CHARACTERIZING BINOCULAR RIVALRY
ACROSS THE LIFESPAN

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BY

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Abstract

Binocular rivalry allows for the unique examination of the neural processes associated with binocular vision by instigating a disruption of normal stereoscopic vision. Although binocular rivalry has been examined extensively in young adults, we know relatively little about its developmental trajectory across the human lifespan. This thesis provides a foundation for characterizing perceptual alternations during binocular rivalry in children and older adults, with a specific emphasis on expanding our understanding of binocular rivalry in older adults. From a theoretical perspective, my studies on aging and binocular rivalry have a specific significance, because unique changes that are known to occur with aging to certain neural mechanisms often associated with characteristics of perceptual alternations allows for the study of aging to serve as a test for many of the current models of binocular rivalry. Overall, my studies provide evidence for a significant transitional period in the binocular visual system at the age of 70 and older, and highlights the developmental trajectories of specific characteristics of binocular rivalry from childhood to senescence.

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Preface

Chapter 1: Introduction

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Chapter 2: Age-related effects of size and contrast on binocular rivalry

Authors: Amanda M. Beers, Allison B. Sekuler & Patrick J. Bennett

Contributions: AMB conceived and designed the study with assistance from PJB and feedback from ABS. AMB conducted the majority of the analyses. PJB conducted the analysis on the difference scores for the sequential pattern of alternations. AMB wrote the manuscript with revisions from ABS and PJB.

Chapter 3: The effects of inter-ocular contrast differences on binocular rivalry in younger and older observers

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Contributions: AMB conceived and designed the study with feedback from ABS and PJB. AMB conducted the analyses. AMB wrote the manuscript with revisions from PJB.

Chapter 4: Visual rivalry and aging

Authors: Amanda M. Beers, Faiza Shafaqat, Allison B. Sekuler & Patrick J. Bennett

Contributions: AMB conceived and designed the study with feedback from FS, ABS and PJB. AMB conducted the analyses. AMB wrote the manuscript with assistance from FS and revisions from PJB.

Chapter 5: Characterizing perceptual alternations during binocular rivalry in children

Authors: Amanda M. Beers, Michael Slugocki, Terri L. Lewis, Allison B. Sekuler & Patrick J. Bennett

Contributions: AMB conceived and designed the study with feedback from MS, TLL, ABS, and PJB. AMB conducted the analyses. AMB wrote the manuscript with revisions from MS and PJB.

Chapter 6: General Discussion

Author: Amanda M. Beers

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Chapter 1

General Introduction

1.1 Interactions with 3-Dimensional Surroundings

We interact with our 3-dimensional (3-D) surroundings countless times throughout our daily routines. Even simple interactions, such as sipping coffee from a cup, require us to encode the 3-D structure of our environment in ways that support reaching, grasping, and manipulating nearby objects. Interactions with 3-D virtual reality in the form of entertainment simulations of varying forms are also becoming increasingly more common, providing an even greater number of examples of our reliance on our ability to encode 3-D structure. Binocular vision, which refers to processes that integrate information from the two eyes, plays an important role in the creation of these 3-D representations of visual space and objects.

Binocular vision, specifically stereoscopic vision, has been studied primarily in young adults. Thus, little is known about how binocular vision may change or remain constant throughout the lifespan. Our limited knowledge of the healthy aging visual system is becoming increasingly problematic with the significant rise in the percentage of older adults within the global population set to continue unabated. It is therefore important to understand how potential changes in the binocular visual system with healthy aging could potentially impact how older adults perceive and interact with their 3-D surroundings.

The human visual system has evolved to integrate information from two eyes placed at slightly different locations at the front of the head. Due to the slight difference in each eye's location, each eye receives slightly different input from the environment about the location of an image in space. This position shift is known as binocular disparity. In normal binocular vision, this binocular disparity allows the brain to utilize information from the two retinal images to form a single 3-D representation. If the inputs received by each eye vary too greatly, (e.g., if the retinal images consist of sine-wave gratings that differ in orientation by 90 deg) the brain is unable to combine the two images to form a single representation. Instead typical observers experience a dynamic percept which alternates between the two retinal images, with the retinal image in one eye often becoming dominant for periods of time while the other image is suppressed from conscious awareness. This phenomenon is known as binocular rivalry.

There are a multitude of ways in which to instigate rivalry dichoptically (see Blake, 2001, p. 9 for review). This variety in potential experimental stimuli means binocular rivalry has been used to investigate a wide assortment of experimental questions associated with an array of topics associated with visual perception, including social and cultural factors (Bagby, 1957; Moore, 1966) and consciousness (Blake et al., 2014). My specific intent with this thesis is to utilize binocular rivalry as a tool to study the disruption of normal stereoscopic vision in children and older adults, and by doing so develop a foundation to help us better understand the binocular visual system throughout the lifespan. The premise of instigating binocular rivalry in order to amplify perceptual characteristics of neural mechanisms associated with binocular vision is outlined in this introduction, and expanded upon within the introductory section of each chapter.

1.2 Historical Background

Here I will briefly highlight some of the important milestones in the experimental investigation of binocular rivalry in the context of my thesis. Specifically, I will focus on the theoretical perspectives of a select few individuals and how they have shaped our understanding of binocular rivalry and its use as a tool for understanding binocular vision. While descriptions of the phenomenon of binocular rivalry were published as far back as the sixteenth century (Porta, 1593), the first experimental investigation of binocular rivalry is credited to Wheatstone (1838). The invention of Wheatstone's mirror stereoscope allowed for the development of controlled conditions for studying binocular rivalry. In his description of the alternations between images when a different letter was shown to each eye, using his mirror stereoscope, Wheatstone noted that these alternations seem outside of willful control. This characteristic of binocular rivalry is still relevant for discussion in this thesis (see Chapter 4).

Since Wheatstone's initial investigations, an extensive body of literature has developed on the characteristics of binocular rivalry. One of the next major milestones in the history of the investigation of binocular rivalry was the publication of a monograph by Breese (1899). Breese commented on some features that would later be recognized as key to our understanding of predominance (e.g., motion and luminance), and introduced the concept of monocular rivalry, where an alternation in dominance occurs between two distinct images shown to the same eye.

Robert Fox also focused on the investigation of monocular qualities of perception during binocular rivalry, particularly on ways of quantifying the suppression of information shown to one eye that occurs during binocular rivalry. Fox developed a test-probe procedure to test sensitivity to information presented to the suppressed eye during binocular rivalry (for description see Chapter 1 in Blake, 2005). Although not utilized within this thesis, the test-probe procedure has proven instrumental in our understanding of binocular rivalry throughout the lifespan. For instance, Norman et al. (2007) used this type of procedure to demonstrate that older adults have poorer sensitivity in the non-dominant eye during binocular rivalry, and thus greater suppression. This characteristic of greater suppression during binocular rivalry with aging is important for the theoretical discussion of the association of rivalry characteristics with neural mechanisms, specifically discussed within Chapter 2.

In the 1950's, Asher (1953) championed the permanent rivalry hypothesis. First proposed by Du Tour (1760), this theory claimed that the visual system was constantly in a state of rivalry, and normal perception was based on only the image from one eye at a time. According to this theory, the phenomenon of binocular rivalry is simply when conflicting images in each eye make this permanent rivalry noticeable. But subsequent studies have disproved this theory (O'Shea, 1987), and led to our current conceptualization of binocular rivalry as a disruption of normal stereoscopic vision rather than being a standard component of normal vision. This modern conceptualization of rivalry laid the foundation for a series of studies in the 1960's, including those by Levelt discussed in the next section.

1.3 Testing Levelt's Propositions in Older Adults

To establish a foundation for future studies of binocular rivalry across the lifespan, it is important to refer to traditional components used to study rivalry in younger adults. Historically, a prominent source of information on rivalry characteristics has involved the investigation of varying external features of rivaling stimuli, such as size and contrast. Levelt (1965) manipulated contrast to study the impact of stimulus strength on dominance during binocular rivalry, and presented the results in a monograph that has served as a hallmark of experimental investigations of binocular rivalry.

The four propositions introduced within Levelt's monograph outlined the relationship between binocular rivalry and inter-ocular differences in stimulus strength. Brascamp et al. (2015) recently outlined revised versions of Levelt's propositions that incorporate findings from the past half-century of research on binocular rivalry. Neither the original nor the revised versions of Levelt's propositions have been tested within age groups other than younger adults. Since some form of these propositions have formed the basis for a large portion of theoretical ideology about binocular rivalry, it seems important to understand if these propositions are applicable to spectrums of the lifespan other than younger adults. This question is investigated in Chapter 3.

Recently it has been suggested that Levelt's propositions are relevant to other forms of visual rivalry, besides binocular rivalry, such as perceptual rivalry. Binocular rivalry and perceptual rivalry are two forms of visual rivalry. While binocular rivalry is instigated by dichoptic presentation of images that differ, perceptual rivalry occurs when the same ambiguous stimulus, or reversible figure, is presented to both eyes.

There is some evidence that various types of visual rivalry are modulated by the same neural mechanism (Andrews and Purves, 1997; Logothetis, 1988; Wolfe, 1996; Blake and Logothetis, 2002), but other evidence suggests different neural mechanisms control different types of visual rivalry (Fox and Herrmann, 1967; Levelt, 1966; Meng and Tong, 2004). Aydin et al. (2013) suggested their findings of slower perceptual rivalry in older adults also provides evidence that similar developmental trends are associated with binocular rivalry and perceptual rivalry. However, this study did not use a within-subject design and did not report potentially confounding variables, such as the cognitive demographics of its older subjects. To further investigate if different forms of visual rivalry are affected by aging in a similar manner, and thus provide compelling support for the theory that similar neural mechanisms are associated with various forms of visual rivalry across the lifespan, Chapter 4 presents a within-subject design of correlations between binocular and perceptual rivalry, and also investigates the reliability of each of these types of visual rivalry across various time periods.

1.4 Characterizing Binocular Rivalry in Special Populations

As previously mentioned, there are a number of experimental methods that can be used to instigate binocular rivalry. Because this thesis involves participants from special populations, specifically children and older adults, our method was a relatively simple one that used red/cyan glasses to dichoptically present orthogonal, oblique sine-wave gratings. Other techniques used to instigate binocular rivalry could have presented potential complications. For example, the use of a mirror stereoscope requires each participant to undergo a complicated and time-consuming calibration procedure, and shutter glasses may have provoked unwanted consequences from sensitivity to flicker, which may be potentially more prevalent in these special populations.

The investigation of binocular rivalry in children and older adults, special populations in which little is currently known about perceptual reactions to experiencing binocular rivalry, also makes it paramount to avoid basing investigations on prior assumptions. By simply reporting only one or the other of the most common measures of rivalry, such as the average duration or proportion of time spent viewing a percept, important information could possibly be lost. For this reason, this thesis stresses a distinction should be made between whether a percept occurs once for a long duration of time or occurs frequently for short periods of time when developing a foundational understanding of the characteristics of binocular rivalry in special populations. Also, while the average duration and proportion of time measures reveal useful information about rivalry, these measures do not necessarily make it easy to infer how rivalry percepts change dynamically throughout a trial. The reporting of sequential transitions in younger and older adults within this thesis provides a unique measure for developing a more comprehensive understanding of the dynamic qualities of binocular rivalry in these populations. The importance of a comprehensive investigation when establishing the preliminary foundation for our understanding of binocular rivalry across the lifespan is discussed in more detail in Chapter 2.

Throughout this thesis, it is also stressed that reporting Mixed percepts (i.e., percepts comprised of some combination of the images shown to both eyes) is important when establishing the basic characteristics of binocular rivalry in a special population. Only allowing for the report of Exclusive percepts (i.e., percepts comprised entirely of an image shown to one eye), like in many previous papers, forces participants to make a judgment about which of the two Exclusive percepts to report they are viewing, even if their percept is Mixed and does not match either Exclusive percept. When this type of selected reporting occurs it has the potential to hide an entire spectrum of information about the characteristics of rivalry. Although using limited measures is sometimes appropriate for the investigative question, it is important for our understanding of potential changes in binocular rivalry to take a more comprehensive approach to establishing a foundation for the characteristics of rivalry across the lifespan.

Studying binocular rivalry in a special population, such as older adults, not only allows us to learn more about the aging of the binocular visual system, but also allows us to test many computational models and theories of binocular rivalry. Certain neural mechanisms known to change with aging, such as inhibition (Betts et al., 2005) and internal noise (Betts et al., 2007; Bogfjellmo et al., 2013; Pardhan, 2004), have been fundamental in proposals of the neural correlates associated with binocular rivalry. Therefore, older adults serve as a useful model for theoretical treatises of binocular rivalry, such as the computational model proposed by Brascamp et al. (2006). The work presented throughout this thesis provides some of the first empirical tests of these models.

The study of normal development of binocular vision throughout childhood also provides a unique perspective on the visual system. The majority of the chapters in this thesis focus on expanding our knowledge of the characteristics of binocular rivalry in older adults, but it is important to recall that there is also a lack of information about binocular rivalry in children. Chapter 5 within this thesis provides the first comprehensive examination of characteristics of binocular rivalry throughout childhood. Specifically, this work provides an example of the first empirical record of Mixed percepts during binocular rivalry in children. These records of Mixed percepts are of particular interest since the commonly accepted theory suggested by Kovács and Eisenberg (2005), that children experience a greater proportion of Mixed percepts, has never been directly tested. This thesis highlights that protocol can be developed to appropriately measure comprehensive characteristics of binocular rivalry in special populations throughout the lifespan.

1.5 Primary Contributions

The main contribution of this thesis is that it begins to fill the gaps in our knowledge of binocular rivalry across the lifespan by establishing the basis for the fundamental knowledge of characteristics of binocular rivalry in areas of the lifespan that previously received little attention from researchers: children and older adults. The arguments laid out in this thesis also highlight how populations with special neural characteristics, such as older adults, can serve as models for testing important theoretical constructs of binocular rivalry. Thus, this work provides a crucial contribution to our understanding of the phenomenon of binocular rivalry and its relationship with specific neural mechanisms that potentially influence general aspects of binocular vision throughout human development.

This thesis also describes research that provides a starting point for further investigations of the practical implications of research in binocular vision across the lifespan. For example, in recent years the entertainment industry has attempted to capitalize on our expanding scientific understanding of binocular vision in an effort to create 3-D forms of entertainment, such as 3-D films and video games. Expanding upon my work could prove a vital tool for these industries in their goal of attracting new customers of various ages by developing products that provide a higher quality experience.

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Chapter 2

Age-related effects of size and contrast on binocular rivalry

Abstract

The current study measured binocular rivalry in young adults (aged 20-29), junior-seniors (aged 61-69), and senior-seniors (aged 71-78). Size (diameter = 2.4^o or 4.4^o) and contrast (0.2 or 0.8) varied across trials. On each trial, participants tracked alternations among four types of percepts (two Exclusive, Mixed, and Fading/Other). Consistent with previous reports (Jalavisto, 1964; Ukai et al., 2003), average durations for Exclusive percepts were longer in older adults. Additionally, the strength of monocular dominance increased with age, and the proportion of Mixed percepts decreased with age. In the low-contrast conditions, senior-seniors reported a statistically higher proportion of Other percepts, presumably representing a greater amount of stimulus fading. The sequential pattern of alternations between percepts also varied across age groups. Overall, across all measures, the senior-seniors were the most

statistically different. Control experiments indicate that these results were not due to age differences in motor response time or retinal illuminance.

2.1 Introduction

Normal stereoscopic perception involves the brain integrating visual input from both eyes. The slight variation of spatial information from each eye allows for the formation of a single 3-Dimensional (3-D) percept. When the two retinal images differ sufficiently the visual system is unable to integrate the two images, and the observer experiences a dynamic percept that alternates between several states. This phenomenon of binocular rivalry, in which the two retinal images compete with each other for perceptual dominance, provides the unique opportunity to study what occurs when the normal processes involved in stereoscopic visual system are disrupted.

Binocular rivalry is influenced by a variety of factors, such as the size and contrast of the images that instigate rivalry. For instance, the rate of rivalry increases with increasing pattern contrast (Hollins, 1980; Levelt, 1965). Also, the proportion of time spent viewing Exclusive percepts (i.e., percepts comprised entirely of an image shown to one eye), is affected by stimulus contrast (Hollins, 1980), and the proportion of time spent viewing Mixed percepts (i.e., percepts comprised of some combination of the images shown to both eyes) is influenced by stimulus size (Blake et al., 1992; O'Shea et al., 1997). In recent years, an importance has been placed on associating such characteristics of rivalry with specific neural mechanisms, and binocular rivalry has been used as a tool to evaluate theories of binocular interactions that may occur in normal binocular vision and stereopsis (Blake, 2001). However, it is important to note that to date investigations of binocular rivalry have focused primarily on young adults. The development of a more comprehensive knowledge of the binocular rivalry characteristics of older adults allows for the expansion of these neural models of binocular vision. For example, the neural characteristics associated with the aging visual pathway of older adults, such as reduced inhibition (Betts et al., 2005) and evidence indicating higher internal noise under certain conditions (Betts et al., 2007; Bogfjellmo et al., 2013; Pardhan, 2004), also provide a model for testing current theories of binocular rivalry that associate certain neural factors, such as inhibition and internal noise, with specific characteristics of binocular rivalry.

Many facets of stereoscopic perception appear well-preserved with aging under optimal conditions (Norman et al., 2008), although some features, such as depth perception, have been shown to deteriorate with age (Norman et al., 2000, 2006). However, little is currently known about binocular rivalry in older adults. Previous research indicates the average duration of Exclusive percepts of the images shown to each eye lengthen with increasing age (Jalavisto, 1964; Ukai et al., 2003), suggesting a slowing of the rivalry process. Older adults also have been shown to exhibit stronger suppression during binocular rivalry (Norman et al., 2007). The current set of experiments examine the effects of size and contrast on binocular vision across the adult lifespan. By studying size and contrast, factors with well-known effects on binocular rivalry, we can begin to establish a foundation for future studies of binocular vision and aging. In addition to estimating standard parameters, such as the average duration and proportion of time spent viewing Exclusive percepts, we also conducted detailed analyses of Mixed percepts and sequential transitions in percepts. These additional analyses provide unique insights into how the phenomenology of binocular rivalry changes with age.

2.2 Experiment 1: Age-Related Effects of Size and Contrast

2.2.1 Method

Observers

The current study measured binocular rivalry alternations in three age groups: young adults, junior-seniors, and senior-seniors. There were eight observers in each age group (four males). Young adult observers were undergraduate and graduate students recruited from McMaster University. Older observers were recruited from the McMaster Vision and Cognitive Neuroscience Lab Senior Participant List. Table 2.1 shows demographic characteristics of each group. All observers had normal or corrected-to-normal visual acuity, as well as normal stereoscopic vision. Observers of all ages had a minimum stereoacuity threshold of 50 seconds of arc at 16 inches, measured with the Randot Stereotest (Stereo Optical Company). Inter-ocular differences in contrast sensitivity, measured with the Pelli-Robson chart, were minimal for all age groups. All participants wore appropriate corrective lenses during the experiments. Older observers performed normally for their age groups on the Mini-Mental-State-Examination (MMSE; Bleecker et al., 1988). No observers reported any general or psychological health issues. Observers were compensated for their time with either partial course credit or a monetary reimbursement at a rate of $10.00/hour. The McMaster University Research Ethics Board approved all experimental protocols, and all participants gave informed consent prior to participating in the study.

Table 2.1: The mean age (years), Snellen acuity (decimal), inter-ocular difference in Pelli-Robson contrast sensitivity (I.D.P.R.), MMSE, and years of education for subjects in Experiment 1.

Age Group	Age (σ)	Snellen Acuity	I.D.P.R.	MMSE	Education
Young Adults (20-29 yrs)	24.0 (2.9)	1.58	0.09	NA	17.56
Junior-Seniors (61-69 yrs)	65.2 (2.9)	1.13	0.06	29.13	15.69
Senior-Seniors (71-78 yrs)	73.6 (3.1)	1.05	0.06	28.63	14.00

Apparatus

Stimuli were generated on a Macintosh Pro 4 using MATLAB 7.10 (R2010a) (Mathworks, Natwick, MA, USA) and the Psychophysics Toolbox (Brainard, 1997). The stimuli were displayed on a 30-inch Apple Cinema HD display with a resolution of 2560 × 1600 pixels. Red/cyan glasses were used to present different images to each eye. The display was carefully calibrated to ensure that the stimuli delivered to each eye had the same average luminance after passing through the red/cyan glasses. A RESPONSEPixx (VPixx Technologies, Inc.) handheld button box was used to record participant responses. All devices (button box, display monitor, and computer) were connected to a DATAPixx (VPixx Technologies, Inc.) data and video processor to enable accurate synchronization of stimulus presentation and response acquisition.

Stimulus Displays

Stimuli were pairs of orthogonal oblique sine-wave gratings presented dichoptically. The spatial frequency was 5 cy/deg. On each trial, the contrast of both gratings was 0.2 or 0.8. Contrast was modulated by a circular window that had a diameter of 2.4 or 4.4 deg. Average luminance was 37.7 cd/m^2. Observers viewed the stimulus display from a distance of 100 cm. Viewing position was stabilized with a chin rest/head rest.

Procedure

During each trial, participants used the button box to track alternations among four percepts: two Exclusive percepts (i.e., a grating tilted clockwise or counter-clockwise from vertical), a Mixed percept, and a so-called "Other" percept. Observers were instructed to press the rightmost (red) button while they perceived an exclusively clockwise-oriented grating, and the leftmost (green) button while they perceived the counter-clockwise oriented grating. Observers were told that they might experience multiple forms of a Mixed percept (e.g., a plaid-like image, a puzzle-like image, or wave-like transition from one Exclusive to the second Exclusive), and were instructed to press both the red and green buttons simultaneously for the entire duration that they perceived a Mixed stimulus. Finally, participants were instructed to report the Other percept if they perceived fading of the stimuli or any percept that was not Exclusive or Mixed by releasing all the buttons for the duration of the Other percept. It was stressed to the observers that there were no right or wrong responses and that the length of each perceptual state may vary, and that they should respond as quickly as possible to attain the most accurate reports. All observers were naïve to the phenomenon of binocular rivalry before participating in this study. Example images were shown during the instructions, and participants were given a practice trial, which used a size/contrast combination that was selected randomly from the four stimulus conditions, before beginning the experimental sessions to allow them to become comfortable with the task.

A testing session consisted of 16 trials. Each participant completed two testing sessions, with a 5-15 minute break in-between sessions. At the start of each session, observers adapted to the average luminance of the display in the dark room for one minute. The presentation order of the four condition types was randomized within each session. There were four trials per condition within a session, yielding a total of 32 trials across both sessions. Each trial lasted for a duration of 40 s and the inter-trial interval was 20 s to allow after-effects to diminish. Observers were instructed that they could rest their eyes and ease their focus on the fixation point during the inter-trial intervals. At the end of each inter-trial interval the fixation point flickered in synchrony with a series of three high pitched beeps. This alerted the observer that the next trial was beginning and to refocus their attention on the fixation point.

2.2.2 Analyses

The primary dependent measures were the average duration and the proportion of time spent in each of the four perceptual states recorded. Average duration represents the average amount of time spent perceiving a particular percept before transitioning to a different perceptual state; proportion of time represents the average overall proportion of time a particular percept was dominant. Previous studies commonly have reported only one of these two measures. However, the two measures convey different information, and therefore we report both.

Perceptual states with durations less than 300 ms were excluded from our analyses in order to remove any incidental button presses. Additionally, a trial was excluded from further data analyses, if an observer either recorded only a single percept for the span of the entire trial, or did not press any buttons. Three observers had at least one trial excluded for that reason: a large size/low-contrast trial for a young adult (female); four large size/low-contrast and one small size/high-contrast trials for a junior-senior (female); and three small size/low-contrast, three small size/high-contrast, two large size/low-contrast, and two large size/high-contrast for a junior-senior (male). Valid trials and responses for both our average duration and proportion of time measures were subjected to separate 3 (age group) × 2 (size) × 2 (contrast) ANOVAs for each of the four reported percepts (two Exclusive; Mixed; and Other). Generalized eta squared values (η_N^2) are reported for effect sizes (see Olejnik and Algina, 2003; Bakeman, 2005, for review).

The two Exclusive percepts were analyzed in a manner to identify the Exclusive percept with a greater dominance per trial. Since, here each Exclusive percept is correlated to a specific eye we label the dominant Exclusive percept Eye 1 (E1), and the other Exclusive percept Eye 2 (E2). For the average duration measure, E1 for each trial was defined as the eye that yielded the Exclusive percept with the longest average duration, and E2 was defined as the other eye. For the proportion of time measure, E1 for each trial was defined as the eye that yielded the exclusive percept in which the observer spent the greatest proportion of time, and E2 was defined as the other eye. Thus, whether the right eye or the left eye was labeled E1 could vary across trials and dependent measures. Preliminary analyses indicated that the number of trials that the same eye was labeled E1 for average duration or for proportion of time did not differ among age groups, and the number of trials in which the same eye was defined as E1 for both average duration and proportion of time also did not differ across groups ($p \geq 0.259$ in all cases). Hence, it is unlikely that group differences in the consistency of which eye was defined as E1 contributed to any observed group differences in our primary dependent measures.

