis that the CCompE has the same effects on the ERP as the CCE. In fact, the ERPs associated with processing of CavHom vs. BW8 stimuli were strikingly similar, and the highly localized early CCompE effect around 100 ms that can be seen in the topographic plot (red dot in left parietal occipital region in Figure 4.8) seems to be related to a slight delay in the CavHom-ERP that can be seen in the left hemisphere of Figure 4.6 beginning at 100 ms. This finding is counter to what would be predicted given the delay in P100 associated with BW2 relative to BW8 stimuli (Lass et al., 2014), and counter to what would be expected given the relatively faster processing of CavHom stimuli compared to BW8 stimuli (Salvagio and Peterson, 2012), which might predict an earlier P100 in the CavHom condition.

Exploratory analyses identified a temporal interval in which ERP amplitude was sensitive to the CCompE. In particular, the N250 peak was larger (i.e., the trough was lower) for higher competition BW8 stimuli compared to CavHom stimuli, which is consistent with the hypothesis that increased competition evoked different processing. Most interestingly, the difference in activation between low vs. high competition conditions – the CCompE$_{N250}$ – was correlated with the CCompE$_{Beh}$, indicating that individuals with strong behavioural differences exhibited weak activation differences at N250 and *vice versa*. These findings, illustrated in Figure 4.9, are consistent with the idea that the CCompE$_{N250}$ is high for those who can overcome the higher competition and resolve BW8 stimuli similarly to the way they can resolve lower competition CavHom stimuli. On the other hand, those who do not alter processing in response to the higher competition in the BW8 condition, and therefore exhibit a small CCompE$_{N250}$, are less able to resolve the stimuli in favour of the $\{\text{VEX} = \text{Figure}\}$ interpretation in the BW8 condition.

Overall, Experiment 4.1 found no evidence that the competition underlying the CCompE is similar to the early activation effects detected in suppression of familiar shape representations reported by Trujillo et al. (2010) and Sanguinetti et al. (2015). Although, we do know that behaviourally the CCompE is expressed when processing is disrupted through backwards masking within that 100 ms timeframe (Salvagio and Peterson, 2012), which suggests that something may be going on within that time period that can be disrupted (or that the backwards masking causes other interference effects that do not simply effect the processing as indexed through P100). The results presented do not support the hypothesis that the competition underlying the CCompE is similar to the effects underlying the CCE, as the effects on the ERPs differed. The data did, however, allow us to identify a component of the ERP that appears to be sensitive to the competition difference underlying the CCompE, and found evidence that the strength of this CCompE$_{N250}$ is associated with the CCompE$_{Beh}$.

4.2 Experiment 4.2

The purpose of current experiment was to replicate the effects found through exploratory analysis above in a new set of data, and to test the effects of age on all hypothesized competition-related effects. The results presented in Experiment 4.1 found no evidence of hypothesize competition effects in younger observers at 100 ms post stimulus onset; however, this does not mean that the hypothesized competition effect would not manifest in a group of older observers, who show a weaker CCE and stronger CCompE$_{Beh}$ (Lass et al., 2012, 2013). Similarly, while our results allowed us to reject the notion that reduced competition evoked by CavHom stimuli relative to BW8 stimuli might have the same effect as adding context to a BW2 stimulus to make a BW8 stimulus, this effect might manifest in older observers who show a stronger CCompE$_{Beh}$. Finally, while we were able to identify a CCompE$_{N250}$ that appears to be sensitive to the difference in competition across conditions, which was furthermore associate with CCompE$_{Beh}$, this was done in a *post hoc* manner. This observation would thus need to be replicated to constitute as valid evidence. Here we test this *post hoc* finding as an *a priori* hypothesis and specifically test whether this brain activation pattern, and the way it relates to behaviour, helps understand the effects of aging on performance in the figure assignment task.

4.2.1 Methods

The methods were identical to those in used Experiment 4.1, except that both older and younger observers were tested, and the data and analyses therefore incorporated the between groups factor of age. We retested all of the hypotheses tested in Experiment

4.1 to examine whether the different effects might depend on age group. We also tested the specific hypothesis generated from the data exploration conducted on data from Experiment 4.1.

Participants

Eighteen younger ($M = 19.4, sd = 2.6$) and 18 older ($M = 68.3, sd = 5.5$) observers participated in this experiment. Participants in each age group were assigned randomly to one of six groups with the constraint that there was equal n in each group. Presentation order of the various conditions was counterbalanced across groups. All older participants were compensated $10 per hour; several younger subjects also received $10 per hour and the rest received a course credit for participating. One older observer was replaced because she did not follow instructions for completing the task and also reported visual abnormalities that met exclusion criteria. Two younger participants were replaced because it was impossible to record an EEG signal.

4.2.2 Results

Three younger observers were excluded from EEG analysis because they met the exclusion criteria of showing no observable P100, and generally showed no signal. The final sample thus contained 15 younger and 18 older observers.

Behavioural results

The behavioural observations are depicted in Figure 4.10, which contains box plots for each condition by age group, and Figure 4.11, which shows distributions of CCEs and CCompEs for each age group. The left panel Figure 4.10 shows that a relatively weak CCE in the younger group, which can be seen clearly in the left panel of Figure 4.11, is driven by relatively high P(VEX = Figure) with BW2 stimuli (compare this to BW2 box plot in Figure 4.4, which shows BW2 data from Experiment 4.1). The left panel Figure 4.10 also shows that, in younger observers, P(VEX = Figure) is higher for CavHom than BW8 stimuli, corresponding to the strong CCompE, which can be seen as different than zero in the left panel of Figure 4.11. The right panel of Figure 4.10 shows that the older group performed near chance for both BW2 and BW8 conditions but show a very large increase in P(VEX = Figure) in the CavHom condition, relative to performance in the BW8 condition, which corresponds to the relatively low CCE and large CCompE in older observers (see right panel of Figure 4.11) compared to that shown by the younger group.

The variance of the CCE and CCompE scores differed significantly between groups (CCE: Bartlett's $K^2(1) = 11.7$, $p = .0006$; CCompE: Bartlett's $K^2(1) = 6.7$, $p = .001$), and therefore the means were compared using t-tests that assumed unequal variances in the two age groups. We found a marginally significant effect of age on CCE, $t(22.6) = 1.6$, $p = .06$ (one-tailed), indicating that the CCE was slightly larger in the younger group. The CCE in younger subjects was greater than zero, $t(17) = 1.8, p = .04$ (one-tailed), but the CCE in older subjects was not, $t(17) = 0.31, p = .37$ (one-tailed). Mean CCompEs differed significantly across age groups, $t(25.5) = -3.1$, $p = .002$ (one-tailed), indicating that the the CCompE was weaker in the younger group compared to the older group. The CCompE was significantly different than zero in both the younger, $t(17) = 3.0, p = .004$, and the older group, $t(17) = 5.1$, $p < .0001$. Additionally, P(VEX = Figure) in the BW2 condition was higher than chance in the younger group, $t(14) = 5.4, p < .0001$, and the older group, $t(17) = 1.8, p = .042$ (both one tailed).

EEG results

The initial stage of the EEG analysis involved creating topographic plots of activation differences between CavHom and BW8 conditions for younger and older observers. These were produced to examine the CCompE at all scalp locations, which was important in selecting appropriate electrodes for our analyses. These topographic maps, shown in Figure 4.12, were created for younger (top panel) and older (bottom panel) observers for time windows surrounding each major ERP peak within 350 ms post stimulus onset (including time points around 100, 150, 200, 250, 300, 350 ms). Each plot was created using the same methods as the topographic plots produced in Experiment 4.1. For each observer and electrode, ERP traces were averaged across trials within each condition, and mean amplitude of the ERP for the time window ±10 ms around the peak of interest was calculated. For each electrode, t-statistics were computed across observers at each time point of interested and plotted as heat map values across scalp locations.

Various patterns can be seen in the topographic plots of Figure 4.12, and by comparing the plots within the figure to those from Experiment 4.1 shown in Figure 4.8. One important property to note is the large CCompE observable in the right occipital-parietal

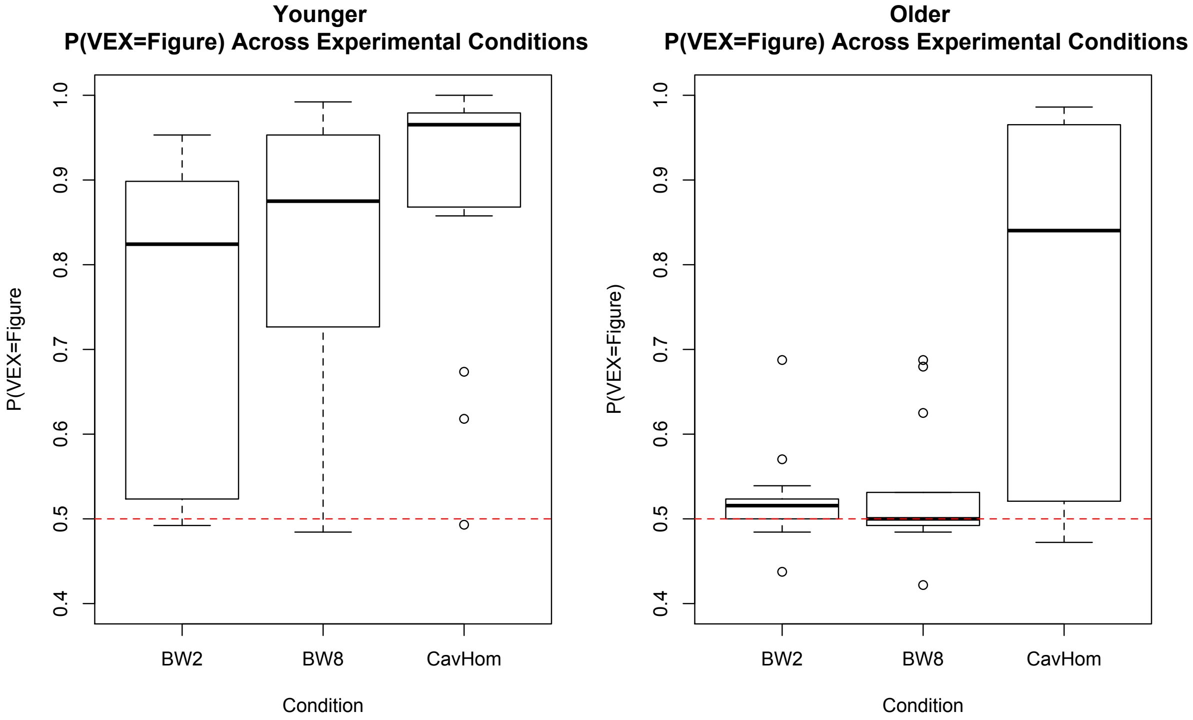

Figure 4.10: Behavioural performance in the three conditions of this experiment for the younger (left panel) and older (right panel) groups. Each box depicts the distribution of scores within a condition. The red dotted line depicts chance performance, i.e., no behavioural bias in that condition.

hemisphere at 250 ms post stimulus onset in younger observers that was observed in both experiments. This result, along with other key findings that can be observed in this figure, will be analyzed and discussed in the context of the hypotheses they relate to below. It is also important to note that the electrodes chosen for analyses of CCompE effects was based on the activation patterns seen in the topographic maps. For the analyses conducted on CCompEs, and to produce figures plotting ERP traces (Figures 4.13 and 4.14), bilateral clusters of occipital-parietal electrodes corresponding to the area where strong CCompEs were detected at N250. These were the electrodes in the parietal-occipital region of the head where a red patch corresponding to strong CCompE can be observed at N250 in the right hemisphere in Figure 4.12 (as well as the highly similar pattern that was observed in Figure 4.8 in that location and time window).

