PERCEPTUAL GROUPING OF SHAPE IN MOTION

PERCEPTUAL GROUPING, MOTION DISCRIMINATION, AND SHAPE COMPLETION OF FOUR-SIDED FIGURES IN YOUNGER AND OLDER ADULTS

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A Thesis Submitted to the School of Graduate Studies in Partial Fulfilment of the Requirements for the Degree Doctor of Philosophy

McMaster University DOCTOR OF PHILOSOPHY (2019) Hamilton, Ontario (Psychology Neuroscience & Behaviour)
TITLE: Perceptual grouping, motion discrimination, and shape completion of four-sided figures in younger and older adults
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NUMBER OF PAGES: ix, 128

Lay Abstract

The visual experience of a human observer is the result of perceptual processing of the brain. The current dissertation focuses on a subset of these processes that concern the grouping of segmented parts into a single shape, while those segmented parts are in motion. This type of visual experience occurs regularly, in situations where part of a visual scene is occluded such as when viewing a moving object through a window occluded by window blinds. In general, we measure an observer's ability to identify the sources of motion, and the ability to infer the shape of the grouped object. In each experiment, the physical stimulus is varied while observers complete tasks using this stimulus. The dissertation characterizes perceptual organization processes using a number of different tasks, stimuli and paradigms in both younger and older adults. Each experimental result characterizes the perceptual abilities of younger and older observers, contributing to the literature of visual perceptual organization in aging.

Abstract

The present dissertation investigates perceptual grouping and shape completion in motion in younger and older observers. The first set of experimental results, Chapter 2, provides a set of exploratory experiments which characterize the nature of a motion grouping task, uncovering accurate direction discrimination when the stimulus contains a cue for global grouping, but compelling illusory motion when the stimulus does not contain that cue. Chapter 3 builds on the findings of Chapter 2 by measuring biases in motion integration that lead to the illusory motion. Chapter 3 extends this paradigm into older adult observers, and explores various stimulus variants and tasks to add to the characterization of this effect. In Chapter 4 the concepts of grouping and motion perception are examined in the context of shape completion by measuring the accuracy of aspect ratio, size, and area discrimination in younger and older adults. Chapter 4 concludes that older adults are worse at discriminating characteristics of shapes, but are similarly affected by incomplete or occluded stimuli as younger adults. On the whole, the dissertation demonstrates several novel findings in the perceptual organization literature, and investigates many of these phenomena into older adults populations. Throughout the dissertation, a central theme concerns the concept of behavioural measurement of perceptual processes, and consequently many of the phenomena are studied using several types of measurements and tasks to ensure a complete picture of the perceptual experience. The current dissertation presents a novel and important addition to the current literature in perceptual grouping and shape completion.

Acknowledgements

To my friends, family, colleagues, and mentors,

I would first like to extend my thanks to my supervisors, Patrick Bennett and Allison Sekuler, for their continual guidance and advice. I have gained countless skills through my experiences in their lab due to their instruction. I would also like to thank my committee members, Daniel Goldreich and Bruce Milliken, for their suggestions and input that provided valuable feedback throughout my graduate student experience. Thank you especially to Bruce for taking me as an undergraduate student and mentoring me throughout my academic experiences.

I owe gratitude to many members of the department of Psychology, Neuroscience, and Behaviour for making our workplace a fun, collaborative, and interactive department. I am lucky to have gained many close and long-lasting friendships. Many members of the vision lab have been both my colleagues and friends, and I owe a lot of my sanity to your companionship. A special mention to Donna Waxman, who's presence was crucial to the scientific process but also for support and friendship along the way.

Thank-you to my family and friends who have supported my decisions every step of the way, and for providing me with a refuge from the academic world. Lastly, thank you to my partner, Kyle, whose support has been crucial to every aspect of my life.

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Chapter 1

General introduction

Visual perception is fundamental to the ability to navigate the external environment and perceive the surrounding world. The subjective experience of a naïve observer might suggest that visual information is processed as a flat image, akin to a photograph taken though the lens of the eye. In reality, the way humans process visual information is much more complex. The visual information we take in is heavily processed through a series of complex functions in the visual system of the brain. The study of visual perception examines how the perceptual system represents the information that is received through the eyes. Many experimental methods exist to guide research in visual perception, each method incorporating the fundamental goal of understanding how information is represented at each stage in the system. In order to provide context for the topics addressed in this dissertation, the current chapter first provides an overview of the visual system as a whole, then subsequently summarizes concepts relevant to the research undertaken, and lastly introduces the specific research undertaken in the present dissertation.

1.1 The Visual System

Information about the shape and spatial arrangement of surfaces in a scene is conveyed in the spatiotemporal patterns of light that form the retinal images in our eyes. The photoreceptors of the retina convert light into electrical signal, and this electrical signal is propagated through multiple pathways into the brain (Svaetichin and MacNichol, 1958). The flow of visual information through the visual system can be classified generally into early, middle, and higher stages. The early stages of visual processing are characterized by relatively simple, local, disjointed analyses of the proximal stimulus. Whereas processing in the middle and higher stages become increasingly complex to form representations of properties of the visual scene rather than retinal images *per se* (Felleman and Van Essen, 1991).

One of the initial stages of cortical visual processing occurs in primary visual cortex, area V1. The neurons of V1 were first discovered to have small receptive fields that respond to straight bars of different brightnesses, representing edges (Hubel and Wiesel, 1962). In later work, V1 was shown to process more complex stimulus features such as orientation, spatial frequency, and spatial phase (Hubel and Wiesel, 1968). As the signal progresses through the visual system, the visual neurons in each area have increasingly complex neural tuning and larger receptive fields. For example, compared to neurons in V1, neurons in area V2 are selective not just for orientation, but also direction of motion, angles, archs, and illusory or perceptually completed contours (Von Der Heydt and Peterhans, 1989).

Visual processing occurring in middle and higher levels of the visual hierarchy is split into two pathways: ventral and dorsal. The distinction between the ventral and dorsal pathways was first described by Mishkin et al. (1983). Classically, the ventral pathway is associated with form, shape, and objects, while the dorsal pathway is associated with motion, object location, and visually-guided action. Current research in this area has suggested that the ventral pathway is primarily responsible for perception of visual scenes whereas the dorsal pathway involves perception for action (Goodale and Milner, 1992). Here too, functions range from simple to complex depending on their location in the hierarchy. For example, processes that occur early in the ventral pathway concern the local integration of edges into shapes and objects while processes occurring higher in the ventral pathway are involved in the representation of faces, buildings, and scenes (Connor et al., 2007; Grill-Spector et al., 2001; Haxby et al., 2001).

Cortical visual processing consists of both feed-forward and feed-back flows of information, which are combined at each stage of processing to form increasingly complex representations of a visual scene (Gilbert and Wiesel, 1990; Gilbert, 1992). The topics of this dissertation concern mid-level visual processing, as the current research focuses on the integration of edges and shapes into objects and the integration of direction signals into global motion.

1.2 The Visual System and the Effects of Aging

A number of elements of the visual system change with age. Many of the components of the eye degrade with age. For example, yellowing and hardening of the lens reduces retinal illuminance and increases light scatter (Weale, 1963; Hennelly et al., 2002), which contributes to age-related changes in visual acuity (Adams et al., 1988). Other age-related changes in vision can be attributed to cortical processing. For example, reduced spatial and temporal contrast sensitivity in older adults (Wright and Drasdo, 1985) has been linked to changes in visual cortical neurons (Wright et al., 1985). The effects of aging on cortical visual mechanisms presumably contribute to age differences in temporal sensitivity (Blake et al., 2008), motion perception (Ball and Sekuler, 1986), visual processing speed (Kline and Birren, 1975), and useful field of view (Ball et al., 1988).

Examining how perception is affected by normal, healthy aging is important for two main reasons. Firstly, the study of perception in aging is important for the health and function of older adults. As discussed above, vision is crucial for navigating and interacting with the outside environment. Secondly, the study of perception in aging provides the ability to test and extend the current models of perception. In the present dissertation, we compare performance between younger and older adults in Chapters 3 and 4 as an extension to concepts that are first established in younger adults. Comparisons in behaviour across age demonstrate how a process changes in the aging perceptual system, which broadens the established model.

1.3 Perceptual Organization

Perceptual organization refers to a variety of processes that are related to our ability to create coherent representations of objects in the world from disjointed and often ambiguous features in the proximal stimulus (e.g., edges, contours, and shapes). Although perceptual organization occurs in all sensory modalities, this dissertation concerns visual perception and therefore only visual perceptual organization is discussed.

Gestalt psychologists created a set of principles that govern the way a visual scene is organized by identifying stimulus characteristics that caused ambiguous stimuli to be perceived in certain ways. For example, the Gestalt principle of good continuation describes a tendency for visual features that fall along a smooth contour to be perceived as forming a coherent unit (Wertheimer, 1923). Gestalt psychologists represented the “whole” or the grouped figure as being qualitatively different from the sum of its parts, meaning that the grouped figure contained properties or characteristics that were not (necessarily) present in the elements forming the group. These grouping characteristics, such as grouping by proximity or similarity, were thought to exist because they produced perceptual units that corresponded to physical units such as surfaces and objects. Modern research in perceptual organization characterizes the visual experience by manipulating the elements of a scene in a way that increases the likelihood that an observer will perceptually organize the stimulus in a particular way, while sometimes probing the characteristics of the perceptual units that the observer can name or describe (see Wagemans et al., 2012, for review).

1.3.1 Perceptual Grouping in Motion

Perceptual grouping is one aspect of perceptual organization that involves binding together spatially distince elements. Perceptual grouping has been studied both in static images and in motion. When grouping is studied in static images, only the information in the retinal image is available. In motion, the observer is required to group across separate local elements within a single static image, as well as grouping temporal information to perceive the motion trajectory of grouped items (Adelson and Movshon, 1982; Williams and Sekuler, 1984; Alais et al., 1998; Braddick, 1993; Snowden and Verstraten, 1999).

An elementary class of motion grouping stimuli are random dot kinematogram (RDK) displays. In these displays, many moving dots are displayed on the screen: most dots move in random directions, while a subset move coherently in one direction. In order to perceive the coherent motion, observers must integrate motion information across space and time (Williams and Sekuler, 1984). The observer is able to perceive the single direction of motion depending on the proportion of dots that are moving coherently (Williams and Sekuler, 1984). If an observer is unable to perceive a single global motion direction in an RDK display, they will instead perceive random dots which do not appear to move in any particular direction. In an RDK, there is no information about direction in a single, static image, and therefore grouping in this task is entirely due to motion.

Ambiguous motion stimuli are often used to study grouping in motion because the physical stimulus offers no single interpretation, yet a single percept is often perceived. The visual system makes inferences about the origin of motion, yielding a single interpretation of the stimulus. Many types of ambiguous motion stimuli have been studied, beginning with Wallach (1935) (see Wuerger et al. (1996) for English translation). A well-studied type of ambiguous motion stimuli are translating gratings and plaids. Viewed alone, gratings translating ambiguously through an aperture are often interpreted to move in the direction perpendicular to the orientation of the grating, although the motion is consistent with many different trajectories (Adelson and Movshon, 1982). Plaids are composed of two superimposed gratings positioned on top of one another, offset by varying degrees from vertical, that are viewed through an aperture (Stoner et al., 1990; Stoner and Albright, 1996). For plaid stimuli, there are two possible interpretations. When the two superimposed gratings are ungrouped, plaids appear as two gratings sliding over one another. When the two gratings are grouped, the percept is a plaid moving coherently in the direction of the resultant vector of the two local motions (Stone et al., 1990). Like RDK stimuli, plaids appear as a specific percept when grouped, but unlike RDK stimuli, plaid stimuli appear as a different specific percept when segmented. Plaids provide an interesting example of motion integration because the exact same stimulus can be seen either as sliding or as coherent by the same participant, at different times. Plaids are useful in studying motion grouping and segmentation because of the two clear percepts they provide in either case, but they do not address integration across space, since the components of the plaid are spatially overlapped.

While the previous examples contain grouping signal in motion and not the static image, some classes of stimuli for grouping in motion combine grouping in a static image of shapes and objects, with grouping signals that occurs when these shapes are in motion. The goal of this area of study is to determine the parameters that cause observers to group segmented edges and lines to perceive completed shapes. Importantly, unlike plaid and RDK stimuli, multiple, spatially separated elements are grouped together, meaning that information relevant for grouping is present in both the static image and in motion. This area of research is important because grouping when elements are spatially distributed is often encountered in natural environments. Lorenceau and Shiffrar (1992) introduced a grouping task in which the observer's task was to determine the direction of orbital translation of squares occluded by apertures of various sizes and visibilities. When apertures were invisible the figure appeared as fragmented pieces, and motion direction discrimination was poor. Yet when apertures were visible, the percept appeared grouped as a single object, and motion direction discrimination was good. Variants of this general task have been used several times (Shiffrar and Lorenceau, 1996; Lorenceau and Alais, 2001; Lorenceau, 1996; Alais et al., 1998; McDermott and Adelson, 2004; Murray et al., 2001), each variant characterizing some aspect of grouping shapes. In general, these studies found that grouping can occur for elements that are separated in space, and grouping is affected by whether the figure is static or in motion.

When motion signals are produced by the same source, accurate interpretation of a complex scene requires integration, even if the motion information differs, such as in an RDK display. Yet when the motion signals are produced by different sources, accurate interpretation of that scene requires segmentation. The perceptual process that determines whether to integrate or segregate distinct motion signals makes use of the perceptual system's ability to maintain measurements of several motion signals at once. Given that the visual motion information can arise from multiple sources, the decision whether to integrate or segment motion is complex. Exactly what leads to integration or segregation is the topic of much study. A large body of research has focused on the physical elements in a particular stimulus. Motion consistent with multiple directions is typically displayed either in an aperture of different shapes and sizes or occluded by an object that varies in shape, size, and contrast with the motion elements. The purpose of these studies is to test how the perception of motion is affected by segregating that motion in either one or more depth plains (e.g., Shimojo et al., 1989; Vallortigara and Bressan, 1991; Trueswell and Hayhoe, 1993; Bressan et al., 1993; Castet and Wuerger, 1997), and modelling the percept based on these types of physical changes to the stimulus (e.g., Weiss et al., 2002; Welch and Bowne, 1990; Anderson and Sinha, 1997).

1.3.2 Grouping: Focusing on Perceptual Experience

Much of the prior research on perceptual grouping focuses on the stimulus properties that lead to grouping or segmentation. This experimental approach is important for many reasons, including those outlined above. However, the binary outcomes of "grouped" or "segmented" does not necessarily capture the complete perceptual experience of the observer. Although a certain type of stimulus may be frequently experienced as grouped, and another type as segmented, this does not mean that the stimuli within a certain category are perceived in the same way. The current dissertation focuses on exploring the characterization of the percept in two situations: in motion grouping and direction discrimination (Chapters 2 and 3) and shape completion (Chapter 4). In order to thoroughly characterize the percept of observers under many variables and situations, the current dissertation adopts various methods including several varieties of objective and subjective measures. In all cases the topic is examined from an important viewpoint: what is the experience of the observer and how does that experience change when the task changes?

1.4 Thesis Overview

The dissertation is composed of five chapters: the current chapter, which is intended to provide a broad overview of the issues that comprise the focus of the dissertation, three experimental chapters, and a General Discussion.

In the first set of experimental results (Chapter 2) an ambiguous motion task is used to explore motion integration and grouping. The stimulus is a square composed of dots, as first displayed by Lorenceau (1996), the addition of local motion noise to the dots encourages global grouping, and leads to better direction discrimination performance. In the first experiment of Chapter 2, the principle effect of the ambiguous motion is displayed; in sum: performance increases as a function of stimulus duration when local motion noise is present, but decreases with increased stimulus duration when local motion noise is absent, reaching below-chance in some observers at the longest stimulus duration. In the second experiment of Chapter 2, a novel noise manipulation is introduced, and shown to increase global grouping. In addition, observers report their confidence in their decisions, which revealed that those who experience illusory direction of motion are likely to be confident about their incorrect responses. Lastly we attempt to explain the illusory motion through an account similar to reference repulsion in a final experiment, but fail to find evidence for this explanation. Broadly, the results of Chapter 2 demonstrate that stimulus noise can promote global grouping in the ambiguous motion task used in the presented experiments, and that confident, incorrect responses can be observed in the absence of correct global grouping.

The focus of Chapter 3 is to measure the bias in visual motion integration by using a variant of the ambiguous motion task of Chapter 2. Experiments 1 and 2 compare direction discrimination performance with measures of integration bias in younger adults, and Experiments 3a and 3b make these comparisons in the context of aging.

In Experiment 4 direction discrimination, integration bias, and ratings of perceived coherence are compared in a separate stimulus with similar properties to that of the prior experiments. Here it is found that ratings of perceived coherence correspond to the degree of integration bias when a grouping cue is present, but not when it is absent.

The final experimental chapter of the dissertation explores many of the themes of Chapters 2 and 3, such as grouping, motion, shape perception, and aging, but examines these themes in the context of perceptual completion. Specifically, Chapter 4 explores how perceptual completion affects the ability to extract the stimulus properties of aspect ratio (Experiment 1) and size (Experiments 2 and 3), and how this ability changes with age. The experiments of Chapter 4 measure how these effects differ with stimulus duration, varying the amount of time the observer has to complete the task of extracting stimulus characteristics. This manipulation is especially relevant in Experiment 1, where older and younger adults produce data that is similar in pattern, but older adults require longer stimulus durations to complete the task at the same proficiency as younger adults.

The final chapter, Chapter 5, brings together the themes introduced in Chapters 2-4 and discusses the implications and future research directions that arise from the results of the current work. The broad themes of the dissertation are discussed in the context of the current state of the research field.