2.2.3 Results

Exclusive Percepts

The ANOVA conducted on the average duration of the E1 percept revealed significant main effects of age, size, and contrast, and a significant age × size interaction (see Table 2.2). As seen in the left panel of Figure 2.1, this interaction reflects the fact that the difference between the E1 average duration in the young adult group and the two older groups was greater with the small stimuli than the large stimuli. Figure 2.1 also makes it apparent both older adult groups had significantly longer E1 average durations across all conditions. The significant main effect of contrast reflects the fact that the average duration of the E1 percept was slightly (0.70 s) longer with low-contrast stimuli, an effect that did not depend significantly on stimulus size or age group.

The results of an ANOVA conducted on the average durations of E2 percepts are shown in Table 2.3. There was a significant main effect of age, as well as a significant age × size interaction. This interaction is illustrated in the right panel of Figure 2.1, where it can be seen that the average duration of E2 percepts was longer in older adults than younger adults for the small and large rivalrous stimuli.

Table 2.2: E1 Percept: Average Duration

	SS	num Df	Error SS	den Df	F	Pr(>F)	η^2_N
Age Group	474.0	2	426.92	21	11.66	< 0.001	0.44
Size	28.6	1	25.77	21	23.34	< 0.001	0.04
Contrast	23.9	1	108.66	21	4.61	0.044	0.04
Age Group × Size	13.4	2	25.77	21	5.48	0.012	0.02
Age Group × Contrast	5.4	2	108.66	21	0.52	0.600	0.01
Size × Contrast	1.4	1	52.17	21	0.57	0.458	< 0.01
Age Group × Size × Contrast	5.6	2	52.17	21	1.12	0.344	0.01

Table 2.3: E2 Percept: Average Duration

	SS	num Df	Error SS	den Df	F	Pr(>F)	η^2_N
Age Group	51.52	2	102.76	21	5.26	0.014	0.26
Size	0.54	1	9.22	21	1.24	0.279	< 0.01
Contrast	2.65	1	22.69	21	2.45	0.132	0.01
Age Group × Size	3.30	2	9.22	21	3.76	0.04	0.02
Age Group × Contrast	5.20	2	22.69	21	2.40	0.115	0.03
Size × Contrast	0.23	1	11.66	21	0.41	0.530	< 0.01
Age Group × Size × Contrast	1.67	2	11.66	21	1.50	0.245	0.01

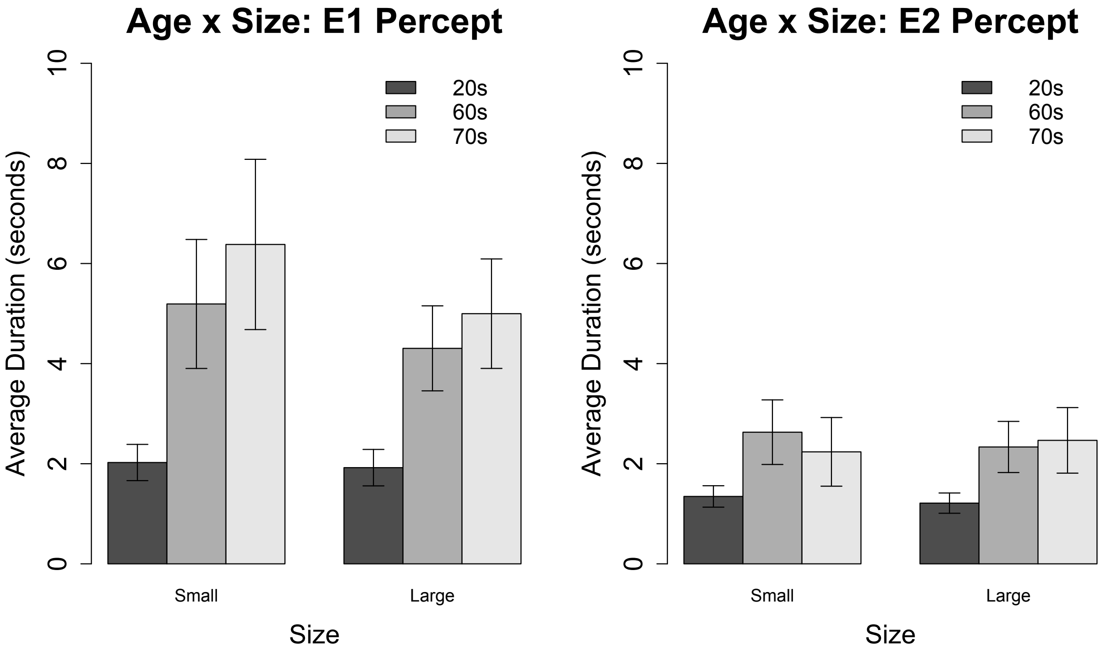


Figure 2.1: Left Panel: Average durations for the E1 percept for the small and large stimuli size conditions, averaged across stimulus contrasts, are shown for each age group. Right Panel: Average duration for the E2 percept for the small and large stimuli size conditions, averaged across stimulus contrasts, are shown for each age group. Error bars represent ±1 SEM.

The results of the ANOVA on the proportion of time spent viewing the E1 percept can be viewed in Table 2.4. As was found with the average duration measure, the ANOVA revealed significant main effects of age group and stimulus size; however, unlike what was found with average duration, there was no main effect of contrast, nor was there any evidence for an age × size interaction. Hence, the ANOVA suggests that the proportion of time seeing the E1 percept increased with age and was slightly (0.05) lower for the large stimulus conditions, irrespective of stimulus contrast. The results of the ANOVA on the proportion of time seeing the E2 percept are shown in Table 2.5. Unlike what was found with the average duration measure, the ANOVA failed to find significant effects of age group and size; however, it did reveal a significant main effect of contrast, indicating that the proportion of time seeing the E2 percept was slightly (0.08) greater in the high-contrast conditions.

As noted above, age affected the proportion of time spent viewing the E1 percept, but not the E2 percept. By taking a difference score of the proportion of time spent viewing E1 and E2 for each age group we unsurprisingly found that this measure of monocular dominance increased with age (see Figure 2.2). Post-hoc t-tests indicated monocular dominance was greater for junior-seniors than young adults ($t(10.45) = -2.81$, $p = 0.018$) and greater for senior-seniors than junior-seniors ($t(12.17) = -3.27$, $p = 0.007$, significant with Bonferroni correction for multiple comparisons).

Table 2.4: E1 Percept: Proportion of Time

	SS	num Df	Error SS	den Df	F	Pr(>F)	η_N^2
Age Group	0.77	2	0.87	21	9.25	0.001	0.36
Size	0.14	1	0.10	21	28.97	< 0.001	0.09
Contrast	0.33	1	0.37	21	0.82	0.374	0.01
Age Group × Size	0.01	2	0.10	21	0.46	0.638	< 0.0
Age Group × Contrast	0.04	2	0.37	21	1.12	0.343	0.03
Size × Contrast	0.00	1	0.04	21	0.20	0.657	< 0.01
Age Group × Size × Contrast	0.00	2	0.04	21	0.78	0.472	< 0.01

Table 2.5: E2 Percept: Proportion of Time

	SS	num Df	Error SS	den Df	F	Pr(>F)	η^2_N
Age Group	0.01	2	0.51	21	0.23	0.797	0.01
Size	0.00	1	0.11	21	00.00	0.979	< 0.01
Contrast	0.34	1	0.27	21	26.66	< 0.001	0.26
Age Group × Size	0.02	2	0.11	21	2.02	0.158	0.02
Age Group × Contrast	0.05	2	0.27	21	2.04	0.155	0.05
Size × Contrast	0.00	1	0.10	21	0.12	0.728	< 0.01
Age Group × Size × Contrast	0.01	2	0.10	21	0.74	0.493	0.01

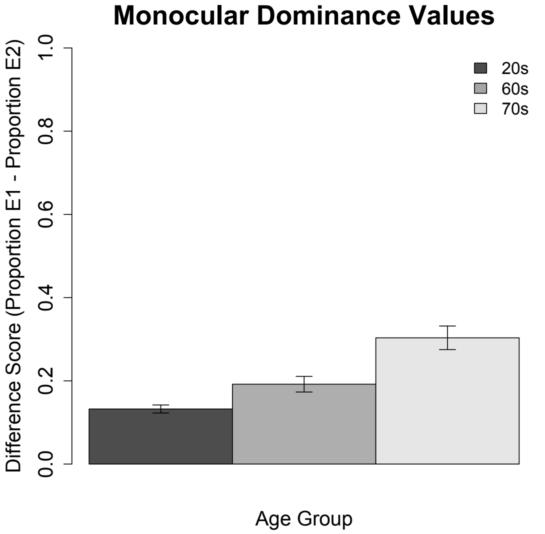


Figure 2.2: Proportion of monocular dominance is shown for each age group. Error bars represent ±1 SEM.

Mixed Percepts

The ANOVA performed on the average duration of Mixed percepts yielded significant main effects of size ($F(1, 21) = 7.24$, $p = 0.014$, $\eta^2_N = 0.05$) and contrast ($F(1, 21) = 8.51$, $p = 0.008$, $\eta^2_N = 0.08$), and a significant age × contrast interaction ($F(1, 21) = 5.15$, $p = 0.015$, $\eta^2_N = 0.10$). The main effect of size was due to the fact that the duration of Mixed percepts was longer for the large stimuli (3.56 s) than the small stimuli (2.60 s). The age × contrast interaction is illustrated in the left-panel of Figure 2.3: the average duration of Mixed percepts was longer for low- than high-contrast stimuli for the junior-seniors group but not the other groups.

The ANOVA performed on the proportion of time spent viewing Mixed percepts revealed significant main effects of age ($F(2, 21) = 4.91$, $p = 0.018$, $\eta^2_N = 0.23$), size ($F(1, 21) = 10.97$, $p = 0.003$, $\eta^2_N = 0.03$), and contrast ($F(1, 21) = 6.35$, $p = 0.020$, $\eta^2_N = 0.08$). None of the interactions were significant ($p > 0.19$ in all cases). The main effect of age is illustrated in the right panel of Figure 2.3: the proportion of time spent perceiving Mixed percepts differed between young adults and senior-seniors ($t(13.91) = 3.10$, $p = 0.008$, two-tailed, significant with Bonferroni correction for multiple comparisons), but not young adults and junior-seniors ($t(13.93) = 1.19$, $p = 0.254$, two-tailed) or junior- and senior-seniors ($t(14.00) = 1.97$, $p = 0.068$, two-tailed). The main effects of size and contrast were due to the proportion of time seeing Mixed percepts being slightly greater for large (0.40) than small stimuli (0.36), and for low- (0.42) than high- (0.35) contrast stimuli. Unlike what was found with the average duration measure, there was no evidence that the effect of contrast on the proportion of time seeing Mixed percepts varied across age groups.

Other Percepts

Subjects in all age groups and conditions were much less likely to report seeing an Other percept than Exclusive or Mixed percepts. Indeed, the average duration and the proportion of time were both near zero in most conditions and age groups. Because of possible floor effects, ANOVAs on these data are not appropriate. Nevertheless, our data suggest that Other percepts may occur for a greater proportion of time and last

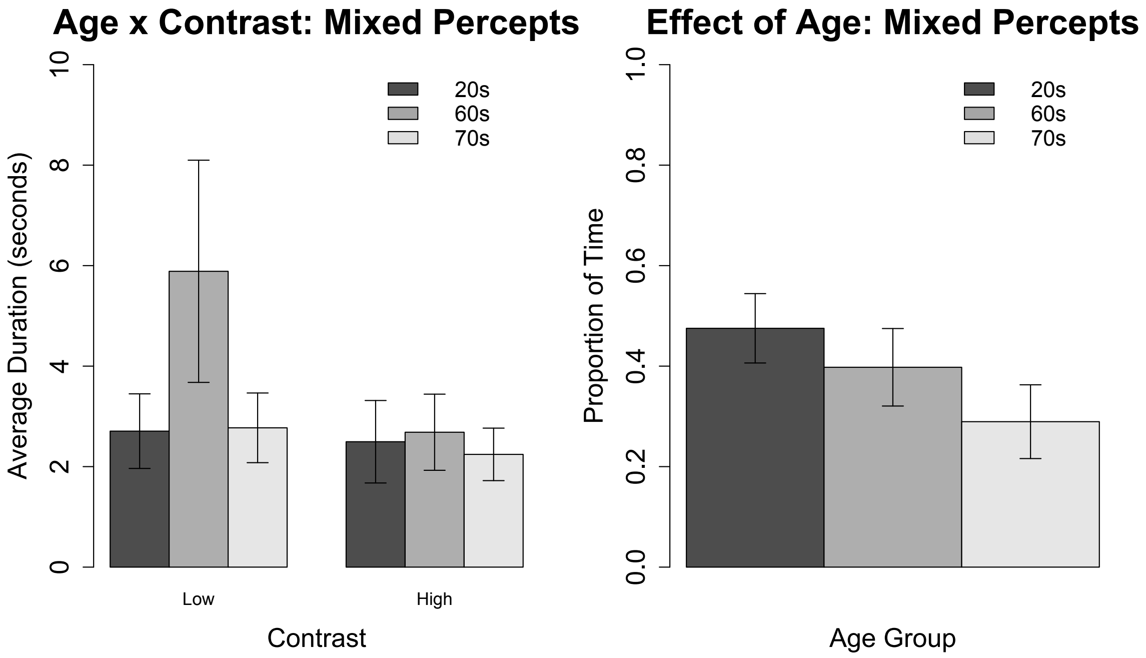


Figure 2.3: Left panel: Average durations for the Mixed percepts for the low- and high-stimuli contrast conditions, averaged across stimulus size, are shown for each age group. Right panel: The proportion of time spent viewing the Mixed percepts is shown for each age group. Error bars represent ±1 SEM.

for longer durations for senior-seniors, especially with low-contrast stimuli (Figure 2.4).

Sequential Pattern of Alternations

The average duration and proportion of time measures reveal useful information about rivalry; however, rivalry percepts change continuously throughout a trial. Therefore, we examined the sequential patterns of perceptual alternations to derive a more comprehensive investigation of how aging affects binocular rivalry. To make the analysis tractable, we started by sorting three-step sequences of percepts into

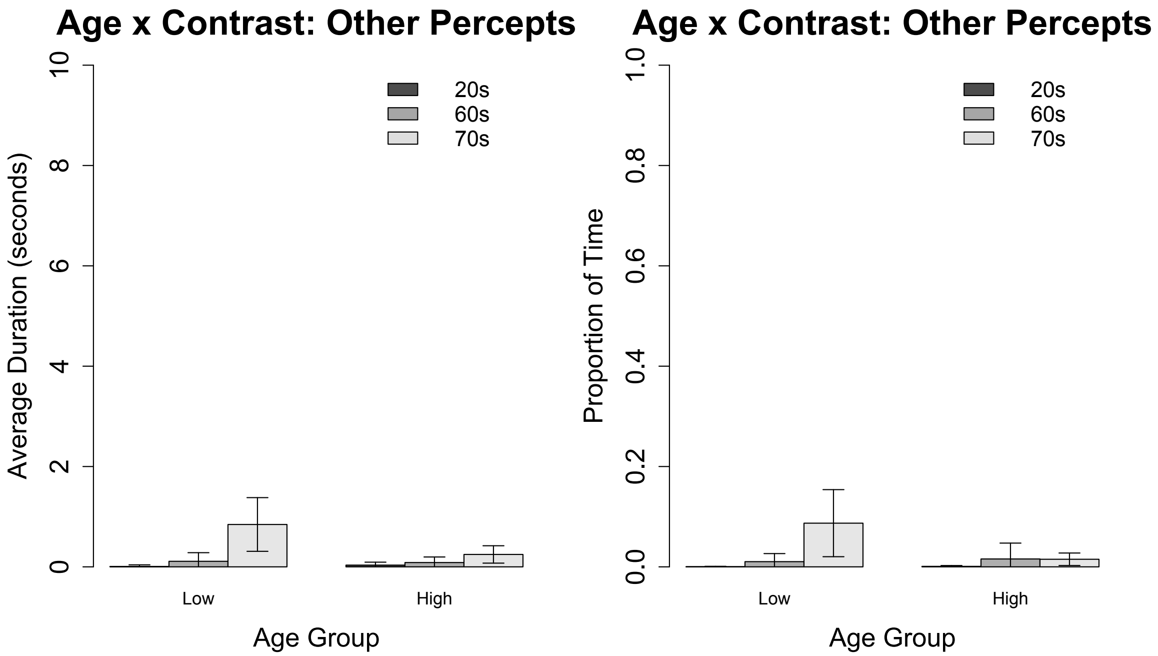


Figure 2.4: Average duration for the Other percepts (left panel) and the proportion of time spent in the Other percepts (right panel) are shown. Results for each age group are shown for both the low- and high-contrast conditions. Error bars represent ±1 SEM.

groups defined by the order of the first two perceptual states, and then analyzed the proportion of all possible third percepts for each of the initial sequential transition pairs. For example, we identified all three-step alternations that began with the initial two-step sequential transition of the E1 percept followed by a Mixed percept (i.e., E1 → Mixed → ?) and then calculated the proportion of times that the third percept in the sequence was E2, E1, or Other. To further simplify the analysis of the 36 potential sequential triads, analyses are only reported here for sequences where the mean occurrence of the initial two-step transition per trial across all conditions and age groups was greater than twenty percent. From this process, the sequential groups of E1 → Mixed → ? and Mixed → E1 → ? were selected for further analysis and are reported below.

The proportions of E1 → Mixed → ? sequences are shown in Figure 2.5. In all conditions and age groups, the E1 → Mixed → Other sequence was much less likely to occur than the E1 → Mixed → E1 and E1 → Mixed → E2 sequences. In the small-pattern, low-contrast condition, the E1 → Mixed → E2 sequence occurred more frequently than the E1 → Mixed → E1 sequence in younger subjects, but not older subjects, in which the two sequences occurred about equally often. In the large-pattern, low-contrast condition, the E1 → Mixed → E2 sequence occurred more frequently than the E1 → Mixed → E1 sequence in the young adults and junior-seniors groups, but the reverse was true for the oldest group. Finally, differences among age groups appeared to be minimal in the high-contrast conditions.

Because the proportions of Other percepts were near zero in most conditions, we simplified our analyses by focusing on the sequences that ended with E1 and E2. First, we conducted separate 3 (age group) × 2 (contrast) × 2 (size) ANOVAs on the arcsine-transformed, since these results were non-normal, E1 and E2 proportions. For the E1 sequence, the ANOVA revealed a significant age × size × contrast interaction ($F(2, 21) = 5.91$, $p = 0.009$, $\eta^2_N = 0.09$). Follow-up analyses revealed a significant simple main effect of age group in the large-pattern, low-contrast condition ($F(2, 21) = 6.51$, $p = 0.006$, $\eta^2_N = 0.38$), but not in the other conditions ($p \geq 0.29$ in all cases). The analyses of E2 proportions yielded a significant main effect of age ($F(2, 21) = 4.71$, $p = 0.02$, $\eta^2_N = 0.10$), which reflected the fact that the proportion of E2 sequences declined with age ($M_{20s} = 0.68$; $M_{60s} = 0.61$; $M_{70s} = 0.50$). There was also a main effect of contrast ($F(1, 21) = 9.55$, $p = 0.006$, $\eta^2_N = 0.09$). None of the interactions with age approached significance ($p \geq 0.10$ in all cases).

Finally, we calculated the difference between the proportions of E1 and E2 percepts (i.e., p(E1) - p(E2)). The difference scores, which are plotted in Figure 2.6, indicate the median scores generally were negative, which means transitions to E2 were, generally, more frequent than to E1. Exceptions to this trend occur for the medians for the oldest group at low contrast with small and large stimuli, and the median for junior-seniors in the small/low-contrast condition. These results were then analyzed with a 3 (age group) × 2 (contrast) × 2 (size) ANOVA. The age × size × contrast interaction was significant ($F(2, 21) = 6.56$, $p = 0.006$, $\eta^2_N = 0.09$), and we therefore evaluated pairwise group differences separately in each condition using Dunnett's T3 test ($\alpha = 0.05$). Our analysis found two significant differences between groups: In the small-pattern, low-contrast condition, the difference between the 20- and 60-year-olds was significant, and in the large-pattern, high-contrast condition, the difference between the 60- and 70-year-olds was significant. In summary, these analyses suggest that E1 → Mixed → E1 sequences were relatively more common in older adults than younger adults, and that this age difference was more apparent at low stimulus contrast.

The proportions of Mixed → E1 → ? sequences are shown in Figure 2.7. In all conditions and age groups, the Mixed → E1 → Mixed sequence was most likely to occur, followed by the Mixed → E1 → E2 sequence. The Mixed → E1 → Other sequence occurred rarely, except in the oldest group where it occurred approximately equally as often as the Mixed → E1 → E2 sequence. We analyzed the arcsine-transformed proportions of E2 and Mixed percepts with separate 3 (age group) × 2 (size) × 2 (contrast) ANOVAs. We did not submit the proportion of Other percepts to an analysis of variance because the data were distributed non-normally, primarily due

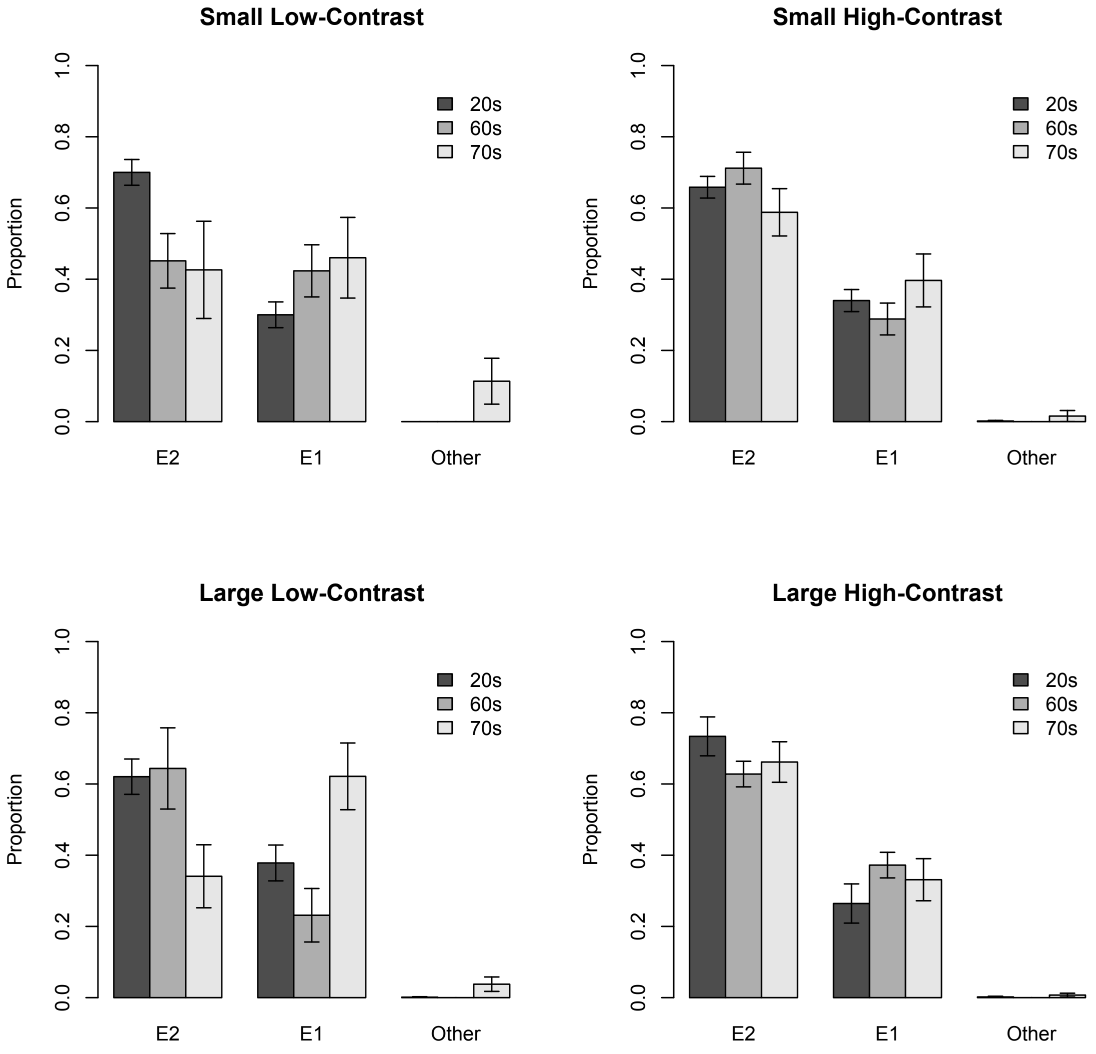


Figure 2.5: Proportion of each sequence in the E1 → Mixed → ? set are shown for each condition and age group. Error bars represent +/- 1 standard error.