Effects of competition at P100

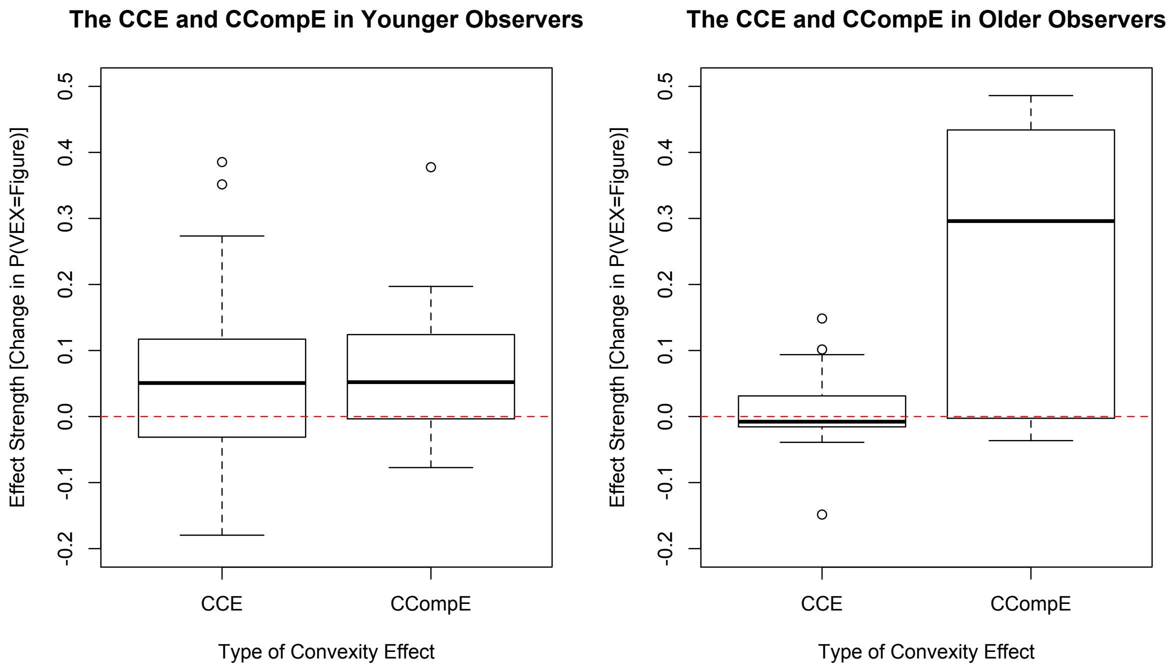

Figure 4.11: Distributions of the CCE and CCompE for Experiment 4.2. The CCE is the difference in P(VEX = Figure) between BW8 and BW2 conditions (see Equation 4.1), and the CCompE is the difference in P(VEX = Figure) between CavHom and BW8 conditions (see Equation 4.2). Each box depicts the distribution of difference scores between conditions, indicating the median (solid line), interquartile range (box), and 1.5 x interquartile range, i.e., tails of distribution (whiskers). The red dotted line depicts an effect of zero, i.e., no difference between performance on conditions contrasted in the CCE or CCompE.

P100 amplitude was analyzed with a 2 (age group) × 2 (hemisphere) × 2 (condition: CavHom vs. BW8) split-plot ANOVA, which found marginally significant main effects of age group, $F(1, 31) = 4.0$, $p = .056$: The younger group had a higher mean amplitude around P100 in both conditions. A marginal effect of condition was also detected, $F(31) = 4.1, p = .050$: the P100 mean amplitude was higher for CavHom compared to BW8 in both groups and hemispheres. No other effects or interactions were significant, all Fs < 1 (except for hemisphere × condition, $F(1, 31) = 1.71, p = .2$). These results suggest that, counter to the prediction, the CCompE did not vary by age group around the P100 for either hemisphere. Additionally, the marginally significant main effect of competition condition was in the opposite direction as was predicted, i.e., amplitude was

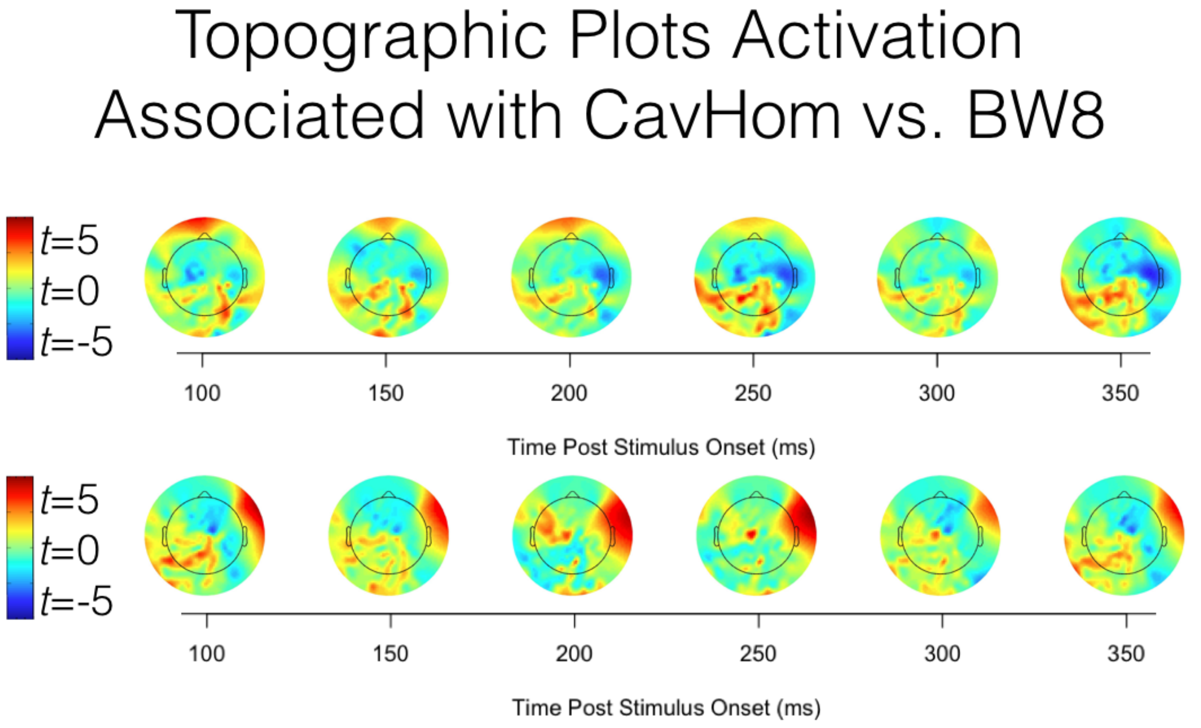

Figure 4.12: Topographic plots of the CCompE for younger (top pane) and older (bottom pane) observers. The heat maps show the t-values comparing the CCompE at each electrode to zero. For each topographic plot in the figure, mean amplitude was calculated for the time window ±10 ms around the time indicated and compared between conditions with a t-test at each electrode. Red values indicate higher amplitude in response to the CavHom condition and blue values indicate higher amplitude in the BW8 condition.

higher in the lower competition CavHom condition, which did not support the hypothesis.

Comparison of CCE & CCompE at P200

We used the amplitudes of the P200 in various conditions to compute CCE and CCompE for each subject. These measures were then analyzed with a 2 (age group) × 2 (hemisphere) × 2 (contrast: CCompE vs. CCE) split-plot ANOVA, which revealed a significant three-way interaction between age group, hemisphere, and contrast, $F(1, 31) = 4.3$, $p = .046$. The interaction was decomposed by conducting separate 2 (age) × 2 (contrast) ANOVAs for each hemisphere. In the right hemisphere, a significant effect of contrast was observed, $F(1, 31) = 6.7, p = .014$, as was a marginally significant effect of age, $F(1, 31) = 4.0, p = .054$. These results, which can be seen by