References

Adams, A. J., Wong, L. S., Wong, L., and Gould, B. (1988). Visual acuity changes with age: Some new perspectives. *American Journal of Optometry & Physiological Optics*, 65(5):403–406.

Adelson, E. H. and Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature*, 300(9):523–525.

Alais, D., Blake, R., and Lee, S. H. (1998). Visual features that vary together over time group together over space. *Nature Neuroscience*, 1(2):160–164.

Anderson, B. L. and Sinha, P. (1997). Reciprocal interactions between occlusion and motion computations. *Proceedings of the National Academy of Sciences*, 94(7):3477–3480.

Ball, K. and Sekuler, R. (1986). Improving Visual Perception in Older Observers. *The Gerontological Society of America*, 41(2):176–182.

Ball, K. K., Beard, B. L., Roenker, D. L., Miller, R. L., and Griggs, D. S. (1988). Age and visual search: Expanding the useful field of view. *Journal of the Optical Society of America A*, 5(12):2210.

Blake, R., Rizzo, M., and McEvoy, S. (2008). Aging and perception of visual form from temporal structure. *Psychology and Aging*, 23(1):181–189.

Braddick, O. (1993). Segmentation versus integration in visual motion processing. *Trends in Neurosciences*, 16(7):263–268.

Bressan, P., Ganis, G., and Vallortigara, G. (1993). The role of depth stratification in the solution of the aperture problem. *Perception*, 22(2):215–228.

Castet, E. and Wuerger, S. (1997). Perception of moving lines: Interactions between local perpendicular signals and 2D motion signals. *Vision Research*, 37(6):705–720.

Connor, C. E., Brincat, S. L., and Pasupathy, A. (2007). Transformation of shape information in the ventral pathway. *Current Opinion in Neurobiology*, 17(2):140–147.

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

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

Gilbert, C. D. and Wiesel, T. N. (1990). The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. *Vision Research*, 30(11):1689–1701.

Goodale, M. A. and Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 14(1):20–25.

Grill-Spector, K., Kourtzi, Z., and Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research*, 41(10-11):1409–1422.

Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., and Pietrini, P. (2001). Distributed and Overlapping Representations of Faces and Objects in Ventral Temporal Cortex. *Science*, 239(5539):2425–2431.

Hennelly, M. L., Barbur, J. L., Edgar, D. F., and Woodward, E. G. (2002). The light scattering characteristics of the eye. *Ophthalmic and Physiological Optics*, 17(2):171–171.

Hubel, D. H. and Wiesel, T. (1962). Receptive fields, binocular interaction and functional architechture in the cat's visual cortex. *Journal of Physiology*, 160(1):106–154.

Hubel, D. H. and Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *The Journal of Physiology*, 195(1):215–243.

Kline, D. W. and Birren, J. E. (1975). Age differences in backward dichoptic masking. *Experimental Aging Research*, 1(1):17–25.

Lorenceau, J. (1996). Motion integration with dot patterns: Effects of motion noise and structural information. *Vision Research*, 36(21):3415–3427.

Lorenceau, J. and Alais, D. (2001). Form constraints in motion binding. *Nature Neuroscience*, 4(7):745–751.

Lorenceau, J. and Shiffrar, M. (1992). The influence of terminators on motion integration across space. *Vision Research*, 32(2):263–273.

McDermott, J. and Adelson, E. H. (2004). The geometry of the occluding contour and its effect on motion interpretation. *Journal of Visionsion*, 4(10):944–954.

Mishkin, M., Ungerleider, L. G., and Macko, K. A. (1983). Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences*, 6(C):414–417.

Murray, R. F., Sekuler, A. B., and Bennett, P. J. (2001). Time course of amodal completion revealed by a shape discrimination task. *Psychonomic Bulletin & Review*, 8(4):713–720.

Shiffrar, M. and Lorenceau, J. (1996). Increased Motion Linking Across Edges with Decreased Luminance Contrast, Edge Width and Duration.

Shimojo, S., Silverman, G. H., and Nakayama, K. (1989). Occlusion and the solution to the aperture problem for motion. *Vision Research*, 29(5):619–626.

Snowden, R. J. and Verstraten, F. A. J. (1999). Motion transparency: Making models of motion perception transparent. *Trends in Cognitive Sciences*, 3(10):369–377.

Stone, L. S., Watson, A. B., and Mulligan, J. B. (1990). Effect of contrast on the perceived direction of a moving plaid. *Vision research*, 30(7):1049–1067.

Stoner, G. R. and Albright, T. D. (1996). The Interpretation of Visual-Motion - Evidence for Surface Segmentation Mechanisms. *Vision Research*, 36(9):1291–1310.

Stoner, G. R., Albright, T. D., and Ramachandran, V. S. (1990). Transparency and coherence in human motion perception. *Nature*, 344(6262):153–155.

Svaetichin, G. and MacNichol, E. F. (1958). Retinal Mechanisms for Chromatic and Achromatic Vision. *Annals of the New York Academy of Sciences*, 74(2):385–404.

Trueswell, J. C. and Hayhoe, M. M. (1993). Surface segmentation mechanisms and motion perception. *Vision Research*, 33(3):313–328.

Vallortigara, G. and Bressan, P. (1991). Occlusion and the perception of coherent motion. *Vision Research*, 31(11):1967–1978.

Von Der Heydt, R. and Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity. *Journal of Neuroscience*, 9(5):1731–1748.

Wagemans, J., Elder, J. H., Kubovy, M., Palmer, S. E., Peterson, M. A., Singh, M., and Von Der Heydt, R. (2012). A century of Gestalt psychology in visual perception: I. Perceptual grouping and figure–ground organization. *Psychological Bulletin*, 138(6):1172–1217.

Wallach, H. (1935). On the visually perceived direction of motion. *Psychologische Forschung*, 20(1):325–380.

Weale, R. A. (1963). New light on old eyes. *Nature*, 198:944–946.

Weiss, Y., Simoncelli, E. P., and Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature neuroscience*, 5(6):598–604.

Welch, L. and Bowne, S. F. (1990). Coherence determines speed discrimination. *Perception*, 19(4):425–435.

Wertheimer, M. (1923). Laws of organization in perceptual forms. *Psycologische Forschung*, 4:301–350.

Williams, D. W. and Sekuler, R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research*, 24(1):55–62.

Wright, C. E. and Drasdo, N. (1985). The influence of age on the spatial and temporal contrast sensitivity function. *Documenta Ophthalmologica*, 59(4):385–395.

Wright, C. E., Williams, D. E., Drasdo, N., and Harding, G. F. (1985). The influence of age on the electroretinogram and visual evoked potential. *Documenta Ophthalmologica*, 59(4):365–384.

Wuerger, S., Shapley, R., and Rubin, N. (1996). “On the Visually Perceived Direction of Motion” by Hans Wallach: 60 Years Later. *Perception*, 25(11):1317–1367.

Chapter 2

The effect of local noise on illusory global motion

2.1 Abstract

The perception of the direction of global motion often depends on our ability to integrate local motion signals over space and time. Lorenceau (1996) demonstrated that in some situations observers reliably perceive global motion in the direction opposite to the true direction, and that the perceived direction becomes more accurate when dynamic noise is added to the motion of the local elements in the stimulus. We explore this phenomenon by testing observers in a global motion discrimination task using Lorenceau's stimulus displayed for 4 durations (150, 300, 600, and 1200 ms) at 3 levels of local motion noise (0 dva, 0.027 dva, 0.081 dva). Like Lorenceau we found better direction discrimination with increasing amounts of local noise, and uncovered an interesting effect of below-chance performance in the zero stimulus noise, 1200 ms condition. We then conducted a second experiment requiring confidence ratings on every trial, where we also test whether this effect is specific to position noise of the elements of the stimulus, or if a stimulus background of dynamic white noise could also produce similar results. Experiment 2 revealed high confidence to incorrect responses to zero noise stimuli, and similar effects for position noise and background noise. Finally, in Experiment 3, we test whether cueing attention can adjust how observers interpret the stimulus. We did not find differences in between conditions, suggesting that this task may be unrelated to covert shifts in attention. Taken together,

these results demonstrate that noise can promote global grouping in this stimulus, and that confident, incorrect responses can be observed in the absence of correct global grouping.

Introduction

Perception of global motion requires the integration of multiple signals across space and time (e.g., Adelson and Movshon, 1982; Williams and Sekuler, 1984; Alais et al., 1998; Braddick, 1993; Snowden and Verstraten, 1999). Lorenceau and Shiffrar (1992) examined how different motion trajectories of distinct spatial elements are integrated to perceive coherent global motion of a single object. Their stimulus comprised four lines arranged to form the outline of a square that orbited a central fixation point in a clockwise or counter-clockwise direction. When occluders are placed over the corners of the square, each line undergoes sinusoidal motion only in the direction perpendicular to the line orientation. The direction of the square's global orbital motion – clockwise or counter-clockwise – is determined by the relative phase of the vertical and horizontal motions. Specifically, clockwise orbital motion produces horizontal motion (of the vertical lines) that leads the vertical motion (of the horizontal lines) by 90 deg, whereas counter-clockwise motion produces horizontal motion that lags the vertical motion by 90 deg. Lorenceau and Shiffrar found that observers could discriminate the direction of orbital motion when the occluders were visible but not when the occluders were invisible, which suggests that observers integrated the vertical and horizontal motions and were sensitive to their relative phase only when occluders were visible.

To further examine the factors that allow observers to integrate motion in different directions, Lorenceau (1996) modified the orbiting square stimulus to allow for the addition of non-informative position noise to the local elements comprising the stimulus. Specifically, the four lines outlining a square were replaced with four sets of colinear dots which underwent the same sinusoidal motion as described previously. Gestalt principles such as proximity and common fate would favour grouping the dots into four colinear sets of dots, whereas the perception of global motion requires grouping across at least two perpendicularly arranged sets of colinear dots. Lorenceau (1996) hypothesized that interfering with the local integration could improve global integration. To test this idea, the paths of the individual dots were perturbed by sinusoidal displacements in the direction that was perpendicular to a dot's main path. In line with the prediction, discrimination accuracy for the global orbital direction improved as the amplitude of the local sinusoidal noise increased. Interestingly, Lorenceau also found that discrimination accuracy for some observers was significantly below chance performance for stimulus durations of 300 and 600 ms when the amplitude of the local noise was zero, which suggests that the relative phase of the horizontal and vertical motion components was encoded incorrectly in those conditions.

In the current study, we measured the effects of local motion noise on the discrimination of global orbital motion using the stimulus and methods described by Lorenceau (1996). Our first experiment replicated Lorenceau's findings, including the observation of below-chance performance with long-duration stimuli that lacked local motion noise. A second experiment measured discrimination accuracy while collecting confidence ratings and found that many observers displayed high confidence when they mis-perceived the direction of global motion. This second experiment also found that the effects of a dynamic white noise background were similar to the effects of local position noise. A third experiment demonstrated that the perceived direction of global motion was not influenced by the location of salient cues on the stimulus.

Experiment 1

Method

Observers

Twelve naïve observers (19-27 years old, $M = 23$; 3 female) participated in the experiment. All observers possessed normal or corrected-to-normal Snellen visual acuity. Observers received partial course credit or $10 per hour for their participation. Each participant provided informed consent prior to the start of the experiment, and all experimental protocols were approved by the McMaster University Research Ethics Board.

Apparatus and Stimuli

Stimuli were generated on an Apple iMac computer using MATLAB and the Psychophysics and Video Toolbox (Brainard, 1997; Pelli, 1997), and presented on an NEC MultiSync FE992 100 Hz monitor with a display size of 36 × 27 cm (35 pixels/cm).

Average luminance was 30.5 cd/m^2. A chin and forehead rest was used to stabilize viewing position. Participants viewed the display binocularly through natural pupils from a viewing distance of 114 cm.

The stimulus consisted of four sets of colinear dots that were positioned along the sides of a virtual square (Figure 2.1). Each set contained five dots (diameter = 0.05 deg) that were evenly spaced and spanned 3.2 deg. The dots were white and presented on a uniform grey background (Weber contrast = 2.14). The sets of dots moved sinusoidally, and the parameters of motion were derived in the following way. Consider a square that is moved in the picture plane so that its centre orbits a stationary central fixation point with a rotation amplitude of 0.40 degrees of visual angle and a rotation frequency of 0.83 Hz. Such orbital motion can be decomposed into horizontal and vertical sinusoidal components: the speed of rotation is determined by the frequency of the sinusoidal components, and the direction of the square's orbit (i.e., clockwise vs. counterclockwise) is determined by their relative phase. In our stimuli, the horizontal and vertical motion components were applied to the vertical and horizontal sets of dots, respectively (Figure 2.1). Because the local motion of the dots was horizontal or vertical, the direction of global, orbital motion (clockwise vs. counter-clockwise) that was used to construct the components could be determined only by noting the relative phase of the two component motions. In addition to the main sinusoidal motion components, independent motion noise was added to each dot. The noise varied the location of a dot sinusoidally in the direction that was perpendicular to the main motion. The frequency of the sinusoidal noise was 3 Hz and the starting phase was selected randomly for each dot on each trial. Each dot's motion therefore would be composed of the main component motion – vertical motion for horizontal dots and horizontal motion for vertical dots – and random phase sinusoidal motion in the orthogonal direction. Noise amplitude, which varied across trials, was 0, 0.027, or 0.081 deg.

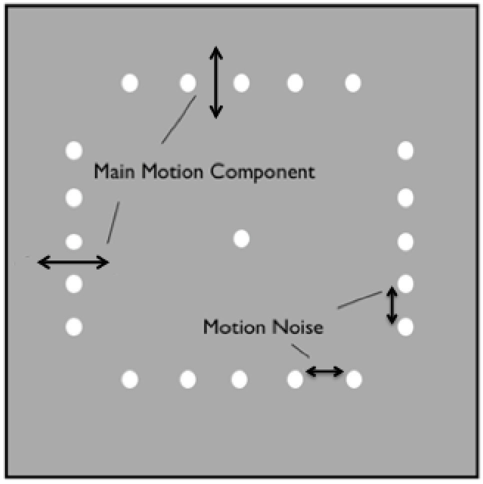


Figure 2.1 – Square stimulus used in Experiments 1-3. The stimulus consisted of 20 white dots arranged into four sets of five dots. Each dot was 0.05 degree of visual angle. Each set of five dots spanned 3.2 deg. The large arrows depict the main sinusoidal motion components: The two horizontal sets of of dots moved vertically and the two vertical sets of dots moved horizontally. The phases of the two main motion components differed by ±90 deg. The small arrows depict the local motion noise: the path of each dot was displaced sinusoidally in the direction perpendicular to the main motion component. The central dot was a stationary fixation point.

Procedure & Experimental Design

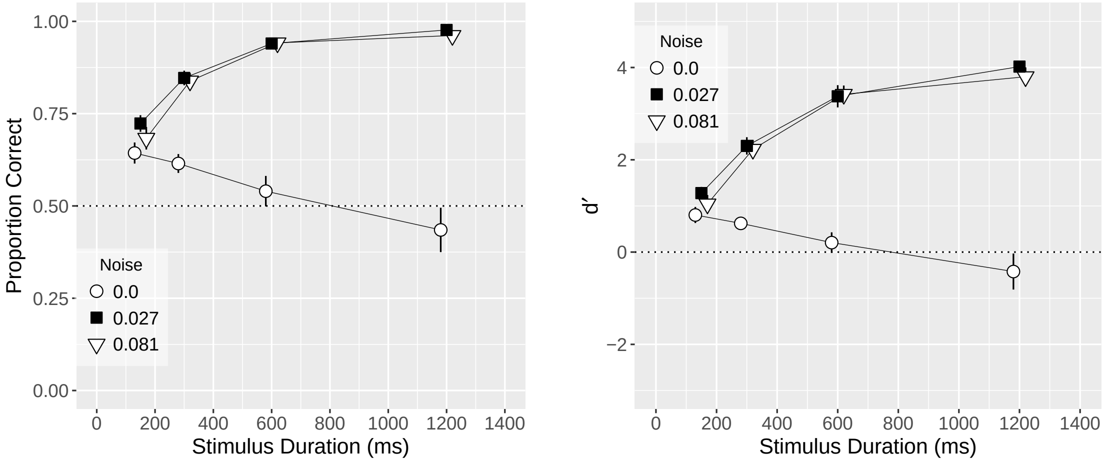
Each trial consisted of the presentation of a central fixation point and a single moving stimulus, followed by a blank, uniform screen. The subject's task was to report whether the direction of global, orbital motion was counter-clockwise or clockwise by pressing one of two labeled keys on a standard computer keyboard. An experimental session began with 10 practice trials in which the stimulus was a square consisting of four high-contrast lines that orbited the fixation point for 600 ms. The 10 practice trials were repeated until a subject responded correctly on at least eight trials. The practice trials ensured that subjects could discriminate clockwise and counter-clockwise motion, understood the task, and could use the keyboard to respond. The experimental trials, which immediately followed the practice trials, used the dot stimulus shown in Figure 2.1. There were four stimulus durations (150, 300, 600, & 1200 ms) and three motion noise amplitudes (0, 0.027, & 0.081 deg of visual angle) for a total of 12 conditions. With our motion parameters, it took 1205 ms for the stimulus to orbit completely around the fixation point; therefore the stimulus did not complete an orbit of the fixation point at all stimulus durations. There were 50 trials per condition, or 600 trials in total. Experimental trials were blocked by stimulus duration; motion noise levels were randomly intermixed within each block. Each block was self-paced, and an experimental session lasted approximately 50 minutes. No feedback was given during the experiment. Each trial began 1500 ms following the response to the previous trial.