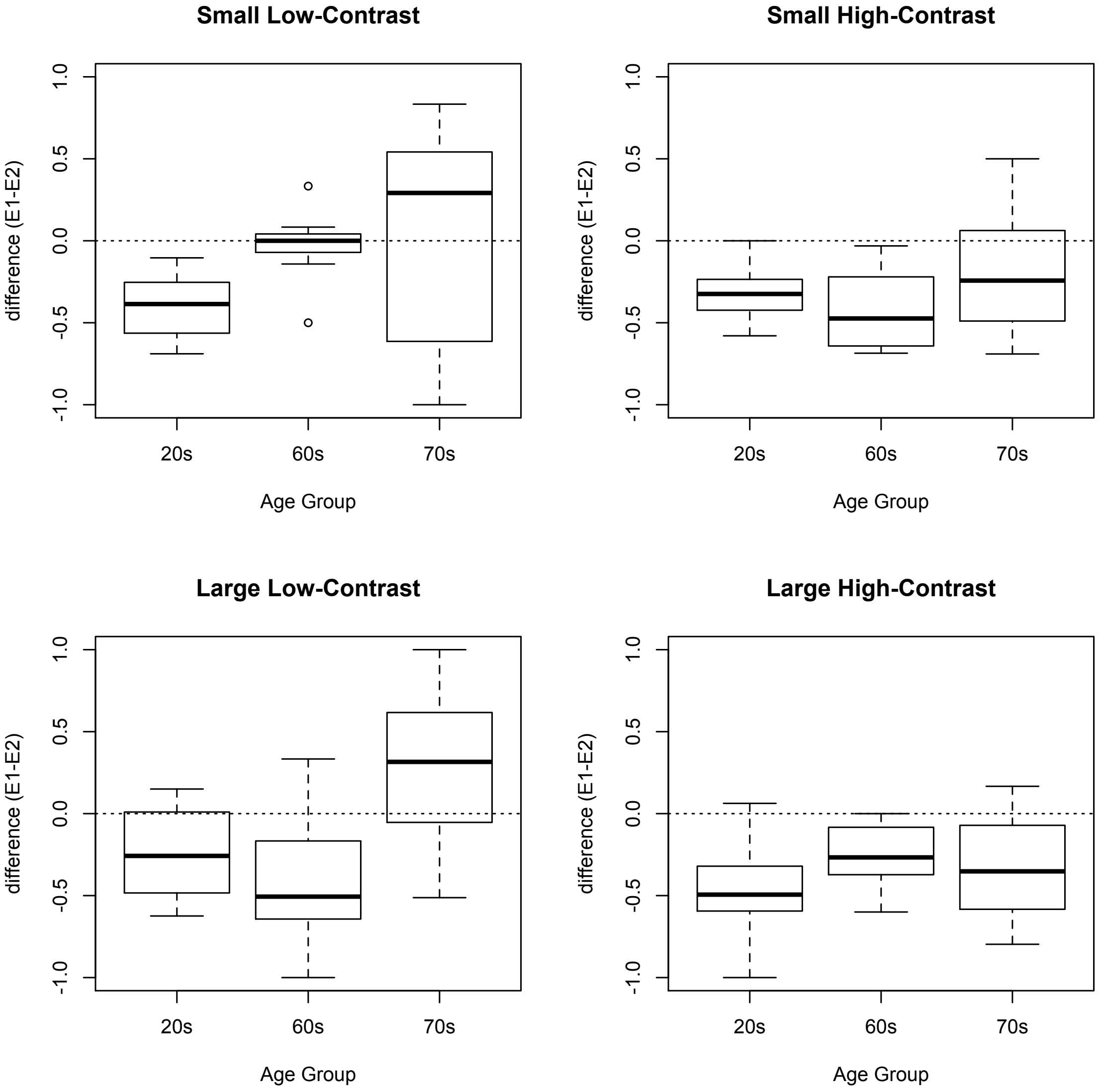


Figure 2.6: Difference scores (p(E1 → Mixed → E1) - p(E1 → Mixed → E2)) are shown for each condition and age group.

to a pronounced floor effect in all conditions for two of the age groups. Nevertheless, Figure 2.7 suggests that Mixed → E1 → Other sequences were more frequent in senior-seniors than the other two groups in all conditions.

As was done with E1 → Mixed → ? sequences, we simplified the data by computing the difference between the proportions of Mixed and E2 percepts (i.e., p(Mixed) - p(E2)). The difference scores, which are plotted in Figure 2.8, generally are positive, which suggests that Mixed→ E1→ Mixed sequences were more common than Mixed→ E1→ E2 sequences. Unlike what was found with E1 → Mixed → ? sequences, there is no obvious effect of age group. The results were analyzed with a 3 (age group) × 2 (size) × 2 (contrast) ANOVA. None of the effects of age approached significance ($p \geq 0.10$ in all cases). In summary, these analyses suggest that relative proportions of Mixed → E1 → Mixed and Mixed → E1 → E2 sequences do not change significantly with age.

Aging differences in sequential transitions were driven by the low-contrast conditions; thus, we decided to further investigate these low-contrast results with a secondary analysis. The coefficient of variation (CV) has been utilized to provide an index for the influence of adaptation and noise on rivalry alternations (Kim et al., 2006; Shpiro et al., 2009). The CV is calculated by taking the standard deviation of the sample of average durations divided by mean average durations for that sample. According to this form of analysis, binocular rivalry alternations driven predominantly by neural adaptation would be fairly consistent; thus, the CV value would approach zero. Alternations driven almost entirely by noise would be exponentially distributed; thus, the CV value would approach one. Table 2.6 shows the average CV values for the

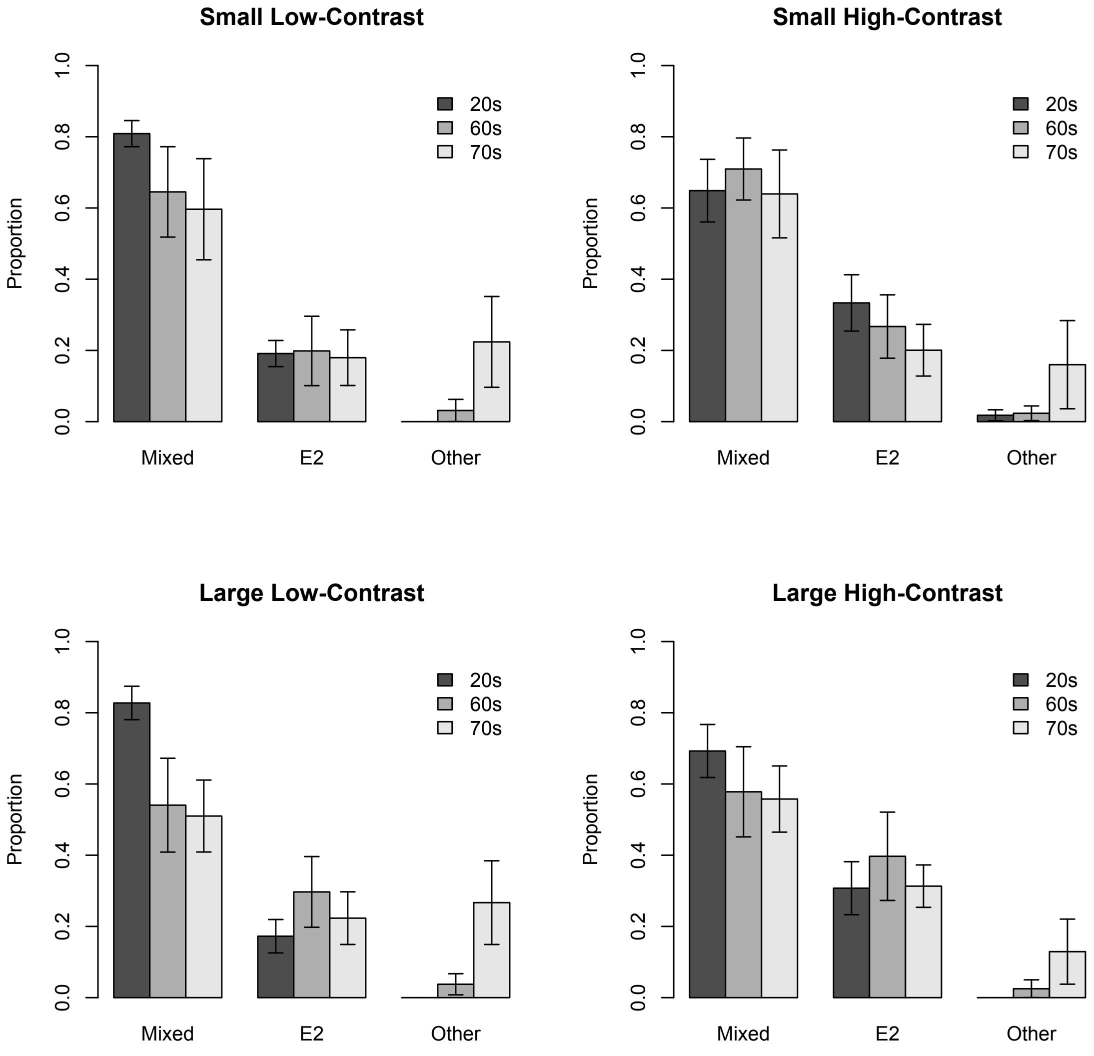


Figure 2.7: Proportion of each sequence in the Mixed → E1 → ? set are shown for each condition and age group. Error bars represent +/- 1 standard error.

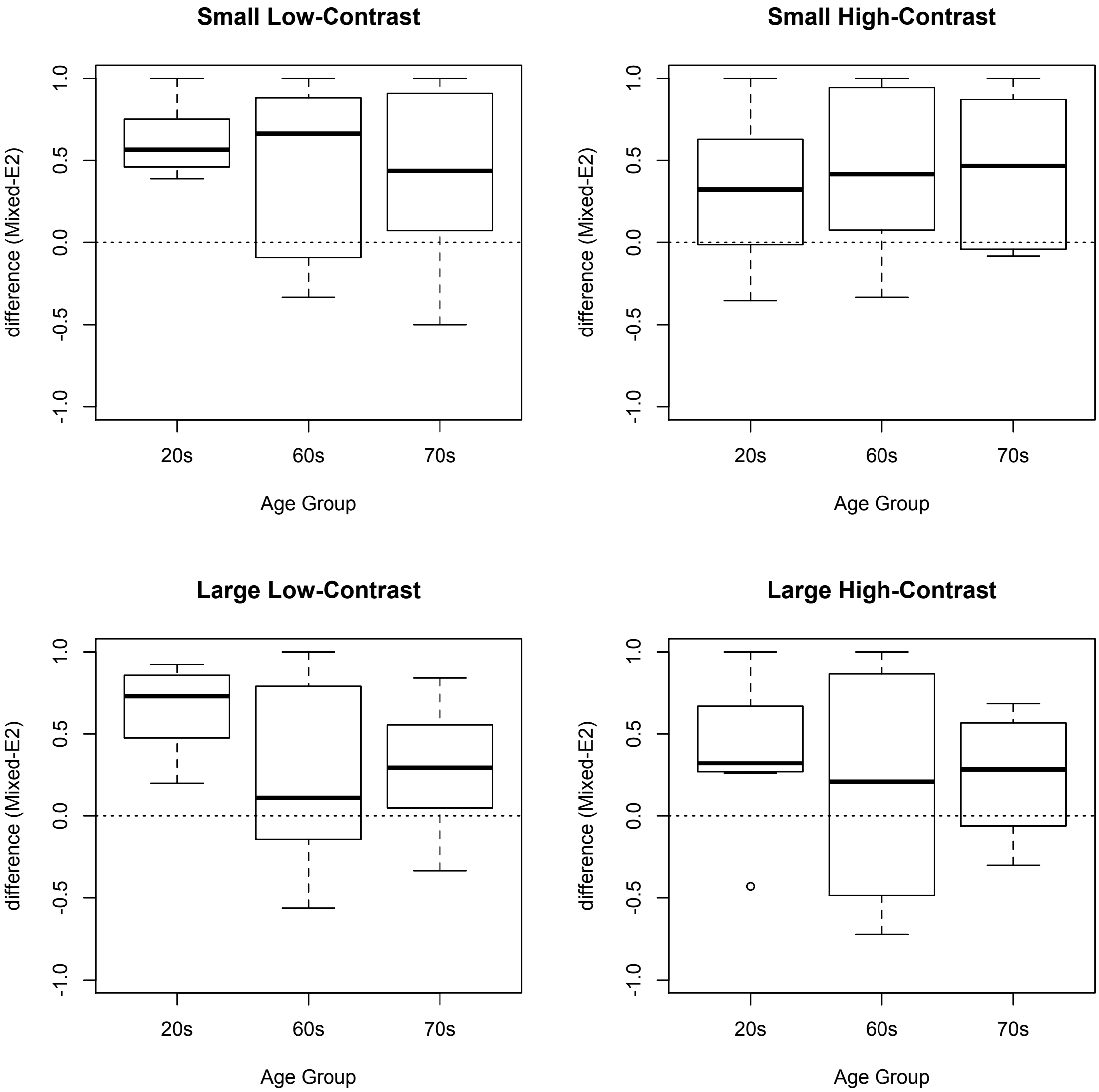


Figure 2.8: Difference scores (p(Mixed → E1 → Mixed) - p(Mixed → E1 → E2)) are shown for each condition and age group.

average durations for E1 and E2 percepts for each age group for the low-contrast conditions. Post-hoc *t*-tests indicated a significant difference between the CV values for older and younger observers, with the senior-seniors expressing a higher CV for both E1 ($t(11.78) = -2.78$, $p = 0.017$, two-tailed, approaching significance with Bonferroni correction for multiple comparisons), and E2 ($t(14) = -3.38$, $p = 0.004$, two-tailed, significant with Bonferroni correction for multiple comparisons). For the E1 percept, the junior-seniors also expressed significantly higher CV values than younger adults ($t(10.24) = -2.48$, $p = 0.032$, two-tailed). There were no significant differences in the CV values for the two senior groups for the E1 ($t(13.27) = 0.15$, $p = 0.885$, two-tailed) or E2 ($t(8.22) = 0.59$, $p = 0.571$, two-tailed) percepts.

Table 2.6: Coefficient of Variation: Low-Contrast

Age Group	E1	E2
Young Adults: 20s	0.53	0.51
Junior-Seniors: 60s	0.69	0.79
Senior-Seniors: 70s	0.69	1.00

2.2.4 Discussion

Previous studies reported that the average duration of Exclusive percepts is greater in older than younger adults (Jalavisto, 1964; Ukai et al., 2003). We replicated this result, and also showed that the age difference in the average duration of the E1 percept, but not the E2 percept, depended on stimulus size. The significant main effect of size for average duration and proportion of time for Mixed percepts is consistent with previous studies of young adults that found increasing the size of rivalrous stimuli increases the duration of Mixed percepts and that the proportion of time viewing

Mixed percepts was greater with larger than smaller stimuli (Blake et al., 1992). Increasing contrast has also previously been shown to increase the proportion of time spent viewing Exclusive percepts in young adults (Hollins, 1980), and here we show that this is due specifically to an increase in proportion of time in the E2 percept and a simultaneous decrease in the proportion of time viewing Mixed percepts. We also found that shorter average duration periods occurred for the E1 percepts for higher contrast conditions. Shorter average durations could be one explanation for increased rivalry rate; thus our finding corresponds with previous findings on contrast that state rivalry rate increases with increasing contrast (Hollins, 1980; Levelt, 1965).

Our results also introduce several novel findings of differences in binocular rivalry characteristics with age. Of particular interest is our finding that monocular dominance increased with aging. It is important to note that, due to the dynamic nature of rivalry, age differences in monocular dominance could influence age differences in other characteristics of rivalry, such as the average duration and/or proportion of time for fading, presumably represented by measures of Other percepts. For example, the strong monocular dominance in older adults may make it difficult for the suppressed Exclusive percept to regain dominance before neural adaptation of the dominant Exclusive percept causes the image to fade, whereas the moderate eye dominance found in younger adults could allow for a perceptual transition between E1 and E2 before adaptation causes fading.

The age differences we found in the proportion of time spent viewing Mixed percepts are particularly interesting, since Mixed percepts are often considered to represent a transitional state between two Exclusive percepts. Neuroimaging studies have provided evidence for an association between activation of the right-hemisphere frontal and parietal areas during transitions in perceptual states (Lumer et al., 1998; Sterzer and Kleinschmidt, 2007). Knapen et al. (2011) provided evidence that the right-lateralized fronto-parietal network also is activated by the perceptual influence of transitions. The fronto-parietal region changes with age (Andrews-Hanna et al., 2007; Madden, 2007) and thus might underlie the decline in Mixed percepts that was found in the current study. It has also been suggested that a lack of effective visual integration may influence the proportion of Mixed percepts. Kovacs and Eisenberg (2005) inferred that the faster switching rate they found in children compared to young adults was due to a greater proportion of Mixed percepts, presumably caused by poor contour integration in children. However, this explanation does not seem to match with the current results showing a decrease of proportion of Mixed percepts in older adults, since older adults also have been shown to have poor contour integration (Roudaia et al., 2008). At the present time there is not sufficient evidence to explain the decrease in Mixed percepts with age. Further research is necessary to determine what factors correspond to the apparent developmental trajectory of proportion of Mixed percepts with aging.

Also, it has been generally assumed that rivalry follows a pattern of switching from one Exclusive percept to a Mixed percept then to the second Exclusive percept. However, this transition sequence is only one of several possible sequences that occur in normal binocular rivalry. So-called “return transitions”, which refers to a sequence of an Exclusive percept followed by a Mixed percept which then is followed by the first Exclusive percept, occur occasionally during rivalry in younger adults (Mueller and Blake, 1989; Brascamp et al., 2006) and are thought to be related to internal noise (Brascamp et al., 2006). Thus, the significant increase in return transitions in older adults, specifically the senior-senior age group, could reflect the influence of age-related increases in internal noise in the neural circuitry underlying rivalry, just as previous studies have found evidence for age-related increases in internal noise in other visual tasks (Betts et al., 2007; Bogfjellmo et al., 2013; Pardhan, 2004). This claim is weakened somewhat by the observation that Brascamp et al.'s computational model predicts that elevated internal noise should also be associated with a lengthening of the average duration of Mixed percepts. However, overall we did not find evidence for increased average durations for Mixed percepts in older adults. Therefore, our results suggest that i) the age-related increase in return transitions were not caused by elevated internal noise; or ii) that the link between return transitions and internal noise embodied in Brascamp et al.'s computational model needs to be modified.

Because of this ambiguity, a secondary analysis, the coefficient of variation (CV), was conducted to allow us to further investigate whether higher internal noise may be a factor in the alternation sequences of older adults in low contrast conditions. The CV values listed in Table 2.6 suggest internal noise is a greater factor in binocular rivalry for older adults than in younger adults. The CV values for the E2 average durations are particularly striking. The average CV for young adults suggests the influence of both neural adaptation and internal noise, while the average C.V. values for the senior-senior group suggests the influence of primarily internal noise. Overall, these CV values and the significantly higher number of return transitions for the E1 percept indicate the strong potential for a greater influence of internal noise on binocular rivalry alternations with aging.

Before the potential implications of these findings can be discussed in greater detail in relation to theoretical facets of binocular rivalry, it is important to rule out several physiological factors that may have caused differing results in younger and older adults. The following experiments serve to provide supplementary investigations to distinguish between whether these findings are likely due to neural changes in the binocular visual system with aging or other factors.

2.3 Experiment 2: Reporting Accuracy (Motor Delay and Pseudo-rivalry)

Many of the aging differences in binocular rivalry highlighted in Experiment 1 have interesting theoretical implications if due to neural changes. It is important to examine whether factors associated with aging, other than neural changes, could be causing these results. In our experiments, Exclusive percepts and Mixed percepts were reported by pressing different buttons, whereas Other percepts were reported by releasing all buttons. Hence, potential age differences in motor control might have contributed to the age differences that we attributed to differences in binocular rivalry. The following experiment examined whether age-related changes in motor responses could account for the age differences found in Experiment 1.

2.3.1 Method

Observers

All of the observers from Experiment 1 participated in Experiment 2 on the following day.

Apparatus

Same as in Experiment 1.

Stimulus Displays

For Experiment 2a, on each trial the red and cyan channels displayed the same oblique grating. Thus both eyes always viewed the same Exclusive percept, and therefore observers should not experience binocular rivalry. As in Experiment 1, Experiment 2a presented stimuli at two stimulus sizes and two contrasts. Experiment 2b was similar to Experiment 2a, except that a series of alternating Exclusive percepts was presented on each trial. These presentations of Exclusive states represent a form of pseudo-rivalry.

Procedure

Before the start of Experiment 2a there was a one minute adaptation period, during which the observer attended to a fixation point, presented in the center of the monitor. At the start of each trial, the fixation point and rectangular frame were presented for 1.5, 2.25, 3, or 3.75 s. This period of time was randomized across trials to discourage the observers from guessing when they should begin to respond. On each trial, either a clockwise or counter-clockwise grating was presented to both eyes. Observers were instructed to press the corresponding button for the entire duration the grating appeared on the screen. The duration of each grating was randomly chosen from a set of stimulus presentation times that spanned the typical average duration for Exclusive percepts: 1.73, 2.25, 2.68, 4.56, 5.93, and 7.07 s. Stimulus durations of 1.73 and 4.56 s corresponded to the mean average duration for Exclusive percepts for younger and older adults, respectively, that were measured during pilot experiments. Each duration was presented twice with each stimulus orientation for each size-contrast condition, resulting in 16 trials.

Individuals were allowed a short break (e.g., 5-15 minutes) after the completion of 2a before beginning Experiment 2b. Experiment 2b began with a one minute adaptation period. Observers were instructed to track their perceptual states in the same manner as Experiment 1. The observers were not informed that alternations in perceptual state were controlled by the computer, rather than by binocular rivalry as in Experiment 1. However, observers were told that they would only need to respond to the two Exclusive percepts and that unlike Experiment 1 Mixed percepts would not be experienced. To prevent observers from guessing when to switch button responses, the duration of the two Exclusive stimuli presented by the computer were randomly selected from a set of stimulus durations consisting of 1.73, 2.25, 2.68, 4.56, 5.93, and 7.03 s. Each possible duration was assigned to each Exclusive stimulus (i.e., counterclockwise and clockwise grating) once per trial. Trials were approximately 40 s, and inter-trial intervals were 20 s. There were four trials in each of four conditions (2 sizes × 2 contrasts), for a total of 16 trials.

2.3.2 Results and Discussion

For each trial in Experiment 2a, we computed the absolute value of the difference between the stimulus duration recorded by the observer and the actual stimulus presentation. These values were submitted to a 2 (age group) × 2 (size) × 2 (contrast) mixed model ANOVA. The results are shown in Table 2.7. No main effects or interactions were found. This indicates younger and older adults have similar accuracy when reporting percepts. Thus, the differences in average durations between younger adults and older adults in Experiment 1 are most likely not caused by age differences in motor response.

Table 2.7: Motor Response Times

	SS	num Df	Error SS	den Df	F	Pr(>F)	η^2_N
Age Group	0.04	2	5.35	21	0.08	0.926	< 0.01
Size	0.07	1	3.97	21	0.37	0.552	0.01
Contrast	0.00	1	0.87	21	0.03	0.868	< 0.01
Age Group:Size	0.36	2	3.97	21	0.94	0.406	0.03
Age Group:Contrast	0.02	2	0.87	21	0.19	0.827	< 0.01
Size:Contrast	0.00	1	0.63	21	0.08	0.779	< 0.01
Age Group:Size:Contrast	0.00	2	0.63	21	0.04	0.961	< 0.01

Because of the accuracy reporting Exclusive percepts found for both age groups in Experiment 2a, for Experiment 2b only the Other percept category was analyzed for Experiment 2b. As seen in Table 2.8 and 2.9, a 3-way ANOVA (age group × size × contrast) for both the average duration and proportion of time spent in the Other percept failed to find any significant main effects or interactions. The absence of a main effect of age and any interactions involving age indicates that the differences between age groups in both the proportion of time and average duration of the Other percept that were found in Experiment 1 probably are not due to differences in motor responses.

Table 2.8: Pseudo-rivalry (Other Percepts Average Duration)

	SS	num Df	Error SS	den Df	F	Pr(>F)	η^2_N
Age Group	0.06	2	0.27	21	2.40	0.116	0.07
Size	0.00	1	0.27	21	0.02	0.907	< 0.01
Contrast	0.00	1	0.16	21	0.18	0.677	< 0.01
Age Group:Size	0.00	2	0.27	21	0.16	0.857	0.01
Age Group:Contrast	0.00	2	0.16	21	0.27	0.765	0.01
Size:Contrast	0.00	1	0.09	21	0.60	0.449	< 0.01
Age Group:Size:Contrast	0.01	2	0.09	21	1.17	0.328	0.01

Table 2.9: Pseudo-rivalry (Other Percept Proportion)

	SS	num Df	Error SS	den Df	F	Pr(>F)	η^2_N
Age Group	0.00	2	0.00	21	1.88	0.177	0.05
Size	0.00	1	0.00	21	0.15	0.701	< 0.01
Contrast	0.00	1	0.00	21	0.06	0.816	< 0.01
Age Group:Size	0.00	2	0.00	21	0.38	0.690	0.01
Age Group:Contrast	0.00	2	0.00	21	0.12	0.887	< 0.01
Size:Contrast	0.00	1	0.00	21	0.91	0.350	0.01
Age Group:Size:Contrast	0.00	2	0.00	21	1.59	0.227	0.02

2.4 Experiment 3: Neutral Density Filters (Luminance Control)

Retinal luminance declines with age (Weale, 1961). A reduction in retinal luminance induces a variety of changes in the visual pathway, and these changes may affect binocular rivalry. Hence, it is important to examine whether reductions in retinal luminance contributed to the age differences found in Experiment 1. The current experiment examined this issue by measuring the effects of retinal luminance on binocular rivalry in a group of young adults.

2.4.1 Method

Observers

Eight young adult observers (four male) participated in this experiment. None of the observers participated in previous experiments and all were naïve to the experience of binocular rivalry. All observers had normal or corrected-to-normal visual acuity, as well as normal stereoscopic vision. Demographics for this set of participants can be found in Table 2.11. As in other Experiments, observers were compensated for their time with either a partial course credit or reimbursement at a rate of $10.00/hour. All participants gave informed consent prior to participating in this study, and the McMaster University Research Ethics Board approved experimental protocols.