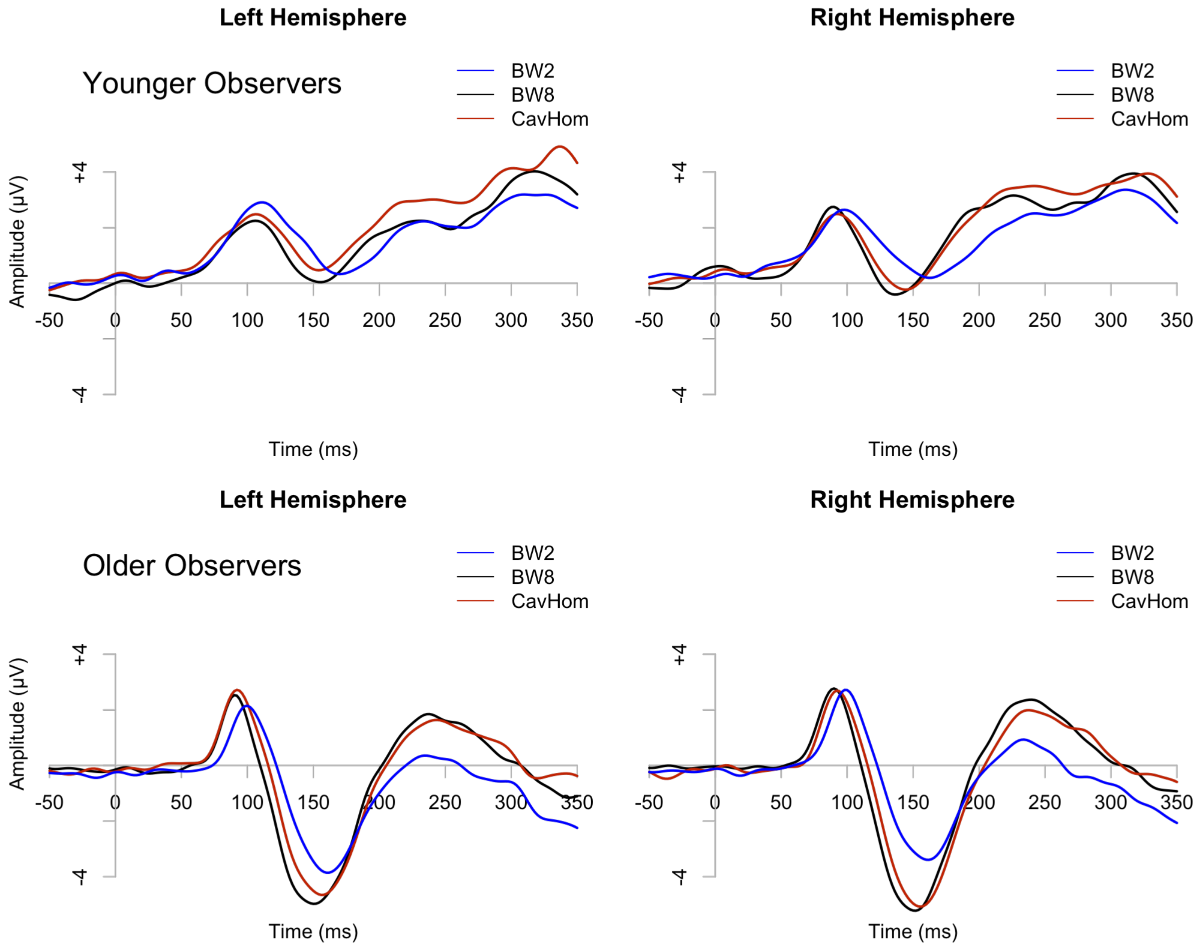

Figure 4.13: ERP plots for younger (top panes) and older (bottom panes) observers for left (left panes) and right (right panes) hemisphere occipital/parietal electrodes indicated as showing large effects in the topographic plots of the younger observers of the current experiment (Figure 4.12, top panel), which was a similar cluster observed to show large effects in Experiment 4.1 (see Figure 4.8) .

comparing the various traces in the right panels of Figure 4.14, indicate that in both age groups, the right hemisphere CCE was significantly greater than the CCompE at 200 ms after stimulus onset. In the left hemisphere, there was a significant age × contrast interaction, $F(1, 31) = 4.3, p = .04$, which reflects the difference between the CCE and CCompE at P200 being greater in the older group compared to the younger group. The difference between the CCE and CCompE was not significant in the younger group, $F(1, 14) = 0.11, p = .74$, but was significant in the older group, $F(1, 17) = 6.8, p = .019$. The left hemisphere results can be seen in the left panel of Figure 4.13, which shows

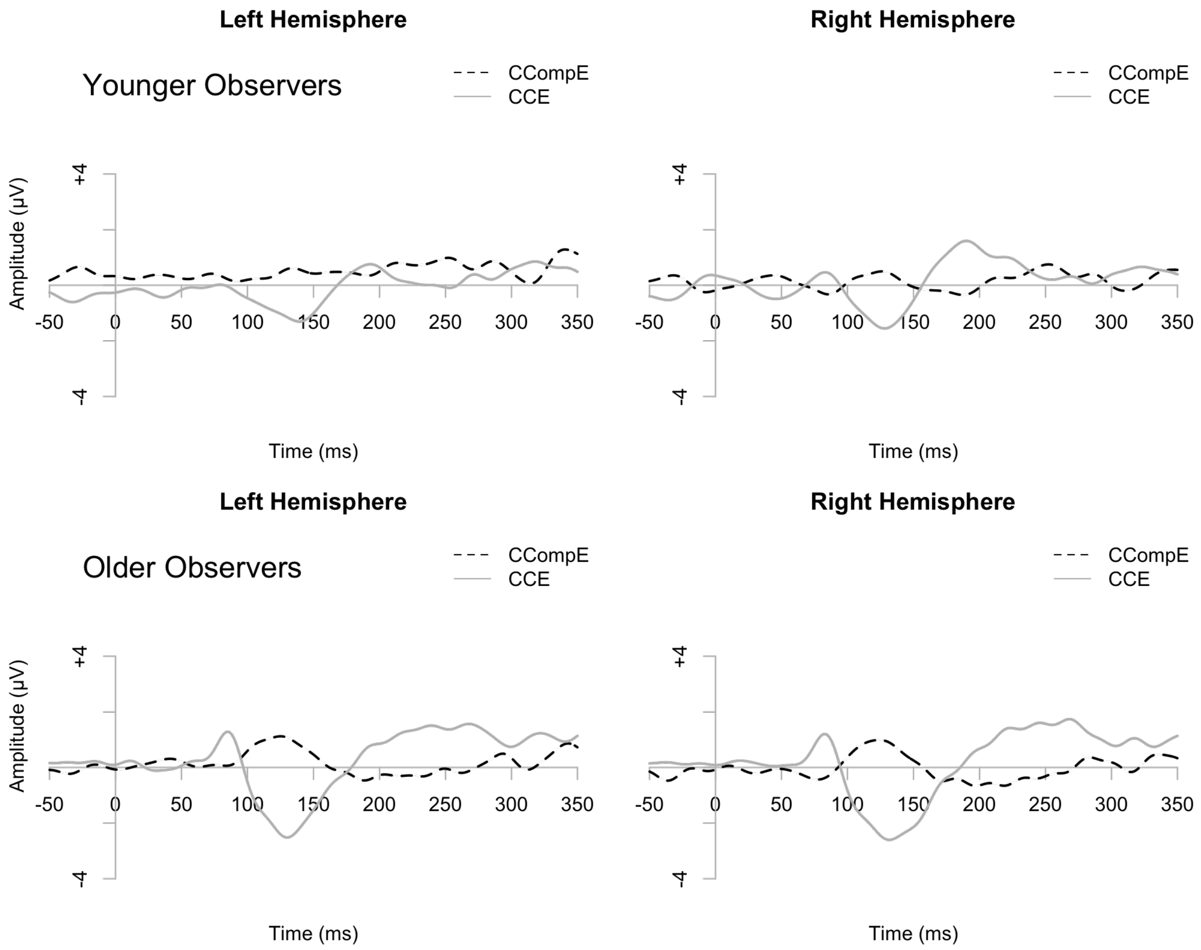

Figure 4.14: ERP difference waves representing CCompEs ($ERP_{CavHom} - ERP_{BW8}$) and CCEs ($ERP_{BW8} - ERP_{BW2}$) for younger (top panes) and older (bottom panes) observers for left (left panes) and right (right panes) hemisphere electrodes indicated as showing large effects in the topographic plots of Experiment 4.1 (Figure 4.8) and the younger observers of the current experiment (Figure 4.12 top panel).

that, around the P200, the difference in ERP traces for BW2 compared to BW8 are much smaller than they are in every other plot presented here and in Lass et al. (2014); similarly, it can be seen in the upper left panel of Figure 4.13 that the CCE and CCompE do not differ at P200 as they do in every other plot of ERP difference waves. Put more simply, the complex three-way interaction is driven by the unusually small, nonsignificant, CCE effect at P200 for younger observers in the left hemisphere. This anomaly causes the contrast of CCE to CCompE amplitude around P200 in that group and hemisphere to be smaller that it is in any other condition, which in turn causes a contrast

× hemisphere interaction in younger observers that is not significant in older observers, which in turn causes the age × contrast ×hemisphere interaction.

Overall, besides the anomalous lack of CCE reflected in the ERP in the left hemisphere of the younger observers at the P200, the results here indicate that, based on previously reported CCE effects on the ERP (Lass et al., 2014), the CCE and CCompE differently effect the ERP. This can be clearly seen by comparing ERP traces for each of the conditions (Figure 4.13) or ERP difference traces corresponding to the CCE and CCompE (Figure 4.14).

Relation between Behavioural CCompE and the CCompE-N250 Effect

A CCompE on the N250 was identified in the data exploration of Experiment 4.1 and associated with behavioural performance. In Experiment 4.2, we explored the relation between this CCompE_{N250} and CCompE_{Beh} to in attempt to replicate the effect *a priori* and explore what it might tell us about FG organization differences across age groups. The data are plotted in Figures 4.12 & 4.13, which show the topographic plots by age groups and average ERP traces for each age group and hemisphere, respectively. Figure 4.13 illustrates that the difference in N250 traces between CavHom and BW8 conditions, representing the CCompE, is present in younger observers but not in older observers. The significance of the CCompE_{N250} was tested here using a 2 (age group) × 2 (hemisphere) × 2 (condition: CavHom vs. BW8) split-plot ANOVA. This analysis found a significant age × condition interaction, $F(1,31) = 5.3$, $p = .028$; no other main effects or interactions were significant ($F \leq 2.0$, $p \geq .16$ in all cases). The age × condition interaction was decomposed with separate 2 (hemisphere) × 2 (condition) ANOVAs for each age group which found that the difference between CavHom and BW8 conditions was significant in the younger group, $F(1,14) = 4.6$, $p = .025$, but not the older group, $F(1,17) = 1.0$, $p = .17$. Contrary to the finding that the CCompE_{N250} was only significant in the right hemisphere in Experiment 4.1, here, no interaction between condition and hemisphere was found, $F(1,14) = 1.1$, $p = .31$, indicating that competition affected the N250 in younger observers similarly in both hemispheres (see Figures 4.12 & 4.13).