Results

Statistical analyses were performed in R (R Core Team, 2017). The Huynh-Feldt estimate of sphericity ($\tilde{\epsilon}$) was used to adjust p values of F tests conducted on within-subject variables with more than 1 degree of freedom. Either partial eta-squared (η_p^2) or Cohen's d are reported as a measure of association strength and effect size.

Response accuracy and sensitivity (d') are plotted as a function of stimulus duration and noise amplitude in Figure 3.8. On average, when the noise amplitude was greater than zero, response accuracy and sensitivity increased with increasing stimulus duration; however, in the zero noise condition, response accuracy and sensitivity *decreased* with increasing stimulus duration.

We analyzed d' and arcsine-transformed proportion correct with separate 4 (Duration) × 3 (Noise) ANOVAs. The two ANOVAs yielded very similar results, and therefore we report only the results of the ANOVA on proportion correct. The main effects of Noise and Duration were significant, as was the Noise × Duration interaction (Table 2.1). The Noise × Duration interaction reflects the fact that accuracy increased with increasing stimulus duration in the non-zero noise conditions, but decreased with increasing duration in the zero noise condition (Figure 3.8). The linear trends of response accuracy across stimulus durations were positive and significantly different from zero in the 0.027 degree noise condition ($t(11) = 11.74$, $p < 0.001$, $d = 4.79$) and the 0.081 degree noise condition ($t(11) = 8.61$, $p < 0.001$, $d = 3.52$), whereas the linear trend was negative and significantly different from zero in the 0 noise condition ($t(11) = 3.67$, $p = 0.002$, $d = 1.50$).



(a) Response accuracy **(b)** Sensitivity

Figure 2.2 – Response accuracy and sensitivity (d') measured in Experiment 1 plotted as a function of stimulus duration and motion noise amplitude. Error bars represent ±1 SEM.

Interestingly, mean response accuracy was below chance at the longest stimulus duration in the zero-noise condition. That is to say, observers were, on average, reporting that the stimulus was moving in the direction opposite to the veridical direction of global motion. Although the mean accuracy in the 1200 ms condition was not significantly different from chance ($t(11) = -1.08$, $p = 0.302$, $d = -0.44$), inspection of the data suggested that accuracy in several individuals was significantly below chance. To test this idea further, we used Bonferroni-corrected ($\alpha_{FW} = .01$) binomial tests to determine which of the 12 subjects had a response accuracy that was significantly below 0.5 in the zero-noise, 1200 ms condition. This method identified three participants with response accuracies that were significantly below 0.5, and the mean proportion correct for these subjects was 0.167. Thus, the data suggest that a few participants responded at below-chance levels in that condition.

Effect	**df**	$\tilde{\epsilon}$	**MSE**	**F**	η_p^2	p_{adj}
Noise	2, 22	0.72	0.05	110.08	.72	<.0001
Duration	3, 33	0.39	0.04	24.34	.40	<.0001
Noise × Duration	6, 66	0.50	0.02	47.10	.50	<.0001

Table 2.1 – Experiment 1 ANOVA table.

Discussion

We found that the effect of stimulus duration on response accuracy in a global motion discrimination task depends on the presence of local motion noise. When the local motion noise was present, accuracy increased with increasing stimulus duration. However, when local noise was absent, accuracy *decreased* with increasing duration (Figure 3.8). Indeed, at the longest stimulus duration (1200 ms), mean accuracy in some younger adults in the zero-noise condition was below chance. These findings replicate results reported by Lorenceau (1996).

Lorenceau (1996) suggested that the addition of stimulus noise reduces the tendency to organize the stimulus into two sets of parallel, collinear arrangements of dots, and therefore makes it more likely that the dots are grouped into a single, coherently moving object. According to this logic, when there is more evidence that the stimulus should be grouped globally, and less evidence the stimulus should be grouped locally, global motion direction is perceived more accurately. This hypothesis is consistent with the results of several studies (e.g., Lorenceau and Shiffrar, 1992; Lorenceau, 1996; Shiffrar and Lorenceau, 1996; Lorenceau and Shiffrar, 1999) as well as the results of Experiment 1.

Like Lorenceau (1996), we found that the response accuracy in some individuals was below chance in zero-noise conditions with relatively long stimulus durations. Because all participants successfully completed a block of practice trials, and because below-chance performance was found only in two conditions, it is unlikely that the below-chance performance occurred because participants were confused about the mapping of the response keys or misunderstood the instructions. Rather, participants presumably perceived global motion in the direction opposite to the veridical direction. In the following two experiments we focus on testing this phenomenon.

Experiment 2

Experiment 2 investigated two issues. The first issue concerned the nature of the position noise used by Lorenceau (1996) and in Experiment 1. Specifically, we examined whether the observed effects of the noise are specific to sinusoidal position jitter or whether they could be elicited by other types of noise. Experiment 2 therefore included a condition that embedded the stimulus in a dynamic white noise background. The second issue concerned the clarity of the global motion percept in conditions that yielded below chance performance in some observers. In Experiment 2, while reporting the direction of global motion, observers also reported whether they felt the motion was “definitely”, “probably”, or “maybe” moving in the reported direction.

Method

Observers

Twelve naïve observers (17-23 years, $M = 19$ years, 10 female) participated in the experiment. All observers had normal or corrected-to-normal Snellen visual acuity. Subjects received partial course credit or $10 per hour for their participation. All participants provided informed consent, and all experimental protocols were approved by the McMaster University Research Ethics Board.

Stimuli

The experimental apparatus was the same as in Experiment 1. The stimuli also were the same as those used in Experiment 1, except for the following changes. Experiment 2 used only three levels of stimulus motion noise: 0, 0.0135, and 0.027. We did not include a noise amplitude of 0.081 because Experiment 1 found that performance was unaffected by increasing noise beyond 0.027. In addition, we added a condition where the uniform $5.22 \times 5.22\,\mathrm{deg}$ background was replaced with a dynamic Gaussian white noise consisting of $0.05 \times 0.05\,\mathrm{deg}$ square pixels. On each video frame, the contrast of each noise pixel was selected randomly and independently from a zero-mean Gaussian distribution with a standard deviation of 0.11. Finally, stimulus duration was fixed at 600 ms. We chose 600 ms because mean accuracy at this duration in Experiment 1 was near chance with zero-noise stimuli, and therefore there was a reasonable chance of seeing performance increase or decrease in conditions that used noise.

Procedure

The procedure was similar to the one used in Experiment 1, except that it was modified to allow participants to register the confidence of their direction judgment on each trial. Specifically, the response screen that immediately followed the stimulus offset prompted observers to respond whether the stimulus "definitely", "probably", or "maybe" moved clockwise or counter-clockwise. We refer to these three response alternatives as representing high, moderate, and low confidence, respectively.

The two types of background (uniform vs. dynamic noise) were crossed factorially with three levels of local motion noise (0, 0.0135, and 0.027) to yield a total of six experimental conditions. There were 74 trials per condition, yielding a total of 370 trials. All trial types were intermixed. Prior to the experimental trials, all participants completed the same practice session that was used in Experiment 1. The experiment took approximately 50 minutes to complete.

Results

Our analyses address two main questions: 1) How does background noise affect performance in this task compared to motion noise?; and 2) How confident are observers when they make incorrect and correct decisions? As in Experiment 1, the Huyhn-Feldt estimate of sphericity ($\tilde{\epsilon}$) was used to adjust the degrees of freedom of within-subject F tests, and either partial eta-squared (η_p^2) or Cohen's d are reported as a measure of association strength and effect size.

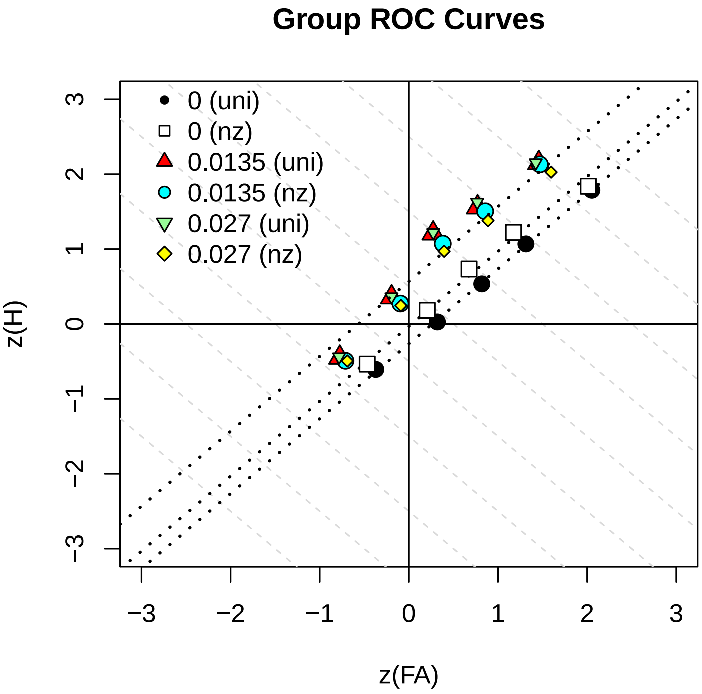
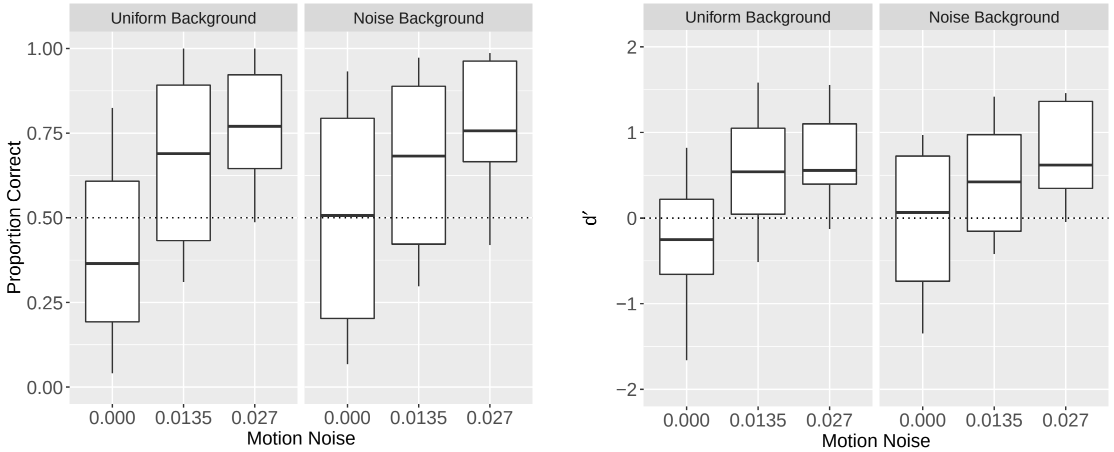


Figure 2.3 – Group ROC data measured with uniform (uni) and noise (nz) backgrounds and local motion noise amplitudes of 0, 0.0135, and 0.027. Each point represents the mean z-transformed false alarms and hits for 12 subjects. The dotted lines represent the best-fitting equal-variance Gaussian ROC (i.e., the slope was fixed at 1.0). The ROC curves for the non-zero motion noise conditions were very similar, so only a single ROC, estimated from the average across those four conditions, is drawn. The light grey lines with a slope of -1 represent constant criterion lines (i.e., $c = \frac{1}{2} \times (z(H) + z(FA))$).

Response Accuracy & Sensitivity

Group Receiver Operating Characteristic (ROC) curves were constructed from all participant data and are displayed in Figure 2.3. The slopes of the ROCs were approximately 1, which demonstrates the validity of using the equal-variance Gaussian model (Wickens, 2002) for calculating d' from these data. The curves also highlight the differences in average performance between the motion noise levels, specifically when the stimulus included motion noise (0.0135 and 0.027) and when it did not (zero motion noise).



(a) Response Accuracy **(b)** Sensitivity (d')

Figure 2.4 – Proportion correct (a) and sensitivity (b) for all conditions in Experiment 2. Sensitivity was estimated from confidence ratings using the equal-variance Gaussian model (Wickens, 2002).

Response accuracy, ignoring confidence ratings, and d', calculated from confidence ratings from each observer using the equal-variance Gaussian model (Wickens, 2002), are plotted as a function of motion noise and background type in Figure 2.4. Accuracy and sensitivity increased with increasing motion noise with both uniform and dynamic noise backgrounds. In addition, performance measured with non-zero motion noise was similar with uniform and noise backgrounds, but performance in the zero motion noise condition was poorer with a uniform background than with a dynamic noise background. Finally, in the zero-noise, uniform background condition, median response accuracy was below chance and d' was less than zero.

We first determined if participants in Experiment 2 performed similarly to participants in Experiment 1 by comparing performance in the zero-noise, uniform-background condition in Experiment 2 to performance in the zero-noise, 600 ms condition in Experiment 1. Mean response accuracy in the zero-noise uniform-background did not differ significantly from chance in Experiment 2 ($M = 0.406$, $t(11) = -0.699$, $p = 0.498$, $d = -0.51$), nor did it differ from the mean response accuracy measured in the comparable condition in Experiment 1 ($t(17.33) = -1.399$, $p = 0.179$, $d = -0.63$). Similarly, sensitivity (d') in the zero-noise, uniform-background condition did not differ significantly from zero in Experiment 2 ($M = -0.304$, $t(11) = -1.462$, $p = 0.172$, $d = -0.60$), nor did it differ significantly from mean sensitivity measured in the comparable condition in Experiment 1 ($t(21.9) = -1.672$, $p = 0.109$, $d = -0.68$). These results suggests that participants performed similarly in the comparable conditions in Experiments 1 and 2.

Arcsine-transformed proportion correct data, as well as d', were analyzed with a 3 (motion noise) × 2 (background) within-subject ANOVA. Essentially identical results were obtained with both ANOVAs, so only the results of the ANOVA performed on accuracy are described here. There was a significant main effect of Motion Noise that was modulated by a significant Motion Noise × Background interaction (Table 2.2). The interaction reflected the fact that the linear trend of accuracy across levels of motion noise was larger with a uniform background ($t(11) = 9.23$, $p < .0001$, $d = 3.77$) than with a dynamic noise background ($t(11) = 4.50$, $p = .0009$, $d = 1.84$).

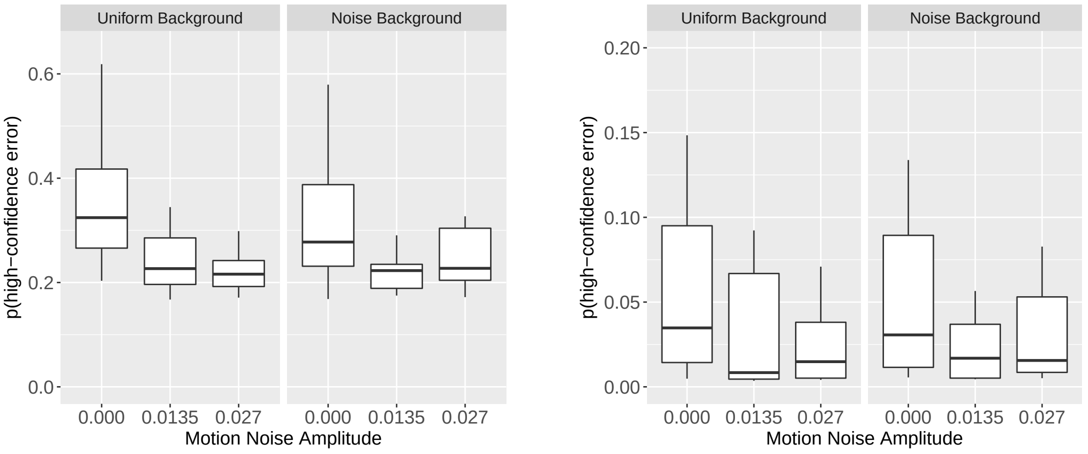
We also analyzed the Motion Noise × Background interaction by comparing the effect of background at each level of motion noise. We found that the difference between accuracy with uniform and dynamic noise backgrounds was significant in the zero motion noise conditions ($t(11) = 3.36$, $p = .006$, $d = .97$), but did not differ with motion noise of 0.0135 ($t(11) = -0.816$, $p = 0.432$, $d = .24$) or 0.027 ($t(11) = -0.069$, $p = 0.946$, $d = .02$). These analyses suggest that the effect of a dynamic background noise on discrimination accuracy was greatest when the stimulus did not include local motion noise.

Effect	**df**	$\tilde{\epsilon}$	**MSE**	**F**	η_p^2	p_{adj}
Noise	2, 22	1	0.02	57.71	.21	<.0001
Background	1, 11	-	0.01	2.14	.002	.17
Noise × Background	2, 22	1	0.01	9.05	.01	.001

Table 2.2 – Experiment 2 ANOVA table.

High-Confidence Errors

Figure 2.5 shows the proportion of high-confidence ratings given an incorrect response plotted as a function of local motion noise, background (uniform vs. noise), and the direction of global motion. Overall, more high-confidence errors were made for counter-clockwise than clockwise global motion. However, for both counter-clockwise and clockwise stimulus motion, the median proportion of high-confidence errors was higher in the absence of local motion noise. In addition, the effect of motion noise was, to a first approximation, similar in the uniform and noise background conditions.



(a) Counter-clockwise motion **(b)** Clockwise motion

Figure 2.5 – Proportion of high-confidence, incorrect responses obtained with (a) counter-clockwise and (b) clockwise global stimulus motion. Note that the scale of the y-axis differs in the two panels.