Apparatus

The apparatus was the same as Experiment 1 with the following additions. A black hard plastic covering blocked the exterior regions of the monitor. This covering

Table 2.10: Mean age (years), (I.D.P.R.), MMSE, and years of education for subjects in Experiment 3.

Age Group	Mean Age	S.D. Age	Age Range
Young Adults: 18-20s	21.00 years	SD = 2.07	18-24 years

Age Group	I.D.P.R.	MMSE Score	Years of Education
Young Adults: 18-20s	0.08	NA	17.25

allowed only a circle in the center of the monitor (18 cm in diameter) to be viewed. Supports on the front of this covering allowed for the attachment of neutral density filters, which were used to vary display luminance.

Stimulus Displays

The stimulus displays were identical to those described in the Stimulus Displays section of Experiment 1. The average luminance without the neutral density filters was 37.7 cd/m ^{2} and the average luminance with the neutral density filters was 10.0 cd/m ^{2}.

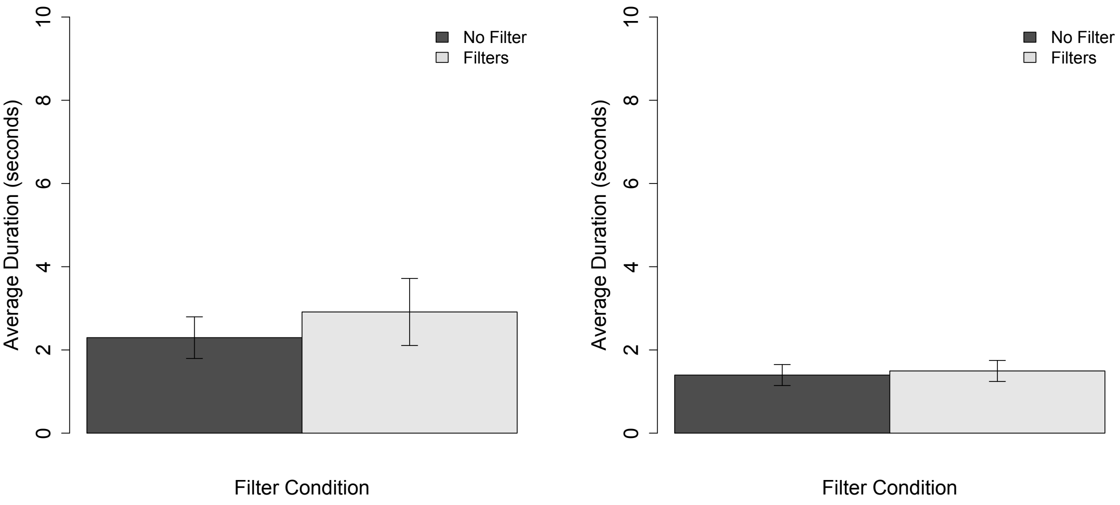
Procedure

The procedure was the same one used in Experiment 1, except the experiment was completed with and without neutral density filters. Both the non-filter condition and the filters condition were completed on the same day with a minimum of a half hour break between the two conditions. Half of the participants completed the no-filter condition first and the other half completed the filters condition first.

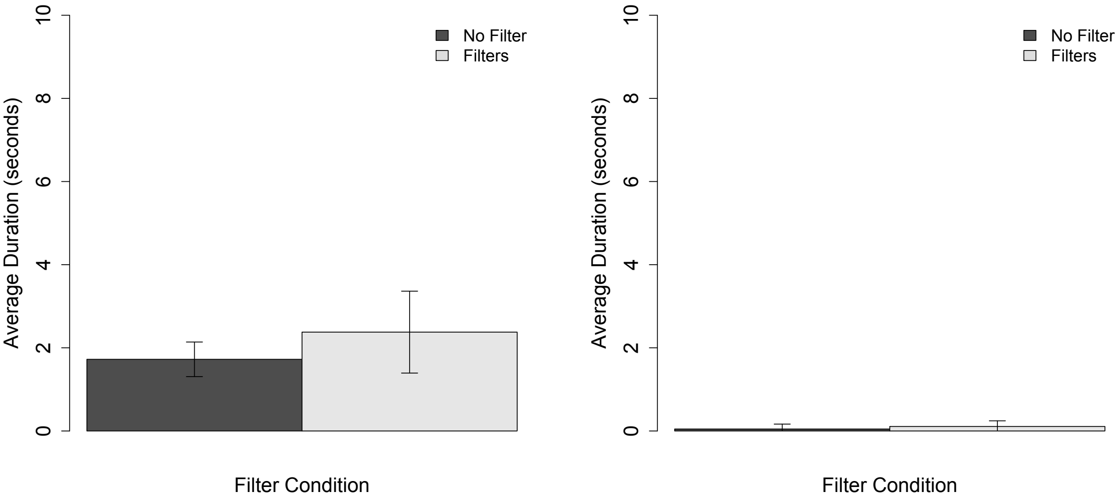
2.4.2 Results and Discussion

A 3-way ANOVA (filter condition × size × contrast) found no significant interactions of the filter conditions for the average duration of time spent viewing E1, E2, Mixed, or Other percepts; however, there was a main effect of filter condition for the E1 and Mixed percepts. These effects can be viewed in Figure 2.9. As a reminder, the most prominent age differences in Experiment 1 were found for the average duration of the E1 percept. As can be seen by viewing Figure 2.9, there is a slight trend for longer E1 percepts when luminance is lowered. However, it is important to note that this increase is minimal and does not account for the far larger increase in average duration that occurs with aging in Experiment 1. There is also a slight trend for increasing average duration with lower luminance for Mixed percepts. However, overall percepts had relatively minimal differences between the two luminance conditions (see Figure 2.9). A 3-way ANOVA (filter condition × size × contrast) found no significant main effects or interactions of the filter conditions for the proportion of time spent viewing E1, E2, Mixed, or Other percepts ($p \geq 0.088$ in all cases); thus these results are not shown.

We also examined how luminance affected the sequences of percepts with a 3-way ANOVA (filter condition × size × contrast). No main effects or interactions with the neutral density filter conditions were found with ANOVAs performed on E1 → Mixed → ? ($p \geq 0.101$ in all cases) and Mixed → E1 → ? ($p \geq 0.144$ in all cases) sequences, which were shown to have age-related differences in Experiment 1. These results indicate that age-related differences in retinal illumination probably were not responsible for the age differences in binocular alternations noted in Experiment 1.



(a) E1 Percept (b) E2 Percept



(c) Mixed Percepts (d) Other Percepts

Figure 2.9: Average duration of a.) E1 b.) E2 c.) Mixed and d.) Other percepts are shown for the two filter conditions.

2.5 Experiment 4: Ghosting (Mixed Percepts Control)

Like any method used to present images to each eye, with anaglyph glasses there is the potential for "ghosting", also known as crosstalk. Ghosting occurs during dichoptic presentations when information for an image meant to be shown exclusively to one eye is also visible to the eye for which the image was not intended. This phenomenon has the potential to create confounds in a laboratory setting, so it is important to test for potential ghosting in our apparatus. One potential confound is an increase in the proportion of Mixed percepts, since overlapping information is presented during ghosting. For this study, since we found an age difference for Mixed percepts it is important to test if this difference in Mixed percepts is potentially caused by an age difference in the influence of ghosting on perception.

2.5.1 Method

Observers

Six young adults and six older adults participated in this experiment. There were an equal number of males and females in both age groups. All observers had normal or corrected to normal visual acuity, as well as normal stereoscopic vision. Demographic information is presented in Table 2.11. Young adult observers were undergraduate and graduate students at McMaster University. Older observers were recruited from the Greater Hamilton Area. No psychological or cognitive disorders were reported by observers. Older observers completed the Mini-Mental-State-Examination. Observers were compensated for their time with either completion credit for course requirements or a monetary reimbursement at a rate of $10.00/hour. All participants gave informed consent prior to participating in this study. The McMaster University Research Ethics Board approved all experimental protocols.

Table 2.11: Demographics for Experiment 4

Age Group	Mean Age	S.D. Age	Age Range
Young Adults: 20s	22.17 years	SD = 1.60	20-24 years
Senior-Seniors: 70s	74.33 years	SD = 2.88	70-79 years

Age Group	I.D.P.R.	MMSE Score	Years of Education
Young Adults	0.10	NA	17.33
Senior-Seniors	0.08	29.33	16.00

Apparatus

The apparatus was the same as in Experiment 1.

Stimulus Displays

Stimuli were orthogonal oblique sine-wave gratings. During each trial, a grating was presented to one color channel (either the red or cyan color channel), and thus one eye via the red/cyan glasses. Spatial frequency was 5 cy/deg and the diameter of the stimuli were 2.4 deg visual angle. Stimuli were presented at an average luminance of 37.7 cd/m^2 for five contrast levels (0.01, 0.02, 0.04, 0.08, and 0.32).

Procedure

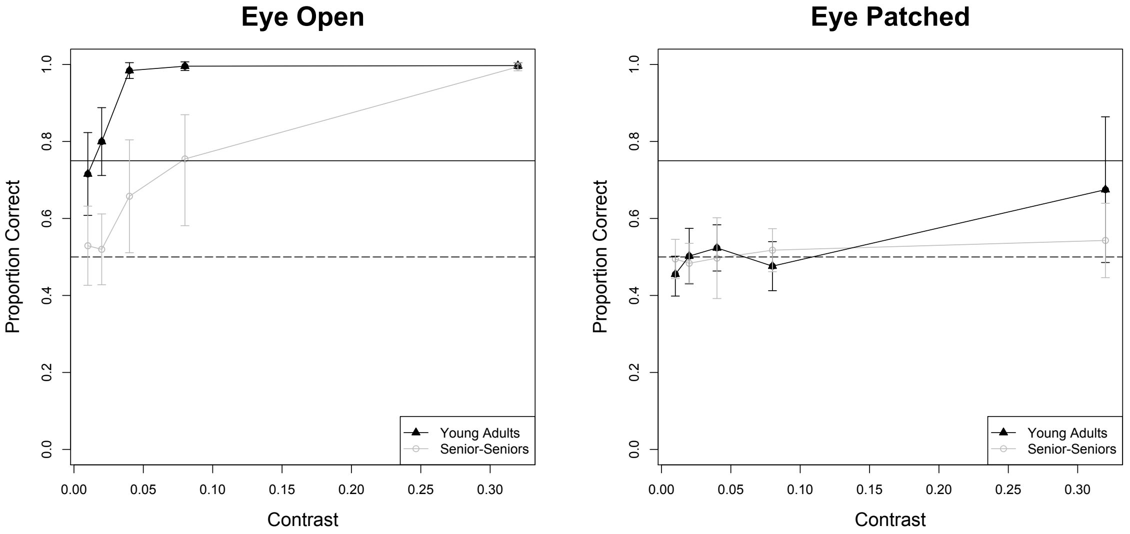
The experimental sessions took place in a dark room. There were two experimental sessions, with a short break (e.g., 5-15 minutes) between them. An eye patch was used under the red/cyan glasses worn by the participant to allow for monocular viewing.

The experimenter switched the eye being covered by the eye patch at the end of the break before beginning the second session. The order of the eye that was patched first (right eye or left eye) was randomized for participants in both age groups. At the beginning of each session, observers focused on the fixation point for one minute to allow for dark adaptation. There were 240 trials within each session. Each trial was presented for a duration of 500 ms. Between each trial there was an interval of 2 s. The amount of trials presented to each eye were equivalent, and the order of monocular presentation to the two eyes was randomized across trials within each session.

Observers were instructed to indicate whether the lines within the image presented during each trial were pointing counter-clockwise or clockwise from vertical by pressing a blue or red key, respectively, on a computer keyboard. All participants were shown example images of the orientations of the two potential oblique gratings before the start of the experiment. Observers were told the image occasionally might be very difficult to see, but to try their best to give an accurate response.

2.5.2 Results and Discussion

The average proportion of correct responses was calculated for both the open eye and the patched eye across both sessions at each of the five contrast levels (0.01, 0.02, 0.04, 0.08, and 0.32). If ghosting did not occur then participants should have an accuracy close to chance (0.5) when the grating was shown to the color channel corresponding with the patched eye, since no image should be visible. By viewing Figure 2.10, age differences can be seen in the level of contrast required for younger and older adults to respond at or above a threshold of 0.75 accuracy for the eye



(a) (b)

Figure 2.10: a.) The proportion correct for the images directed to the open eye is shown. Error bars represent 95% confidence interval. b.) The proportion correct for the images directed to the patched eye is shown. Error bars represent 95% confidence interval.

open condition; however, it is important to note the contrast level required for both age groups to reach 0.75 accuracy is below the low-contrast level (0.2) tested in Experiment 1. These results indicate both younger and older adults are able to accurately report the orientation of Exclusive percepts during binocular rivalry at relatively low contrast levels. Figure 2.10 also shows that even at the highest contrast level tested, where ghosting is the most likely to occur, the 95% confidence interval range still includes chance performance for the patched eye condition for both age groups.

The highest contrast level tested in this experiment was 0.32; however, Experiment 1 used an extremely high contrast level of 0.8. While the current experiment does not directly rule out an age-related impact of ghosting on the perception of Mixed percepts for extremely high contrast levels it is important to note that there was no significant difference between Mixed percepts for the low- (0.2) and high-contrast (0.8) conditions for young adults ($t(7) = 1.11$, $p = 0.303$, two-tailed) and senior-seniors ($t(7) = 0.62$, $p = 0.555$, two-tailed) in Experiment 1. Thus, it is reasonable to conclude potential age differences of the impact of ghosting did not lead to the aging differences in Mixed percepts seen in Experiment 1, and also that ghosting is not significantly different in young adults and senior-seniors at the thresholds tested in this current experiment.

2.6 General Discussion

The results of this study indicate that not only is the process of binocular rivalry slower with aging, it also has different characteristics. For example, the strength of monocular dominance increases with age and the proportion of time spent viewing Mixed percepts decreases with age. The slowing of rivalry is due to a lengthening of the average duration of Exclusive percepts, with no overall trend of differences with aging between the average duration of Mixed percepts. As has been reported for age-related changes in motion perception (Bennett et al., 2007), the largest age differences in binocular rivalry that we observed were between young adults and senior-seniors (i.e., adults ≥ 70 years of age). The results of our supplementary control experiments (Experiments 2-4) support the notion that age differences found in Experiment 1 were not due to age differences in motor response time, retinal illuminance, or differential effects of ghosting, but rather reflect changes in the neural mechanisms that underlie rivalry.

Together the various findings of this study form an intriguing and coherent story of the aging visual system. The diversity of information gathered on binocular rivalry and aging particularly allows for the comparison of these results with current theories and computational models of binocular rivalry. One such model, proposed by Lehky and Blake (1991), will be examined in detail here, since it has previously been used by Norman et al. (2007) to explain their results of greater suppression in binocular rivalry with aging. Two interacting mechanisms are proposed by this theory. The first mechanism, reciprocal inhibition between discrepant visual input, has been labeled the gating circuitry and produces strong mutual inhibition between the two eyes. The effects of reciprocal inhibition are modulated by a secondary mechanism termed the matching circuitry. This secondary mechanism can be thought of as a control mechanism that prevents one of the visual inputs from gaining an extreme perceptual dominance. If the operation of the matching circuitry was disrupted, so that its modulation of the gating circuitry was reduced, then the control that prohibits strong dominance of one percept or the other would no longer be in place and one would predict longer periods of Exclusive percepts and greater monocular dominance. It should be noted previous research has found evidence for weakened inhibition in senescent monkeys (Schmolesky et al., 2000; Leventhal et al., 2003), as well as in older adult humans (Betts et al., 2007). If this weakened inhibition affected this secondary mechanism outlined by Lehky and Blake (1991), then their model provides a potential explanation for our findings of increased monocular dominance with aging. Other components of binocular rivalry and aging that have been noted by this study and previous research can also be summarized by this theory. For instance within the constraints of this theory, strong inhibition in the secondary mechanism would result in the weaker suppression previously found in young adults during binocular rivalry

(Norman et al., 2007), as well as shorter average durations of Exclusive percepts. The stronger suppression (Norman et al., 2007) and longer Exclusive average durations found in older adults, would thus result from a weaker inhibition in the secondary mechanism according to this model.

Interestingly, Lehky and Blake (1991) suggested that this dual circuitry model could have implications for other aspects of binocular vision besides binocular rivalry. For instance, while many aspects of stereopsis remain unchanged with age, some facets of stereoscopic vision, such as depth perception, show some deficits with aging (Norman et al., 2000, 2006). While the current study greatly enriches our current knowledge, further research is required to develop a fully integrated representation of the changes that occur within the visual pathway with aging.

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Chapter 3

The effects of inter-ocular contrast differences on binocular rivalry in younger and older observers

Abstract

Monocular dominance during binocular rivalry increases significantly with aging (see Chapter 2). To further investigate age-related changes in monocular dominance, we measured binocular rivalry in younger (aged 20-28) and older (aged 70-79) adults using pairs of orthogonal, oblique sine-wave gratings that differed in contrast. In baseline conditions, rivalry was measured with equal stimulus contrasts (0.2 or 0.8) presented to both eyes. In the test condition, stimulus contrast was 0.2 in one eye and 0.8 in the other eye, with the eye viewing the higher contrast counter-balanced across trials. During each trial, participants reported their perceptual state (the two Exclusive percepts, Mixed, or Other) by pressing buttons on a response box. Monocular dominance was defined as the difference between the proportion of time a participant reported seeing each Exclusive percept. Monocular dominance in the baseline conditions was significantly greater in older than younger adults, supporting our previous findings. However, monocular dominance did not differ between age groups in the test condition. The introduction of an inter-ocular contrast difference of 0.6 caused monocular dominance to increase significantly in younger adults, whereas the contrast difference had an insignificant effect in older adults who already had shown strong monocular dominance in baseline conditions. A follow-up experiment measured binocular rivalry in younger adults with a wider range of inter-ocular contrast differences: 0, 0.2, 0.4, and 0.6. A contrast difference of 0.4 was needed to produce a level of monocular dominance that was approximately equivalent to that found in older adults with contrast-matched stimuli. These results demonstrate that a large difference in inter-ocular contrast is required to produce monocular dominance in younger adults that is equivalent to the monocular dominance found in older adults, suggesting neural changes in binocular vision with aging.

3.1 Introduction

The human visual system uses binocular disparity to create a representation of the 3-dimensional (3-D) structure of a visual scene. Although some disparity is necessary for 3-D vision, variations between the two retinal images that are too drastic (e.g., different orientations of gratings) cannot be integrated into a single visual percept and under certain circumstances may produce the phenomenon of binocular rivalry. During binocular rivalry, the observer's percept alternates between the two images presented to each eye. When the perceptual state of one image is dominant for a period of time the other image is suppressed from conscious perception. Binocular rivalry, conceptualized as a disruption of normal stereopsis, can be used to gain a better understanding of the neural factors that underlie binocular vision. The current literature on binocular rivalry and binocular integration focuses primarily on the visual system of younger adults. This leaves a tremendous gap in our understanding of binocular vision across the lifespan. It becomes particularly important to fill these gaps with the drastic aging of the current global population. The goal of the current paper is to address this gap in the literature by studying in more detail age-differences in monocular dominance during binocular rivalry.

Chapter 2 provided foundational evidence binocular rivalry is not only slower in older adults compared to younger adults (Jalavisto, 1964; Ukai et al., 2003), but there are also different characteristics of rivalry with aging. One such characteristic is the finding of increased monocular dominance with aging. This result is particularly interesting because Chapter 2 held constant inter-ocular factors that are known to influence perceptual dominance during rivalry. These findings raise interesting questions about whether varying inter-ocular stimulus factors, such as inter-ocular differences in contrast, might affect perceptual dominance during rivalry differently in older and younger adults. It has been well-documented that external factors that influence the salience of the image shown to each eye can influence perceptual dominance, with the more salient image having greater dominance (see Blake, 2001, p. 14 for review). In fact, a number of stimulus factors for which salience can be manipulated (e.g. luminance, velocity, countour density, etc.) have been shown to influence dominance during binocular rivalry when the salience is varied inter-ocularly. The influence of inter-ocular variation of contrast levels is one of the most well-studied examples of these stimulus factors, with the higher contrast image gaining a greater dominance over the lower contrast image (Levelt, 1965; Mueller and Blake, 1989).

The goal of this study was to investigate the effect of stimulus salience, on monocular dominance, an equivalent measure to perceptual dominance, with aging. As mentioned above, in younger adults, it has been shown that varying the strength of stimulus factors, in particular contrast levels, has a prominent influence on proportion of dominance. It is unclear if inter-ocular contrast differences will have a similar effect in older adults. If the external manipulation of stimulus factors has a similar result in older adults, who have already been shown to have strong levels of monocular dominance for contrast-matched stimuli, the resulting monocular dominance could be extremely drastic. However, if the apparent neural mechanisms controlling this shift in monocular dominance with aging are resistant to influences by external stimulus factors there may not be a significant change.

3.2 Experiment 1

3.2.1 Method

Observers

All observers were naïve to the purpose of the experiment. Two age groups participated in this experiment, young adults and older adults. Ten young adults (mean age = 23.1 years, SD = 2.61, range = 20-28 years) were undergraduate and graduate students at McMaster University. Ten older adults (mean age = 74.3 years, SD = 3.37, range = 70-79 years) were recruited from the Greater Hamilton Area. An additional younger and four older observers participated but were excluded based on pre-established exclusion criteria discussed in the Analyses Section 3.2.2. Observers were compensated for their time either with partial course credit or reimbursement at a rate of $10.00/hour. All participants gave informed consent prior to participating in this study, and the McMaster University Research Ethics Board approved experimental protocols. Observers reported no psychological or neurological health concerns that are known to influence binocular rivalry. Older observers performed normally for their age group on the Mini-Mental-State-Examination (MMSE), with a mean score of 28.4.

Visual acuity was normal or corrected-to-normal for all participants and all participants had normal stereoacuity when evaluated using the Randot Stereotest (Stereo Optical Company). Contrast sensitivity for each eye was measured with the Pelli-Robson Contrast Sensitivity Test. An inter-ocular contrast sensitivity difference value was determined for each participant by calculating the absolute difference between the Pelli-Robson contrast sensitivity for each eye. These difference values ranged from 0 to 0.3 for both age groups, with a mean of 0.06 inter-ocular difference for young adults and 0.11 for older adults. A two-tailed t-test indicated there was no significant difference in inter-ocular differences in contrast sensitivity between younger and older adults, ($t(16.997) = -0.72$, $p = 0.4821$).

Apparatus

Stimuli were generated on a Macintosh Pro 4 using MATLAB 7.10 (R2010a) (Mathworks, Natwick, MA, USA) and the Psychophysics Toolbox (Brainard, 1997). The stimuli were displayed on a 30-inch Apple Cinema HD display with a resolution of 2560 × 1600 pixels. Red/cyan glasses were used to present different images to each eye, with Gamma corrections made to ensure that the red and cyan were equiluminant. A RESPONSEPixx (VPixx Technologies, Inc.) handheld button box was used to record participant responses. All devices (button box, display monitor, and computer) were connected to a DATAPixx (VPixx Technologies, Inc.) data and video processor to enable accurate synchronization of stimulus presentation and response acquisition.

Stimulus Displays

Pairs of orthogonal oblique (i.e., ±45 deg from vertical) sine-wave gratings were presented dichoptically. The diameter of the stimuli was 2.4 deg visual angle. The spatial frequency was 5 cy/deg and average luminance was 37.7 cd/m^2. In baseline conditions, the gratings presented to each eye had the same contrast (i.e., either 0.2 or 0.8). In test conditions, stimulus contrast was 0.2 in one eye and 0.8 in the other eye, with the eye viewing the higher contrast counter-balanced across trials.

Procedure

Observers were instructed to use the button box to record their perceptual alternations among four percepts: two Exclusive percepts (i.e., counter-clockwise and clockwise gratings), Mixed percepts, and Other percepts/fading. The four types of percepts were described, and observers were told that they might experience multiple forms of a Mixed percept (e.g. a plaid-like image, a puzzle-like image, or wave-like transitions). Observers were instructed to press and hold the rightmost (red) button while viewing an exclusively counter-clockwise oriented grating, press and hold the leftmost (blue) button when viewing an exclusively clockwise oriented grating, and to press and hold both buttons simultaneously when viewing a Mixed percept. If observers viewed any other kind of percept, or if any part of the image faded from view, observers were instructed to not press any buttons.