In relating brain activity to behavioural performance, we plotted the CCompE_{N250} as a function of CCompE_{Beh} across observers in both age groups (Figure 4.15). The figure suggests that the association between the CCompE_{N250} and CCompE_{Beh} was similar to the effect seen in the exploratory analysis in Experiment 4.2 (compare these results to Figure 4.9). The correlation was negative although not significant in the younger group, $r(13) = -.24$, $p = .38$, and negative and marginally significant in the older group, $r(16) = -.43$, $p = .076$. Across all observers of the two groups combined, the correlation between CCompE$_{N250}$ and CCompE$_{Beh}$ was significant, $r(31) = -.46$, $p = .0078$.

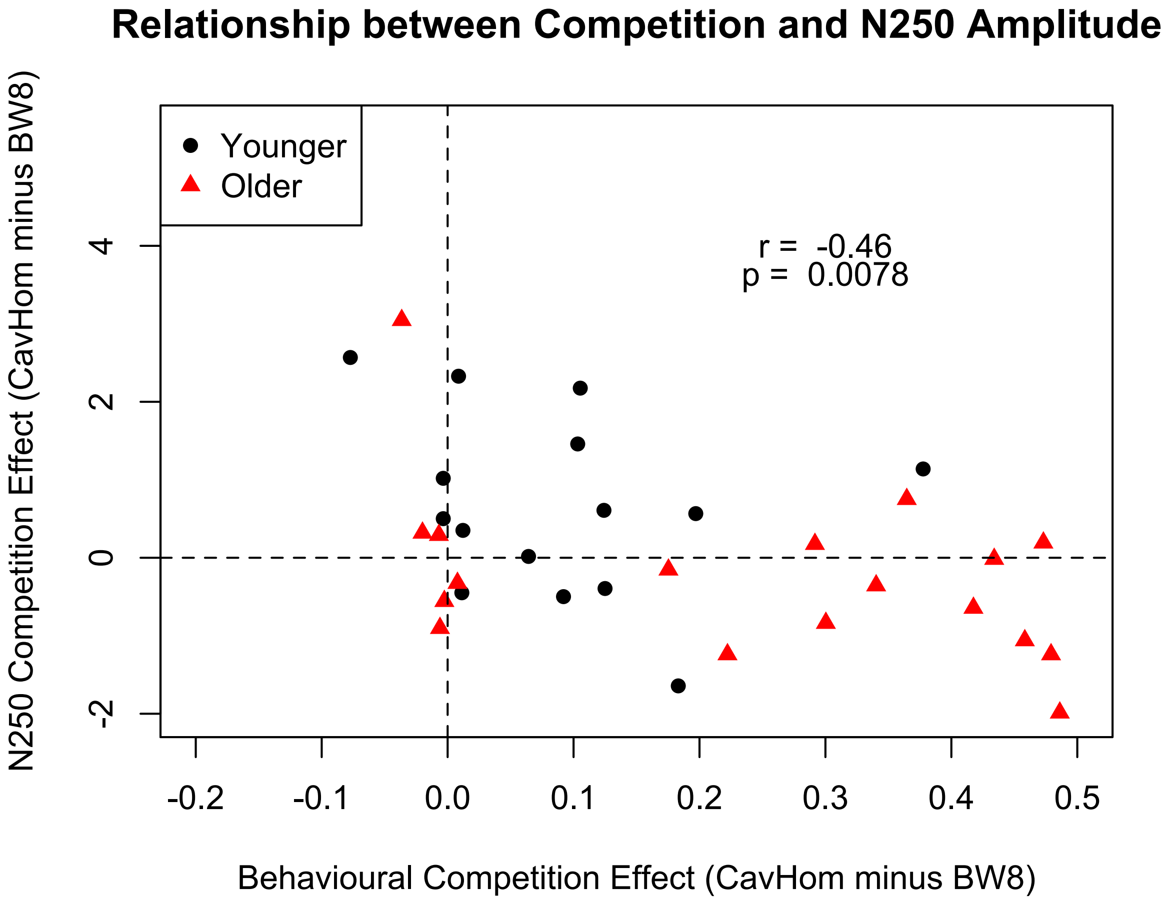

Figure 4.15: Scatter plot of younger (black circles) and older (red squares) CCompE$_{N250}$ scores as a function CCompE$_{Beh}$ scores. A Pearson correlation indicated a significant relationship between behavioural and N250 amplitude across all observers, $r(31) = -.46$, $p = .0078$: individuals showing high activation differences between conditions around N250 showed low behavioural differences whereas those showing weak/no activation differences showed a strong behavioural CCompE. However, whereas the correlation was present within the older group, $r(16) = -.43$, $p = .076$, it was not detected within the younger group, $r(13) = -.24$, $p = .38$.

4.2.3 Discussion

The findings of Experiment 4.2 replicated the findings of Experiment 4.1 and extended them to test the effects of aging on competition resolution underlying CCEs and CCompEs. Our results allow us to reject the hypothesis that the difference in competition between CavHom vs. BW8 conditions is similar to the difference in competition across region number conditions in either age group. We were also unable to find any evidence that the neural CCompE measured here, i.e., difference in ERP between CavHom and BW8 conditions, was similar to the effects of competition on the P100 reported by Trujillo et al. (2010), which have been argued to capture cross-border competition-mediated suppression (Cacciamani et al., 2015).

However, we did replicate the finding that the ERP around 250 ms post stimulus onset is sensitive to the CCompE in younger observers, but we found no evidence of the same effect in the older group. We also replicated the association between CCompE$_{Beh}$ and CCompE$_{N250}$ (Figure 4.15), which indicate that brain response across individuals is related to the effect of competition at the behavioural level: observers who show a higher CCompE$_{N250}$ show lower CCompE$_{Beh}$ and those showing lower CCompE$_{N250}$ show a larger CCompE$_{Beh}$. This finding is consistent with the hypothesis that individuals who can mediate processing mechanisms in response to the relatively higher competition in BW8 compared to CavHom conditions are able to resolve the stimulus equally well across competition conditions. On the other hand, those who do not alter processing in response to the differential competition are less able to resolve the higher competition BW8 stimuli compared to the lower competition CavHom stimuli.

This pattern of results suggests that the ability of the younger group to resolve the high competition in BW8 stimuli might be explained by the ability to appropriately mediate inhibitory competition processing mechanisms to resolve the higher competition. On the other hand, the older groups here and in Lass et al. (2012, 2013, 2014, 2015) show a stronger CCompE$_{Beh}$, driven by relatively low P(VEX = Figure) in BW8 conditions, compared to younger observers. The lack of CCompE$_{N250}$ in the older group suggests that the relatively reduced ability of older observers to resolve the higher competition BW8 stimuli might stem from impairment to the competition resolution processing mechanisms underlying FG organization. Thus, these results suggest that the age-related reduction to the CCE is related to group differences in ability to effectively mediate processes underlying FG competition resolution. Older observers are particularly impaired in high competition conditions with ambiguous stimuli.

4.3 General discussion

4.3.1 Main findings

The current experiments explored the effects of aging and competition on FG processing at behavioural and neural levels. Our results indicated that the effects of competition due to homogeneity of VEX regions are different from the effects due to region number, which may also entail competition, with respect to how they are reflected in the ERP. We also failed to find evidence that the competition involved in our figure assignment task is similar to other reports of local competition-mediated ground suppression in a task where performance required suppression of high vs. low competition grounds (Peterson and Skow, 2008; Trujillo et al., 2010; Sanguinetti et al., 2015; Cacciamani et al., 2015). This suggests that the effects of manipulations to the convexity stimuli on FG competition resolution processing is of different nature than the processing underlying suppression of familiar configurations. CCompEs thus appear to have different effects than the local competition-mediated suppression of local ground side figures, which are detected surprisingly early in the evolution of the neural response.

Instead, Experiment 4.1 found evidence that a later neural component, specifically the N250, is sensitive to the competition for figural status across CaVHom and BW8 conditions. This is consistent with the notion that the CCompE reflects *global FG segmentation* that affects this later portion of the ERP (Caputo and Casco, 1999), and consistent with the interpretation of CCEs a resulting from spreading of inhibitory suppression across spatially separated background segments (Peterson and Salvagio, 2008). The CCompE$_{N250}$ was also inversely related to the behavioural effect of competition across individuals. This suggests that adjusted processing, reflected in the CCompE$_{N250}$, is required to resolve the higher competition stimuli to the same degree as the lower competition stimuli, as indexed by behavioural performance differences across conditions. The overall CCompE$_{N250}$ effect was replicated in a second sample of younger observers but was not observed in a sample of older observers. The correlation between neural and behavioural responses was not replicated in the younger group of Experiment 4.2, possibly due to the relatively higher proportion of individuals who showed high P(VEX = Figure) in the BW8 condition and the correspondingly reduced CCompE$_{Beh}$ compared to the sample in Experiment 4.2. However, the brain-behaviour relationship did hold across the combined sample of older and younger observers (see Figure 4.15).

Overall, these results indicate that the difference in neural responses across age groups is associated with the differential behavioural effects of competition. The findings suggest that older adults are impaired in their ability to invoke the altered processing required to resolve the higher competition stimuli.

4.3.2 Alternative explanations

We propose that the differential mean amplitude at N250 across competition conditions reflects altered – possibly increased – neural response invoked to resolve increased competition between perceptual interpretations. However, an examination of other interpretations might be informative.

Is it possible that the N250 amplitude simply reflects the degree of competition as opposed to the response of processing mechanisms required to resolve the the competition? Given that the negative amplitude trough is larger in the higher competition condition, results of the younger group are consistent with this possibility. However, the differences across age groups and the correlation between behaviour and brain activity, seem to be at odds with this alternative. The notion that CCompE$_{N250}$ reflects competition encountered is inconsistent with the observation that the ERP effects was observed only in those individuals who were able to resolve stimuli equally well, i.e., low CCompE$_{Bhv}$/high CCompE$_{N250}$ younger observers. This account would seeming predict that those who are unable to resolve the higher competition stimulus, i.e., high CCompE$_{Bhv}$/low CCompE$_{N250}$ younger observers and older observers, should also show strong sensitivity of the ERP to the stimulus competition. Our data thus fit better with the notion that the CCompE$_{N250}$ reflects some sort of response to the competition. This does not completely rule out the possibility that the N250 may reflect the competition propagating through the system, but such explanations seem less parsimonious than the interpretation presented above.