To examine these trends quantitatively, we analyzed the arcsine-transformed data in Figure 2.5a & b with separate 3 (Motion Noise) × 2 (Background) within-subject ANOVAs. With counter-clockwise motion, the main effects of local motion noise ($F(2,22) = 14.568$, $\eta_p^2 = 0.29$, $\tilde{\epsilon} = 0.508$, $p_{adj} = 0.0027$) and background ($F(1,11) = 5.089$, $\eta_p^2 = 0.003$, $p = 0.0454$) were significant, as was the noise × background interaction ($F(2,22) = 7.380$, $\eta_p^2 = 0.02$, $\tilde{\epsilon} = 0.925$, $p_{adj} = 0.0045$). The interaction was significant because the proportion of errors was higher in the uniform background condition compared to the noise background condition when the local motion noise amplitude was zero ($t(11) = 2.723$, $p = 0.0193$, $d = 0.79$) or 0.0135 ($t(11) = 2.076$,

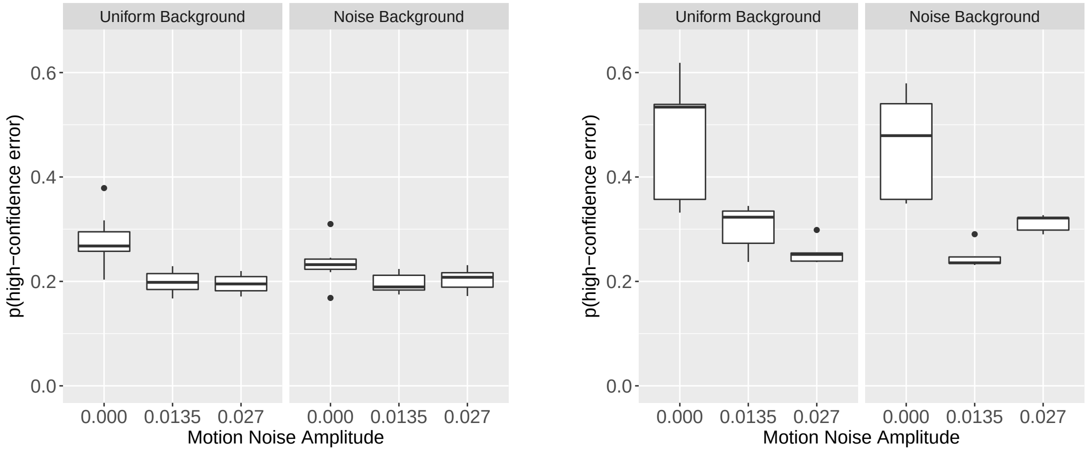
$p = 0.062$, $d = 0.60$), but it was lower in the uniform background condition when the motion noise amplitude was 0.027 ($t(11) = -3.426$, $p = 0.006$, $d = 0.99$). However, in both background conditions more high confidence errors were made in the zero motion noise condition than in the 0.0135 motion noise ($t(11) = 3.854$, $p = 0.008$, $d = 1.11$) or 0.027 motion noise ($t(11) = 3.791$, $p = 0.008$, $d = 1.09$) conditions.

With clockwise stimulus motion, the ANOVA yielded a significant main effect of local motion noise amplitude ($F(2, 22) = 9.137$, $\eta_p^2 = 0.11$, $\tilde{\epsilon} = 0.527$, $p_{adj} = 0.010$). The main effect of background ($F(1, 11) = 1.903$, $\eta_p^2 = 0.003$, $p = 0.195$) and the noise × background interaction ($F(2, 22) = 2.288$, $\eta_p^2 = 0.01$, $\tilde{\epsilon} = 0.773$, $p_{adj} = 0.140$) were not significant. Pairwise comparisons across the three levels of local motion noise, after averaging across the two background conditions, indicated that the proportion of high confidence errors was higher in the zero noise amplitude condition compared to the 0.0135 ($t(11) = 3.369$, $p = 0.0063$, $d = 0.97$)) and 0.027 ($t(11) = 2.824$, $p = 0.0166$, $d = 0.82$) conditions, but that 0.0135 and 0.027 conditions did not differ from each other ($t(11) = -0.269$, $p = 0.793$, $d = -0.08$).

These analyses suggest that high-confidence errors occurred significantly more frequently when there was no local motion noise. In addition, the effects of motion noise were similar, though not identical, in the uniform and noise background conditions, which means that high-confidence errors in our experiment were more affected by local motion noise than by the nature of the background.

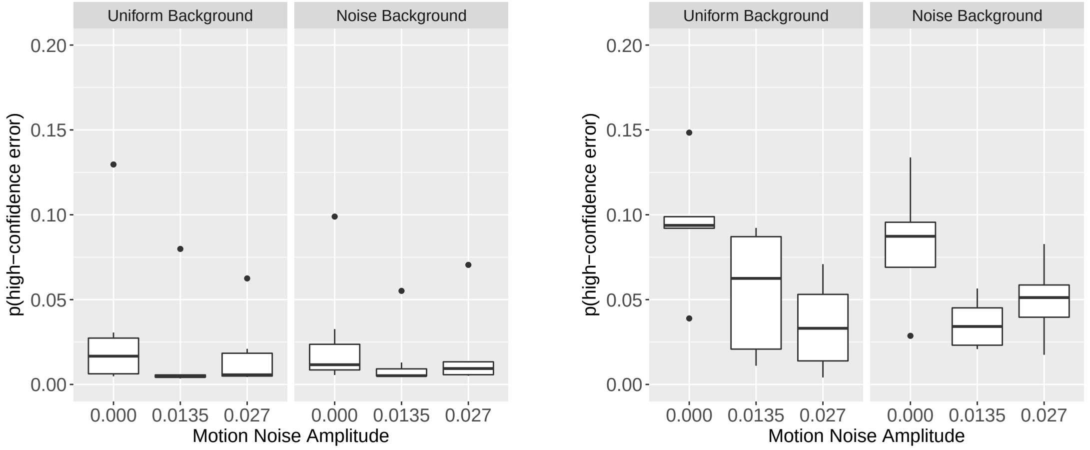
Experiment 1 suggested that some, but not all, younger observers consistently report seeing global orbital motion in the direction opposite to the veridical motion. We wondered whether the effects of local and/or background noise shown in Figure 2.5 differed between observers who were or were not prone to seeing global motion in the incorrect direction. Therefore, we divided participants into two groups depending on whether their overall accuracy across all conditions was above or below chance performance (0.50): Five participants produced overall accuracy scores lower than 0.50, while the remaining seven participants produced overall accuracy above 0.50. Figure 2.6 shows the proportion of high-confidence, incorrect responses as a function of local motion noise, background, the direction of global motion, and observer performance. Overall, the low performing observers made more high confidence errors compared to the high performing observers, especially when the stimulus contained no local motion noise.

We analyzed the data in Figure 2.6 using a linear contrast that tested whether the



(a) Counter-clockwise motion, > chance observers

(b) Counter-clockwise motion, < chance observers



(c) Clockwise motion, > chance observers

(d) Clockwise motion, < chance observers

Figure 2.6 – Proportion of high-confidence, incorrect responses obtained with (a & b) counter-clockwise and (c & d) clockwise global stimulus motion. Results for seven participants with above-chance accuracy are shown in a & c; results for five observers with below-chance accuracy are shown in b & d. Note that the scale on the y-axis differs between figures in the top and bottom rows.

arcsine-transformed proportion of high-confidence errors in the zero noise condition differed from the mean proportion of high-confidence errors in the 0.0135 and 0.027 noise conditions. With counter-clockwise global motion, the proportion of errors in the zero noise condition was higher than in the other two noise conditions ($F(1, 10) = 21.99$, $p = 0.001$, $\eta_p^2 = 0.69$), and this effect of motion noise differed significantly between the low- and high-performance groups ($F(1, 10) = 7.86$, $p = 0.018$, $\eta_p^2 = 0.44$). Similar results were obtained for clockwise global motion: the proportion of errors was greater in the zero noise stimulus condition than in the 0.0135 and 0.0270 noise conditions ($F(1, 10) = 12.686$, $p = 0.005$, $\eta_p^2 = 0.559$); however, although the difference in the linear contrast between the low- and high-performance groups was in the correct direction, it was not statistically significant ($F(1, 10) = 4.689$, $p = 0.055$, $\eta_p^2 = .319$). Taken together, the analyses provide evidence that the effects illustrated in Figure 2.5 differed for low- and high-performance observers.

Discussion

The data from Experiment 2 clarifies and extends the findings of Experiment 1. We found that dynamic background noise affected global direction discrimination only when the stimulus did not contain local motion noise. Recall that we manipulated the stimulus background to determine if the addition of white noise acted similarly to local motion noise, and therefore increase discrimination accuracy. Our results were consistent with our predictions: adding background white noise to stimuli that had zero local motion noise significantly increased response accuracy from approximately 40% correct (i.e., below chance) to approximately 50% correct (i.e., chance) in the global motion discrimination task (see Figure 2.4). This result raises the possibility that the local motion noise used here is not particularly special, but instead is just one of several types of noise that leads to higher performance in this task.

The second major finding of Experiment 2 concerns the confidence of observers when they make errors. Several observers in Experiment 1 consistently performed below chance in some conditions, which suggests that they perceived the direction of the global orbital motion incorrectly. By analyzing the confidence ratings to incorrect discrimination, Experiment 2 showed that observers often are *confident* in their incorrect responses, and this effect was larger in observers who were more likely to perceive incorrect global motion. These analyses suggest that the below-chance performance found in some conditions represents a genuine mis-perception of global motion direction rather than an effect of response bias and/or guessing on trials in which no clear direction was perceived.

Experiment 3

Experiment 3 examined whether the illusion of opposite motion is due to differences in attention in noise absent and noise present stimuli. According to this hypothesis, when the stimulus is grouped (i.e., when noise is present), attention is allocated to the entire stimulus as one object, whereas when it is not grouped (i.e., when noise is absent), attention is allocated to only one motion component. Importantly, attending to only one motion component could cause the motion of the second component to be computed in reference to the attended component, as is found in the Duncker illusion (Zivotofsky, 2004) and the reference repulsion effect (Rauber and Treue, 1998). To test this idea, we changed the colour of a single dot in each of two sets of collinear dots from white to red. The red dots were placed either within the same motion component (i.e., on parallel sets of dots) or different motion components (i.e., on perpendicular sets of dots). According to saliency models of attention (Itti and Koch, 2000), the red dots should draw visual attention to those locations and therefore bias observers to attending to the corresponding motion components. If attending to a single motion component is causing the illusion of opposite motion in the zero noise condition, then increasing the saliency of a single motion component should decrease response accuracy in the noise present condition. On the other hand, increasing the saliency of dots positioned on different motion components should make it more likely that observers will attend to both motion components and therefore increase response accuracy in the noise absent condition.

Methods

Observers

Five observers participated in the experiment (20-34 years, M = 24 years, 5 female). To increase the likelihood that the fixation instructions would be followed reliably, Experiment 3 used only experienced psychophysical observers. One observer was one of the authors and the other four were experienced psychophysical observers who were naïve to the purpose of the experiment. All observers had normal or corrected-to-normal Snellen visual acuity. All participants provided informed consent, and all experimental protocols were approved by the McMaster University Research Ethics Board.

Stimuli

The experimental apparatus was the same as in Experiments 1 and 2. The stimuli were similar to those used in Experiments 1 and 2 with the following exceptions. Experiment 3 used only two levels of local motion noise: 0 and 0.027 dva, and the stimuli were presented only on a uniform grey background for a duration of 1200 ms. There were three stimulus conditions. In the no cue condition, the stimulus consisted entirely of white dots, as in the prior experiments. In the perpendicular cue condition, the stimulus contained two red dots, one replacing the second dot from the left on the top set of dots, and the other replacing the second dot from the top on the right set of dots. Each red dot was easily discriminated from the neighbouring white dots, and therefore this manipulation potentially provides an attentional cue that could promote integration of the two different motion components associated with the two sets of dots. Stimuli in the parallel cue condition contained two red dots that replaced the second dot from the left in the top and bottom sets of dots. If attention to particular motion components is important in this task, this stimulus would encourage local grouping, because the red dots provide an attentional cue to group the two parallel lines that are part of the same motion component.

Procedure

Observers completed three blocks of 100 trials. As in previous experiments, each trial began with the presentation of a fixation point followed by the stimulus. Participants judged whether the global orbital motion was clockwise or counter-clockwise, and the next trial began 1500 ms after the response. No feedback was given. Observers were instructed to maintain central fixation throughout the entire experiment. Half of the trials contained stimuli with zero motion noise and half with 0.027 dva motion noise. Also, half of the trials contained clockwise motion and half counter-clockwise motion. Observers completed the no-cue condition first, followed by the perpendicular cue condition and then the parallel condition. Unlike Experiment 1 and 2, observers did not complete a practice session. The experiment lasted approximately 15 minutes.

Results

Response accuracy is displayed for all conditions in Figure 2.7. Response accuracy was significantly greater than chance in all noise-present conditions (all $p < 0.041$, $d > 1.33$) and was significantly less than chance in all zero noise conditions (all $p < 0.006$, $d > 2.18$). A 3 (Cue) × 2 (Noise) within-subjects ANOVA on arcsine-transformed accuracy revealed a significant main effect of Noise ($F(1,4) = 20.5$, $p = 0.01$, $\eta^2_G = 0.77$). The main effect of Cue ($F(2,8) = 2.67$, $p_{\text{adj}} = 0.16$, $\eta^2_P = 0.03$) and the Cue × Noise interaction ($F(2,8) = 1.06$, $p_{\text{adj}} = 0.38$, $\eta^2_G = 0.01$) were not significant. The effect of cue also was not significant when the the noise-present ($F(2,8) = 1.56$, $p_{\text{adj}} = 0.28$, $\eta^2_P = 0.28$) and noise-absent ($F(2,8) = 2.99$, $p_{\text{adj}} = 0.13$, $\eta^2_P = 0.43$) conditions were analyzed separately.

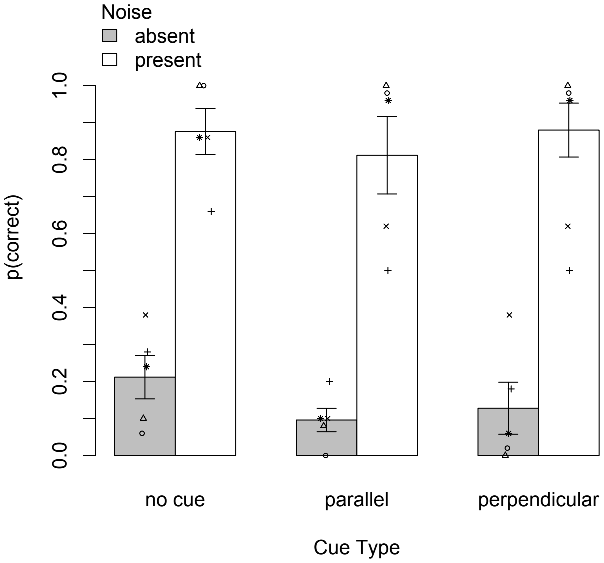


Figure 2.7 – The effects of cues on response accuracy in Experiment 3. The bars indicate the mean cueing effect for each noise level and each cue type. The symbols show accuracy for for individual participants. Error bars represent ±1 SEM.

Discussion

Experiment 3 was designed to test whether manipulating the saliency of one or both motion components using visual cues would change response accuracy relative to a no cue condition. We found no evidence that the cues influenced accuracy: in all cue conditions, accuracy was well above chance in the noise-present conditions and well below chance in the noise-absent conditions. Hence, these findings demonstrate that the perceived global motion was not affected significantly by cues that should draw attention (Itti and Koch, 2000) to a one or both motion components, and reduces the likelihood that the illusory motion seen in zero noise stimuli was caused by observers covertly attending to one of the two motion components

General Discussion

In Experiment 1 we successfully replicated a surprising result reported by Lorenceau (1996), namely that adding local motion noise significantly improves the performance in a global motion discrimination task, especially for long stimulus durations. Interestingly, several observers showed below-chance performance when the stimulus was displayed for long durations and did not contain local motion noise. The local motion noise added to the stimulus perturbed the direction of each dot, but maintained the global spatial distribution of the stimulus. Hence, local noise improved global motion perception presumably by increasing the likelihood of grouping the different motion trajectories into a single percept.

Experiment 2 examined the reliability of the below-chance performance by asking observers to rate their confidence in their responses. We found that observers were often confident about their incorrect decisions in conditions where the group average response accuracy was below chance. Furthermore, the the probability of making high confidence errors was greater in observers whose overall response accuracy was below chance. These results suggest that observers genuinely perceived global motion in the wrong direction. Experiment 2 also showed that the addition of a dynamic white noise to the stimulus background increased discrimination accuracy from below-chance to near-chance levels. This lends support to the idea that the local motion noise used by Lorenceau (1996) and in Experiment 1 is not the only type of noise that can increase response accuracy. We suggest that any stimulus manipulations that reduce the tendency of the individual dots to be grouped into four linear units would make it easier for the dots to be grouped into a single, moving global form.

Experiment 3 was conducted to test the specific hypothesis that the illusion of opposite motion in zero noise stimuli is due to selecting a single motion component as a motion reference. Salient colour cues were placed in the stimulus at locations that ought to bias observers to attend to either a single motion component or to both motion components. The results of Experiment 3 demonstrated that performance was largely unaffected by this manipulation. A motion reference account of illusory motion does not seem to provide an adequate explanation in the current task.

Eye movements have been implicated in various motion illusions such as the peripheral drift illusion (Faubert and Herbert, 1999; Beer et al., 2008), the Enigma illusion (Troncoso et al., 2008) and the Filehne illusion (Mack and Herman, 1973). In the present experiments, we instructed participants to maintain central fixation throughout the experiment, although we did not record eye movements. Despite the lack of eye-tracking data, there are several reasons for suspecting that eye movements did not contribute significantly to this illusion. Firstly, the illusion depends strongly on the presence or absence of noise (Figure 3.8), and it is not clear why eye movements would differ significantly in those conditions. Secondly, although naïve observers were used in Experiments 1 and 2, Experiment 3 also found the illusion in experienced psychophysical observers who (at least in some conditions) are better able to maintain fixation (Cherici et al., 2012) and who were confident that they maintained fixation during each trial. Finally, informal observations by the authors have shown that switching between central fixation and deliberately tracking one set of dots does not affect the clear percept of illusory motion in the zero noise stimulus.