Following the instructions, the room was darkened and observers were asked to focus their gaze on a small, high-contrast fixation dot in the middle of the screen for 60 s. After the adaptation period, two practice trials were conducted to allow observers to become familiar with the task. To avoid extreme monocular dominance during practice trials, which could limit practice recording rivalry transitions and/or create a future expectation bias, the stimulus contrast was the same in each eye and the order of the two contrasts (0.2 and 0.8) was determined randomly for each observer. The practice trials were followed by the block of experimental trials. Practice trials and experimental trials were both 40 s in duration. The inter-trial duration was 20 s. Prior to the start of each trial, the fixation dot flashed several times in synchrony with a series of high pitched beeps to alert the observer to refocus their attention for the upcoming trial. For baseline trials, both eyes were shown the same contrast, either low-contrast (0.2) or high-contrast (0.8). For test trials, there was an inter-ocular contrast difference of 0.6, with one eye viewing the high-contrast (0.8) and the other viewing the low-contrast (0.2). The block of experimental trials consisted of 24 trials: six trials of each of the baseline conditions (stimulus contrast of 0.2 and 0.8) and six test trials with the high-contrast grating presented to the left eye, and 6 test trials with the high contrast grating presented to the right eye. Four pseudo-rivalry trials (one per stimulus condition) immediately followed the experimental trials. Observers were not told of the change from experimental to pseudo-rivalry trials and responded using the same instructions as for all previous trials. During the pseudo-rivalry trials, the computer controlled the alternations perceived by the observer, by presenting the same image to both eyes, and alternating these images between the two Exclusive percepts (clockwise and counter-clockwise grating). This method of stimulus presentation should produce no binocular rivalry, and therefore enables us to measure the accuracy of each observer's judgements. The duration for each stimulus presentation was selected randomly from a set of four durations (1.73, 2.68, 4.56, and 7.068 s) that fall within the range of durations of rivalrous, Exclusive percepts in younger and older adults found during pilot experiments.

3.2.2 Results

If rivalry was not reported during a trial (e.g., the participant either reported seeing a single percept for the entire trial or did not press any buttons), then the trial was excluded from further data analysis. An observer was excluded from the experiment if all six of the trials in one of the four conditions (i.e., low- and high-contrast baseline conditions, and the left- and right-eye high-contrast test conditions) were excluded due to a lack of rivalry. As noted above, one younger observer and four older observers were excluded based on these criteria. Finally, percept durations of less than 400 ms were assumed to reflect button press errors and therefore were excluded from further analyses.

Monocular dominance was computed for each trial by calculating the absolute difference between the proportion of time spent in each of the two Exclusive percepts. To determine if monocular dominance differed in the low- and high-contrast baseline conditions, monocular dominance in each condition was compared with paired t tests for each age group. The difference between conditions was not significant in either younger ($t(9) = 1.67$, $p = 0.132$) or older adults ($t(9) = 1.75$, $p = 0.114$), and therefore we combined the data across conditions to obtain a single baseline monocular dominance value for each observer. Monocular dominance values in the baseline and test conditions are shown in Figure 3.1 for each age group. Monocular dominance in the baseline condition differed significantly between age groups ($t(11.07) = -2.30$, $p = 0.042$), but there was a minimal, non-significant, difference between the age groups in the test condition ($t(17.99) = -0.06$, $p = 0.954$). In younger observers, the difference between monocular dominance in the baseline and test conditions was significant ($t(9) = -5.84$, $p = 0.001$), but the difference between monocular dominance in the two conditions was not significant in older observers ($t(9) = -1.514$, $p = 0.164$).

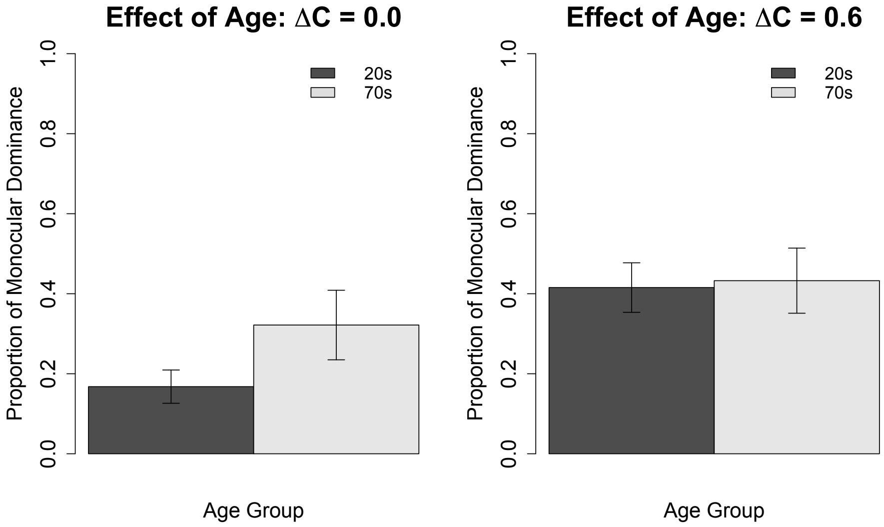

Figure 3.1: In the left-panel, the average proportion of monocular dominance is shown for each group for baseline conditions. In the right-panel, the proportion of monocular dominance is shown for each age group for test conditions. Error bars represent +/- 1 standard error.

For the test condition, where a large inter-ocular contrast difference (0.6) was presented, the number of trials in which the Exclusive percept with the higher contrast

(0.8) was the same as the Exclusive percept perceived for the greater proportion of time, referred to here as matching trials, was also analyzed. These results are depicted for each age group in Figure 3.2, which shows that the Exclusive percept with the higher contrast was more likely to be the same as the reported dominant percept in younger adults than older adults. A Mann-Whitney test indicated a significant difference between the two age groups ($U = 79$, $p = 0.018$).

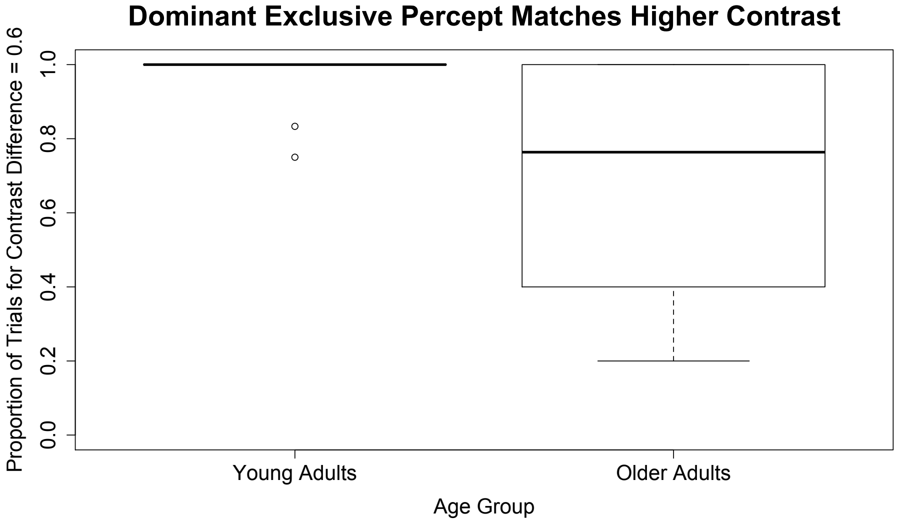

Figure 3.2: The proportion of trials in which the dominant percept was the same as the higher contrast stimuli is depicted above for each age group.

Pseudo-rivalry trials consisted of a series of alternating Exclusive stimuli (i.e., the same oblique grating presented to both eyes). During each individual Exclusive stimulus presentation, a response was considered incorrect if the participant reported seeing the incorrect Exclusive percept, alternations between multiple percepts, and/or the Mixed or Other percepts for longer than 400 ms. Both age groups exhibited high response accuracy: accuracy was 95.0% and 93.5% in younger and older adults, respectively.

Since only alternating Exclusive stimuli were presented on pseudo-rivalry trials, differences in the duration of Other percepts, which were reported by releasing all buttons, could be used to examine the effects that age-related changes in motor delay (Smith et al., 1999) had on our results. We found no significant difference between age groups for either average duration ($t(18) = -1.15$, $p = 0.265$) or proportion of time ($t(18) = -1.39$, $p = 0.182$) for Other percepts. This suggests that age differences in motor processing had relatively minor effects on our dependent measures.

3.3 Experiment 2

3.3.1 Method

Observers

A new group of eight undergraduate and graduate students recruited from McMaster University (mean age = 21.23 years, SD = 1.64, range = 20-24 years) participated in Experiment 2. The participants were naïve to the purpose of the experiment. Visual acuity was normal or corrected-to-normal for all participants, and all participants had normal stereoacuity when evaluated using the Randot Stereotest (Stereo Optical Company). Contrast sensitivity for each eye was measured with the Pelli-Robson Contrast Sensitivity Test. The absolute value of the inter-ocular difference in contrast sensitivity ranged from 0 to 0.15, with a mean of 0.06. Participants were compensated for their time either with a partial course credit or reimbursement at a rate of $10.00/hour. All experimental protocols were approved by the McMaster University Research Ethics Board.

Apparatus

The experimental apparatus was the same as in Experiment 1.

Stimulus Displays

Pairs of orthogonal oblique sine-wave gratings were presented dichoptically. Stimulus diameter was 2.4 deg and the spatial frequency was 5 cy/deg. Average luminance was 37.7 cd/m^2. In baseline conditions, stimulus contrast was 0.8 in both eyes. In the test conditions, stimulus contrasts (0.2, 0.4, 0.6, 0.8) differed between the two eyes, resulting in three levels of inter-ocular contrast differences (0.2, 0.4, and 0.6), with the eye viewing the higher contrast counter-balanced across trials.

Procedure

The procedure was similar to the procedure for Experiment 1, with the exception of the number of trials and the conditions. There were two practice trials that consisted of only baseline stimuli (i.e., 0.8 contrast in both eyes). The experimental block consisted of 42 trials: six trials of the high contrast (0.8) baseline condition, as well as six trials for each eye being presented the higher contrast stimulus for the test conditions of varying inter-ocular differences (0.2, 0.4, and 0.6). The order of the baseline and test conditions were randomized within the experimental block of trials. Upon the completion of the experimental block, seven pseudo-rivalry trials (one trial per condition type) were immediately presented. The pseudo-rivalry trials were presented in the same manner as described in the procedure for Experiment 1. Observers were given the same instructions for experimental and pseudo-rivalry trials, and were not informed of the difference. The durations of each trial and the inter-trial interval were the same as in Experiment 1.

3.3.2 Results

Response accuracy on pseudo-rivalry trials was defined the same way as in Experiment 1. As was found in that experiment, response accuracy was very high (i.e., 95.3%) on pseudo-rivalry trials, which indicates that observers were attending to the stimulus and could easily control the response box. For each experimental trial, monocular dominance, defined as the absolute difference between the proportion of time spent in each of the two Exclusive percepts, was calculated. Monocular dominance for each inter-ocular contrast difference is shown in Figure 3.3. Pairwise comparisons of the monocular dominance values for the inter-ocular contrast differences can be viewed in Table 3.1.

Table 3.1: Monocular Dominance Comparisons

Comparison	t	Df	p
0:0.2	-1.27	7	0.243
0:0.4	-4.41	7	0.003
0.2:0.4	-4.23	7	0.004
0.4:0.6	7.33	7	< 0.001

For each test condition in which the inter-ocular contrast difference was greater than zero, we calculated the proportion of trials where the dominant Exclusive percept corresponded to the stimulus that had the higher contrast, referred to as matching trials (Figure 3.4). Both the conditions of 0.4 and 0.6 inter-ocular contrast difference had significantly higher proportion of matching trials than the inter-ocular contrast difference of 0.2, with $t(7) = -3.99$, $p = 0.005$ and $t(7) = -5.45$, $p = 0.001$ respectively

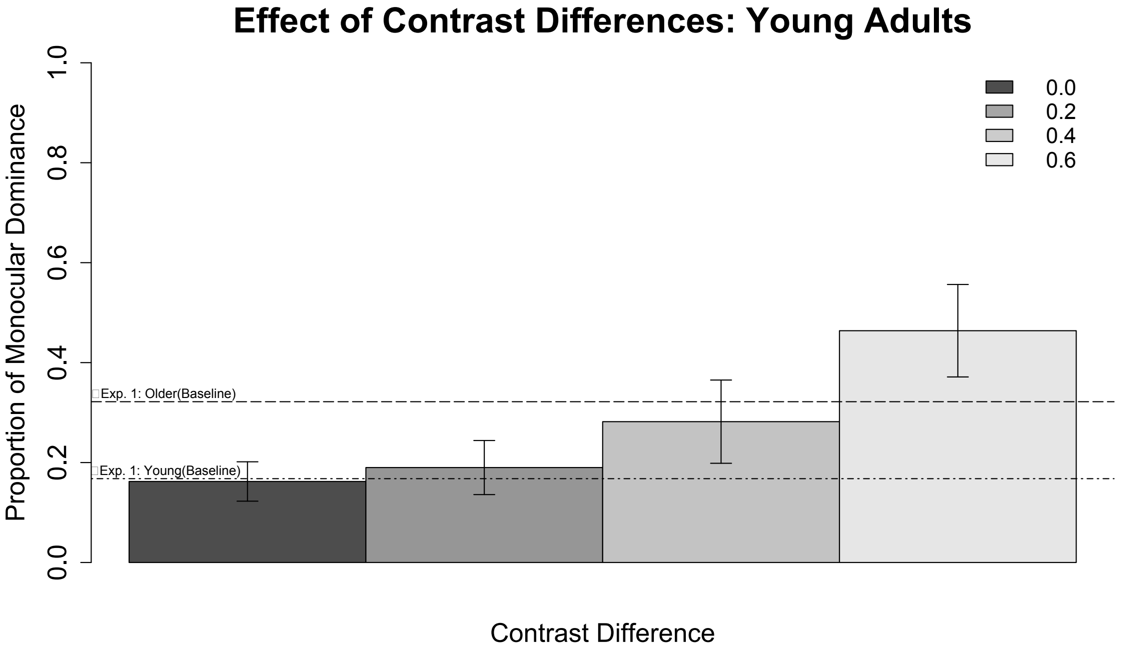

Figure 3.3: The average proportion of monocular dominance is shown for each interocular contrast difference. Error bars represent +/- 1 standard error. The dash-dot line represents the average proportion of monocular dominance for the baseline condition found in Experiment 1 for younger adults and the dashed line represents the baseline result for the older adults in Experiment 1.

with Bonferroni correction for multiple comparisons. The inter-ocular contrast differences of 0.4 and 0.6 did not show a significant difference ($t(7) = -1.84$, $p = 0.108$). However, this appears to potentially be due to a ceiling effect. It can be observed in Figure 3.4 that there is still a trend of increasing matching trials with this increase of inter-ocular contrast difference.

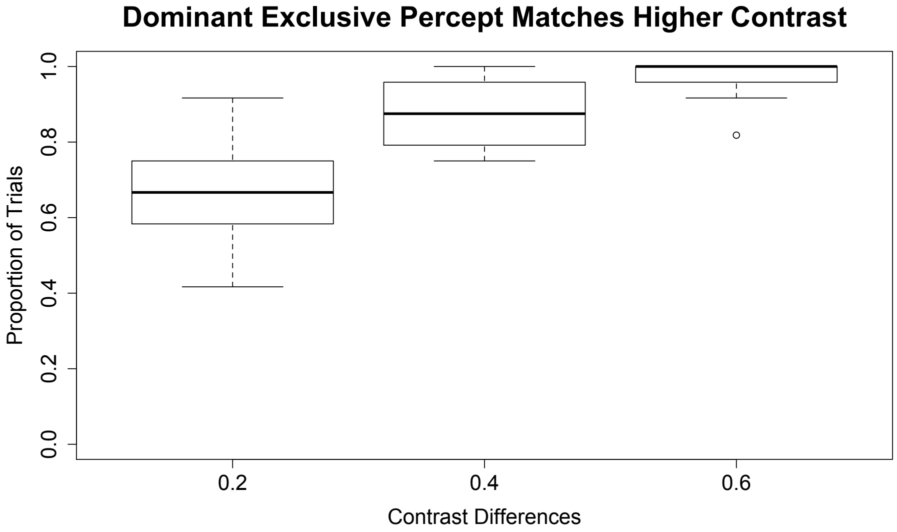

Figure 3.4: The proportion of trials in which the dominant percept was the same as the higher contrast image is depicted above for each inter-ocular contrast difference.

3.4 Discussion

To our knowledge this study is the first to investigate the applicability of Levelt's propositions to older adults. Specifically, this study investigated Levelt's first proposition, which states the salience of the image shown to each eye during binocular rivalry can influence perceptual dominance, and the image with the higher salience will be dominant a greater proportion of time. Our finding that inter-ocular contrast difference does not significantly affect monocular dominance for older adults indicates that Levelt's first proposition, currently a hallmark for the basis of many binocular rivalry studies, is not an appropriate description of the characteristics of binocular rivalry in older adults.

Monocular dominance was shown in Experiment 1 to be greater for older adults compared to younger adults when external stimulus factors known to affect perceptual dominance during binocular rivalry were kept constant, replicating previous findings (see Chapter 2). As expected based on other previous findings (Levelt, 1965; Mueller and Blake, 1989), monocular dominance increased with inter-ocular contrast difference for younger adults. Monocular dominance for older adults did not significantly differ between baseline and the inter-ocular contrast difference. Older adults were also less likely to report the image with the higher contrast as the more dominant percept during trials with an inter-ocular contrast difference than younger adults.

In Experiment 2 we found that monocular dominance in younger adults was approximately linearly related to the squared value of the inter-ocular contrast difference. Furthermore, we found that an inter-ocular contrast difference of approximately 0.4 was required to increase monocular dominance in younger adults to levels that were similar to the monocular dominance found in older adults in Experiment 1. It is unlikely that optical factors in senescent eyes produce inter-ocular contrasts differences as large as 0.4, and therefore the current results suggest that the age difference in monocular dominance that was observed in Experiment 1 is unlikely to be caused solely by age differences in optics. Instead, our study suggests that age differences in monocular dominance are likely due to neural factors. Also, the fact that younger adults require an inter-ocular contrast difference of 0.4 to experience monocular dominance that is on par with that found in older adults at baseline suggests that the age difference that we found in Experiment 1 is indeed a *large* effect.

This *large* effect coupled with the lack of significant differences in monocular dominance between baseline and trials where the inter-ocular contrast differed for older adults indicates the strength of apparent neural changes with aging to resist specific exogenous factors, such as contrast. This indicates a rather prominent role of neural changes with aging within the binocular visual system and could possibly be related to poor depth perception that has been noted in older adults (Norman et al., 2000, 2006). This prominence of neural factors is also important for future projects that may wish to utilize techniques developed to counter monocular dominance that interferes with stereoscopic abilities in amblyopes using video-games (Hess et al., 2011; To et al., 2011) to improve stereoscopic vision in older adults. Training studies utilizing video games have also shown improvements in contrast sensitivity functions for healthy younger adults (Li et al., 2009). This poses an interesting question about the effects of similar training on healthy older adults, who have been shown to have losses in contrast sensitivity (Owsley et al., 1983; Allard et al., 2013). It would be interesting for future studies to investigate if the little known qualities of neural plasticity of healthy older adult brains would allow for similar enhancements in contrast sensitivity via video-game training and whether an enhancement in contrast sensitivity may influence monocular dominance dominance levels in older adults at various inter-ocular contrast differences. Recent evidence has concluded neural plasticity is still present in older adults (Ball and Sekuler, 1986; Andersen and Bower, 2010). However, further studies are necessary to understand if visual training protocol that rely on neural plasticity would succeed in lessening the extreme monocular dominance levels found in older adults, especially with the apparent strength of the neural factors associated with monocular dominance shown by the current study. It will be important for future studies to explore whether inter-ocular differences during binocular rivalry of external stimulus factors, other than contrast, may influence monocular dominance levels in older adults to thoroughly understand these apparent neural changes in the binocular visual system.

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Chapter 4

Visual rivalry and aging

Abstract

Perceptual rivalry occurs when the same ambiguous stimulus, or reversible figure, is presented to both eyes: observers typically see the figure's appearance change over time. Binocular rivalry occurs when different stimuli are presented to each eye: over time, observers see a stimulus presented to one of the eyes (i.e., Exclusive percepts), as well as mixtures of the stimuli presented to both eyes. Compared to young adults, older adults are believed to experience slower perceptual (Aydin et al., 2013) and binocular rivalry (Jalavisto, 1964; Ukai et al., 2003). These similar developmental trends have been used as evidence that the same neural processes are likely to be associated with both perceptual and binocular rivalry. The current study investigated this possibility by determining whether measures of perceptual and binocular rivalry are correlated within individual subjects. We assessed the reliability of our dependent measures by measuring perceptual and binocular rivalry in younger and older adults in two sessions within the same day and on two days a week apart. In the binocular

rivalry task, Exclusive percepts had longer average durations in older than younger subjects. However, unlike previous findings by Aydin et al. (2013), in the perceptual rivalry task, there were minimal age differences in the average durations of Exclusive percepts. There was a general trend for durations of Mixed percepts to have shorter average durations in older subjects in the perceptual rivalry task, but this effect was significant only in the first session of the second day of testing. Measures of binocular rivalry were more reliable than measures of perceptual rivalry and there was an extremely high reliability overall on day two. Correlations between the two types of rivalry were not significant. Thus, developmental changes in visual rivalry are unlikely to be explained by age-related changes in a common set of processes.

4.1 Introduction

Visual rivalry is a perceptual phenomenon that occurs when the brain is unable to integrate visual information into a single interpretation of an image. Two forms of visual rivalry include perceptual rivalry and binocular rivalry. Perceptual rivalry occurs when the same ambiguous visual stimulus is presented to both eyes and the visual percept changes over time. The Necker Cube, a two dimensional pattern that evokes distinct three-dimensional percepts that alternate over time (see Figure 4.1a) is an example of perceptual rivalry. Binocular rivalry occurs when different visual stimuli are presented to each eye. Binocular rivalry is commonly induced using images of dichoptic gratings that differ in orientation (see Figure 4.1b). In this case, the eyes signal to the brain that two different objects exist at the same location in space at the same time. Visual perception alternates between the two images, with the image in one eye becoming dominant for periods of time while the other image is suppressed

(a) Necker Cube (b) Dichoptic Gratings

Figure 4.1: Examples of Perceptual Rivalry and Binocular Rivalry Stimuli

from consciousness.

Binocular rivalry has been suggested to occur at early stages of the visual cortex (V1), resulting from mutual inhibition between V1 neuronal populations associated with each percept (Blake, 1989; Blake et al., 1980; Nguyen et al., 2001). This finding is supported by functional magnetic resonance imaging (fMRI) studies that have found that neural activity in monocular regions of the V1 change similarly in time with alternations of percepts (Haynes et al., 2005; Lee et al., 2005, 2007; Meng et al., 2005; Polonsky et al., 2000; Tong and Engel, 2001). In contrast, other studies have suggested that binocular rivalry involves competition between stimulus patterns in higher-level areas of the visual system rather than competition between the eyes (Kovács et al., 1996; Leopold and Logothetis, 1996; Logothetis and Sheinberg, 1996; Sheinberg, D. L. and Logothetis, 1997). Perceptual rivalry also is suggested to involve higher-level extra-striate areas of the visual system (Kleinschmidt et al., 1998; Tong and Engel, 2001; Meng and Tong, 2004). Both forms of rivalry demonstrate similar temporal dynamics, conforming closely to gamma or log-normal distributions (Fox and Herrmann, 1967; Walker, 1975; Carter and Pettigrew, 2003).

The fact that both forms of visual rivalry share similar characteristics has lead to the proposal that a single neural mechanism is accountable for both perceptual rivalry and binocular rivalry (Andrews and Purves, 1997; Logothetis, 1988; Wolfe, 1996; Blake and Logothetis, 2002). Studies of age-related changes in visual rivalry, which show that the rates of perceptual (Aydin et al., 2013) and binocular rivalry (Jalavisto, 1964; Ukai et al., 2003) decline with age, are consistent with this common-mechanism view. However, other investigators have argued that their studies provide evidence that different neural mechanisms are responsible for different forms of visual rivalry (Fox and Herrmann, 1967; Levelt, 1966; Meng and Tong, 2004). Therefore, it remains unclear whether the rates of perceptual and binocular rivalry are governed by a common set of mechanisms. To investigate this issue, we measured the rates of perceptual and binocular rivalry in younger and older adults to determine if aging had similar effects on the two types of rivalry, and whether the rates of perceptual and binocular rivalry were correlated within-subjects.

4.2 Method

4.2.1 Observers

Twelve young adults (mean age = 21, SD = 1.95, range = 20-26) and twelve older adults (mean age = 64, SD = 2.35, range = 60-67) participated in this study. Young adults were undergraduate and graduate students recruited from McMaster University. Older adults were recruited from the Greater Hamilton Area. Observers were compensated with monetary reimbursement at a rate of $10.00/hour. All participants provided informed consent prior to participating in the study, and the McMaster University Research Ethics Board approved all experimental protocols.

All subjects had normal or corrected-to-normal visual acuity and normal stereoscopic vision. Stereoacuity was measured using the Randot Stereotest (Stereo Optical Company). Young adults had an average stereoacuity threshold of 25 seconds of arc at 16 inches and older observers had an average threshold of 35 seconds of arc at 16 inches. Subjects contrast sensitivity for each eye was estimated using the Pelli Robson Contrast Sensitivity Test. Inter-ocular differences in contrast sensitivity were minimal for both age groups (mean inter-ocular difference: young adults = 0.075; older adults = 0.1). Older adults completed the Mini-Mental-State-Examination (MMSE) with a score of 27 or higher (mean score = 29.25). Older adults also scored an average of 27 on the Montreal Cognitive Assessment (MOCA), indicative of normal cognitive abilities. Young adults and older adults reported similar education levels, with an average level of 17.83 reported by young adults and 16.25 reported by older adults. Education level was defined by years of school completed.