Could the ERP difference associated with processing of CavHom vs. BW8 stimuli, i.e., the CCompE$_{N250}$, be the result of *repetition suppression* (e.g., Desimone, 1996)? Our results are inconsistent with that possibility, because individuals showing strong ERP effects showed weak, if any, behavioural difference across conditions (see Figures 4.9 and 4.15). Those who did show a strong behavioural effect tended to show no ERP effect, which is where the repetition suppression would be expected considering it is those observers who would have a different P(VEX = Figure) response rate with CavHom compared to BW8 stimuli. Thus, if repetition suppression caused an ERP difference at N250, we would expect the amplitude difference to be strongest in observers who had largest behavioural effects, specifically in this case the people showing a high CCompE_{Beh}. Our data are also inconsistent with the possibility that the CCE_{P200} might be explained by repetition suppression. Since observers had higher P(VEX = Figure) in BW8 condition compared to BW2 condition, a repetition suppression account would predict reduced amplitude for the BW8 condition, which has higher proportion of {VEX = Figure} trials, compared to the BW2 condition. However, the ERP data show the opposite pattern: the P200 amplitude is higher for the BW8 condition.

4.3.3 Questions and future directions

Given our findings of effects of aging on FG perception at behavioural and neural levels, one important extension would involve linking our findings to the observation of Trujillo et al. (2010) that found a similar effect of competition in younger observers but at a different temporal trajectory. The competition-mediated suppression of familiar shaped grounds involves suppression of a local region adjacent to the contour of interest, whereas the CCompE is reflected later, in time windows linked to global FG segmentation (Caputo and Casco, 1999). This makes sense given that the CCE is mediated by spreading of inhibitory suppression across grouped CAV regions (Peterson and Salvagio, 2008), which takes time (Salvagio and Peterson, 2010, 2012), as does integration across the global scenes (Han et al., 1999a,b). Our results raise the question of what the ERPs of older observers would look like in the silhouette classification task. Similarly, how would *competition-mediated suppression* in older observers compare to that seen in younger observers in processing networks resolving FG through hierarchical feedback loops (Likova and Tyler, 2008), and with suppression of ground-responsive fMRI voxels, measured using the categorization task and high vs. low competition silhouette stimuli (Cacciamani et al., 2015)?

Interestingly, a very recent study explored the effects of aging on FG perception using the silhouette stimuli and task. Anderson et al. (2016) observed that younger observers had quicker RTs for high competition compared to low competition stimuli. This is consistent with the idea that increased processing was invoked in response to the increased competition between interpretations of the stimulus, which caused an increase in overall speed. However, older observers exhibited the opposite pattern: responses were slower when categorizing the higher competition compared to lower competition silhouettes. This finding is consistent with the idea that the inability of older observers to recruit additional inhibitory processing resources poses a challenge when faced with higher competition between perceptual interpretations that slows responses. Given that younger observes have elevated P100 amplitude associated with the high relative to low competition stimuli (Trujillo et al., 2010), our current results suggest that older observers might exhibit a reduced effect of competition on amplitude of P100 compared to younger observers. We would predict that the weak, or lack of, P100 difference between high and low competition silhouettes in older observers would correspond to their reduced ability to resolve the relatively high competition silhouettes. This result would be analogous to the lack of CCompE$_{N250}$ seen in the older group in Experiment 4.2 here that corresponded to their reduced ability to resolve relatively higher high competition BW8 stimuli. Given our current results, we might also expect the effects of familiar ground competition reflected neurally (indexed by P100 amplitude) to relate to the effects of competition reflected behaviourally (indexed by RT).

It would also be interesting to compare both neural and behavioural performance between the figure assignment task used here vs. the silhouette classification task used by Trujillo et al. within the same younger and older observers. Performance on the two FG competition tasks should be correlated if they measure the same impacts of inhibition but different if they measure two isolated mechanisms that function, and perhaps are affected by aging, independently of each other. One important control in comparing the performance across these indices of FG competition would be to make the tasks more comparable to each other in order to remove the effects of task, which could theoretically affect the way the information is processed at stages reflected in our ERP results.

4.3.4 Conclusion

This paper explored the effects of aging on the processing underlying FG organization. This was done by manipulating context and competition properties of the stimuli to examine the effects on perceptual processing at behavioural and neural levels. We identified a relatively late visual ERP, the occipital-parietal N250, that is sensitive to the degree of competition between convexity stimuli and perhaps reflective of additional competition-mediated processing required to resolve such stimuli. We presented evidence that this neural response varies with individual behavioural responses to differing degrees of FG competition, and showed that this response is not present in older observers, who have impaired FG perception particularly in the high competition conditions. Taken together, the results presented here provide strong evidence consistent with the theory that the inhibitory processing mechanisms underlying resolution of FG competition are impaired in healthy aging.

4.4 References

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Chapter 5

General Discussion

This thesis explored the effects of aging on perceptual organization with specific focus on Figure-Ground (FG) perception. This chapter reviews the results across the other chapters, integrates the findings, discusses implications and questions left open at this juncture, and outlines some future directions that would further this program and related research efforts.

5.1 Summary of findings

The work composing this dissertation examined age differences in performance in a FG assignment task. We used convexity stimuli to test the impacts of aging on convexity and context effects, i.e., convexity context effects (CCEs), in order to investigate competition resolution processing underlying FG organization. This involved examining figure assignment performance in younger and older observers using 2-region stimuli where a single border separated one convex (VEX) from one concave (CAV) region, and a variety of contextual manipulations including the addition of surrounding CAV/VEX regions that were homogeneously or heterogeneously filled, and addition of motion to VEX and/or CAV regions that produced texture accretion-deletion and region edges. The effects of context and competition were explored at both behavioural and cortical levels to assess the processing underlying CCEs and the influences of aging on that processing.

5.1.1 Convexity context effects in older observers

The experiments in Chapter 2 demonstrated that aging does indeed affect FG perception. Specifically, we found a reduced CCE in older observers relative to younger observers. Younger observes replicated the CCEs observed by Peterson and Salvagio (2008), i.e., that the probability of perceiving VEX regions as figures increases with alternating VEX and homogeneously filled CAV regions surrounding the border of interest. However, older observers showed reduced reliance on convexity and reduced influence of context on the convexity effect (Experiment 2.1). This age effect could not be accounted for by low-level visual factors of reduced spatial integration or slowed processing time in the older group (Experiments 2.2 and 2.3). However, our observation of strong increase in the {VEX = Figure} interpretation was observed when competition between perceptual interpretations of the display was reduced using stimuli with heterogeneous VEX and homogeneous CAV regions (Experiment 2.4). These *CavHom* stimuli have properties consistent with the {VEX = Figure} and {CAV = Background} stimulus interpretation, and therefore reduce conflict between FG interpretations of the display compared to multi-region black and white (BW8) stimuli (Salvagio and Peterson, 2010, 2012; Goldreich and Peterson, 2012). The strong convexity effect emerging in older observers under reduced competition is consistent with the idea that perceptual processing deficits impair FG resolution in older observers, particularly in high competition.

5.1.2 Convexity context effects and motion

A further exploration of the reduced CCE in aging used motion in the same stimulus set (Chapter 3). The results ruled out the possibility that CCEs are partially due to reduced presumption of depth in the older observers and supported the conclusions of our prior work. These experiments added horizontal motion to texture filling CAV and/or VEX regions that accreted/deleted at leading/lagging region edges. Unbiased motion added to both region types simultaneously but in opposite directions, which presumably increased evidence of depth (Froyen et al., 2013), did not increase CCEs in younger or older observers (Experiments 3.1, 3.2, and 3.3), which was hypothesized given a Bayesian model replicating convexity context and competition effects (Goldreich and Peterson, 2012). However, in Experiment 3.4, a biased CAV-motion stimulus set was used in which only CAV regions were moving and accreting/deleting at region boundaries, which is consistent with a moving CAV ground occluded by stationary VEX regions. With

CAV-motion, convexity and motion cues were both consistent with the $\{VEX = Figure\}$ interpretation, which should reduce competition relative to a static or unbiased motion condition. In the CAV-motion condition, the older observers who could detect the motion showed a strong increase in $P(VEX = Figure)$, consistent with the idea that the reduced CCE in aging results from reduced ability to resolve high competition for figural status. The combined findings of a null effect of unbiased motion across observers, which increases evidence of depth but adds no information about depth order, and a strong effect of biased CAV motion in the older group, supports the hypothesis that age × CCE interaction stems from perceptual processing deficit to the system that resolves conflict between stimulus interpretations. Considering results from across the thesis, conditions in which age effects were observed, and the pattern of differences in performance across conditions, suggest that older observers are particularly impaired in high competition contexts with ambiguous stimuli.

5.1.3 Neural processing associated with figure-ground competition in aging

We used electroencephalography (EEG) to explore the temporal dynamics of processing mechanisms underlying the context and competition effects (Chapter 4). Exploratory analyses suggested that younger observers, who were able to resolve both high and low competition stimuli (BW8 and CavHom, respectively), exhibit a change in N250 amplitude between those conditions (Experiment 4.1). Specifically, the stimuli in the high competition BW8 condition evoked a larger N250 than stimuli in the low competition CavHom condition, consistent with the idea that adjusted processing is required to resolve higher FG competition. Interestingly, this N250 effect was correlated with the behavioural difference in performance across conditions: those who showed a large decrease in $P(VEX = Figure)$ in the BW8 relative to the CavHom condition showed no ERP difference; those showing a small behavioural differences across conditions (i.e., no difference in $P(VEX = Figure)$, indicating the ability to resolve high and low competition equally well, showed a strong N250 amplitude effect. This *post hoc* finding was tested *a priori* in a sample of older and younger participants and we observed the same N250 effect for younger observers but not for older observers (Experiment 4.2). At the level of individual differences, the correlation between behavioural and N250 ERP amplitude was replicated across all observers, but the correlation was not observed in the younger group alone. This may be because the second sample of younger observers tended to show weaker behavioural and strong N250 effects of competition condition compared to the sample in the previous experiment (i.e., without much variance on performance measures within the younger group, the correlation could not be detected). In this second experiment, the younger group replicated the tendency to show strong ERP/weak behavioural effects of competition, while older observers tended to fall in the weak ERP/strong behavioural effect region of the N250 vs. behavioural competition scatterplot. Overall, the EEG results are consistent with the idea that younger adults resolve high FG competition through adjusting perceptual processing mechanisms, which is reflected at the cortical level in the N250. The results are also consistent with the hypothesis that older observers' inability to resolve the high conflict may be due to inability to invoke, or alter, the processing mechanisms used by younger observers to resolve high FG competition.