Previous research using the orbiting square stimulus in Figure 2.1 has focused on the stimulus manipulations that enable observers to integrate the motion components to perceive the correct global motion rather than how or why observers consistently perceive global motion in the wrong direction (Lorenceau and Shiffrar, 1992; Lorenceau, 1996; Shiffrar and Lorenceau, 1996; Lorenceau and Shiffrar, 1999). Lorenceau (1996) discussed several explanations for the effect, including the possible contribution of pursuit eye movements, but did not experimentally explore the phenomenon. Shiffrar and Lorenceau (1996) examined the perceived global orbital motion of stimuli consisting of four contours arranged to form a diamond and found that discrimination accuracy was below chance when the stimulus comprised wide, low luminance contours, which suggests that the effects reported in this paper are not unique to the specific manipulations we used here. Instead, they may be present whenever perceived global direction depends on relative phase of different motion components in stimuli that lack compelling cues for global grouping.

The current study has important methodological implications for research on grouping and perceptual organization. In most studies of perceptual organization that use a two-alternative task, high response accuracy is thought to occur in conditions in which the stimulus is organized correctly whereas a proportion correct of about 0.50 usually is assumed to occur when the stimulus input is not organized, the resulting percept is ambiguous, and the observer guesses. However, near-chance performance in a two-alternative task also could occur in conditions in which stimulus input is organized so that the stimulus is unambiguous on every trial but the observer's judgement is correct on only half the trials. In Experiment 2, we obtained confidence ratings to distinguish these two possibilities, and found that some observers behaved as though they clearly and consistently perceived global motion in the incorrect direction in some conditions. It would be interesting to see if our measures of confidence are correlated with ratings of motion coherence (e.g., McDermott and Adelson, 2004). Our results suggest that observers may sometimes see coherent motion in an incorrect direction, and therefore measures of perceived coherence may not always correspond to measures of accuracy.

The three experiments reported here explore how relative phase integration in motion can be understood using a discrimination task in the presence and absence of global grouping cues. In general, we found good performance when global grouping cues were present, and below-chance performance in the absence of grouping cues. This below-chance performance is important for research in perceptual grouping in motion because it is suggestive of a bias in information integration that maybe be present in other types of integration or grouping tasks.

References

Adelson, E. H. and Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature*, 300(9):523–525.

Alais, D., Blake, R., and Lee, S. H. (1998). Visual features that vary together over time group together over space. *Nature Neuroscience*, 1(2):160–164.

Beer, A. L., Heckel, A. H., and Greenlee, M. W. (2008). A Motion Illusion Reveals Mechanisms of Perceptual Stabilization. *PLoS ONE*, 3(7):1–7.

Braddick, O. (1993). Segmentation versus integration in visual motion processing. *Trends in Neurosciences*, 16(7):263–268.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4):433–436.

Cherici, C., Kuang, X., Poletti, M., and Rucci, M. (2012). Precision of sustained fixation in trained and untrained observers. *Journal of Vision*, 12(6):31–31.

Faubert, J. and Herbert, A. M. (1999). The peripheral drift illusion: A motion illusion in the visual periphery. *Perception*, 28(5):617–621.

Itti, L. and Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research*, 40:1489–1506.

Lorenceau, J. (1996). Motion integration with dot patterns: Effects of motion noise and structural information. *Vision Research*, 36(21):3415–3427.

Lorenceau, J. and Shiffrar, M. (1992). The influence of terminators on motion integration across space. *Vision Research*, 32(2):263–273.

Lorenceau, J. and Shiffrar, M. (1999). The linkage of visual motion signals. *Visual Cognition*, 6(3-4):431–460.

Mack, A. and Herman, E. (1973). Position constancy during pursuit eye movement: An investigation of the Filehne illusion. *The Quarterly Journal of Experimental Psychology*, 25(1):71–84.

McDermott, J. and Adelson, E. H. (2004). Junctions and cost functions in motion interpretation. *Journal of Vision*, 4(7):552–563.

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

R Core Team (2017). *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria.

Rauber, H. J. and Treue, S. (1998). Reference repulsion when judging the direction of visual motion. *Perception*, 27(4):393–402.

Shiffrar, M. and Lorenceau, J. (1996). Increased motion linking across edges with decreased luminance contrast, edge width and duration. *Vision Research*, 36(14):2061–2067.

Snowden, R. J. and Verstraten, F. A. (1999). Motion transparency: Making models of motion perception transparent. *Trends in Cognitive Sciences*, 3(10):369–377.

Troncoso, X. G., Macknik, S. L., Otero-Millan, J., and Martinez-Conde, S. (2008). Microsaccades drive illusory motion in the Enigma illusion. *Proceedings of the National Academy of Sciences*, 105(41):16033–16038.

Wickens, T. D. (2002). *Elementary Signal Detection Theory.* Oxford University Press, Oxford.

Williams, D. W. and Sekuler, R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research*, 24(1):55–62.

Zivotofsky, A. Z. (2004). The Duncker illusion: Intersubject variability, brief exposure, and the role of eye movements in its generation. *Investigative Ophthalmology and Visual Science*, 45(8):2867–2872.

Chapter 3

Phase integration bias in a motion grouping task

3.1 Abstract

We examined motion binding using a task requiring integration of relative phase. Observers completed two tasks involving clockwise and counter-clockwise motion in a stimulus comprising four sets of linearly arranged dots, two moving horizontally and two moving vertically along sinusoidal trajectories differing in phase. Across conditions, noise jitter was added along the trajectory perpendicular to each dot's motion. The addition of noise in this task acts as a grouping cue to improve performance, but, surprisingly, the absence of noise causes consistent below chance performance. Here we test the hypothesis that observers perceive reverse motion because their representation of the relative phase of the motion components is systematically biased. We asked observers to adjust the relative phase of motion components to produce the most compelling clockwise or counter-clockwise motion with stimuli that did or did not contain noise. We also measured discrimination accuracy for clockwise and counter-clockwise motion. In three separate groups of observers the correlation between phase adjustment error and discrimination accuracy were significant in both noise conditions. This relationship held in younger and older adult observers. In a separate experiment, a different stimulus containing the same motion components was used to measure perceived coherence. We find a similar systematic bias in motion integration using this different stimulus, and show that stimuli that lead to this bias are also viewed

as less coherent. Our results support the hypothesis that observers misperceive the direction of motion without noise because their representation of the relative phases of motion components is biased. Generally, this result raises the possibility that an integration bias could exist in other motion tasks.

Introduction

The integration of information across space and time is a fundamental aspect of motion perception. Such integration occurs over multiple spatial scales: for example, motion perception is thought to depend on the integration of information across multiple features on a single object, as well as the integration of information across multiple moving objects. The current paper focuses on the integration of spatially-separated sets of elements that have different motion trajectories. Previous studies examining this issue focussed primarily on the question of whether the moving sets of elements were or were not integrated into a pre-determined, correct motion percept (Lorenceau and Alais, 2001; Lorenceau and Shiffrar, 1992; McDermott and Adelson, 2004; Murray et al., 2001; Shiffrar and Pavel, 1991). This forced-choice aspect of the experimental method may have missed some important characteristics of motion integration. Therefore, the current experiments examined motion integration using a continuous measure of integration that allowed for the possibility that subjects perceived illusory or anomalous integrated motion.

Relative Phase Integration

We used a stimulus created by Lorenceau (1996) to study issues related to the integration of sinusoidal motion trajectories that differ in phase. First consider a stimulus consisting of four contours that are arranged to form a square, and that occluders are placed over the square's four corners. When the square moves in a circular orbit around a central point, the presence of the occluders means that each horizontal and vertical contour undergoes sinusoidal motion in a direction that is perpendicular to its orientation. In other words, the contours move only along horizontal or vertical trajectories, and the direction of orbital motion (i.e., clockwise vs. counter-clockwise) is conveyed by the relative phase of the horizontal and vertical components. Nevertheless, observers typically report seeing the square orbit the central point and are capable of discriminating clockwise and counter-clockwise motion, which implies that observers somehow integrate the horizontal and vertical motions and are sensitive to their relative phase. To investigate this integration process, Lorenceau modified the moving square stimulus by replacing the four contours with four colinear sets of five evenly-spaced, high-contrast dots, and each set of dots underwent sinusoidal motion in the direction perpendicular to its orientation. Hence, like the original square stimulus, the modified stimulus contained motion only in the horizontal and vertical directions, and the relative phase of the horizontal and vertical components could be adjusted such that the motion in the modified stimulus was identical to that produced by clockwise or counter-clockwise orbital motion in the original stimulus. Lorenceau measured response accuracy in a task that required observers to discriminate clockwise and counter-clockwise global motion. Across conditions, he varied the amount of dynamic, independent motion noise that was added to the trajectory of each individual dot. Surprisingly, he found that accuracy *improved* as the level of dynamic noise increased. However, he also found that accuracy was significantly *below* chance at long stimulus durations when the stimulus did not contain dynamic noise. That is to say, observers consistently misperceived the direction of motion in some conditions. We recently replicated both of these findings (Chapter 1). Furthermore, we found that below-chance performance occurred even when we restricted our analyses to trials on which observers were confident in their responses, which suggests that observers genuinely perceived the stimulus moving in the incorrect direction.

The Present Study

The current study focusses on the factors that produce below-chance performance. We assume that the perception of the global, orbital motion in the Lorenceau stimulus requires observers to encode the relative phase of the horizontal and vertical motion components, and that a misperception of the direction of motion occurs when the phase is encoded incorrectly. The fact that previous studies found that some observers *consistently* misperceived the direction of motion in some conditions suggests that there was a consistent error, or bias, in the perceived relative phase of the two components. To test our hypothesis, we measured the magnitude of each observer's phase bias on every trial, and measured the association between bias and their direction discrimination responses made to the same stimuli. Specifically, we asked users to adjust the relative phase of the horizontal and vertical motion components until the stimulus appeared to be rotating clockwise or counter-clockwise (specified at the beginning of each trial). We calculated the difference between the observer's setting and the actual relative phase that was required to produce the desired motion. In Experiment 1 we found that phase bias was significantly associated with response accuracy measured in a separate direction discrimination task. In Experiments 2 and 3 we extend the findings of Experiment 1 among several groups of observers, varying the degree of stimulus noise (Experiment 2) and age of the observers (Experiment 3). In a final experiment, we test whether the present findings are stimulus specific by measuring the relation between phase bias and perceived direction with a related stimulus that produces the chopstick illusion (Anstis, 2007). We compare subjective and objective measures of motion integration by collecting ratings of perceived coherence, and conclude that objective and subjective measures of motion integration produce comparable results, although subjective measures are not able to detect evidence of illusory percepts such as those discussed in the current paper.

Experiment 1

Method

Observers

Thirty naïve observers between the ages of 18 and 29 ($M = 20$ years; 22 female) participated in Experiment 1. All observers possessed normal or corrected-to-normal Snellen visual acuity. Observers participated for course credit or received 10$ per hour for their participation. Participants provided informed consent to participate in this experiment, and all experimental protocols were approved by the McMaster Research Ethics Board.

Apparatus & Stimuli

Stimuli were generated on an Apple iMac computer using MATLAB and the Psychophysics and Video Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented on an NEC MultiSync FE992 monitor with a frame rate of 100 Hz. The height and width of the viewable screen were 27 and 36 cm, respectively (35.6 pixels/cm).

The stimulus consisted of four sets of five equally-spaced, collinear dots arranged along the four sides of a square (Figure 3.1). Each dot subtended 0.05 deg. Each set of dots subtended 3.2 deg from the edge of the first dot to the opposite edge of the fifth dot. The entire stimulus subtended 3.7 deg vertically and horizontally. The luminance of each dot was 95.6 cd/m^2 and background luminance was 43.9 cd/m^2.

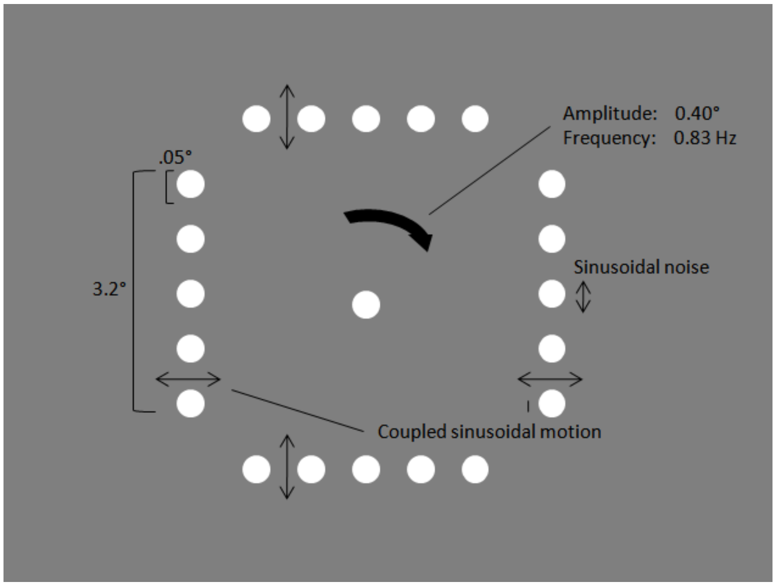


Figure 3.1 – Diagram of stimulus used in experiments 1, 2, and 3. Each of the two parallel lines of dots contained the same sinusoidal motion. In the adjustment task observers were able to adjust the relative phase of these two motion components using a dial. In the discrimination task observers viewed one of two combinations of relative phase that corresponded to either clockwise or counter-clockwise motion.

Each set of dots moved along a sinusoidal trajectory that was perpendicular to its principal axis: the horizontal dots moved vertically, and the vertical dots moved horizontally. When the four sets of dots coherently orbit the central fixation point, the direction of the global motion is determined by the relative phase of the horizontal and vertical motions: Clockwise orbital motion produces horizontal motion (of the vertical sets of dots) that leads the vertical motion (of the horizontal dots) by 90 deg, whereas counter-clockwise motion produces horizontal motion that lags the vertical motion by 90 deg. Relative phases between 0 and ±90 deg produce clockwise/counter-clockwise motion that is elliptical rather than circular: Reducing relative phase from ±90 deg to 0 deg results in progressively narrower elliptical motion, and a relative phase of 0 deg corresponds to diagonal motion. We measured the direction of global motion that was perceived when the relative phase of the horizontal and vertical motions was set to different values. Because there was no actual orbital motion in the stimulus, the horizontal and vertical motions were, individually, uninformative, and therefore the direction judgement could be based only on the relative phase of the two motion components. In our experiments, the amplitude and frequency of the sinusoidal motions were set to values that corresponded to a global orbital rotation amplitude of 0.4 deg and a frequency of 0.83 Hz. Finally, in addition to the main sinusoidal motion, the trajectory of each dot was perturbed by sinusoidal jitter, or noise, in the direction that was orthogonal to the main motion. The amplitude of this sinusoidal motion jitter was either 0 or 0.027 deg, the frequency was 3 Hz, and the starting phase was selected randomly for each dot on each trial.

Procedure & Experimental Design

Sensitivity to relative phase was measured with an adjustment task and a discrimination task. In the adjustment task, each trial began with the instruction “please adjust the stimulus until it is clockwise/counter-clockwise” which was presented in the center of the display for 2 s. The stimulus was presented immediately after the instruction was removed. On each trial, observers adjusted relative phase by turning a knob until they perceived global motion in the pre-specified direction (i.e., clockwise or counterclockwise). Observers were informed that rotating the knob varied relative phase over a limited range (i.e., ±720 deg, or ±2 cycles) around the starting value. Specifically, observers were told that if they felt they had hit a “wall" in stimulus space, to continue exploring the stimulus by turning the dial in the other direction. Observers were encouraged to adjust the stimulus to achieve the most compelling percept of the target global motion possible and, when they were satisfied, to press the space bar on a computer keyboard to end the trial. On 50% of the trials, the initial setting of relative phase was correct: it was set to the value (-90 or 90 deg) that corresponded to the target direction of global, orbital motion. On the remaining 50% of the trials the starting phase was set to uninformative values of 0 or 180 deg. When the starting relative phase was 0 deg, the four sets of dots formed a square that moved coherently along a diagonal path from the lower-left to the upper-right of the stimulus display. When the starting relative phase was 180 deg, the four sets of dots moved coherently along a diagonal path from the lower-right to the upper-left of the display. For each initial value of relative phase, on half of the trials the adjustments made by the observer altered the phase of the horizontal motion (of the vertical dots) and on the other half the adjustments varied the vertical motion (of the horizontal dots). There were a total of 96 trials. On 48 trials the trajectories of the individual dots were perturbed by sinusoidal noise (amplitude = 0.027 deg) and on the remaining 48 trials the stimulus did not contain noise. Noise and no-noise stimuli, as well as all initial values of relative phase, were presented in a random order.

In the discrimination task, on each trial the relative phase was set to produce either clockwise or counter-clockwise circular motion (i.e., ±90 deg) and observers reported whether they perceived global motion in the clockwise or counter-clockwise direction. Observers completed 100 trials, 50 with local, sinusoidal noise and 50 with no noise. For each type of noise, the global motion was clockwise on half of the trials and counter-clockwise on the other half. The type of noise and direction of global motion were randomly intermixed. Stimulus duration was 600 ms and was followed by a response screen that contained six buttons that indicated three levels of confidence – "maybe", "probably", "definitely" – that the global motion was in the clockwise or counter-clockwise direction. Participants indicated their response by selecting one button with a computer mouse.