4.2.2 Apparatus

A 30-inch Apple Cinema HD display with a resolution of 2560 × 1600 pixels was used to present the stimuli. Stimuli were viewed using red/cyan glasses from a distance of 100 cm. The red and cyan were made equiluminant using Gamma corrections. The viewing position of the participant was stabilized using a chin rest. A RESPONSEPixx (VPixx Technologies, Inc.) handheld button box was used to record participant responses. Stimuli were generated on a Macintosh Pro 4 using MATLAB 7.10 (R2010a) (Mathworks, Natwick, MA, USA) and the Psychophysics

Toolbox (Brainard, 1997). The computer was connected to a DATAPixx (VPixx Technologies, Inc.) data and video processor. All other devices were connected to the DATAPixx box for accurate synchronization.

4.2.3 Stimulus Displays

Red/cyan glasses allowed for different images to be presented to the subjects left and right eye during the binocular rivalry task. For the perceptual rivalry task, a single ambiguous image was presented to both eyes. Subjects wore the red/cyan glasses for both rivalry tasks as a control measure. For the perceptual rivalry task, the stimulus was a Necker Cube (Viperlib, http://viperlib.york.ac.uk). For the binocular rivalry task, the stimuli were pairs of orthogonal oblique sine-wave gratings presented dichoptically. The diameter of the stimuli were 2 deg visual angle and 2.4 deg visual angle for the perceptual rivalry task and binocular rivalry task, respectively. The spatial frequency of the binocular rivalry stimuli was 3 cy/deg. The stimulus contrast level for both rivalry stimuli was 0.8 and the average luminance was 37.7 cd/m^2.

4.2.4 Procedure

Each subject was tested at approximately the same time on two days, a week apart. On each day, the tasks alternated between blocks of perceptual and binocular rivalry and each subject completed each task twice during each day. Half of the subjects in each age group completed the perceptual rivalry task first on Day 1 and the binocular rivalry task first on Day 2, and the remaining subjects completed the tasks in the reverse order. Each subject completed two rivalry sessions on each day, with each session being composed of two rivalry tasks: perceptual rivalry and binocular rivalry.

There was a short break ($\approx$ 5 minutes) between each session.

Each day started with a 60 s adaptation period, during which time the subjects were instructed to direct their gaze to a central fixation point located within a rectangular frame. After the adaptation period, subjects completed a rivalry session that consisted of two blocks of trials (i.e., one block with each task): each block included one practice trial followed by eight, 30 s experimental trials. The second rivalry task in a session began with a 10 s adaptation period. The inter-trial interval within each session was 15 s to allow for afterimages to diminish. Subjects were instructed to rest their eyes and ease their focus on the fixation point during the inter-trial intervals. At the end of each inter-trial interval the fixation point flickered in synchrony with three high pitched tones to alert the subject that the next trial was beginning and to refocus attention on the fixation point.

Participants tracked alternations between Exclusive, Mixed, and Other percepts using a handheld button box. Example images of these types of percepts were presented for each rivalry task along with instructions. For the binocular rivalry task, subjects were instructed to press down the rightmost (red) button for the entire duration that they perceived the Exclusive percept of a clockwise (i.e., +45 deg) grating; the leftmost (blue) button for the duration that they perceived the Exclusive percept of a counterclockwise (i.e., -45 deg) grating; and both the red and blue buttons simultaneously for the duration they perceived forms of a Mixed percept (e.g., a plaid-like image, a puzzle-like image or wave-like transitions). For the perceptual rivalry task, subjects were instructed to press down the rightmost (red) button for the entire duration that they perceived an Exclusive percept in which they saw the bottom of the Necker Cube; the leftmost (blue) button for the duration they perceived an Exclusive percept in which they saw the top of the Necker Cube; and both the red and blue buttons simultaneously when they perceived a Mixed percept or when they were unsure whether they are seeing the top or bottom of the cube. (Note: Although rare, these percepts were reported to occur during perceptual rivalry by some individuals in pilot experiments. Thus, they were included as a reporting option.) In both tasks, subjects were instructed to not press any buttons while they perceived so-called Other stimuli (e.g., perceptual fading or no stimulus at all). It was stressed to the subjects that the length of each perceptual state may vary and that it is important to respond as quickly as possible to attain the most accurate reports from button presses.

4.3 Results

4.3.1 Average Durations

Trials on which rivalry did not occur (e.g., the observer either stayed in a single percept for the entire trial or did not press any buttons) were excluded from the data analyses. Four-way ANOVAs (one between-subject factor (age group) and three within-subject factors (rivalry type, day and session)) were conducted on the average durations of the reported Exclusive and Mixed percepts. Generalized eta squared values (η^2_N) are reported for effect sizes (see Olejnik and Algina, 2003; Bakeman, 2005, for review). Average duration for the Exclusive percepts category was determined by calculating the mean duration for the two Exclusive percepts. Other percepts were rarely reported, and are not relevant to the specific focus of this study. Therefore, Other percepts are not reported here.

Exclusive Percepts

There were significant main effects of age ($F(1, 22) = 8.41$, $p = 0.008$, $\eta^2_N = 0.16$), rivalry type ($F(1, 22) = 14.64$, $p < 0.001$, $\eta^2_N = 0.12$), and day ($F(1, 22) = 6.30$, $p = 0.020$, $\eta^2_N = 0.03$). The day × session interaction was significant ($F(1, 22) = 5.28$, $p = 0.031$, $\eta^2_N = 0.04$) age × rivalry type interaction was marginally significant ($F(1, 22) = 4.15$, $p = 0.054$, $\eta^2_N < 0.01$), and the rivalry type × session ($F(1, 22) = 4.66$, $p = 0.042$, $\eta^2_N = 0.01$) and age × rivalry type × session ($F(1, 22) = 4.66$, $p = 0.042$, $\eta^2_N < 0.01$) interactions were significant.

To deconstruct the age × rivalry type × session interaction, separate 2 (age group) × 2 (rivalry type) × 2 (day) ANOVAs were conducted on the average duration of Exclusive percepts for Session 1 and Session 2. For Session 1 there were significant main effects of age ($F(1, 22) = 8.14$, $p = 0.009$, $\eta^2_N = 0.16$) and rivalry type ($F(1, 22) = 11.83$, $p = 0.002$, $\eta^2_N = 0.12$), as well as a significant age × rivalry type interaction ($F(1, 22) = 6.26$, $p = 0.020$, $\eta^2_N = 0.07$). For Session 2 there were significant main effects of age ($F(1, 22) = 7.59$, $p = 0.012$, $\eta^2_N = 0.16$), rivalry type ($F(1, 22) = 13.92$, $p = 0.001$, $\eta^2_N = 0.12$), and day ($F(1, 22) = 10.28$, $p = 0.004$, $\eta^2_N = 0.04$).

The results for the average duration of Exclusive percepts, averaged across days, can be seen in Figure 4.2. The figure indicates that for the perceptual rivalry task, older adults appear to have slightly longer average durations than younger adults for both sessions. This age difference appears greater for Session 2, because younger adults experienced shorter average durations for Exclusive percepts in Session 2 compared to Session 1 ($t(11) = 2.50$, $p = 0.030$), while older adults did not significantly differ across sessions, ($t(11) = 2.03$, $p = 0.068$). However, the differences between age groups was not significant for either session (Session 1: $t(21) = -0.82$, $p = 0.420$; Session 2: $t(22) = -1.47$, $p = 0.155$). Figure 4.2 also shows that the age difference was far greater for binocular rivalry, with older adults reporting significantly longer average durations while viewing the Exclusive percepts compared to younger adults for both sessions (Session 1: $t(15) = -4.18$, $p < 0.001$; Session 2: $t(19) = -3.57$, $p = 0.002$), though the age difference appears slightly smaller for Session 2 compared to Session 1. While there was no significant difference between the average durations reported in each session of binocular rivalry for the younger adults ($t(11) = 2.05$, $p = 0.065$), older adults experienced a significantly shorter average duration for Exclusive percepts in Session 2 compared to Session 1, $t(11) = 4.45$, $p = 0.001$.

Mixed Percepts

Average durations of Mixed percepts were analyzed with a 2 (age group) × 2 (rivalry type) × 2 (session) × 2 (day) ANOVA. The ANOVA revealed a significant main effect or rivalry type ($F(1, 22) = 21.32$, $p < 0.001$, $\eta_N^2 = 0.11$), a significant rivalry type × day ($F(1, 22) = 5.81$, $p = 0.025$, $\eta_N^2 = 0.02$) interaction, and a marginally significant age group × rivalry type × day × session interaction was observed for the average duration for Mixed percepts ($F(22) = 4.08$, $p = 0.056$, $\eta_N^2 < 0.01$). To further deconstruct the 4-way interaction, separate 2 (age group) × 2 (rivalry type) × 2 (session) ANOVAs were conducted on the average duration of Mixed percepts for Day 1 and Day 2. For the Mixed percepts reported for Day 1 there were significant main effects of rivalry type ($F(22) = 5.08$, $p = 0.035$, $\eta_N^2 = 0.05$) and a marginally significant main effect of session ($F(22) = 4.32$, $p = 0.050$, $\eta_N^2 = 0.02$). For the Mixed percepts reported for Day 2 there was a main effect of rivalry type

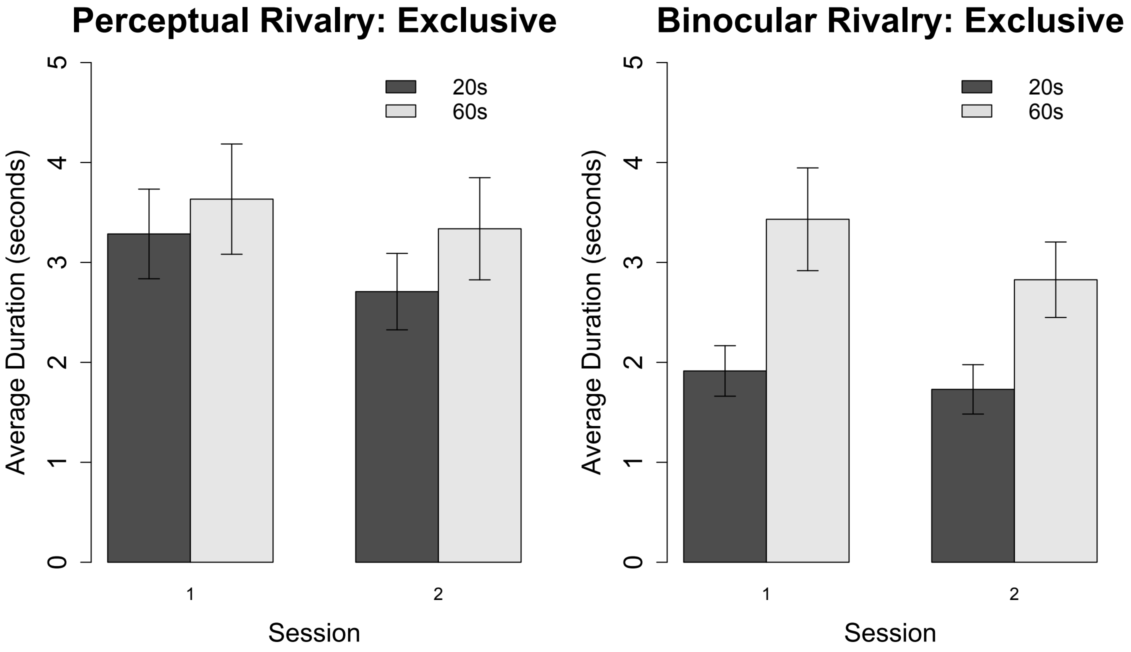


Figure 4.2: Average duration for Exclusive percepts are shown for the perceptual rivalry task (left panel) and the binocular rivalry task (right panel). Results for each age group are shown for both the first and second session across both days. Error bars represent +/- 1 standard error.

$(F(22) = 21.47$, $p < 0.001$, $\eta_N^2 = 0.18)$.

The top panel of Figure 4.3 shows the reported average duration of Mixed percepts for Day 1. By viewing this graph it can be seen that for Day 1 Mixed percepts were reported for slightly longer for binocular rivalry than for perceptual rivalry. On Day 2 (see Figure 4.3: bottom panel), this difference between rivalry type appears even greater. The marginally signicant main effect of session for Day 1 appears to be due to a slight decrease in the average duration of Mixed percepts, and seems primarily driven by the decrease in average duration for older adults from Session 1 to Session 2 for perceptual rivalry. While there were no significant main effects or interactions of age for either Day 1 or Day 2, by viewing Figure 4.3 suggests that the average duration of Mixed percepts was slightly shorter for older adults in the perceptual rivalry task, and this age difference was slightly larger on Day 2.

4.3.2 Within-Subject Correlations

The data were further analyzed by conducting within-subject Pearson correlational analyses between rivalry type, days, and sessions for Exclusive and Mixed Percepts. Subjects were excluded from a correlation analysis if they had an average duration that was +/- 3 standard deviations away from the group mean. In such cases, an adjusted correlation value, designated r', is reported.

Figure 4.4 shows a comparison between the average duration of Exclusive percepts and Mixed percepts for each rivalry type. Measures of correlation between the average duration of Exclusive percepts and Mixed percepts can be viewed in the following tables for each of the within-subjects factors: rivalry type (Table 4.1), days (Table 4.2), and sessions (Table 4.3). Additionally, Spearman's rank correlational analyses

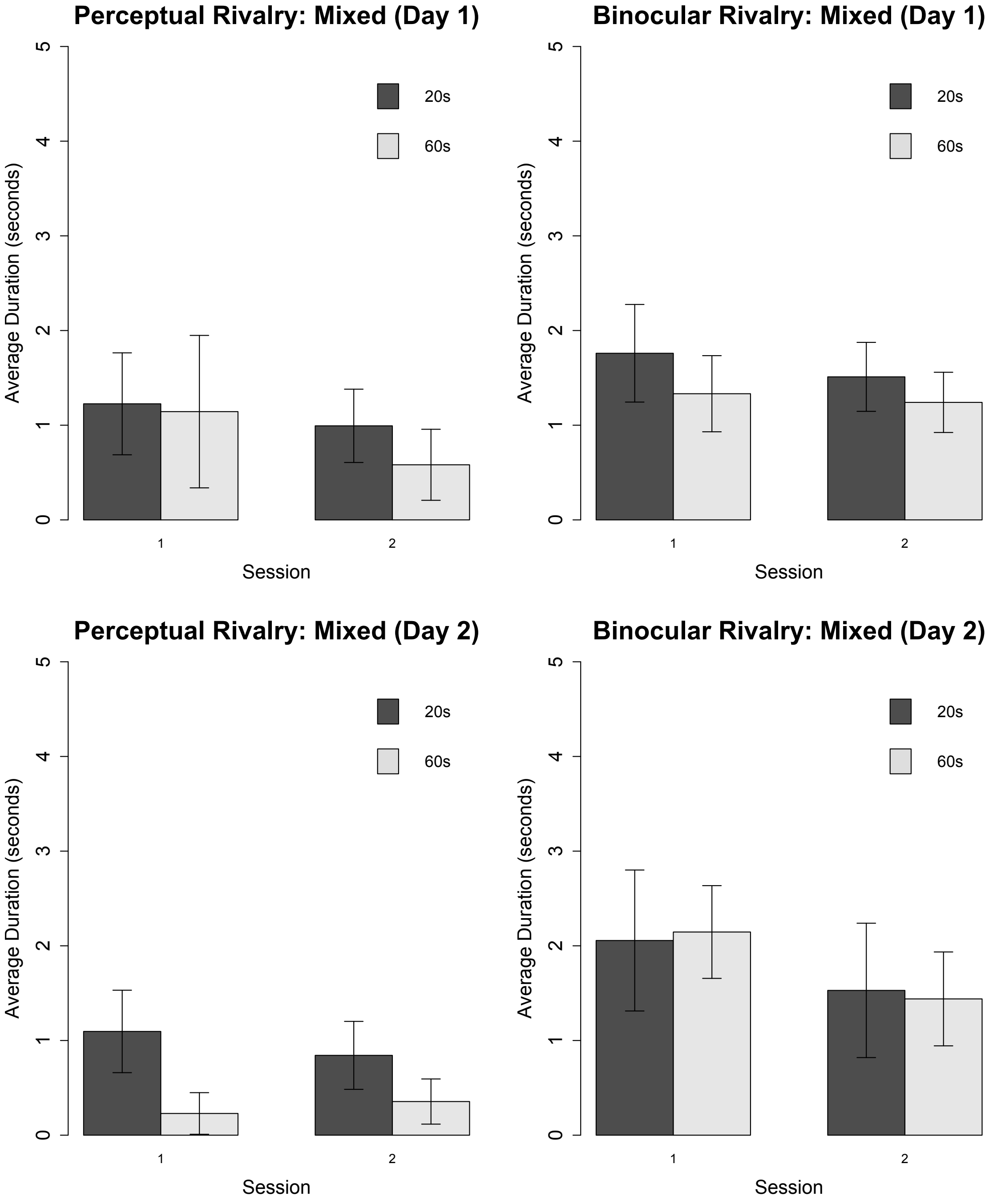


Figure 4.3: Average duration for Exclusive percepts are shown for the perceptual rivalry task (left panel) and the binocular rivalry task (right panel). The top panel shows results from Day 1 and the bottom panel from Day 2. Results for each age group are shown for both the first and second sessions for either Day 1 or Day 2. The error bars represent +/- 1 standard error.

were calculated for the factor rivalry type for Exclusive and Mixed percepts, and there were no significant correlations.

Table 4.1: Correlations (r) Between Average Durations for Two Rivalry Types

Age Group	Exclusive Percepts	Mixed Percepts
Young	0.36	0.54
Older	0.50	0.77** ($r' = 0.91$**)

(* $p < 0.05$; ** $p < 0.001$)

Table 4.2: Correlations (r) Between Average Durations on Days 1 & 2

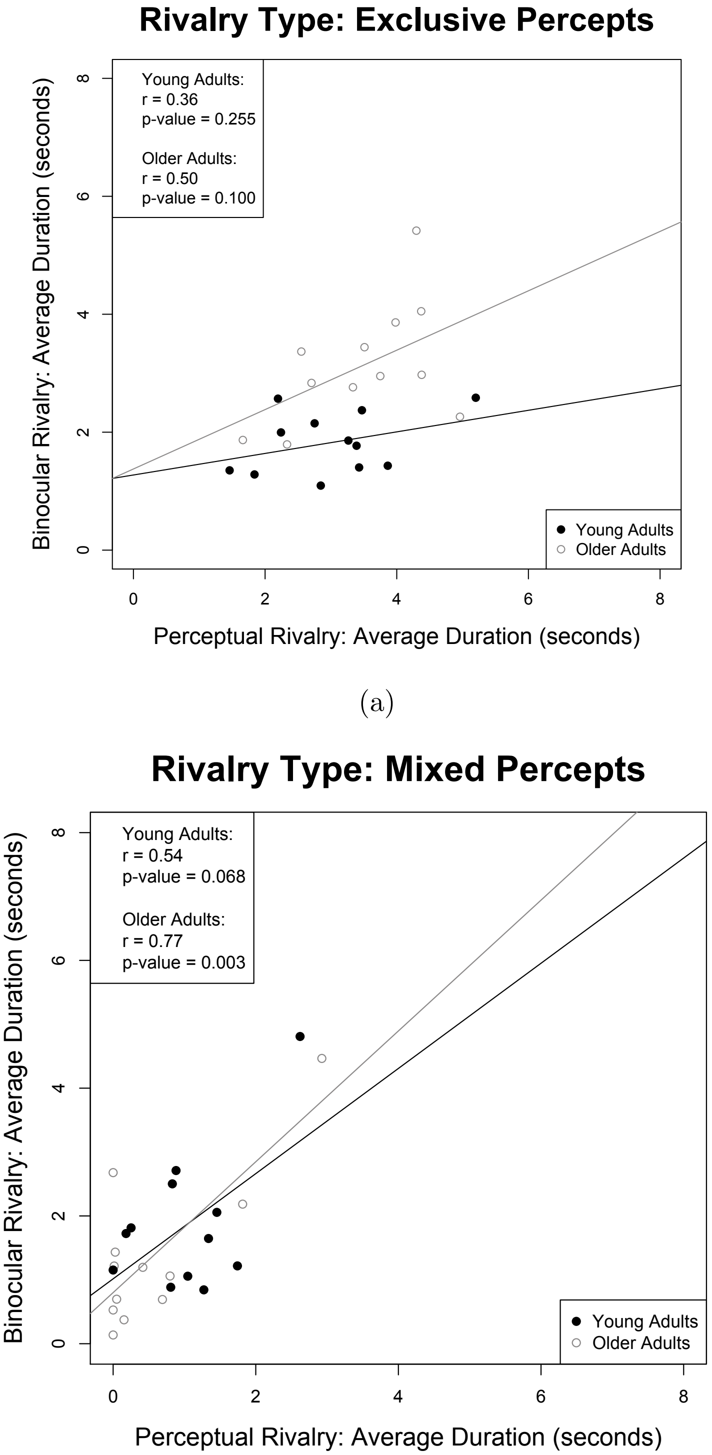
Age Group	Rivalry Type	Exclusive Percepts	Mixed Percepts
Young	Perceptual	0.76**	0.75**
Older	Perceptual	0.45	0.62** ($r' = 0.93$**)
Young	Binocular	0.15 ($r' = 0.76$**)	0.67*
Older	Binocular	0.90**	0.96**

(* $p < 0.05$; ** $p < 0.001$)

Table 4.3: Correlations (r) Between Average Durations on Sessions 1 & 2

Age Group	Rivalry Type	Day	Exclusive Percepts	Mixed Percepts
Young	Perceptual	1	0.50	0.54
Older	Perceptual	1	0.44	0.75**
Young	Perceptual	2	0.86**	0.70
Older	Perceptual	2	0.91**	0.91**
Young	Binocular	1	0.84**	0.42
Older	Binocular	1	0.77**	0.87**
Young	Binocular	2	0.90**	0.87**
Older	Binocular	2	0.86**	0.97**

(* $p < 0.05$; ** $p < 0.001$)



(a)

(b)

Figure 4.4: Within-Subjects Correlations for Rivalry Type

4.4 Discussion

The results of this study provide further evidence that binocular rivalry slows with aging, since the average duration of Exclusive percepts was longer in older compared to younger adults. However, for the perceptual rivalry task, we found no significant differences in the average durations of Exclusive percepts with aging. The current results differ from previous findings by Aydin et al. (2013) that indicated older adults experience longer average durations during perceptual rivalry. It should be noted that Beer et al. (1989) compared measures of alternation rates in young and older adults during perceptual rivalry and found stronger correlations between exogenous factors, such as years of education and verbal ability, than chronological age. In the current study, older adults did not differ from young adults in education level ($t(18) = 1.23$, $p = 0.233$). Older adults participating in the current study also did not demonstrate significant cognitive decline as they scored 27 or higher (mean score = 29.25) on the MMSE and an average of 27 on the MOCA, results indicative of normal cognitive abilities. Interestingly, when looking specifically at the older adult age group there is no correlation between age and Exclusive average duration for perceptual rivalry ($r = 0.37$, $p = 0.236$). However, there is a correlation between education level and Exclusive average duration for perceptual rivalry for the older adult age group ($r = 0.61$, $p = 0.036$). Thus, it seems likely that equivalent education levels and cognitive abilities between the two age groups may have resulted in a lack of results indicative of a significant slowing of perceptual rivalry with age in this study. Discrepancies between the current findings and past findings of age-differences in perceptual rivalry alternations could also potentially be due to a difference in the stimuli as a Rubin vase-face figure was used in the study by Aydin et al. (2013) to induce perceptual rivalry, in comparison to the Necker cube used in the current study. Although both stimuli are ambiguous images shown to each eye, and thus are likely to induce similar binocularly related neural processes, Schwartz et al. (2012) suggested that different perceptual binding processes are associated with each of these stimuli. Future research on the variations in neural components of perceptual binding for various forms of stimuli may prove of interest for researchers of visual rivalry.

There were also differences between binocular rivalry and perceptual rivalry for the dependent measure of the average duration of Mixed percepts. There was a general trend for durations of Mixed percepts to have shorter average durations in older subjects in the perceptual rivalry task. The increase in this age difference that seems to occur for Day 2 compared to Day 1 may be related to the low reliability of perceptual rivalry measures we calculated for Day 1. No significant differences were observed between age groups for the average duration of time spent viewing the Mixed percepts for binocular rivalry, a result that is consistent with the binocular rivalry experiments presented in Chapter 2, which showed that the proportion, but not the average duration, of Mixed percepts decreases with age.

Mixed percepts, which are often thought of as transitional states between Exclusive, rivalrous percepts, are one of the few areas of rivalry that has been investigated with neuroimaging. Recent neuroimaging studies have observed activation of the right-lateralized fronto-parietal network during the perceptual influence of transitions in rivalry (Knapen et al., 2011; Lumer et al., 1998; Sterzer and Kleinschmidt, 2007). The fronto-parietal network of the brain is a major brain network that is impacted by aging. An age-related structural and functional disruption of the fronto-parietal network has been shown to occur with aging (Andrews-Hanna et al., 2007;

Madden, 2007). Behavioural results from the current study suggest this change in neural circuitry in the frontal-parietal network may impact rivalry measures differently depending on the method used to instigate visual rivalry and whether it leads to binocular rivalry or perceptual rivalry. Further exploration of this region and its influence on various forms of visual rivalry at various stages across the human lifespan could prove highly beneficial to gaining a better understanding of the neural components associated with the breakdown of the binocular visual system that occurs during rivalry.