5.2 Implications & future directions

The research presented here, and our interpretation of the findings, have a variety of implications and lead to even more questions. The goal of the section below is to set out various implications and, for each implication, discuss a number of the questions and research directions it opens up.

5.2.1 General implications

Taken together, the results presented in this dissertation tell a clear story that is relevant to our understanding of vision and aging. This work identified an impairment to FG organization in healthy aging, measured as a reduced CCE in aging that cannot be accounted for by low-level visual factors. Rather, the current results support the hypothesis that perceptual organization processes underlying FG perception are impaired in older adulthood. Specifically, older observers exhibit difficulty resolving high competition between FG interpretations of a stimulus, which occurs under conditions of ambiguity. Investigation of the neural activity associated with the FG processing is consistent with the idea that younger adults are, on average, significantly altering visual processing mechanisms under high competition conditions, which allows them to resolve the stimulus. However, older adults, who are not able to resolve the high competition, apparently do not invoke the different processing that was observed in the younger group. Taken together, these observations support the notion that FG processing is changed in the senescent visual system, perhaps due to a reduction in the efficacy of inhibitory mechanisms, or a change in the inhibitory/excitatory balance, that occurs with aging (Leventhal et al., 2003; Schmolesky et al., 2000; Pinto et al., 2010).

Our findings are consistent with notion that decreased cortical inhibition in aging might cause deficits to FG organization, as has been hypothesized for visual abilities involving inhibitory processing. From the perceptual organization perspective, this evidence adds to the story of competition-mediated suppression as underlying FG resolution by demonstrating what happens when a visual system that is speculated to have reduced cortical inhibitory control (e.g., Pinto et al., 2010) engages in a FG task that entails inhibitory processing (Peterson and Salvagio, 2008; Peterson and Skow, 2008). Our results provide evidence that such a visual system would have reduced ability to resolve FG competition, particularly under high ambiguity. These findings suggest that drugs that decrease cortical inhibition, for example medications that suppress the inhibitory cortical mechanisms (e.g., Valium), might impair FG processing. The results also suggest that other conditions affecting inhibition, like Schizophrenia, which *has* been shown to impact other aspects of perceptual organization (Spencer et al., 2013), might likewise impair FG organization. Nevertheless, how Schizophrenia – and, more generally, the reduction to cortical inhibition – affects FG organization remains an open question.

The results also help understand the nature of convexity effects by showing 1) the neural signals sensitive to competition driven by CAV-region homogeneity are different from those sensitive to region number manipulations; 2) these signals are detectable at time points different from indices reflecting more local FG competition (Trujillo et al., 2010; Sanguinetti et al., 2015) but overlap in time with FG contextual effects known to index global FG segregation (Caputo and Casco, 1999); 3) the presence of this ERP difference correlates with behavioural performance that also reflects ability to resolve high competition; and 4) this ERP-behaviour correlation is consistent with the explanation of our age effects as resulting from changes to cortical mechanisms supporting visual processing. Further exploring the cortical mechanisms of FG resolution, and how these are impacted in aging, will yield further insight into the mechanics of FG organization.

From the aging perspective, these results support the hypothesis that aging impacts FG perception, among the other aspects of visual processing impacted in senescence that include more basic perceptual mechanisms like contrast sensitivity and luminance sensitivity, (Owsley et al., 1983; Spear, 1993), different aspects of perceptual organization (Roudaia et al., 2010, 2013; Pilz et al., 2010; Blake et al., 2008; Spencer et al., 2010), and “higher-level” visual functions like facial information processing (Habak et al., 2008; Rousselet et al., 2009). It would be worth exploring which aspects of visual perception are correlated with each other throughout the aging process, a question that is discussed below. Yet, our findings do stand on their own in supporting the theory that age-related decreased cortical inhibition impairs FG segregation. We demonstrated that high competition between perceptual interpretations, caused by increased ambiguity, particularly impairs older observers on our FG task. This finding is important for projects trying to characterize and ameliorate the challenges associated with aging. The exploration of how impaired FG in aging relates to functioning in visually-related health and overall well-being is another important research direction discussed below.

5.2.2 Aging and figure-ground organization: Extending beyond convexity context effects

This thesis unveiled much about how CCEs are influenced by aging, which yields a variety of implications and future directions. Yet, one direct follow up would involve continuing to explore the questions guiding our specific research program: How does aging affect CCEs and FG perception more generally?

We showed that older observers have trouble resolving high competition between alternative perceptual interpretations of a display. However, reducing competition by making the colour or motion cue consistent with the $\{\text{VEX} = \text{Figure}\}$ interpretation increased older observers’ ability to resolve the stimuli. We might wonder how much contextual information would be enough to bring FG resolution in older observers to the level of younger observers? It would be interesting to show that equating performance across age groups is possible by combining many cues to disambiguate the stimulus. For example, we could use stimuli that combine the motion and colour cues, or manipulate the relative areas of various regions, which has been shown to mediate figure assignment in other tasks using convexity stimuli (Froyen et al., 2013). We could also add other configural cues, like symmetry, to VEX regions or introduce stimulus properties indicating depth like disparity. The ability to manipulate different combinations of cues would allow for a more granular exploration of the effects of aging by decomposing the stimulus piecemeal and conducting a more extensive examination of multiple FG-related properties, and then pushing perceptual biases closer to ceiling in both age groups. This would also allow us to better explore visual systems of different individuals, and groups, in terms of how they process varying degrees of ambiguity.

Taking this method one step further, it would be informative to vary each of these parameters to get a more refined measure of sensitivity to stimulus properties affecting FG organization. Convexity of an edge could be varied from flat, sinusoidal, and/or CAV to VEX; motion could be varied in degrees of coherence or speed of CAV relative to VEX region fills; colour could be manipulated binomially (VEX/CAV = homogeneous vs. heterogeneous) as done in our experiments; area could be manipulated by widening/narrowing CAV vs. VEX regions. In a series of experiments, which explore each factor and combinations of factors, each of these region properties could be manipulated to varying degrees of congruency with the {VEX = Figure} interpretation. One goal of this series of experiments would be to attempt to bring older observer performance to ceiling to demonstrate that combining cues allows them to successfully resolve stimuli at the same level as younger observers. However, since the design would involve the combination of multiple other cues, the approach begins to speak to FG much more generally, moving beyond the CCEs explored by our project thus far.

As we have seen in the context effects described here, however, the problem of understanding FG inherently cannot escape the grouping side of the perceptual organization coin. Another interesting approach that could be employed to study effects of FG on aging more broadly would entail manipulating FG structure through grouping. Lee and Blake (1999) demonstrated grouping based on temporal synchrony of a dense array of Gabor patterns that changed location on each frame and the correlation between direction changes varied between the figure and ground regions. Guttman et al. (2005) extended these findings by showing that the synchrony signal could be split amongst a number of different stimulus properties: figural regions could be defined by changes split across orientation, spatial frequency, phase, and contrast of Gabor elements could be detected, so long as the change was temporally synchronous. Guttman et al. (2007) later showed that the FG structure defined by grouping is actually dependent on *temporal structure* more than temporal synchrony (i.e., the temporal patterns of changes rather than the exact synchronous timing of the changes). Blake et al. (2008) reported results that suggest that healthy aging is associated with a decrease in grouping by temporal structure but not luminance or motion-defined regions.

This *mixed-messenger signalling temporal structure* technique could be used to systematically explore the strength of FG resolution by varying correlation in temporal structure, as well as *similarity* in each Gabor property independently. Figure regions could be defined by Gabor orientation, spatial frequency, size, phase, or temporal structure of changes within and across features. This would allow us to investigate the effects of FG in relation to grouping in a psychophysical manner: each cue could be manipulated to wide degrees and objective correct/incorrect performance could be measured along the stimulus-property dimensions to obtain psychophysical parameters of performance. This technique would also allow for the combination of multiple cues at the same time. Such a design might even allow us to use convexity and other classic configural border properties to shape the figure region that is detected in the temporal structure task. Previous studies have used a rectangular figural region that is placed in one half or quadrant of the screen in a 2-alternative forced choice (2-AFC) or 4-AFC task. However, the theories of inhibitory competition-mediated suppression underlying FG perception (Peterson and Skow, 2008; Likova and Tyler, 2008; Salvagio and Peterson, 2012; Sanguinetti et al., 2015; Cacciamani et al., 2015) would suggest that if the figure had VEX borders it would be more salient than if it were CAV in shape because the temporal structure-defined CAV region would be suppressed by convexity, which should make it harder to detect the figure.

More generally, such control over the stimulus might provide a much more extensive measuring instrument for exploring the general effects on processing mechanisms underlying FG and grouping in perceptual organization. Such a tool could be used to explore which aspects of this processing are maintained vs. deteriorated in aging, and might serve as an adaptable paradigm that could be used in developing diagnostic tests for identifying impairments to perceptual organization. Such a psychophysical measure of FG ability might also be useful in further exploring the neural mechanisms of FG and perceptual organization and how they support perceptual organizational processing.