The inter-trial interval in both tasks was 1 s. All participants completed the adjustment task first followed by the discrimination task.

Results

Statistical analyses were performed in R (R Core Team, 2017). Either adjusted R-squared (R^2_{adj}) or Cohen's d are reported as a measure of association strength and effect size.

Adjustment Task

Data are reported as phase adjustment error from the value that produces the desired target motion. An error of 0 means the stimulus was adjusted to the correct value. Errors *between* $\pm\pi/2$ mean that phase was set to values that produce elliptical (rather than circular) global motion in the correct direction. An error of exactly $\pi/2$ or $-\pi/2$ means that relative phase was set to a value that produces diagonal global motion. Finally, errors between $\pi/2$ and π or between $-\pi/2$ and $-\pi$ mean that phase was set to a value that produces elliptical global motion in the incorrect direction. The sign of the phase error was not informative. Consequently, the absolute value was taken for all responses for the purpose of analysis. The 20% trimmed mean was calculated to estimate the average phase error in each condition for each observer[1].

Figure 3.2 displays data from several representative observers. In each figure, the adjustment errors from individual trials are divided into four sets depending on whether the stimulus did or did not contain local noise, and whether the initial global motion was in the correct direction or was ambiguous. The results from most observers resembled the results from observers 5 and 11, who responded correctly in the noise condition but incorrectly in the no-noise condition. Indeed, most of the errors on no-noise trials fell between $\pi/2$ and π, or between $-\pi/2$ and $-\pi$, which is consistent with the hypothesis that observers perceived the global motion in the wrong direction (Chapter 1). Observers 7 and 25 did not perform differently on the noise and no-noise trials: the adjustment errors suggest that observer 7 nearly always perceived global motion in the direction opposite to the true motion, whereas observer 25 nearly always correctly perceived the direction of global motion.

The boxplots in Figure 3.3a illustrate the distributions of average phase error in the zero noise and high noise conditions in π radians. Average phase error was greater in no-noise trials than high noise trials, ($t(29) = 9.31$, $p < 0.0001$, $d = 1.70$). The possible range of phase errors spans from 0 to 1 π radians. If an observer was responding randomly, a uniform distribution of responses would be expected, leading to an average phase error of 0.50 π radians. Therefore, to determine if observers perceived illusory motion, t tests compared average phase error in the zero-noise and high-noise conditions to 0.50 π radians. One-tailed t tests indicated that phase error was significantly greater than 0.50π in the zero-noise condition ($t(29) = 3.28$, $p < 0.003$, $d = 0.60$) and significantly less than 0.50π in the high-noise condition ($t(29) = 8.18$, $p < 0.0001$, $d = 1.10$).

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[1] Similar results were obtained when average error was calculated as the mean rather than the trimmed mean.

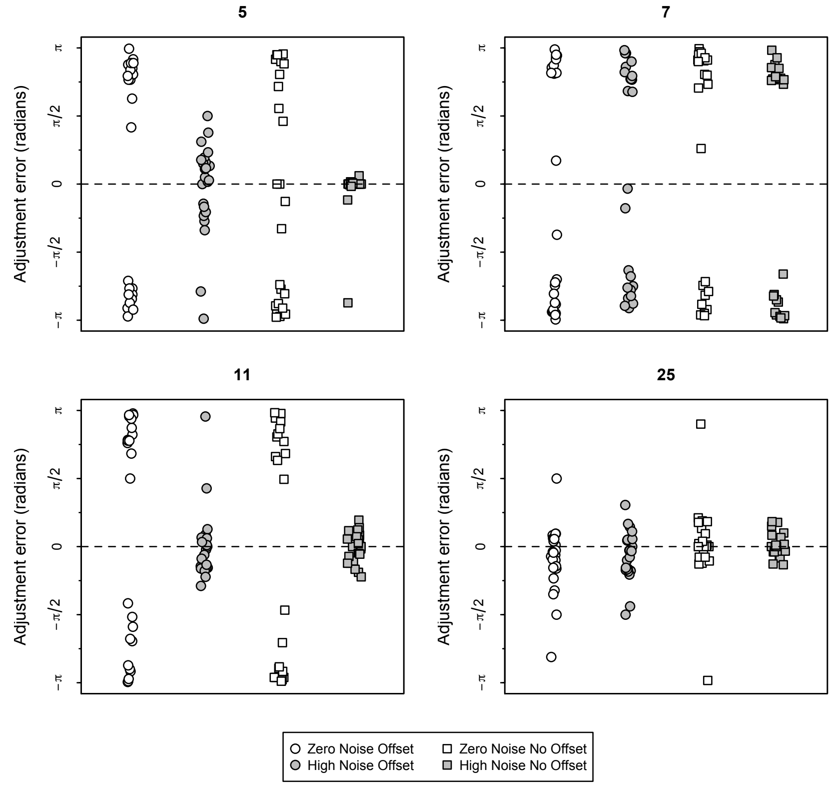
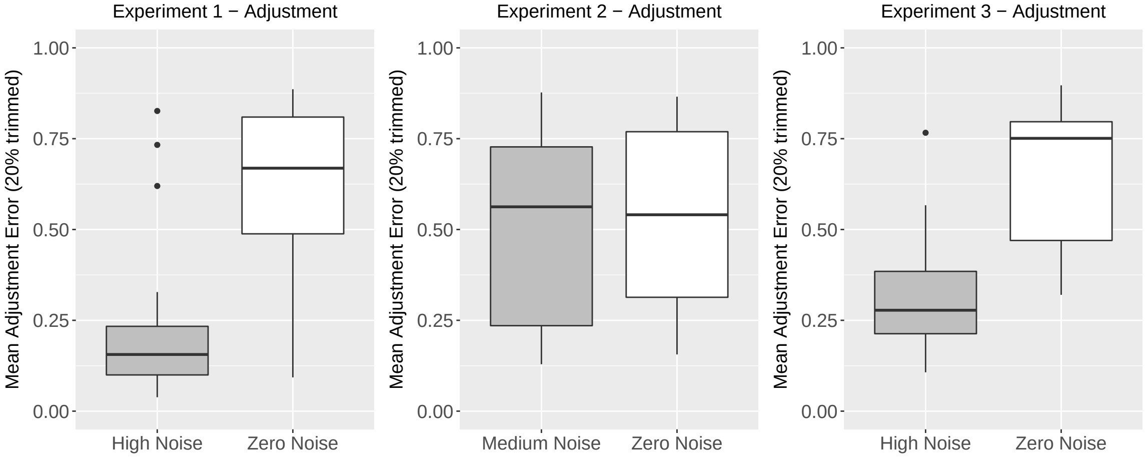


Figure 3.2 – Phase adjustment data from four representative observers in Experiment 1. Each symbol corresponds to a phase setting from a single trial. Results from high-noise and zero-noise trials are represented by filled and unfilled symbols, respectively. The square and circle symbols indicate results from, respectively, trials in which the initial global motion was in the correct direction (i.e., no offset; relative phase was -90 or 90 deg) or was in an ambiguous direction (i.e., offset; relative phase was 0 or 180 deg).



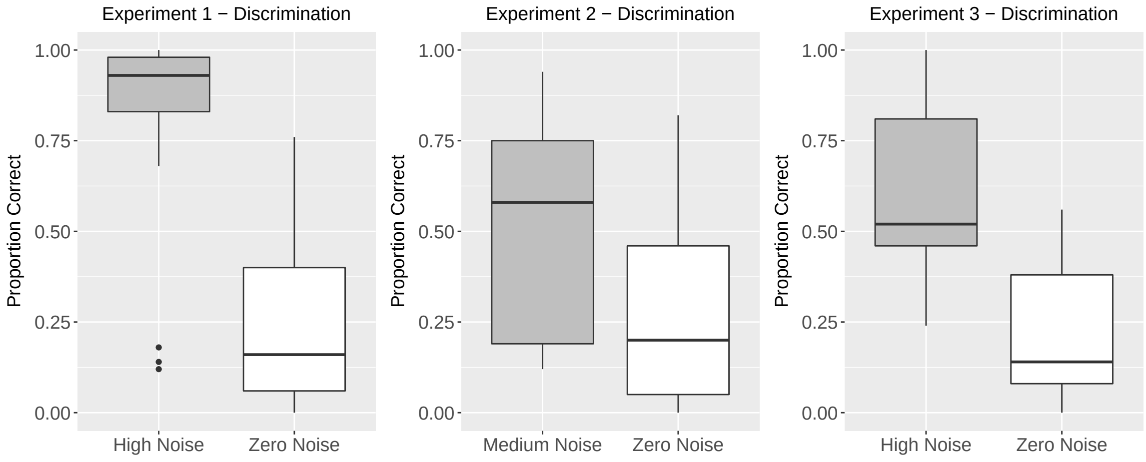
(a) Experiment 1 **(b)** Experiment 2 **(c)** Experiment 3b

Figure 3.3 – Boxplots illustrating the distributions of average (i.e., 20% trimmed mean) phase error across observers in Experiments 1, 2, and 3b. In each plot, phase error is plotted in units of π (i.e., $1 = \pi$ radians). In the noise present condition, the stimulus contained local, sinusoidal jitter with an amplitude of 0.027 (Experiments 1 & 3b) or 0.0135 (Experiment 2). Young adults were tested in Experiment 1 ($M_{\text{age}} = 20$; n=30) and Experiment 2 ($M_{\text{age}} = 19$; n=15); older adults were tested in Experiment 3b ($M_{\text{age}} = 73$; n=15). Perfect performance corresponds to 0 phase error. Phase error of 1 (i.e., π radians) corresponds to the opposite direction of global motion.

Discrimination Task

The proportion of correct responses in the discrimination task, collapsing across all confidence ratings, is shown in Figure 3.4a. The difference between proportion correct on high-noise ($M = 0.838$) and no-noise ($M = 0.239$) trials was significant ($t(29) = 12.37$, $p < 0.0001$, $d = 2.25$). Furthermore, accuracy on zero noise trials was significantly below 0.50, which represents chance performance ($t(29) = 6.55$, $p < 0.0001$, $d = 1.20$), whereas accuracy on high noise trials was significantly above 0.5 ($t(29) = 7.46$, $p < 0.0001$, $d = 3.38$).

Figure 3.5a displays the average proportion of high-confidence responses (i.e., observers selected “definitely” on the response screen) that were *incorrect*. Three participants are removed from this analysis because they did not make at least one high-confidence response in both noise levels. The mean proportions in the zero-noise ($M = 0.15$) and high-noise ($M = 0.76$) conditions differed significantly ($t(26) = 7.42$, $p < .0001$, $d = 11.42$).



(a) Experiment 1 **(b)** Experiment 2 **(c)** Experiment 3b

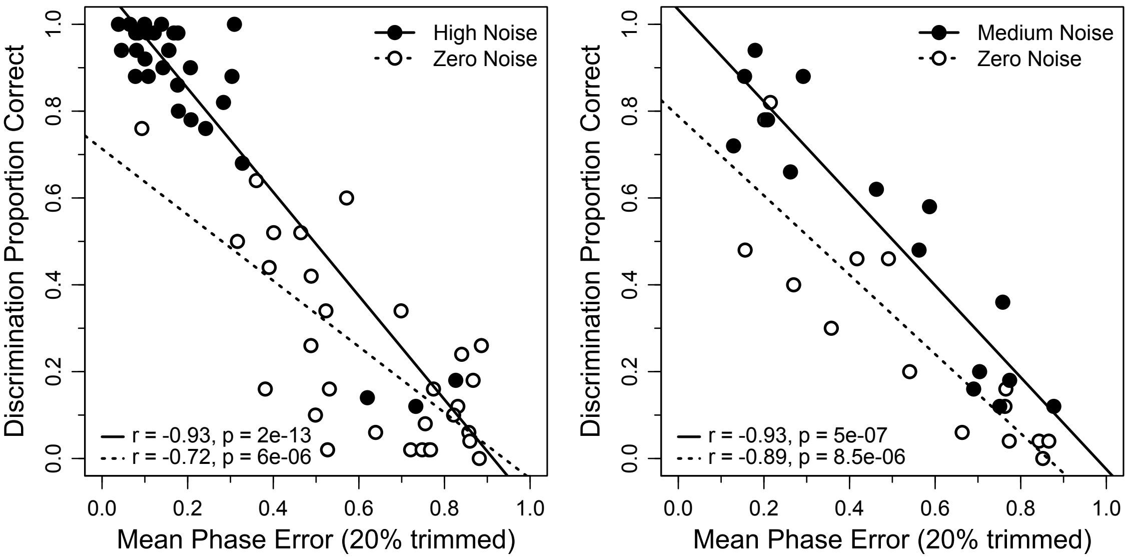
Figure 3.4 – Proportion correct in the discrimination task, ignoring confidence ratings. The amplitude of local, sinusoidal jitter was 0.0135 and 0.027 deg in the medium and high noise conditions, respectively. Young adults were tested in Experiment 1 ($M_{\text{age}} = 20$; n=30) and Experiment 2 ($M_{\text{age}} = 19$; n=15); older adults were tested in Experiment 3b ($M_{\text{age}} = 73$; n=15). Chance performance corresponds to an accuracy of 0.5.

(a) Experiment 1 **(b)** Experiment 2 **(c)** Experiment 3b

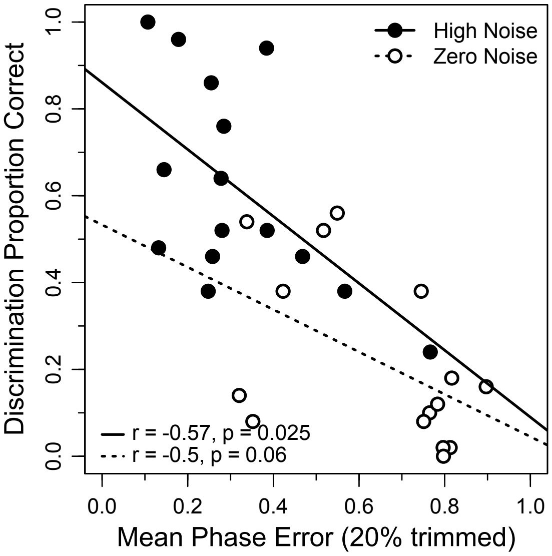
Figure 3.5 – The proportion high-confidence responses that were incorrect (i.e., $p(\text{Incorrect}|\text{Definitely})$) observed in various conditions and experiments. The amplitude of local, sinusoidal jitter was 0.0135 and 0.027 deg in the medium and high noise conditions, respectively. Young adults were tested in Experiment 1 ($M_{\text{age}} = 20$; n=30) and Experiment 2 ($M_{\text{age}} = 19$; n=15);. Older adults were tested in Experiment 3b ($M_{\text{age}} = 73$; n=15).

Relating Adjustment Responses & Discrimination Accuracy

The association between performance in the adjustment and discrimination tasks is depicted in Figure 3.6a. The linear association between response accuracy in the discrimination task and mean phase error in adjustment task was significant in both the high-noise ($b = -1.19$, $t(28) = -13.21$, $p < 0.001$, $R^2_{\text{adj}} = 0.85$) and zero-noise ($b = -0.76$, $t(28) = -5.57$, $p < 0.001$, $R^2_{\text{adj}} = 0.51$) conditions.



(a) Experiment 1 **(b)** Experiment 2



(c) Experiment 3b

Figure 3.6 – Relationship between response accuracy in the discrimination task and the average phase error in the adjustment task. Pearson's r and the *p* value for each regression are shown in the lower left corner in each plot.

Discussion

Experiment 1 examined the relationship between the relative phase of two motion trajectories and the perceived direction of global orbital motion. Using an adjustment task, we found that some participants set the relative phase of motion components to a value that was more than $\pi/2$ radians away from the correct value for the target motion. Importantly, these same participants performed below chance in the direction discrimination task when the stimulus did not contain local motion noise. Furthermore, observers were more likely to make errors in the discrimination task with high confidence when the stimulus did not contain noise. These results can be taken as strong evidence that most participants perceived motion in the direction opposite to the veridical direction when the stimulus did not contain local dynamic noise, and some participants misperceived the direction of motion even when the stimulus did contain noise. The regression shown in Figure 3.6a showed that there was a strong inverse relationship between phase adjustment error and discrimination error accuracy both in the presence and absence of local dynamic noise.

Lorenceau (1996) suggested that local stimulus noise improved global motion discrimination by reducing the motion coupling between the two sets of horizontal dots that moved vertically and between the two sets of vertical dots that moved horizontally, and therefore made it easier to group all four sets of dots into a single form that moved in one global direction. If this is true, reducing the amplitude of the local motion noise should reduce performance in noise-present stimuli. We tested this hypothesis in Experiment 2 by using a noise amplitude that was one half the value used in Experiment 1. Experiment 2 also addressed a potential criticism of Experiment 1, namely that the high correlation between phase adjustment error and direction discrimination accuracy is due primarily to the presence of three outliers who were observers that had large adjustment errors and poor discrimination accuracy in the high-noise condition (see Figure 3.6a). By reducing the amplitude of local noise, we hoped to increase the range of phase errors found in the noise-present condition and therefore derive a more robust estimate of the relationship between adjustment error and discrimination accuracy.

Experiment 2

In Experiment 1, performance in the high-noise condition was accurate in both the adjustment and discrimination tasks. To avoid this ceiling effect, the amplitude of local noise used in Experiment 2 was reduced from 0.027 deg to 0.0135 deg.