In addition to making comparisons between age groups on measures of average duration, we also assessed the reliability of our dependent measures by testing perceptual and binocular rivalry in two sessions on the same day, and on two separate days a week apart. Measures of binocular rivalry were overall more reliable than measures of perceptual rivalry. This could potentially be accounted for if subjects have more attentional control over alternations during perceptual rivalry than during binocular rivalry, resulting in more variability within-subjects and less reliability of measures across sessions and days for the perceptual rivalry task. This goes along with the idea Meng and Tong (2004) previously have proposed that attentional modulation is stronger for perceptual rivalry compared to binocular rivalry. Meng and Tong suggested that compared to perceptual rivalry, binocular rivalry may involve a more automatic, stimulus driven form of rivalry, less biased by selective attention and/or top-down modulation. If true, this theory provides a potential explanation for the greater consistency within-subjects for our binocular rivalry measures compared to our perceptual rivalry measures.

The specific increase in reliability between sessions from Day 1 to Day 2, particularly for perceptual rivalry, indicates the potential for the influence of a practice effect on the influence of strong attentional modulation. None of participants had experience with rivalry tasks in a laboratory setting when they began the current experiment. Therefore, observers may have utilized more variable degrees of attentional modulation and response biases for reporting percepts while adjusting to what can seem like a complicated task for observers inexperienced with rivalry. With an increased exposure to rivalry, specifically perceptual rivalry, the tendency of subjects to exert attentional control over percepts may have decreased and/or stabilized, allowing measures to become more consistent across sessions on Day 2. Based on the correlational results reported in the current study, researchers of perceptual rivalry concerned with maximizing the reliability of their measures within-subjects should consider the addition of an increased amount of practice for inexperienced observers. It is also interesting to note that older adults were overall more reliable in measures across sessions and days compared to young adults. However, this could be representative of a greater reliability of this sample of older adults, which consists of many highly experienced psychophysical observers, and not necessarily representative of rivalry trends in aging.

Overall, correlations between the two rivalry types were insignificant. These findings suggest that developmental changes in visual rivalry across the lifespan are unlikely to be explained entirely by a single neural mechanism. These findings are contrary to a group of previous studies that have suggested similar neural processes underlie various forms of visual rivalry, following observations of similar trends of change in rivalry measures across studies (Blake and Logothetis, 2002; Brascamp et al., 2005; Lehky, 1995; Levelt, 1968). In the present study, measures of perceptual and binocular rivalry were analyzed within-subjects with the hypothesis that if both rivalry types occur by a single neural mechanism, they would change similarly and be highly correlated within-subjects. However, these correlations were determined to be insignificant, suggesting that measures of binocular rivalry and perceptual rivalry are not consistent within-subjects. These results support theories that propose different neural mechanisms are potentially involved while viewing different types of visual rivalry. For example, Blake (2001) has suggested that although different types of visual rivalry exhibit similar temporal fluctuations, which may reflect a fundamental property of neural dynamics, this does not necessary implicate a single common neural mechanism. Further research will be needed if the theory of a single neural mechanism for all types of visual rivalry is to be excluded from discussion, as well as to determine specific neural characteristics of visual rivalry.

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Chapter 5

Characterizing perceptual alternations during binocular rivalry in children

Abstract

Many studies have investigated binocular rivalry in young adults, but we know relatively little about its developmental trajectory. To examine binocular rivalry during childhood, we created a child-friendly task, in which we presented pairs of orthogonal, oblique sine wave gratings hat differed in size (diameter = 1.4 or 4.4 deg) and contrast (0.2 or 0.8) to 7-, 9-, 11-year-olds, and young adults (mean = 21.25 years). On each trial, we measured the average duration and proportion of time participants reported seeing Exclusive, Mixed, and Fading/Other percepts. To estimate response accuracy, we intermixed pseudo-rivalry and experimental trials. Children spent a significantly greater proportion of time viewing Exclusive percepts and less time viewing Mixed

percepts compared to young adults, a finding that is inconsistent with the predictions of increased Mixed percepts in children (e.g., Kovács and Eisenberg, 2005). Average durations for Exclusive percepts did not differ significantly across age groups, contrary to previous reports suggesting faster alternation rates in children(Kovács and Eisenberg, 2005; Hudak et al., 2011). Average durations for Mixed percepts were shorter in children compared to young adults. Sequential patterns of alternations between percepts also varied between children and young adults. For example, with low-contrast stimuli the proportion of return transitions increased from childhood to adulthood.

5.1 Introduction

Binocular rivalry allows for the unique examination of the neural processes associated with binocular vision by instigating a disruption of normal stereoscopic vision. An extensive literature on the characteristics of binocular rivalry in young adults, including the effects of stimulus factors such as size and contrast (see Blake, 2001), has been established. However, far less is known about the characteristics of binocular rivalry across the human lifespan. For aging in adulthood, binocular rivalry has been found to not only slow with aging (Jalavisto, 1964; Ukai et al., 2003), but recent evidence also demonstrates different characteristics as adults age, particularly when individuals are aged 70 or higher, indicating an important developmental shift in the binocular visual system (see Chapter 2). For example, compared to younger adults, older adults spend a greater proportion of time seeing Exclusive percepts (i.e., percepts comprised entirely of an image shown to one eye), a smaller proportion of time seeing Mixed percepts (i.e., percepts comprised of some combination of the images shown to both eyes), and exhibit stronger monocular dominance during binocular rivalry. Differences in the transitional sequences of rivalry percepts have also been noted in older adults compared to younger adults, specifically older adults report a greater proportion of 'return transitions', defined by an Exclusive percept transitioning to a Mixed percept then back to the same Exclusive percept (see Chapter 2). Brascamp et al. (2006) suggested that these forms of transitions, are caused by the influence of internal noise. Interestingly, recent findings have indicated that older adults, a group known to have higher internal noise (Betts et al., 2007; Bogfjellmo et al., 2013; Pardhan, 2004), demonstrate a higher proportion of return transitions (see Chapter 2).

Our understanding of characteristics of binocular rivalry in children is also currently sparse. Kovács and Eisenberg (2005) investigated alternation rates of a group of children aged between 5-6 years and young adults by having participants indicate whenever a change in perceptual state occurred during rivalry. Kovács and Eisenberg found that children alternated between rivalrous images at a faster rate compared to young adults, and suggested that this age difference was due to a greater occurrence of Mixed percepts that consequently resulted in a shorter average duration of Exclusive percepts in children. Consistent with this idea, Hudak et al. (2011) found marginally significant shorter average duration of Exclusive percepts in 9-year old and 12-year old children compared to young adults. Thus, these results seemed to be in agreement with those found by Kovács and Eisenberg (2005). Although these studies have provided a much needed insight into the development of binocular rivalry, they reported only a few limited measures of rivalry in children, and used experimental designs that differ greatly from previous studies with young adults, making it difficult to compare results across studies. To allow for a more direct comparison of rivalry characteristics across the lifespan, the current study therefore used an experimental design that was similar to the design used in a previous study of the effects of aging on binocular rivalry (see Chapter 2). The current experimental design and the recording of a more comprehensive analysis of measures of binocular rivalry in children may reveal important transitional periods that exist in the development of binocular vision, as well as allow for a greater understanding of characteristics of binocular vision across the human lifespan.

5.2 Method

5.2.1 Observers

Participants were 7-year-olds (7 years 0 months ± 3 months, M = 7.06 years, 6 females and 6 males), 9-year-olds (9 years 0 months ± 3 months, M = 8.96 years, 7 females and 5 males), 11-year-olds (11 years 0 months ± 3 months, M = 10.99 years, 6 females and 6 males), and young adults (age range = 20-25 years, M = 21.25 years, 6 females and 6 males). Young adult observers were undergraduate and graduate students recruited from McMaster University and either volunteered to participate (9 participants), received partial completion of credit for course requirements (one participant), or monetary compensation for their time at a rate of $10.00/hour (2 participants). Children were recruited from a database of children whose parents volunteered to participate in research at the time of their child's birth. Children received an age appropriate toy for their participation in this study.

All participants had normal or corrected-to-normal visual acuity of at least 20/20 as measured by the Lighthouse Visual Acuity Chart. Stereoacuity was also normal for all participants as measured by the Randot Stereotest (Stereo Optical Company). Observers of all ages had a minimum stereoacuity threshold of 40 seconds of arc at 16 inches (mean stereoacuity threshold: 7-year-olds = 22.5 seconds of arc, 9-year-olds = 22.5 seconds of arc, 11-year-olds = 21.25 seconds of arc, young adults = 25 seconds of arc). Monocular contrast sensitivity of each eye also was determined for each participant, and minimal inter-ocular differences were found for each age group, 7-year-olds (M = 0.025), 9-year-olds (M = 0.0125), 11-year-olds (M = 0.0125) and young adults (M = 0.0125).

Four observers were replaced for failing visual screening (one 7-year-old, two 9-year-olds, and one 11-year-old). One 7-year-old observer was replaced due to a technical malfunction. Five observers (three 7-year-olds, one 11-year-old, and one young adult) were replaced for failing to meet accuracy criterion for the control trials, and six observers (two 7-year-olds, one 9-year-old, two 11-year-olds, and one young adult) were replaced for failure of rivalry to be instigated for at least one trial in each condition.

5.2.2 Apparatus

Two testing rooms were used to collect data for this study. In the primary experiment room, where most of the data were collected, stimuli were generated on a Macintosh PowerPC G5 using MATLAB 7.10 (R2010a) (Mathworks, Natwick, MA, USA) and the Psychophysics Toolbox (Brainard, 1997). This experimental computer was connected to a DATAPixx lite data and video processor (VPixx Technologies, Inc.). To allow for highly accurate synchronization, all external devices were connected to the DATAPixx box. Stimuli were displayed on a 30-inch Apple Cinema HD display with a resolution of 2560 × 1600 pixels. Participants viewed the stimuli binocularly from a distance of 100 cm. The viewing position of each participant was stabilized with the use of a chin rest. Different images were presented to the observers left and right eye, thus allowing for binocular rivalry, using red/cyan glasses. Gamma corrections were made to ensure that the red and cyan were equiluminant. A RESPONSEPixx (VPixx Technologies, Inc.) handheld button box was used to record participant responses.

Data from one-half of the 7-year old participants were collected in a secondary testing room. In the secondary testing room stimuli were generated on a Macintosh Pro 4 computer, and that this experimental computer was connected to a DATAPixx (VPixx Technologies, Inc.) data and video processor. Preliminary statistical analyses found no differences between the groups of 7-year old participants tested in the two experiment rooms. As noted in the following Stimulus Display section the average luminance differed between the two experiment rooms. Therefore, we also conducted an additional, separate control experiment (not reported) that compared rivalry measures obtained at an average luminance of 18.4 cd/m^2 and 37.7 cd/m^2 on separate groups of 7-year old observers ($n = 6$ per group) and found no significant differences. Therefore, the data from 7-year old participants who were tested in the two rooms were combined into a single group for our main statistical analyses.

5.2.3 Stimulus Displays

Stimuli were pairs of orthogonal oblique sine-wave gratings presented dichoptically with red/cyan glasses at a spatial frequency of 5 cy/deg. Stimuli size (diameter = 1.4 or 4.4 deg) and contrast (0.2 or 0.8) varied across trials. For the primary experiment room the average luminance was maintained within a photopic range of 18.4 cd/m^2 and 37.2 cd/m^2. In the secondary experiment room, the average luminance was 37.7 cd/m^2.

5.2.4 Procedure

Before visual screening, the experimental procedure was explained and all adult participants gave informed consent prior to participating in this study. The parent of each child participant also gave informed consent and each child gave verbal assent. Upon completion of visual screening, the participant was positioned in the apparatus and the following instructions were read aloud by the experimenter:

> "You are an astronaut and your spaceship has just flown by a strange planet controlled by aliens. The aliens are trying to talk to you using special alien pictures, but to see the pictures you need to wear these special glasses [experimenter shows the participant the anaglyph glasses]. Your job will be to record the alien pictures that you see by holding buttons on this special box [experimenter shows the participant the response box]."

Before continuing, the experimenter instructed participants to focus their attention on a laptop display where example images of the perceptual states they would be asked to report were presented. During this presentation, the experimenter explained:

> "If you see a picture with lines pointing towards the blue spaceship, hold the blue button [experimenter points to the blue button on the button box]. If you see a picture with lines pointing towards the red spaceship, hold the red button [points to the red button on the button box]. If you see funny pictures like this or this [points to the example images of Mixed percepts onscreen], hold both the blue and red buttons. If the picture changes from one to another like a wave [show example animation of Mixed percept onscreen], also hold both buttons. If you see something different than these pictures, or the pictures start to disappear, do not press any button. Before each message, there will be a beep and the dot in the middle of the screen will get bigger to let you know to get ready. Make sure to look at this dot when you are recording each message. Also, make sure to switch between holding buttons as quickly as you can!"

Since all observers were naïve to the phenomenon of binocular rivalry, the participants were then asked to press and hold the button that was representative for each type of perceptual state. After ensuring the instructions were clearly understood by the participant, the experimenter initiated a 60 s dark adaptation period followed by a block of two 30 s practice trials. The condition type (small size/low-contrast, small size/high-contrast, large size/low-contrast, large size/high-contrast) was randomized for the first practice trial. The second practice trial was the opposite size and contrast from the first practice trial that was presented. If necessary, a second practice session was completed by the participant. Upon ensuring the participant was attentive and felt comfortable with the task, the experimenter then initiated the experimental block of trials.

The experimental session consisted of 12 binocular rivalry trials. The four trial condition types were randomized within each session. There were three trials of each condition type within the experimental session. Each trial lasted for a duration of 30 s and the inter-trial interval was 15 s to allow after-effects to diminish. Pseudo-rivalry trials, in which a series of alternating unambiguous Exclusive percepts were presented during each trial, were intermixed with the experimental trials of binocular rivalry. There were four of these pseudo-rivalry trials, one of each condition type, that lasted for a duration of approximately 30 s.

5.3 Analyses

To remove any incidental button presses that may have occurred during the course of a trial, all button presses less than 400 ms in duration were discarded before the final analyses. Additionally, if an observer reported only a single percept for the span of the entire trial (binocular rivalry was not instigated), or did not press any buttons, the trial was excluded from further data analysis. Valid trials and responses for measures of average duration and proportion of time were subjected to separate 3-Way ANOVAs, with age (7-, 9-, 11-year-olds, and young adults) as a between-subject factor, and size (1.4 and 4.4 degrees visual angle) and contrast (0.2 and 0.8) as within-subject factors, for each of the three types of reported percepts (Exclusive, Mixed, and Other). Generalized eta squared values (η_N^2) are reported for effect sizes (see Olejnik and Algina, 2003; Bakeman, 2005, for review). Unless otherwise noted, all p values are two-tailed.

5.4 Results

5.4.1 Average Duration and Proportion of Time

Exclusive Percepts Although reported separately, the two Exclusive images (clockwise-oriented grating and counterclockwise-oriented grating) are both considered Exclusive percepts and thus were considered the same type of category of percepts for analysis. Average durations of Exclusive percepts are shown for each age group in Figure 5.1a. There was no significant main effect of age ($F(3, 43) = 0.22$, $p = 0.882$, $\eta^2_N = 0.01$), but there were significant main effects of size ($F(1, 43) = 15.64$, $p < 0.001$, $\eta^2_N = 0.05$) and contrast ($F(1, 43) = 13.92$, $p < 0.001$, $\eta^2_N = 0.05$). However, the difference in the mean average durations for the two size conditions, though significant, was small (i.e., 2.74 s vs 2.37 s in the small and large conditions, respectively). The difference between the low- (M=2.72 s) and high- (M=2.4 s) contrast condition also was relatively small.

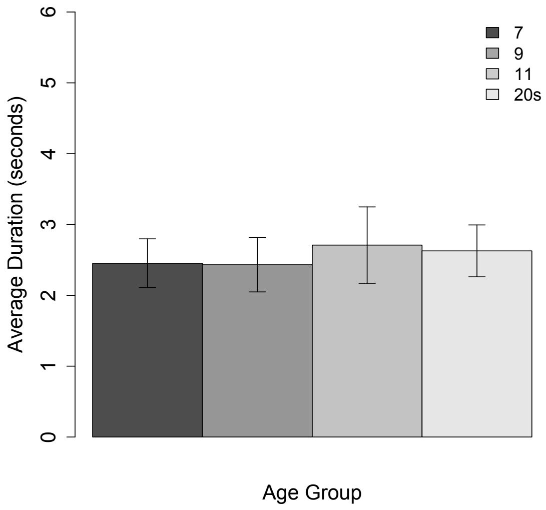
The average proportion of time that Exclusive percepts were seen are shown for each age group in Figure 5.1b. There was a marginally significant main effect of age ($F(3, 44) = 2.76$, $p = 0.054$, $\eta^2_N = 0.10$), which reflects the lower proportion of time young adults spent viewing Exclusive percepts compared to each of the three childhood age groups (7-, 9-, and 11-year-olds). There was also a main effect of contrast ($F(1, 44) = 4.66$, $p = 0.036$, $\eta^2_N = 0.01$) and a size × contrast interaction, ($F(1, 44) = 4.34$, $p = 0.013$, $\eta^2_N = 0.01$). This interaction is a result of a decreased proportion of time spent viewing Exclusive percepts for the larger stimuli compared to the smaller stimuli for high-contrast conditions, but no difference with size for the low-contrast conditions (see Table 5.1).

Table 5.1: Exclusive Proportion of Time: Size × Contrast

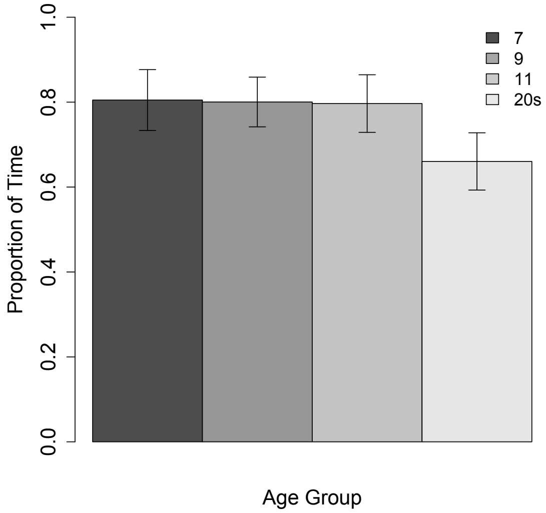
Size	Low-Contrast	High-Contrast
Small	0.75	0.82
Large	0.75	0.74

Mixed Percepts Average durations of Mixed percepts are shown for each age group in Figure 5.2a. The figure suggests that the average duration of Mixed percepts was shorter in children than young adults, but the main effect of age was not significant ($F(3, 29) = 0.78$, $p = 0.514$, $\eta^2_N = 0.04$). There was a significant main effect of size ($F(1, 29) = 5.57$, $p < 0.001$, $\eta^2_N = 0.02$) and a significant size × contrast interaction ($F(1, 29) = 6.42$, $p = 0.016$, $\eta^2_N = 0.03$). Table 5.2 indicates this interaction is driven primarily by an increase of the average duration of Mixed percepts for the large conditions compared to the small conditions at high-contrast.

Figure 5.2b shows the average proportion of time spent viewing Mixed percepts for the various age groups. The main effect of age was significant ($F(3, 44) = 4.99$, $p = 0.005$, $\eta^2_N = 0.18$). This effect was primarily driven by the greater proportion of time young adults spent viewing Mixed percepts compared to each of the childhood age groups (7-, 9-, and 11-year-olds). There was a significant main effect of size ($F(1, 44) = 7.67$, $p = 0.008$, $\eta^2_N = 0.02$) and a size × contrast interaction ($F(1, 44) = 6.05$, $p = 0.018$, $\eta^2_N = 0.01$). By viewing Table 5.3, it can be seen that there were no differences between size conditions for low-contrast conditions, but for high-contrast conditions participants spent a greater proportion of time viewing Mixed percepts than for low-contrast conditions.



(a)



(b)

Figure 5.1: a.) Average duration for Exclusive percepts is shown for each age group. Error bars represent +/- 1 standard error. b.) Proportion of time spent in the Exclusive percepts is shown for each age group. Error bars represent +/- 1 standard error.

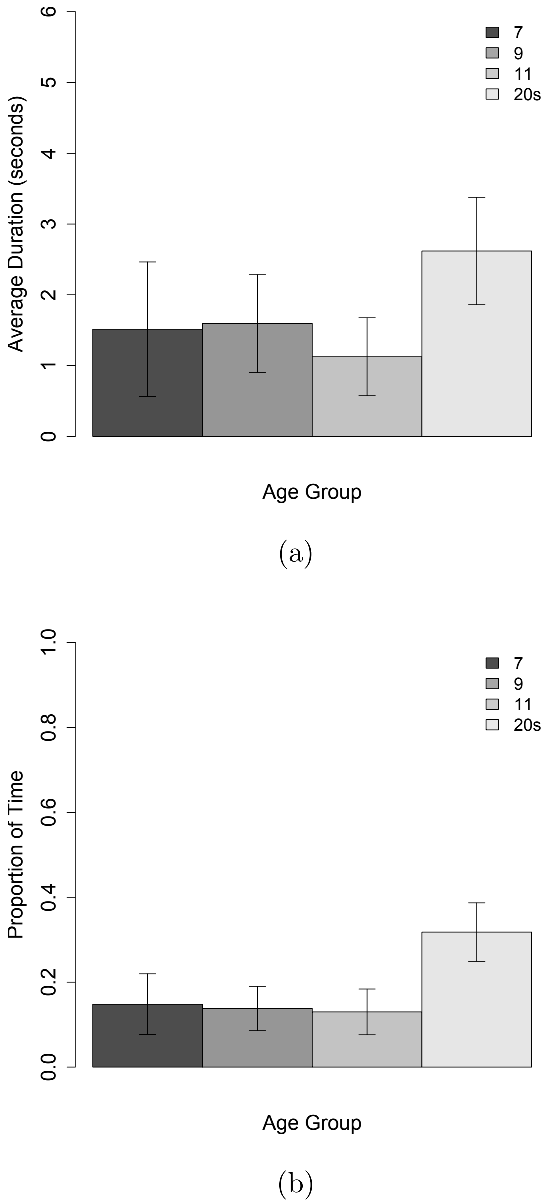


Figure 5.2: a.) Average duration for Mixed percepts is shown for each age group. Error bars represent +/- 1 standard error. b.) Proportion of time spent in the Mixed percepts is shown for each age group. Error bars represent +/- 1 standard error.

Table 5.2: Mixed Average Duration: Size × Contrast

Size	Low-Contrast	High-Contrast
Small	1.81	1.00
Large	1.86	2.15

Table 5.3: Mixed Proportion of Time: Size × Contrast

Size	Low-Contrast	High-Contrast
Small	0.19	0.12
Large	0.19	0.23

Other Percepts Subjects in all age groups and conditions were much less likely to report seeing an Other percept than Exclusive or Mixed percepts. Indeed, the average duration and the proportion of time were both near zero in most conditions and age groups. Because of possible floor effects, ANOVAs on these data are not appropriate. In any case, all differences were minimal, with the largest effect occurring for size (Small, M = 0.06; Large, M = 0.04) still being relatively small.

5.4.2 Sequential Pattern of Alternations

The average duration and proportion of time measures reveal useful information about rivalry; however, rivalry percepts change continuously throughout a trial. Therefore, we examined sequential patterns, specifically consisting of three perceptual alternations, to provide a more comprehensive investigation of binocular rivalry. To make the analysis tractable, we normalized these results by sorting sequential patterns into groups based on a set order of the first two perceptual states, and then analyzed the proportion of all possible third percepts for each of the initial sequential transition pairs. It has been generally assumed that rivalry follows a pattern of switching from one Exclusive percept to a Mixed percept then to the second, alternative Exclusive percept, and Chapter 2 found unique age-related differences associated with the proportion of transitions from one Exclusive percept to a Mixed percept and returning to the same Exclusive percept. Therefore, we decided to focus our analysis specifically on the First Exclusive → Mixed → ? group of sequential triads. For the purposes of this analysis "First Exclusive" refers to the first Exclusive percept in the triad, and can be either an exclusively counter-clockwise grating percept or clockwise grating percept. "Second Exclusive" refers to the Exclusive percept that is opposite to the First Exclusive percept. Each analyzed sequence potentially could be seen by different numbers of participants from each age group because not all participants necessarily reported all possible sequences in each stimulus condition.

Sequences ending with a transition to Other percepts (i.e., First Exclusive → Mixed → Other) were rare for all age groups and thus were not statistically analyzed, but it can be seen in Figure 5.3 that while there is a slight increase in the proportion of this sequence at low-contrast, age differences are minimal. Therefore, we focussed on the effects of age, pattern size, and pattern contrast on the proportion of times participants reported seeing First Exclusive → Mixed → Second Exclusive and First Exclusive → Mixed → First Exclusive sequences.