5.2.3 Compensatory mechanisms

Our results demonstrated an overall age effect on FG perception at the group level that related to cortical activation differences associated with performing the task. In an exploration of the effects of aging in the cognitive domain, McIntosh et al. (1999) and Cabeza et al. (2002) found that older adults generally performed more poorly than younger adults on tasks assessing memory and attention. Interestingly, a subset of the older group exhibited the same neural activity pattern, as indexed by positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), as younger adults, whereas another subset of the older group showed a markedly different pattern of activation. Furthermore, observers showing the same activation pattern seen in younger participants had significantly reduced performance, but those who showed a unique pattern that involved significantly more frontal lobe activation performed at the same level as the younger group. This result was consistent with the idea that the processing invoked by older adults could no longer support high performance on the task unless individuals recruited additional neural resources. We failed to find evidence of such compensatory mechanisms, but instead found evidence of an opposite pattern. At the group level, the older group showed differential processing compared to the younger group. However, at the individual level, the subset of younger observers who showed similar brain activity patterns as the older group also exhibited behavioural performance similar to older observers. From the compensatory mechanism perspective, our results thus seem to indicate that it is some of the younger observers who are able to invoke a sort of compensatory processing that allows them to resolve higher competition. Our results are consistent with the possibility that the ability to overcome high FG competition, which is typical in younger observers, is not preserved into late adulthood when inhibitory properties of cortical neurons become degraded (Leventhal et al., 2003; Schmolesky et al., 2000; Pinto et al., 2010).

Unfortunately, our sample did not contain enough older participants who performed behaviourally similar to the younger group, but it would be interesting to measure neural activity patterns sensitive to the competition in such a sample of older observers. Doing so would yield insight into how the aging brain might be able to overcome this challenge accompanying senescence.

5.2.4 Configural cues: Prior knowledge and perceptual learning

How are configural relations learned? Research has shown that use of such cues in determining FG organization is ecologically valid (Fowlkes and Martin, 2007): the natural scene statistics of convexities and FG relations are distributed such that figures are more likely to be VEX than CAV, and VEX regions are more likely to be figures than grounds. Correspondingly, people are biased in their depth perception towards {VEX = Figures} interpretations (Bertamini and Lawson, 2008; Burge et al., 2010). So it seems reasonable to conclude that, through engaging with the world and learning relationships between different variables including depth/FG relations and curvature/shape of objects, the Bayesian brain builds priors of these relations that bias perception, including the development of a convexity bias (Goldreich and Peterson, 2012).

Why then, as we observed here, would aging see a reduced convexity bias, as measured most purely in the contrast of younger to older performance using 2-region black and white (BW2) displays? The findings of this dissertation provide compelling evidence that older observers are impaired in resolving high competition/ambiguity, which speculatively relates to decreased inhibitory mechanisms shown to relate to cellular tuning of direction/orientation in animal models (Leventhal et al., 2003; Schmolesky et al., 2000) and the excitatory-inhibitory balance in human cortical tissue (Pinto et al., 2010). Yet, from a Bayesian perspective, we might expect the convexity bias to be more stable or even extreme in aging, as aging individuals continue to gain experience with the environment and the configural properties within. How can we reconcile these perspectives?

One possibility is that impairments to other aspects of vision in aging might reduce the ability to efficiently extract curvature information from stimuli. For example changing of the optics might defocus or blur edges (Weale, 1963), or impaired contour integration (Roudaia, 2013) might be impaired in a way that makes it difficult to extract edge shape (especially with multi-component complex-texture real-world objects against similarly complex backgrounds; e.g., consider a VEX tree contour composed of leafy texture with gaps in its structure, which is presented against a grassy background). When certain aspects of visual information processing become less reliable (i.e., certain aspects of perception become detuned or noisy), the ideal integration strategy is to shift weight to other inputs/channels carrying information about the same properties of stimuli (Ernst and Banks, 2002). If, in aging, the use of convexity as a cue to determining depth was reduced in quality compared to other sources inputted to the perceptual inference mechanism, then older observers would rely more on other cues that tend to be more reliable in determining depth or FG structure. For example, if use of disparity yielded more reliable information in determining FG or depth structure as people progress into late adulthood, then older observers would shift more weight to disparity in the integration of cues used to infer depth (see Burge et al., 2010, for a discussion on the integration of disparity and convexity in inferring depth, and presentation of human data speaking to this integration process). So, it is possible that aging, through differential change in reliability of various inputs to FG organization processing, causes a shift away from the use of convexity in particular and region curvature more generally. This would lead the integration mechanism to more strongly weight information from other cues that are more reliable, which would be more adaptive for the senescent visual system in inferring depth. However, all of this is a speculative possibility that remains open to question.

Another possibility considers perceptual learning in a scenario where perceptual organization rules are generalized to a new set of stimuli: how does the aging visual system form new priors or apply priors learned throughout life to a new class of blobby/pointy stimuli? At the start of our experiments, observers had no prior experience with these convexity-context stimuli, so they applied the general convexity bias learned through navigating the {VEX = Figure} biased environment and, hypothetically, as observers gain experience they form priors about our specific class of stimuli based on previous perception (because no correct/incorrect feedback was given). Our overall results do not rule out this possibility and may be consistent with it: in some experiments, P(VEX = Figure) was higher for 2-region stimuli when the first condition was 8-region and lower in 8-region stimuli when 2-region stimuli were presented first in both age groups. This finding suggests that when processing our new stimulus set, initial perception is biased by general rules of perceptual organization and susceptible to contextual factors yielding interpretations of stimuli, which influence later processing of similar stimuli. Given the small effect size and inconsistency (and *post-hoc* nature) of the result, however, it might be informative to explore this hypothesis more thoroughly in an experiment designed to test how priors are formed for the new stimulus set and how this effect differs between older and younger observers. Experimental design could involve the use of false, manipulated, correct/incorrect feedback that attempts to bias the way observers think stimuli are supposed to be perceived. Techniques could also manipulate task instructions that bias perception one way or the other, for example explaining that the task involves viewing black or white figures, or making the background homogeneous with CAV vs. VEX regions, so that one region type blends in and the other stands out as figures. Examining this question would yield insight into why older adults show a reduced 2-region convexity bias, as well as providing a means for exploring how the aging visual system can be trained to acquire new perceptual organization principles that might be useful in overcoming visual impairments.

5.2.5 Implications of the relationship between figure-ground and depth in aging

Conceptually, FG and depth perception seem related: they both have to do with distribution of objects in 3D space. FG perception involves assigning adjacent regions with figure or ground labels, which involves suppression of ground regions (Peterson and Salvagio, 2008; Peterson and Skow, 2008; Cacciamani et al., 2015) and irrelevant stimulus interpretations (Salvagio and Peterson, 2010, 2012). Depth perception involves determining depth order through other cues (including occlusion, which is also considered a FG cue) and metric depth relation from cues like disparity. The issue of the relation between depth and FG came up as a challenge in the motion work presented in this thesis. Our hypothesis was that reduced presumption of depth in the task could lead to reduced ability to infer FG structure. The task for those experiments was actually a depth judgement ("which region, light or dark, was closer?"). The complex relation between FG and depth perception is a topic that deserves deep focus in its own right.

In fact, it has been strongly demonstrated that cues to FG, convexity in specific, bias perceived depth, suggesting it to be a metric depth cue. Observations have demonstrated that convexity-disparity incongruence slowed responses in a depth judgement task (Bertamini and Lawson, 2008). Additionally, psychophysically measured depth from stereopsis depended on the convexity of the border between regions separated in stereoscopically- induced depth (Burge et al., 2010). Given our observed decreased convexity effects in aging, we would expect a decreased influence of convexity on depth judgements. This would be an interesting question to address because it would yield insight into the implications of the FG impairment identified in this dissertation to other aspects of visual perception, which might also serve as a link to the functional consequences of the age-related FG impairments. The relation between FG and depth remains an open question for exploration. However, the fact that FG impacts depth perception in younger observers (Burge et al., 2010) further motivates that FG be studied as part of the effort to quantify, and develop a battery of tests that can identify, vision's role in the challenges facing seniors.

5.2.6 Linking figure-ground to real world functioning in older adults

One of the major pursuits that must follow from our findings is determining whether FG is an indicator of visual deficits associated with negative outcomes in the senior population. It is conceivable that impaired ability to resolve FG structure in the environment would pose a challenge to many aspects of functioning, including, for example, driving ability (Wood, 2002; Wood et al., 2005) and avoidance of falls (Källstrand-Ericson and Hildingh, 2009). With convexity being important in determining depth order and biasing perceived depth in younger adults (Burge et al., 2010), and given that older people show impairments to processing that underlies convexity effects, we might expect impaired ability to infer depth relations of curved objects in older observers. Thus, investigating the relation between FG organization with tasks like driving and trips/falls seems necessary. While other visual and cognitive factors are undoubtedly important in the incidence of driving incidents (Ball et al., 1993), how would decreased ability to segregate objects from backgrounds or infer depth in scenes with fast moving objects play a role in, and interact with these other identified factors, in affecting the every day independence-enabling task of driving? Given our finding of the age-related FG deficit particularly under high competition/ambiguity, and similar findings for other aspects of perceptual organization (e.g., Pilz et al. 2010; Spencer et al. 2010; Roudaia et al. 2013), it is likely that FG impairments might not be an issue under clear, noiseless, well-let viewing conditions. It might be the case that reduced FG resolution ability becomes and impairment in non ideal conditions, and, as our results suggest, such deficits might become dangerous, as information becomes noisier through viewing conditions, like rain or low light. Similarly, FG resolution might become particularly impaired as other optical factors or visual functions deteriorate in and of themselves.

The research presented here thus implores other research programs that explore the effects of age-related sensory and perceptual declines in every day tasks, like the Can-Drive project (Langford et al., 2013; Marshall et al., 2013), to include FG organization as part of the investigation. This will allow researchers to characterize the role of FG organization in age-related functional deficits, may eventually lead to the inclusion of FG perception tests as part of a diagnostic battery to identify visual aging and determine when a person's ability to perform specific tasks becomes compromised, and inform different efforts working towards overcoming this deficit. Together with the FG results recently reported by Anderson et al. (2016), our findings suggest measures of FG processing that might be useful individual indicators of the presence of, or future risks to, aspects of seniors' ability to function normally.

The use of perceptual training to enhance perception and overcome impairments in older adults has proven possible. For example the useful field of view (UFOV), which is the ability to efficiently extract information surrounding a fixation, is another characteristic of the visual system impaired in aging (Ball and Owsley, 1993; Sekuler et al., 2000). Yet, training in a divided-attention task with a peripheral component led to increased ability to overcome the divided-attention in both older and younger observers, although, the increase in UFOV did require more training in the older group (Richards et al., 2006). Findings like this are promising in the effort to improve visual functions compromised in aging that have been implicated in every day tasks, like driving (Wood, 2002; Wood et al., 2005). One study with older adults demonstrated that *speed-of-processing* training improved measures of UFOV that transferred to some aspects of driving ability, and that driving simulator training improved other aspects of driving ability. Some of these promising training effects were still present 18 months after training (Roenker et al., 2003).