Methods

Observers

Fifteen naïve observers between the ages of 18 and 21 ($M = 19$ years; 11 female) participated in the experiment. All observers possessed normal or corrected-to-normal Snellen visual acuity. Observers participated for course credit or received 10$ per hour for their participation. Participants provided informed consent to participate in this experiment, and all experimental protocols were approved by the McMaster Research Ethics Board.

Apparatus, Stimuli & Procedure

The experimental method and stimuli were the same as in Experiment 1 except that the amplitude of the local sinusoidal noise was reduced from 0.027 to 0.0135 deg.

Results

Statistical analyses were performed in R (R Core Team, 2017). Either adjusted R-squared (R^2_{adj}), Cohen's d, or partial eta-squared (η^2_P) are reported as a measure of association strength and effect size.

Adjustment Task

Results from the adjustment task from four representative observers are displayed in Figure 3.7 in radians. Average phase error in π radians for all observers is shown in Figure 3.3b. Average phase error in the medium noise trials ($M = 0.54$) was slightly greater than the average error in the zero noise condition ($M = 0.49$), a difference that was statistically significant ($t(14) = 2.44$, $p = .028$, $d = 0.63$). Phase error did not differ from chance (.50 phase error) for zero-noise trials ($t(14) = 0.67$, $p = .517$, $d = 0.17$) or medium-noise trials ($t(14) = -0.10$, $p = .918$, $d = 1.86$).

An ANOVA comparing performance on noise present and noise absent trials in Experiment 1 and Experiment 2 yielded a significant Experiment × Noise interaction ($F(1, 43) = 30.97$, $p > .0001$, $\eta_P^2 = 0.42$). The phase adjustment error was significantly greater in medium noise (Experiment 2) than high noise (Experiment 1) ($t(21.7) = 3.65$, $p = 0.001$, $d = 1.28$), but the average phase error in zero noise trials did not differ significantly between experiments ($t(23.2) = 1.03$, $p = 0.31$, $d = 0.35$).

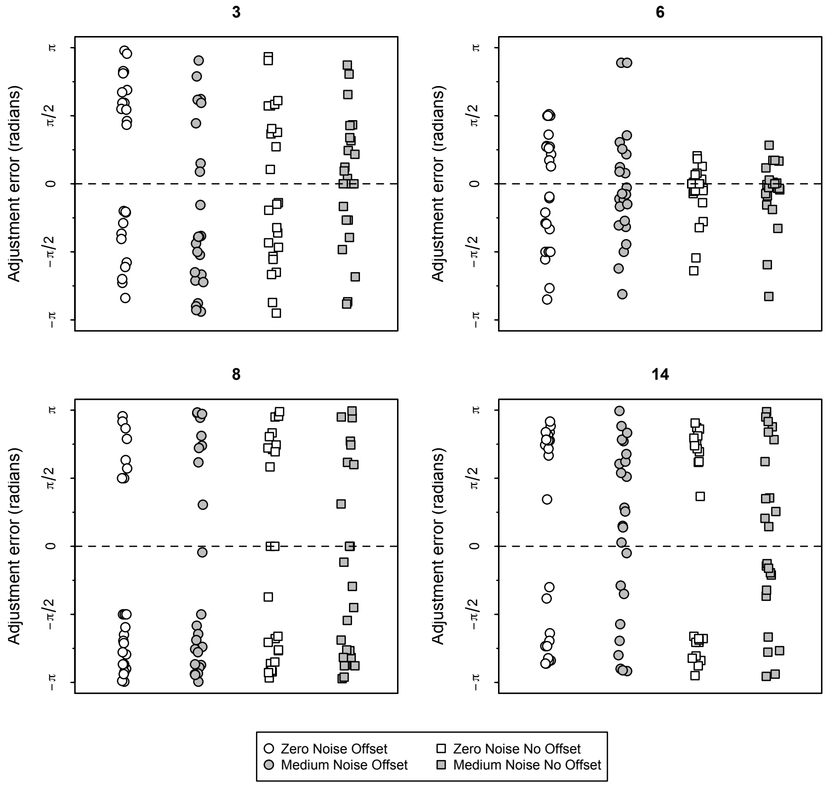


Figure 3.7 – Phase adjustment data from four representative observers in Experiment 2. Symbol conventions are the same as in Figure 3.2.

Discrimination Task

The average proportions of correct responses from the discrimination task, ignoring confidence ratings, are shown in Figure 3.4b. The difference between proportion correct in the medium-noise ($M = 0.512$) and zero-noise ($M = 0.291$) was significant ($t(14) = 5.99$, $p < 0.0001$, $d = 1.54$). Hence, as we found in Experiment 1, adding local motion noise improved direction discrimination accuracy. Furthermore, as was found in Experiment 1, response accuracy in the zero-noise condition was significantly below chance performance ($t(14) = 3.03$, $p = 0.009$, $d = 0.78$). Accuracy on medium-noise trials did not differ significantly from chance ($t(14) = 0.15$, $p = 0.879$, $d = 1.70$)

A 2 (Noise Present vs Noise Absent) × 2 (Experiment) ANOVA comparing proportion correct in Experiments 1 and 2 found a significant Experiment × Noise interaction ($F(1, 43) = 26.37$, $p < .0001$, $\eta_P^2 = 0.38$). Two-sample t tests comparing accuracy in Experiments 1 and 2 found that accuracy differed on noise-present trials ($t(23.8) = 3.62$, $p = 0.001$, $d = 1.22$) but not noise-absent trials ($t(23.6) = 0.65$, $p = 0.52$, $d = 0.22$).

Figure 3.5b displays the average proportion of high-confidence responses (i.e., trials on which observers selected "definitely" on the response screen) that were incorrect. Two participants were excluded from this analysis because they did not make at least one high-confidence response for each noise level. The proportion of high-confidence errors in the zero-noise (0.78) and medium-noise (0.45) conditions differed significantly ($t(12) = 3.44$, $p = .005$, $d = 0.95$).

An ANOVA comparing the proportion of high-confidence errors on noise present and noise absent trials in Experiments 1 and 2 revealed a significant interaction between noise and experiment ($F(1, 38) = 4.33$, $p = .044$, $\eta_P^2 = 0.10$). Two-sample t tests comparing the proportion of high-confidence errors in Experiments 1 and 2 found a significant difference on noise-present trials ($t(19.2) = 2.46$, $p = .023$, $d = 0.91$) but not noise-absent trials ($t(26.8) = 0.16$, $p = .874$, $d = 0.05$).

Relating Adjustment Responses & Discrimination Accuracy

Figure 3.6b displays the relationship between performance on the adjustment and discrimination tasks for all participants in Experiment 2. As predicted, reducing the amplitude of the local dynamic noise in this experiment resulted in broader distributions of phase adjustment error and discrimination accuracy in the high noise condition than was found in Experiment 1. Nevertheless, as was found in Experiment 1, response accuracy in the discrimination task was significantly linearly associated with average phase error in the adjustment task in both the noise-present ($b = -1.06$, $t(13) = -9.14$, $p < .0001$, $R^2_{\text{adj}} = .855$) and noise-absent conditions ($b = -.91$, $t(13) = -7.06$, $p < .0001$, $R^2_{\text{adj}} = .777$).

The relation between phase adjustment error and discrimination accuracy in Experiments 1 and 2 was analyzed with a linear model that included phase error as a continuous predictor variable, experiment as a categorical predictor variable, and a phase error × experiment interaction term. Noise-present and noise-absent conditions were analyzed separately. In the noise-present condition, the linear association between phase error and discrimination accuracy in Experiment 1 was significant ($b = -1.19$, $t(41) = -9.36$, $p < 0.001$), and neither the effect of experiment ($b = -0.06$, $t(41) = -0.91$, $p = .367$) nor the phase error × experiment interaction ($b = 0.14$, $t(41) = -0.96$, $p = .341$) were significant. Similar results were obtained in the noise-absent condition: the association between phase error and discrimination accuracy was significant in Experiment 1 ($b = -0.76$, $t(41) = -5.87$, $p < 0.001$), but neither the effect of experiment ($b = 0.07$, $t(41) = 0.61$, $p = 0.545$) nor the phase error × experiment interaction ($b = -0.15$, $t(41) = -0.78$, $p = 0.439$) were significant. Hence, these analyses suggest that the relation between phase adjustment error and direction discrimination accuracy was similar in the two experiments.

Discussion

In Experiment 1, phase adjustment error was very small and direction discrimination accuracy was very high in the high-noise condition. To avoid this ceiling effect, Experiment 2 used a local dynamic noise amplitude that was half the amplitude used in Experiment 1. As expected, reducing the amplitude of the noise resulted in a wider distribution of phase adjustment error and discrimination accuracy across participants (cf. Figures 3.6a & 3.6b), and therefore provided a more reliable estimate of the relation between performance in the adjustment and discrimination tasks. Overall, the results of Experiment 2 were consistent with those obtained in Experiment 1: in both experiments, response accuracy in the discrimination task was higher in the noise present condition than in the zero noise condition, discrimination accuracy was significantly below chance in the zero noise condition but not in the medium-noise condition, and discrimination accuracy in both conditions was significantly correlated with phase error in the adjustment task. One difference between experiments is that discrimination accuracy in the noise present condition was significantly above chance when the local dynamic noise amplitude was 0.027 dva (Experiment 1) but not 0.0135 dva (Experiment 2).

Experiment 3

Several aspects of motion perception change during normal healthy aging (Hutchinson et al., 2012). For example, minimum motion thresholds and motion coherence thresholds increase with age (Snowden and Kavanagh, 2006), meaning that older adults need faster speeds to accurately perceive coherent motion. Furthermore, older adults are less sensitive to global motion in random dot kinematograms, and identify its direction less accurately (Bennett et al., 2007; Ball and Sekuler, 1987; Roudaia et al., 2010).

Lorenceau (1996) reported that observers sometimes mis-perceived the direction of global motion when the stimulus did not contain local motion noise. The nature of this result was examined in Experiments 1 and 2, by allowing observers to adjust the phase of the stimulus directly. In Experiments 3a and 3b we examine how older adults perceive the global motion of the stimulus. In Experiment 3a, we test a group of twelve older adults in a replication of Lorenceau (1996). In Experiment 3b, investigate age-related changes in motion perception by testing fifteen older adults in both phase adjustment and discrimination tasks used in Experiments 1 and 2.

Experiment 3a

Methods

Observers

Twelve observers (64-78 years, $M = 70$; 7 female) participated in the experiment. All participants possessed normal or corrected-to-normal Snellen visual acuity. Participants were recruited through local newspaper advertisements and received \$10 per hour for their participation. Some individuals had completed other visual experiments, but all participants were naïve to the purposes of this experiment and had not taken part in studies that used tasks or stimuli that were similar to those used in the current experiment. Participants provided informed consent prior to the start of the experiment and all experimental protocols were approved by the McMaster University Research Ethics Board.

Apparatus & Stimuli

The experimental apparatus was the same as in Experiments 1 and 2. The stimuli used in Experiment 3a were similar to those used in Experiments 1 and 2 (Figure 3.1). There were three amplitudes of local sinusoidal position noise (0, 0.027, 0.081 deg) and four stimulus durations (150, 300, 600, & 1200 ms) for a total of 12 conditions.

Procedure

Each trial began with a central fixation point and a single moving stimulus, followed by a blank, grey screen. The observer reported the direction of global, orbital motion by pressing a key labeled "CC" (counter-clockwise) or "C" (clockwise) on a standard computer keyboard. Each experimental session began with 10 practice trials in which the stimulus was a square consisting of four high-contrast lines that orbited the fixation point for 600 ms. The 10 practice trials were repeated until a observer responded correctly on at least eight trials. The practice trials ensured that observers could discriminate clockwise and counter-clockwise motion, understood the task, and how to use the keyboard to respond. The experimental trials immediately followed the practice trials. There were 50 trials in each of the twelve conditions, or 600 trials in total. Experimental trials were blocked by stimulus duration; motion noise levels were randomly intermixed within each block. Each block was self-paced, and an experimental session lasted approximately 50 minutes. No feedback was given during the experiment. Each trial began 1500 ms following response to the previous trial.

Results

The Huynh-Feldt estimate of sphericity ($\tilde{\epsilon}$) was used to adjust p values of F tests conducted on within-subject variables with more than 1 degree of freedom. Either partial eta-squared (η_p^2) or Cohen's d are reported as a measure of association strength and effect size.

Response accuracy is plotted as a function of stimulus duration and noise amplitude in Figure 3.8. On average, the effects of noise and duration on both measures were qualitatively similar in older adults compared to the results of younger adults in prior work, although numerically accuracy was lower in older adults here (Lorenceau 1996, Chapter 1). When the noise amplitude is non-zero, response accuracy increases with increasing stimulus duration. When noise amplitude is zero, response accuracy decrease with increasing stimulus duration and drops below chance (0.50) at the longest stimulus durations.

The arcsine-transformed proportion correct were analyzed with a 4 (Duration) × 3 (Noise) ANOVA. The main effect of Noise was significant, as was the Noise × Duration interaction (Table 3.1).

Effect	**df**	$\tilde{\epsilon}$	**MSE**	**F**	η^2_p	p_{adj}
Noise	2, 22	0.67	.07	21.89	.18	<.0001
Duration	3, 33	0.49	.09	1.65	.02	.22
Noise × Duration	6, 33	0.48	.05	12.96	.15	<.0001

Table 3.1 – Experiment 3a ANOVA table.

The significant Noise × Duration interaction reflects the fact that accuracy increased with increasing stimulus duration in the non-zero noise conditions, but decreased with increasing duration in the zero noise condition (Figure 3.8). The linear trend of response accuracy across stimulus durations were positive and significantly different from zero in the 0.027 degree noise ($t(11) = 2.13$, $p = .028$, $d = 0.87$), and 0.081 degree noise ($t(11) = 4.62$, $p < 0.001$, $d = 1.89$) conditions, whereas the linear trend was negative and significantly different from zero in the 0 noise condition ($t(11) = 3.91$, $p = 0.001$, $d = 1.60$).

Average proportion correct was below chance at stimulus durations of 600 ms (M= .40) and 1200 ms (M = .26) ms in the zero noise condition. We tested whether proportion correct in each subject was below 0.5 using Bonferroni-corrected ($\alpha_{FW} = .01$) binomial tests. Four observers had response accuracies significantly below 0.5 at 600 ms stimulus duration: The average performance of these observers was 0.06. With the 1200 ms stimulus, ten of the twelve observers performed significantly lower than 0.5: the average proportion correct for these observers was 0.14. These data suggests that older adults are susceptible to illusory backwards motion in zero noise stimuli.

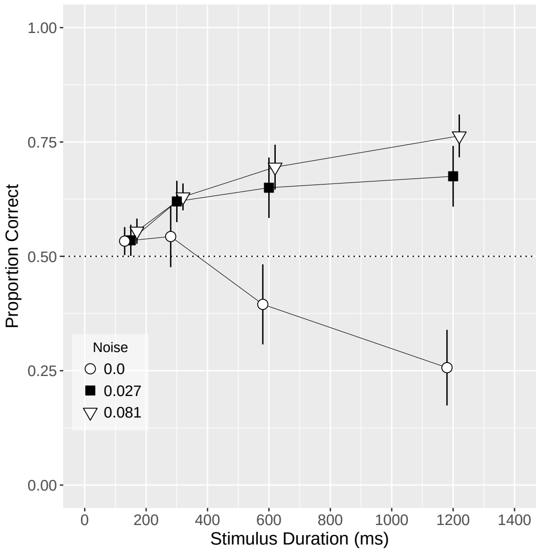


Figure 3.8 – Response accuracy measured in Experiment 3a plotted as a function of stimulus duration and motion noise amplitude. Error bars represent ±1 SEM.

Discussion

The focus of Experiment 3 is to explore how the integration of global motion changes with age. In Experiment 3a, we found that older adults are similarly effected by stimulus noise in this task as found in prior experiments with younger adults (Lorenceau 1996, Chapter 1). Specifically, motion discrimination accuracy increased with increasing stimulus duration when noise was present, but decreased with increasing stimulus duration when noise was absent. The perception of illusory motion in zero-noise stimuli may be stronger in older adults than younger adults (Figure 2, Chapter 1). In the current experiment, ten out of twelve older adults performed significantly below chance at the longest stimulus duration, whereas in Chapter 1, only three of twelve younger adult participants performed significantly below chance. Having shown that older observers produce similar patterns of data to younger adults, we now directly measure the relationship between the relative phase of the two motion components and perceived global motion in Experiment 3b to be able to directly compare motion integration in this task across the adult lifespan.

Experiment 3b

Methods

Observers

Fifteen naïve participants between the ages of 62 to 85 years ($M = 73$ years; 9 female) took part in the experiment. Participants were recruited in the same manner as Experiment 3a. All participants had normal or corrected-to-normal Snellen visual acuity, provided informed consent prior to the start of the experiment, and received $10 per hour for their participation. All experimental protocols were approved by the McMaster Research Ethics Board.

Apparatus & Stimuli

The stimuli and method were the same as in Experiment 1, with the exception of the following change in the adjustment task for participants 8 to 15. Based on feedback given by participants 1-7, for participants 8-15 the target direction and trial number were written at the top of the response screen in order to reduce memory demands during the trial and to provide feedback about the time remaining in the experiment.

Results

Statistical analyses were performed in R (R Core Team, 2017). Either adjusted R-squared (R^2_{adj}), partial eta-squared (η^2_P), or Cohen's d are reported as a measure of association strength and effect size.

Adjustment Task

Average adjustment error from observers 1-7 was compared to observers 8-15 to check for differences that may have occurred due to the change in experimental procedure described above. A two-sample t test revealed no difference between the two groups for the adjustment task ($t = 0.59$, $p = 0.56$, $d = 0.23$), and so the data was combined across groups for the following analyses.