An ANOVA on the proportion of times participants reported seeing a First Exclusive → Mixed → Second Exclusive sequence yielded a significant age × contrast interaction ($F(3, 24) = 5.17$, $p = 0.007$, $\eta^2_N = 0.11$). This interaction is illustrated in Figure 5.3, which shows the proportion of sequences, averaged across stimulus sizes, for each age group and contrast. As seen in Figure 5.3, the effect of age was much

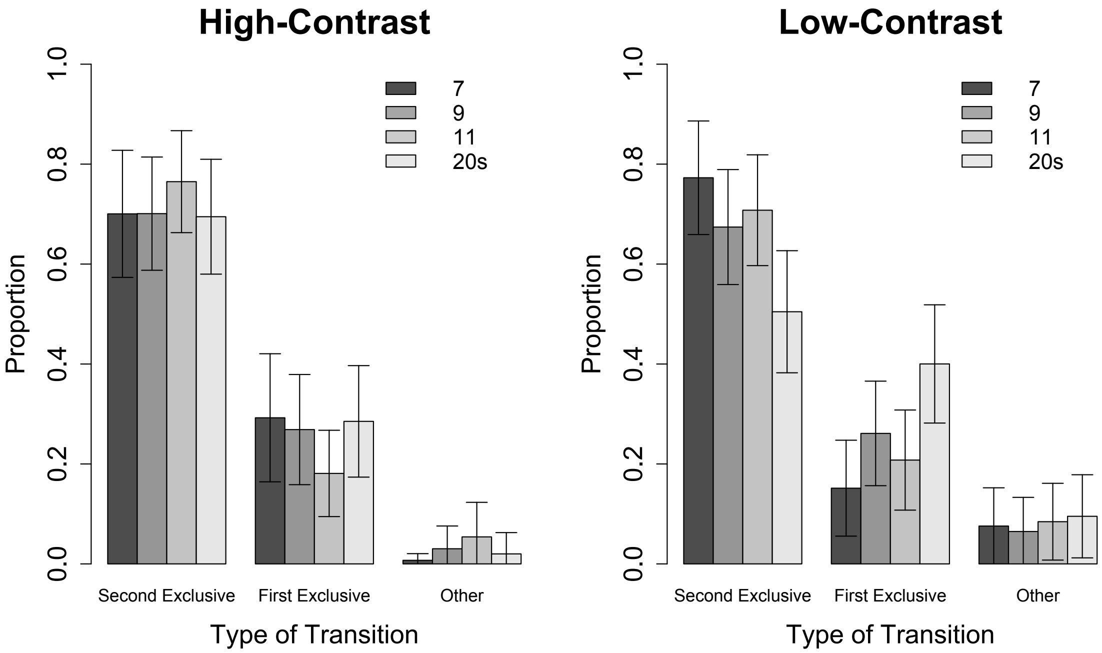


Figure 5.3: 3-Step Transitional Sequences. Proportion of each of the potential sequences in the First Exclusive → Mixed → ? group are shown for both high-contrast (left panel) and low-contrast (right panel). Error bars represent +/- 1 standard error.

greater with low-contrast stimuli. Specifically, in the low-contrast condition the proportion of First Exclusive → Mixed → Second Exclusive was higher in children than adults, whereas in the high-contrast condition there was no obvious difference among age groups.

An ANOVA on the proportion of times participants reported seeing a return transition (i.e., First Exclusive → Mixed → First Exclusive sequence) also yielded a significant age × contrast interaction ($F(3, 25) = 5.33$, $p = 0.006$, $\eta^2_N = 0.09$). Figure 5.3 shows that this interaction was also driven by the low-contrast conditions, with children demonstrating a smaller proportion of this type of transitional sequence for low-contrast conditions. Note that this age difference is opposite to the one obtained with the First Exclusive → Mixed → Second Exclusive sequence, which is not surprising because the proportion of sequences that ended with Other percepts was low in all age groups, and therefore the proportion of sequences that ended with First Exclusive and Second Exclusive percepts were constrained to sum to a value near 1.0. In summary, we found evidence of an age difference in First Exclusive → Mixed → ? sequences in low-contrast, but not high-contrast, conditions. Specifically, children were less likely to report seeing so-called return transitions (i.e., First Exclusive → Mixed → First Exclusive) than young adults in low-contrast conditions.

5.5 Control Trials: Pseudo-rivalry

As mentioned in the Procedure (see Section 5.2.4), pseudo-rivalry trials were intermixed with the experimental trials. All participants were required to meet 75% accuracy on both the ability to report the correct Exclusive percept shown and in their accuracy of reporting the appropriate proportion of time spent viewing each percept shown. Participants that did not meet these accuracy criterion were excluded from further analyses and replaced as discussed in the Observers section (see Section 5.2.1). Further analyses were conducted on all participants that passed the exclusion criteria to determine if the developmental effects reported above were due to differences in either motor delay or reporting accuracy.

Overall, across all stimulus durations participants in each age group accurately reported the correct Exclusive percepts shown onscreen (7-year olds = 84.11%, 9-year olds = 88.28%, 11-year olds = 87.76%, and young adults = 95.05%). Since our interest was specifically whether there were age differences between children and young adults at each of the four pseudo-rivalry stimulus durations presented (1.73 s, 2.6815 s, 4.56 s, and 7.068 s) pairwise comparisons also were conducted. The only significant differences between age groups were found for the two longest stimulus durations, 4.56 s and 7.068 s (see Table 5.4), with younger children being less accurate. These durations are longer than any current or previously reported average duration for Exclusive percepts for these age groups. Kovács and Eisenberg (2005) has also reported inaccuracies in children reporting longer controlled durations when asked to report perceptions during pseudo-rivalry, but no differences in accuracy for durations within the reported range of durations for children and young adults.

Table 5.4: Proportion of Accurately Matching Reports (p-values reported)

Age Group	1.73 s	2.6815 s	4.56 s	7.068 s
7-year olds	0.359	0.145	<0.001	0.007
9-year olds	0.126	0.197	0.103	0.038
11-year olds	0.074	0.080	0.117	0.128

For the proportion of time reported for each percept compared to the accurate duration the percept was shown, there were no significant differences between each of the childhood age groups and young adults for any stimulus duration for pairwise comparisons. However, there was a marginally significant difference between 9-year olds and young adults ($t(19.88) = -2.03$, $p = 0.056$) for the longest duration of 7.068 s, with 9-year olds responding with a slightly lower proportion of time. It should be noted that this is in the opposite direction of the age-effects demonstrated for proportion of time spent viewing Exclusive percepts for the experimental trials.

5.6 Discussion

This is the first study to analyze proportion of time spent viewing any percept during binocular rivalry in children. For Exclusive percepts, children viewed these percepts for a greater proportion of time than young adults. This age difference could be due to children either experiencing a greater occurrence of Exclusive percepts and/or spending a longer average duration viewing an Exclusive percept before switching perceptual states. However, contrary to previous reports (Kovács and Eisenberg, 2005; Hudak et al., 2011), we found that the average durations of Exclusive percepts were similar in children and young adults. One possible explanation for the different findings is that the experimental methods and data analysis used in previous studies may have yielded an inaccurate representation of self-report responses from children. For example, children in the Kovács and Eisenberg study were instructed "to press a button whenever the grating orientation changed". This reporting method makes it impossible to separate Exclusive and Mixed percepts for analysis. Our results indicate that average durations of Mixed percepts in children are slightly shorter than in young adults. Thus, combining all reported changes in perceptual state may have led Kovács and Eisenberg to the erroneous conclusion that children have shorter Exclusive percepts when our results indicate children have shorter Mixed percepts. It is also important to note that Kovács and Eisenberg included all button presses in their data analysis, whereas the current study included only presses with durations $>$ 400 ms to prevent the inclusion of accidental button presses. By including all button presses previous studies may have included artificial button presses that were not representative of perceptual states, and instead representative of accidental motor impulses. Thus, biasing their results towards faster alternations for children, since control studies in this study and prior work (Kovács and Eisenberg, 2005) has shown increased instances of these short accidental button presses in young children required to press one button for a long duration of time (see Section 5.5).

Like Kovács and Eisenberg (2005), Hudak et al. (2011) also found that older children (9-year olds and 12-year olds) reported a shorter average duration for Exclusive percepts than younger adults. Participants in the Hudak et al. study reported perceptual alternations by moving a joystick, and Exclusive percepts included all instances where the 75% threshold of maximal joystick tilt was surpassed either to the left or right side. Note that this definition of Exclusive percepts could potentially include instances of Mixed percepts, depending on response bias (i.e., distinguishing Mixed and Exclusive percepts) and/or an inability to finely control the tilt of the joystick. Once again, although the current study found no age differences in the average duration of Exclusive percepts, we did find that the average durations of Mixed percepts were shorter in children. With the potential for inclusion of Mixed percepts, it is possible that the results reported by Hudak et al. of the average duration of Exclusive percepts in children is biased towards shorter durations. Interestingly, Hudak et al. did not report any analyses of Mixed percepts, even though their observers were asked to report these states. Thus, while at first these results for Exclusive percepts seem contrary to previous findings of studies of binocular rivalry in children, it is our belief that differences in experimental design and analysis provide plausible explanations for varying findings.

One important component of the current study is that it is the first study to report measures of Mixed percepts in children during binocular rivalry. Our findings for the effects of size and contrast are similar to previous results indicating young adults experience an increase in the average duration of Mixed percepts with increased size and an increase in the proportion of time spent viewing Mixed percepts with larger stimuli (Blake et al., 1992; O'Shea et al., 1997), and suggests these effects may be dependant on contrast. In our study, young adults viewed Mixed percepts for a greater proportion of time than children. These results are contrary to the inferences made by Kovács and Eisenberg (2005) . It should be noted that in forming their hypothesis of the occurrence of greater Mixed percepts in children Kovács and Eisenberg (2005) relied on anecdotal reports from children, as well as circumstantial evidence from alternative experiments comparing alternation rates during binocular rivalry in adults by varying a stimulus component known to produce different levels of Mixed percepts (e.g., small and large stimuli). The direct evidence of reports of Mixed percepts from the current study indicates the currently accepted theory about characteristics of binocular rivalry in children proposed by Kovács and Eisenberg (2005) involved too many assumptions and should be revised.

Our finding of age differences in Mixed percepts is also interesting because it is consistent with the notion that the activation of fronto-parietal region is related to Mixed percepts during binocular rivalry. Neuroimaging studies have provided evidence for an association between activation of right-hemisphere frontal and parietal areas during transitions in perceptual states (Lumer et al., 1998; Sterzer and Kleinschmidt, 2007). A recent study expanded upon this evidence and concluded a component of the right-lateralized fronto-parietal network is also activated by the perceptual influence of transitions (Knapen et al., 2011). Fair et al. (2007) have recently shown that the circuitry of the fronto-parietal region is not fully adult-like even during adolescence. Thus, the lack of completed circuitry of the fronto-parietal region in children compared to young adults may provide an explanation for the differences in results for both average duration and proportion of time viewing Mixed percepts.

Interestingly, the fronto-parietal region has been shown to change with age (Andrews-Hanna et al., 2007; Madden, 2007), and the proportion of time viewing Mixed percepts has been shown to decrease throughout adulthood with aging (see Chapter 2). Thus, there could be a potential connection between an incomplete fronto-parietal network and lower proportions of time spent viewing Mixed percepts. However, unlike the shortened average duration of Mixed percepts in children compared to young adults shown by the current study, Chapter 2 found no difference in average duration of Mixed percepts between young and older adults. Therefore, if fronto-parietal activation is related to Mixed percepts, then it appears that the link between neural activity and Mixed percepts is different in children and older adults. Thus, the Mixed percept results from the current study of children actually provide unique insight into the preservation of the neural mechanisms associated with the average duration of Mixed percepts with age, while other neural mechanisms associated with the proportion of time seem to deteriorate with age. Further neuroimaging studies will be needed to clarify the potential role of the fronto-parietal region in relation to Mixed percepts throughout the lifespan and to further understand the potential impact of the preservation of some components of the neural mechanisms associated with the binocular visual system with aging.

Our analysis of sequential transitions also provides a unique insight into binocular rivalry. Traditionally it has been assumed that rivalry follows a pattern of switching from one Exclusive percept to a Mixed percept then to the other Exclusive percept. The current study provides further evidence that other types of transitions commonly occur. The increase in the proportion of return transitions (e.g., the First Exclusive → Mixed → First Exclusive sequence) from childhood to young adulthood for low contrast conditions is of distinct interest, particularly due to previous findings that return transitions increase with aging in adulthood at low-contrast, but not for high-contrast conditions (see Chapter 2). According to a computational model by Brascamp et al. (2006), increased internal noise causes a greater proportion or return transitions. Shpiro et al. (2009) introduced the coefficient of variation, a mathematical index that juxtaposes the influence of adaptation and internal noise to quantify the influence of these two factors on binocular rivalry. Thus, if the current results of fewer return transitions in children are taken to infer lower internal noise, according to the return transition theory introduced by Brascamp et al. (2006), children would be expected to have a greater influence of adaptation on binocular rivalry than young adults. This is supported by the conclusions of Hudak et al. (2011) that their analysis of correlations of dominance durations with prior history during binocular rivalry indicated a greater relative contribution of neural adaption in children. On the contrary, previous analyses have indicated a greater contribution of internal noise on binocular rivalry with aging in adulthood (see Chapter 2). Since return transitions involve Mixed percepts, it is important to address the possibility that differences between children and young adults for Mixed percepts may arise because children do not understand or report Mixed percepts properly. It should be noted that if this was true, then we would expect similar reports of Mixed percepts to occur in all stimulus conditions. The fact that age differences in Mixed percepts depend on stimulus contrast argues against a simple explanation of age difference in terms of response bias and/or a failure to follow instructions. The presence of differences for children between contrast conditions for sequential transitions that include Mixed percepts provides evidence that children were competent in the identification of Mixed percepts. Thus, the results for return transitions in children demonstrated in the current study provides important evidence for a developmental trend throughout the human lifespan, and highlights the important need for further research on how adaptation and internal noise operate throughout the lifespan at varying contrasts.

In conclusion, our studies provide strong evidence for several developmental changes in binocular rivalry that occur throughout the lifespan, and for important similarities and differences in development that occurs during childhood and senescence. For example, our studies have now shown that both children and older adults view Exclusive percepts for a greater proportion of time, and Mixed percepts for a smaller proportion of time, compared to young adults. Also, our analysis of sequential transitions found that the proportion of return transitions increases from childhood to young adulthood and continues to increase with aging. On the other hand, our studies show the average duration of Exclusive percepts is longer in older than younger adults, but does not differ between children and young adults. Also, the average duration of Mixed percepts is shorter in children than young adults, but does not differ between younger and older adults. This comprehensive analysis of the characteristics of perceptual alternations during binocular rivalry in children will hopefully provide a foundation for neural models of binocular vision in children, as well as allow further comparisons of the development of binocular vision across the lifespan.

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Chapter 6

General Discussion

This thesis addressed gaps in our knowledge of the characteristics of binocular rivalry across the lifespan. My studies demonstrated how the development of experimental techniques that are appropriate for a variety of ages, yet still rooted in the experimental principals used to study binocular rivalry in a laboratory setting for centuries, allows for the detailed investigation of age-related changes in rivalry. The importance of a comprehensive investigation of rivalry characteristics when establishing the foundational framework of our understanding of rivalry in special populations, such as children and older adults, is highlighted by this thesis. My comprehensive examination of binocular rivalry in older adults also is a useful model for testing theoretical models of binocular rivalry. The following discussion highlights the most prominent findings from this thesis, how they can be integrated into theories of binocular rivalry, and how this thesis forms the foundation for avenues of future research.

6.1 Summary of Results

My experiments on binocular rivalry found that the average duration of Exclusive percepts were longer in older than younger adults, a result that is consistent with previous studies that found an overall slowing of binocular rivalry alternations (Jalavisto, 1964; Ukai et al., 2003). This thesis also demonstrates that other characteristics of binocular rivalry also vary across the lifespan. For example, a significant increase in monocular dominance was found with aging in Chapter 2. This increase in monocular dominance with age was replicated in Chapter 3. Chapter 3, also provided intriguing evidence that monocular dominance is not significantly affected by inter-ocular differences in contrast for senior-seniors, unlike younger adults. The reliability of measures of binocular rivalry across time periods shown in Chapter 4 for both younger and older adults indicates the robustness of these age-related findings. Chapter 4 also found that unlike in binocular rivalry there were minimal differences between younger and older adults for perceptual rivalry, contradictory to previous findings (Aydin et al., 2013).

This thesis also showed that binocular rivalry characteristics continue to change significantly as older adults age from junior-seniors to senior-seniors, but is comparatively stable throughout childhood (see Chapter 5). However, there are differences between children and younger adults, particularly in Mixed percepts, which had shorter average durations and were seen for a smaller proportion of time in children compared to younger adults. Interestingly, older adults also spend a smaller proportion of time viewing Mixed percepts than younger adults. My experiments also found a developmental trajectory across the lifespan for the sequential transitions of percepts during binocular rivalry. Results from Chapter 2, indicate older adults, particularly senior-seniors, perceive a greater number of return transitions, where the perceptual state transitions from one Exclusive percept through a Mixed percept back to the same Exclusive percept, compared to younger adults. Results from Chapter 5 show children experience fewer return transitions compared to younger adults.

6.2 Implications

The primary significance of this thesis is that it demonstrates that binocular rivalry not only slows with aging, but several characteristics of rivalry also vary across the lifespan. Of particular interest is the discovery of increased monocular dominance with aging shown in Chapter 2 and Chapter 3. Chapter 3 also suggests the neural changes that appear to cause this change in monocular dominance with aging are strong enough to resist the influence of external stimulus factors, such as contrast. This finding is particularly intriguing considering the salience of the image presented to each eye is known to influence perceptual dominance during binocular rivalry for young adults (Levelt, 1965), and specifically when rivalrous images are presented to young adults with inter-ocular contrast differences the image with a higher contrast has a greater dominance than the lower contrast image (Levelt, 1965; Mueller and Blake, 1989). This is known as Levelt's first proposition, and has been a hallmark of binocular rivalry research for over 50 years. However, the findings outlined in this thesis indicate limitations to the applicability of Levelt's first proposition with aging. These limitations will be important for researchers to consider when designing future studies investigating how characteristics of binocular rivalry compare between younger and older adults.

Stronger monocular dominance in older adults compared to younger adults also has potential implications for how we interact with our 3-D surroundings throughout the lifespan. The greater reliance on information from one eye, represented by increased monocular dominance, suggests the possibility of a decrease in the ability of older adults to attain the binocular fusion utilized for stereoscopic vision. This has the potential to lead to altered judgements about 3-D structure of objects as adults age. In fact, previous research has found that some features of stereoscopic vision deteriorate with age (Norman et al., 2000, 2006). However, our general understanding of stereopsis and aging is still minimal and future studies will be required to determine the true implications of increased monocular dominance with aging on our interactions with our 3-D surroundings.

Mixed percepts were also shown to change across the lifespan in this thesis. The results from 2 and Chapter 5 indicate the proportion of time spent viewing Mixed percepts is lower for children and older adults compared to young adults. These results provide the first reported measure of Mixed percepts in these age groups, and seem to contradict the assumptions made by Kovács and Eisenberg (2005) that children perceive a greater occurrence of Mixed percepts compared to young adults. Children also reported a shorter average duration of Mixed percepts, while overall older adults showed no difference in this measure with aging compared to young adults. Little is currently known about the specific neural circuitry involved with Mixed percepts during binocular rivalry. However, a recent line of work investigating the potential connection between the fronto-parietal region and transitions could provide an explanation for this trajectory throughout the lifespan. The circuitry of the fronto-parietal region has been found to be incomplete until age fourteen (Fair et al., 2007), and children tested in this thesis were all younger than fourteen. Therefore, if there is actually a connection between the fronto-parietal region and Mixed percepts an incomplete circuitry in this brain region could explain the differences found between children and young adults. Older adults have been shown to demonstrate differences in the fronto-parietal region compared to young adults (Andrews-Hanna et al., 2007; Madden, 2007). These changes provide a potential explanation for the differences found for Mixed percepts between younger and older adults. The distinction between the development of the complete circuitry of the region and its deterioration may also provide an explanation for children reporting distinctly shorter average durations than younger adults, while there was no statistical difference between average durations for the reported Mixed percepts of older and younger adults. However, the exact relationship between the fronto-parietal region and transitional periods is still under debate (Brascamp et al., 2015).

Sequential transitions are another facet of binocular rivalry that seem to follow a clear developmental trajectory across the lifespan based on the findings presented in this thesis. Specifically, return transitions, where an individual perceives one Exclusive percept and then a Mixed percept followed by a return to the initial Exclusive percept, are shown to be affected by age. The proportion of return transitions increases from childhood to young adulthood and again in older adults (see Chapter 2 and Chapter 5). It has recently been suggested by Brascamp et al. (2006) that internal noise (the random variations of system components) allows for return transitions. Thus, if the computational model proposed by Brascamp et al. (2006) is true the evidence from this thesis indicates the weighting of the influence of internal noise on rivalry increases with age throughout the lifespan. In fact, older adults have been shown to demonstrate increased internal noise, for certain visual tasks (Betts et al., 2007; Bogfjellmo et al., 2013; Pardhan, 2004), which supports this idea.

The most overarching implication of this thesis is that it provides evidence of age-related changes in the neural circuitry associated with binocular rivalry. The developmental variations in average duration demonstrated between types of visual rivalry suggests a change in neural circuitry with aging that is unique to binocular rivalry. While these results contradict recent theories suggesting similar neural mechanisms are associated with various forms of visual rivalry (Brascamp et al., 2015), these results are in agreement with other findings in the literature. For example, cognitive factors, such as years of education, have been shown to be more strongly correlated with alternation rates during perceptual rivalry than age (Beer et al., 1989). In Chapter 4 of this thesis, cognitive demographics were relatively equivalent between younger and older adults, which in agreement with findings should mean there is little change in alternation rate for perceptual rivalry according to Beer et al. (1989).

Specifically, the current results counter the proposal by Aydin et al. (2013), that states declines in attention processes in older adults are related to a general slowing with age of alternations during all forms of visual rivalry. Instead, the lack of correlation between characteristics of perceptual and binocular rivalry found in Chapter 4 provides support for the idea that attention modulation is different in perceptual and binocular rivalry. This finding is in agreement with previous work that suggests a stronger attentional modulation of perceptual alternations for perceptual rivalry compared to binocular rivalry for younger adults (Meng and Tong, 2004). This differentiation in the influence of attention could also provide an explanation for the greater overall reliability of binocular rivalry across different time periods presented within this thesis. The high reliability in measures of binocular rivalry for younger and older adults lends greater weight to the overall findings of age-related differences in characteristics demonstrated throughout this thesis are due to consistent neural changes with aging, and not just a result of chance.

6.3 Future Directions

The novelty of the findings discussed within this thesis leads to numerous questions to be answered by future research. The discovery of age-related differences in characteristics of binocular rivalry across the lifespan provides the most apparent avenue for investigation. Further investigation of these characteristics could provide a significant increase in our understanding of neural components of the binocular visual system, lead to new theories of stereopsis, as well as potentially increase the quality of life of individuals across the lifespan by helping us understand the relationship between variances in characteristics of binocular rivalry and our interactions with 3-D surroundings throughout the lifespan.

One such age-related change demonstrated by this thesis is that the proportion of time spent viewing Mixed percepts varies across the lifespan. This change and the potential, but as of yet unformalized, relevance of these variations to specific neural changes highlight the important need for future research to focus on the investigation of Mixed percepts. In many previous studies, characteristics of the two Exclusive percepts are often the only facets of rivalry to be measured. However, binocular rivalry is a dynamic process that often involves percepts comprised of a mixture of the two Exclusive percepts. Thus, in order to gain a comprehensive understanding of binocular rivalry and its relationship to the breakdown of stereoscopic vision it seems important to gain a better understanding of Mixed percepts and how this characteristic changes across the lifespan.

Another key finding of this thesis is that monocular dominance increases with aging. While this thesis has demonstrated that an external stimulus factor known to influence perceptual dominance in younger adults, inter-ocular contrast differences, has no effect on the strength of monocular dominance in older adults, it remains to be determined if inter-ocular variations in other stimulus or cognitive factors are effective in altering perceptual dominance for older adults. Specifically, cognitive salience has been shown to influence perceptual dominance in younger adults (Blake, 2001), but it is unclear how inter-ocular differences in cognitive salience affect binocular rivalry in older adults. The investigation of such factors on perceptual dominance during binocular rivalry seems advantageous for understanding the aging binocular visual system.

Further research on binocular vision across the lifespan also seems pertinent with the increasing development of forms of technology used for 3-D entertainment and interactions. The finding of increased monocular dominance with aging seems specifically relevant to the conversion and production of 3-D movies, as this technology relies upon the integration of specific information sent to each eye at precise times to create visual effects. While one technical issue known to cause deterioration in the clarity of man-made 3-D images, ghosting, was shown to not significantly vary across the conditions tested within this thesis, it would be interesting to investigate if there are perceptible differences between the visual experiences of older and younger adults for other facets involved in creating 3-D visual effects.

Connections to how the results presented within this thesis relate to the broader spectrum of visual perception impacts overall quality of life for individuals throughout the lifespan is also an important avenue for future research. This seems especially important since many daily activities involve interactions with our 3-D surroundings. The majority of differences in characteristics of binocular rivalry demonstrated between older and younger adults occurred for the individuals aged in their 70s. This raises important questions about whether these changes translate to any differences in visual perception that leads to alterations in how those in their 70s and older translate their perceptions into interactions with their 3-D surroundings.

6.4 Conclusions

Overall this thesis has contributed to our knowledge of characteristics of binocular rivalry throughout the lifespan. Primarily, it has filled gaps in our knowledge of the characteristics of binocular rivalry in children and older adults, and provided evidence of a transitional period in the binocular visual system when individuals are in their 70s. The foundation for future studies of binocular rivalry established by this thesis provides a crucial stepping-stone to more intricate investigations of rivalry, and more generally highlights the important information to be gained by taking a comprehensive and developmental approach to investigations of the binocular visual system.

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