5.2.7 The visual system's trajectory of aging

As I prepare to conclude this dissertation and my time in the Vision and Cognitive Neuroscience Lab, I broaden my focus. My research program on FG perception and aging has found evidence of impaired FG processing in older observers and we argued that this may be an important aspect of vision involved in different tasks critical to normal functioning. Yet, FG is only one aspect of vision that may bear much understanding about the impacts of aging studied in our laboratory. Exploring the combination of multiple such factors simultaneously, along with measures of basic visual function and broader functional capacity, would yield much insight into the covariation of these factors through individual aging trajectories. Such a project would help develop a more comprehensive model of the aging visual system, which might link the different facets of visual functioning impacted by an aging brain. Such an effort will be critical in characterizing the phenomenon of *aging*.

The nature of our older observer pool, and likely that of other long standing visual perception and aging laboratories, is that observers continue to come back over the course of years. It would be interesting to measure a battery of these variables at various age points throughout their tenure in the lab. This would give us the power of a longitudinal design with potentially long and detailed individual trajectories. One way to construct this battery would involve creating a master script that runs all tests within the battery, where past and future students would be able to include a fully functioning, self contained script that would be controlled by the master script, run a specific task (with instructions), collect the data, and output a summary datafile that combines performance across tasks. To study the effects of aging would also entail comparing results to a younger group. An even more powerful method, however, would entail the combination of both longitudinal and cross sectional methods into a single cross-sequential design (Schaie and Strother, 1968). This method allows comparison across cohorts and within cohorts as they age, and therefore gives the ability to control for cohort effects while studying a broad range of age brackets.

For a lab studying aging, a cross-sequential study within the older population would be useful. Whereas we studied a single older group of individuals aged 60+ years old, a cross-sequential design could use multiple age brackets spanned throughout older adulthood, for example five age brackets spanning from 60 years to 80 years. Samples of different sub-older groups would have visual abilities and function measured at the study onset. After four years, when each cohort has aged the width of the age brackets, groups would be retested. This data would enable the comparison between age brackets and also give the ability to compare adjacent age bracket effects to the age effect within a longitudinal group. The more retest conducted, the more powerful the data would become. However, the challenge with exploring the effects of aging from younger age group that could be later brought back when they fell into the older group.

One way to really propel such a project forward would involve a more widespread application of this design. For example, a standardized and comprehensive application for researchers could be distributed widely, which could be run by disparate researchers who study aging and visual perception in a collaborative effort to grapple one of the fundamental questions of aging research: how do various aspects of visual processing change through healthy aging, and what implications do these changes have on every day functioning and longevity?

5.3 Challenges & limitations

It is important to acknowledge the challenges faced in conducting this research in order to understand the limitations of what it can tell us.

In this thesis, the work tried to draw a link between human performance on a subjective (i.e., no correct/incorrect response) behavioural task, thought to rely on inhibitory neural mechanisms (Peterson and Salvagio, 2008). However, the research that has linked age-related degradation of inhibitory cortical mechanisms to psychophysical measures of perceptual processing has been conducted in other animals. The observation of disrupted inhibitory/excitatory balance in humans was conducted in post mortem tissue (Pinto et al., 2010). Thus, the *aging-inhibition hypothesis* partially motivating this research program, and some of the conclusions about how the behavioural deficits relate to reduced cortical inhibition in aging, is speculative. Furthermore, unlike what is possible in animal models, we cannot directly manipulate some of the variables examined, like the decrease in GABAergic mechanisms speculated to cause our FG impairment. Whereas in animal studies GABAergic mechanisms can be manipulated to decrease inhibition in younger monkeys or increase inhibition in older monkeys (Leventhal et al., 2003), the best we could do is explore groups that vary in properties of interest. It would be unethical to manipulate the GABA levels in younger or older observers to test the effects on competition resolution, but future research might explore this question by looking at groups of people taking medications that alter cortical GABA levels. Yet, our methods are correlational; evidence from such studies may be consistent with or inconsistent with hypotheses about the cortical inhibition-FG perception link, but it could not prove cause and effect relationships. This challenge pervaded our research and we were limited to finding results *consistent with* the hypotheses laid out at the onset of the program.

One of the most challenging aspects of our research is how to approach *aging* itself. How does one study effects of the aging visual system without a comprehensive model of aging that can be drawn on to ensure control over the various factors associated with aging, and isolate the mechanisms of interest? Furthermore, which variables that covary with chronological age are part of what makes aging what it is, and which factors are to be controlled for? How will the chosen balance between the controlling for the effects associated with age vs. leaving factors that occur as part of aging affect the way the findings generalize to the population of older adults? This challenge is a serious issue in studying any special population, and to some degree permeates the study of any scientific topic. Ultimately, it is only through carefully designed experimentation based on the data we have, and the most plausible interpretations of the data, that the model we rely on will itself progress, refine, and redevelop. Our work was designed to explore a specific aspect of perceptual processing and the effects of aging on it. We were careful in controlling for the effects associated with aging that affect information processing prior to the perceptual processing we are trying to assay. This was done by measuring a battery of visual abilities and demographic data for all participants, designing stimuli and experiments to control for properties known to affect the processes we were examining, and conducting control experiments like Experiment 2.2 and 2.3 to explore whether lower level factors explained the perceptual effects observed. We did our best to work from what is known about aging and vision, and recorded the details needed to explore alternative explanations. Although there is no *ideal older observer* model to help escape this problem associated with studying aging, our research contributed knowledge to the very project of developing a scientific model of aging.

Another challenge faced involved studying weak effects, i.e., the weak CCE in older observers. Indeed the CCE was trending in the correct direction in most samples of older observers throughout the thesis, but statistical power was a severe limitation in significantly detecting the effect much of the time. For example, in Experiments 3.1 and 3.2, the CCE was not statistically significant in the older group, however, the CCE in the older group was detected when the two samples were combined in the between experiments analysis. It was important to remember throughout this work that finding a weak, nonsignificant CCE is expected when sampling from a distribution with a weak effect. Through this experience I learned that studying weak effects can be a difficult task that may be better to avoid when possible, or to ensure large sample sizes when doing so. However, I think the nature of many psychological phenomena, especially when studying effects of aging, is that there are many important but weak effects that do deserve attention and large sample size is not always an option. One way this challenge was bypassed was by focussing analyses on the $Age \times RegionNumber$ interaction that could be used to compare the effects of various manipulations on CCE across age groups. Since in some cases, it may be important to demonstrate the presence of the weak CCE in its own right, we might have better addressed this challenge through using a more powerful measure of the CCE: perhaps if we looked at the linear trend of P(VEX = Figure) across more region number conditions, we may have been able to obtain a more powerful individual measure for the CCE compared to the difference between 2- and 8-region stimuli; however, it is also possible that this would produce a weak effect that would be hard draw conclusions from. Another means for dealing with this issue might have been adapting our conception of the null distribution of older observer CCEs after collecting data in multiple experiments: instead of comparing performance difference across conditions to zero, we could have compared it to the older population CCE distribution, estimated from previous data. Although it would still be hard to detect a weak CCE that differed from zero in many of the samples collected, it would have also likely been difficult to reject the hypothesis that a weak CCE observed in a particular sample was lower than the distribution of weak CCEs previously inferred. Although rejecting a hypothesis of zero effect is very different than failing to reject a hypothesis about an effect varying from what was previously observed, including both analyses might have been one way to address the issue better.

One of the major limitations that comes along with studying aging is that various techniques for studying factors affected by aging, are themselves susceptible to the effects of aging. For example, many studies on FG organization have used paradigms where backwards masking was applied to control processing time (Peterson and Salvagio, 2008;

Salvagio and Peterson, 2010, 2012). Yet studies on aging and visual masking have shown that aging interacts with different kinds of masking in different ways (Kline and Birren, 1975; Farber et al., 2010). Thus, we chose not to use masks in our studies because it would be challenging to interpret the results. Not using masks was a limitation in that we could not precisely control the processing times in our observers. Our approach was to design carefully controlled experiments that allowed us to approach these effects from the other direction. For example, in Experiment 2.2, we manipulated processing time constraints in younger observers in a way we thought comparable to unmasked older observers by reducing stimulus durations in younger observers by up to a factor of four. One idea that might have been useful in retrospect could have been to use masking but to include the presence of masks as a factor in the design. This would allow for controlling the effects of masks in every other combination of conditions, although making conclusions based on this kind of method would assume that the masking does not interact with other stimulus/task factors, which is not necessarily well-founded.

5.4 Conclusion

In this thesis, I presented work demonstrating that FG perception, thought to be achieved through competition-mediated suppression, is impaired in healthy aging. Specifically, older observers had difficulty resolving ambiguous, high competition stimuli and benefited from reducing competition through disambiguating the FG structure by combining consistent cues. A series of motion experiments supported the notion that FG resolution is impaired in older adulthood as opposed to the possibility that depth presumption is reduced in observers, and further supported the theory that high competition poses particular challenge to the aging visual system. An electroencephalographic examination of cortical activity associated with performing the figure assignment task, assaying the neural mechanisms of the underlying processing, indicated a relatively late neural component (the N250) associated with resolving the FG competition. This neural index of the competition was shown in two groups of younger adults but not found in a group of older observers. Interestingly, individual differences in behavioural and neural indices of the competition were negatively correlated: those showing a relatively strong impact of increased competition on behavioural performance showed no ERP effect whereas those showing a weak effect of competition on behavioural performance showed strong ERP differences between competition conditions. This pattern of results support the hypothesis that younger observers are able to alter perceptual processing mechanisms to resolve higher competition stimuli whereas older observers show no index of altered processing and have reduced ability to resolve high competition.

Overall, the work conducted in this thesis indicated an age-related impairment to perceptual organization of FG that is associated with the neural signatures of the underlying processing. This exciting set of findings implicate the processing mechanisms supporting FG organization as an important aspect of perception that changes in senescence, which might lead to age-related challenges to every day functioning. The work presented thus motivates future research that can further investigate, and hopefully capitalize on, the results discovered here: the effects of aging on FG perception.

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