Results from the adjustment task from four representative observers are displayed in Figure 3.9. Average phase errors in the zero- and high-noise conditions are shown in Figure 3.3c, in π radians. Mean error in the two conditions differed significantly ($t(14) = 4.48$, $p < .0001$, $d = 1.16$). Average phase error in zero-noise trials was significantly greater than 0.5 (i.e., the phase error predicted by random responding) ($t(14) = 2.74$, $p = .016$, $d = 0.71$), whereas average phase error in the high-noise trials was significantly less than 0.5 ($t(14) = 4.03$, $p = .001$, $d = 1.78$).

Phase adjustment error measured in older participants was compared to the adjustment error measured in younger participants in Experiment 1 with a 2 (Noise Present vs. Noise Absent) × 2 (Experiment) ANOVA. The main effect of noise ($F(1, 43) = 83.17$, $p > .0001$, $\eta_P^2 = 0.66$) was significant, but the main effect of Experiment ($F(1, 43) = 1.68$, $p = .202$, $\eta_p^2 = 0.04$) and the Noise × Experiment interaction ($F(1, 43) = 1.08$, $p = .305$, $\eta_p^2 = 0.02$) were not.

A comparison of Figures 3.2 and 3.9 suggests that the responses from older adults in Experiment 3b were more variable and less precise than responses from younger adults in Experiment 1. The standard deviations of the absolute value of adjustment error, computed for each participant and condition, and plotted in Figure 3.10. To quantitatively asses this comparison, a 2 (Noise Present vs Absent) × 2 (Experiment) ANOVA compared the mean standard deviation of adjustment errors across conditions and experiments. Unlike what was found by the analysis of mean adjustment error, the analysis of the standard deviation yielded a significant Noise × Experiment interaction ($F(1, 43) = 10.22$, $p = .003$, $\eta_P^2 = 0.19$). A two-sample t test comparing the mean standard deviation in the high-noise condition in Experiments 1 and 3b was significant ($t(30.8) = 2.97$, $p = .006$, $d = 0.91$), but the difference between experiments in the zero-noise condition was not significant ($t(22.5) = 1.12$, $p = .274$, $d = 0.39$).

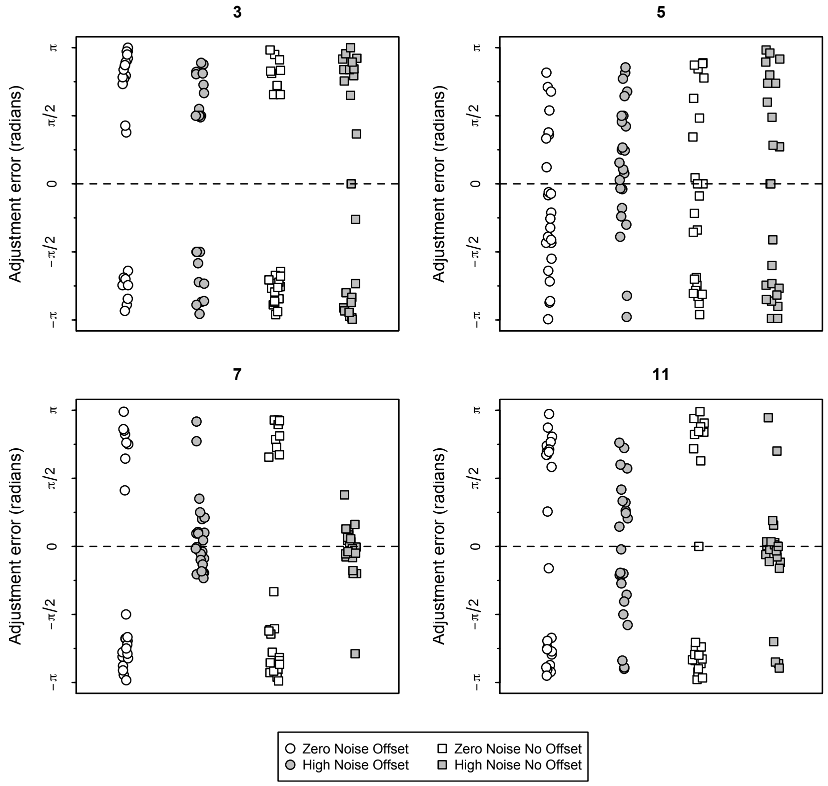
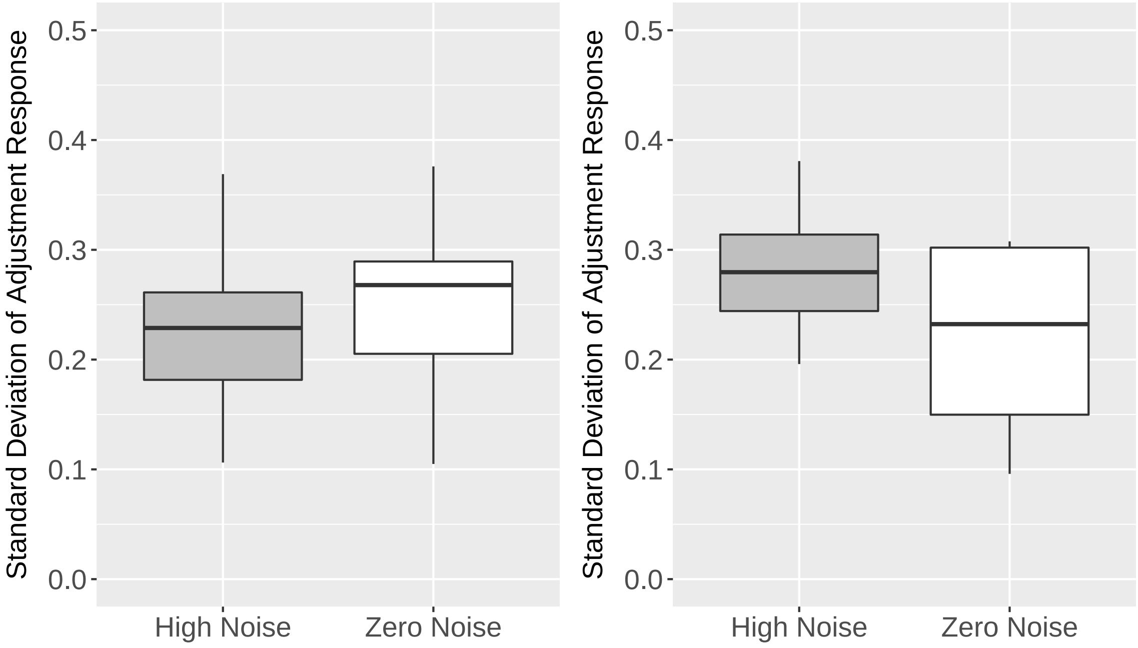


Figure 3.9 – Phase adjustment data from four representative observers in Experiment 3b. Symbol conventions are the same as in Figure 3.2.



(a) Experiment 1

(b) Experiment 3b

Figure 3.10 – Standard deviation of response in adjustment task, calculated within each participant for Experiment 1 ($M_{\text{age}} = 20$; n=30) and Experiment 3b ($M_{\text{age}} = 73$; n=15). The amplitude of local, sinusoidal jitter was 0.0135 high-noise condition and absent in the zero-noise condition.

Discrimination Task

The average proportions of correct responses in the discrimination task, ignoring confidence ratings, are shown in Figure 3.4c. The difference between response accuracy in the high-noise ($M = 0.617$) and zero-noise ($M = 0.219$) conditions was significant ($t(14) = 4.31$, $p < 0.001$, $d = 1.11$). Furthermore, response accuracy in the zero-noise condition was significantly below 0.50, which represents chance performance ($t(14) = 5.43$, $p < 0.0001$, $d = 1.40$), while response accuracy in the high-noise condition was not different from 0.50 ($t(14) = 1.91$, $p = 0.077$, $d = 0.49$).

An ANOVA comparing performance on high-noise and zero-noise trials in Experiments 1 and 3b produced a significant Noise × Experiment interaction ($F(1, 43) = 4.50$, $p = .040$, $\eta^2_P = 0.09$), suggesting that the effect of noise on accuracy differed in younger and older adults. A two-sample t-test found that the difference between accuracy in Experiments 1 and 3b was significant on high-noise trials ($t(29.2) = 2.89$, $p = .007$, $d = 0.90$) but not zero-noise trials ($t(30.4) = 0.31$, $p = .762$, $d = 0.09$).

Figure 3.5c displays the average proportion of high-confidence responses that were incorrect. One participant did not make at least one high confidence response in each noise level and therefore was not included in this analysis. The proportion of high-confidence errors in the zero-noise ($M = 0.82$) and high-noise ($M = 0.41$) conditions differed significantly ($t(13) = 4.14$, $p = 0.001$, $d = 1.11$).

An ANOVA comparing the proportion of high-confidence responses that were incorrect in Experiments 1 and 3b found significant main effects of Noise ($F(1, 39) = 4.31$, $p = .044$, $\eta^2_P = 0.10$) and Experiment ($F(1, 39) = 60.11$, $p < .0001$, $\eta^2_P = 0.61$), but the Noise × Experiment interaction was not significant ($F(1, 39) = 2.23$, $p = .144$, $\eta^2_P = 0.05$). This analysis suggests that high-confidence errors were more frequent in high-noise conditions and more frequent in older than younger subjects, but that the effect of noise was similar in both age groups.

Relating Adjustment Responses & Discrimination Accuracy

Figure 3.6c displays the data and regression line comparing the results of each observer in both tasks in Experiment 3b. Regressing direction discrimination accuracy onto average phase error in the adjustment task yielded a significant relationship on high-noise trials, ($b = .6112$, $t(13) = 2.249$, $p = .0425$, $R^2_{\text{adj}} = .2247$) but not zero noise trials ($b = .3764.$, $t(13) = 2.098$, $p = .056$, $R^2_{\text{adj}} = .1956$). The relationship between discrimination accuracy and adjustment error in Experiments 1 and 3b was evaluated with linear models that included adjustment error as a continuous predictor, Experiment (1 or 3b) as a categorical predictor, and an Adjustment × Experiment interaction. The high-noise and zero-noise conditions were analyzed separately. In the high noise condition, the linear model fit the data reasonably well ($R^2_{\text{adj}} = 0.727$). As noted earlier, the association between discrimination accuracy and adjustment error was significant in Experiment 1 ($b = -1.19$, $t(41) = -9.01$, $p < 0.001$). The difference between the regression slopes in Experiments 1 and 3b was not significant ($b = 0.42$, $t(41) = 1.72$, $p = .093$); however, the intercept of the regression line was lower in Experiment 3b than Experiment 1 (0.86 vs. 1.09, $b = -0.23$, $t(41) = -2.76$, $p = 0.009$). In the zero noise condition, the overall fit of the linear model was poorer ($R^2_{\text{adj}} = 0.405$). As noted earlier, there was a significant relationship between discrimination accuracy and adjustment error in Experiment 1, ($b = -0.76$, $t(41) = -5.25$, $p < 0.001$), and the difference between the regression slopes ($b = 0.27$, $t(41) = -1.05$, $p = 0.297$) and intercepts ($b = 0.27$, $t(41) = -1.05$, $p = 0.297$) in the two experiments were not significant. These analyses suggest that the relation between discrimination accuracy and phase adjustment error was similar in younger (Experiment 1) and older (Experiment 3b) participants, although i) overall accuracy in the high-noise condition was lower in older observers; and ii) the association between discrimination accuracy and phase error was weaker in older compared to younger subjects (cf. Figures 3.6 a & c).

Discussion

Experiment 3b measured the relationship between the perceived relative phase of two motion trajectories and perceived global motion in older adults. Specifically, Experiment 3b tested the hypothesis that the illusion of opposite motion is stronger in older than younger adults.

As expected, we found that phase adjustment error was smaller in the high-noise condition than in the zero-noise condition (see Figure 3.3c). Contrary to our hypothesis, there was no evidence that the magnitude of the effect of noise on phase adjustment error differed between older observers and the younger adults in Experiment 1, although analyses conducted on the standard deviations of phase adjustment errors from each participant indicated that adjustments were more variable in older than younger adults. As was found with younger observers in Experiment 1, discrimination accuracy for older adults was higher in high-noise trials than zero-noise trials; however, this effect of noise was smaller than the effect found in younger observers in Experiment 1. Finally, as was found in Experiments 1 and 2, discrimination accuracy was inversely related to phase adjustment error.

Experiment 4

The prior experiments used stimuli that were similar to the one illustrated in Figure 3.1. In Experiment 4 we sought to extend the findings of the prior experiments by testing whether similar effects are obtained with a different stimulus described by Anstis (2007) which produces the so-called chopstick illusion. The stimulus consisted of a pair of crossed horizontal and vertical bars, each moving sinusoidally in a direction that is orthogonal to the bar's orientation (Figure 3.11). When the motions are out of phase by 90 deg, the summed motion of both the bars is circular in either a clockwise or counterclockwise direction around a central fixation point. In both this stimulus, and those used in the above experiments, it is theoretically possible to monitor each of the motion components separately and sum the phases to get a correct answer to direction of motion, without perceiving a single coherent percept. The responses of observers who completed the task this way, and who perceived the stimulus as multiple, separate components, could be similar to the responses of observers who integrated the two moving lines into a single coherent percept. To gain a better understanding of how behaviour in this task is related to perceived coherence, the current experiment therefore compared discrimination accuracy with ratings of perceived coherence.

Method

Observers

Twenty naïve observers (11 female, mean age 20.25 years) participated in this experiment. One participant withdrew from the study, leaving 19 observers in the final sample. Participants received either partial course credit or 10$ per hour for their participation. All participants had normal or correct-to-normal Snellen visual acuity. Each participant provided informed consent prior to the start of the experiment, and all experimental protocols were approved by the McMaster University Ethics Board.

Apparatus & Stimuli

The apparatus used in this experiment was identical to the prior experiments. The stimulus used in this experiment is depicted in Figure 3.11. The stimulus consisted of a pair of crossed, horizontal and vertical bars white bars presented against a grey background. Each bar was 1.85 deg long and 0.10 deg wide. The luminance of each bar was 95.6 cd/m^2 and background luminance was 43.9 cd/m^2 . Each bar moved sinusoidally along the direction perpendicular to its principal axis (i.e. the horizontal bar moved vertically and the vertical bar moved horizontally). In the discrimination task, the motion of the bars was offset by ±90 deg so that the added motion of the two bars created either clockwise or counter-clockwise motion. In the adjustment task the relative phase of the two bars was adjustable, as in Experiments 1, 2, and 3b. On half of the trials, a thin (0.05 deg visual angle) square boarder surrounded the stimulus.

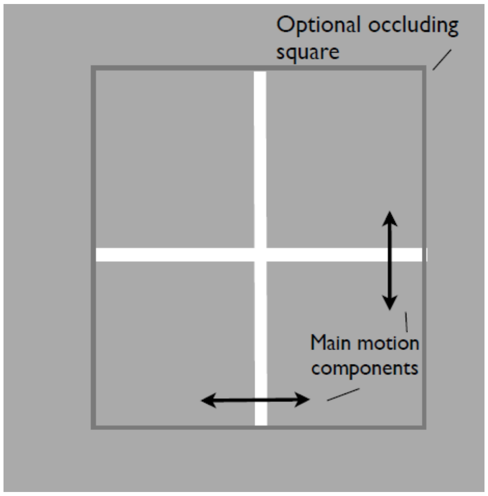


Figure 3.11 – Depiction of the stimulus used in Experiment 4. Each of the white bars displayed sinusoidal motion which varied in phase depending on condition. The grey occluding square was present on half the trials, representing the occluder present/absent manipulation.

Procedure

Prior to the experiment, participants were shown a demonstration consisting of dynamic plaid patterns that was used to explain the concept of motion coherence. Each plaid was displayed in a circular aperture 3.13 deg in diameter. Each grating component moved at a speed of 0.08 deg/s toward either the upper left or upper right corner of the display. The first, coherent plaid consisted of two square wave gratings of 0.68 cpd oriented ±45 deg from vertical, and a total RMS contrast of 0.52. This stimulus evoked a percept of a plaid pattern that drifted coherently upward. The second, incoherent plaid similarly consisted of two square-wave gratings oriented ±45 deg from vertical, but one grating had a fundamental frequency of 1.23 cpd while the other had a fundamental of 0.14 cpd, RMS contrast of 0.56. This plaid did not evoke a percept of coherent upward motion, but rather a percept of each grating sliding over one another (Stoner and Albright, 1996). Participants were shown each type of plaid while the experimenter described the concepts of coherent and incoherent motion, and were asked to describe the motion of each plaid. The stimuli remained visible for as long as was necessary for the participants to understand the distinction between coherent and incoherent motion.

The experimental trials began immediately following the demonstration and followed the same procedures used in Experiments 1, 2, and 3b. Observers completed an adjustment task followed by a discrimination task. In the adjustment task, the target direction of orbital motion was indicated by the word "clockwise" or "counterclockwise" being shown in the center of the display for 2 s at the start of each trial. The moving stimulus then appeared in one of four starting phase: 90 deg, which produced clockwise orbital motion, -90 deg which produced counter-clockwise motion, and two neutral phases (0 & 180 deg) that produced diagonal motion. As in the previous experiments, the participant used a dial to adjust the relative phase of the stimulus to produce the target motion and pressed the space bar when satisfied. Unlike prior experiments, participants then used the mouse to click a button on the screen to rate the motion coherence on a four point (0-3) scale: 0 was labelled 'low coherence' and the 3 was labelled 'high coherence'. The following trial began 1500 ms following the coherence rating. Participants completed 32 occluder-present trials and 32 occluder-absent. The adjustment task lasted approximately 40 minutes.

The discrimination task was similar to prior experiments, except that observers made motion coherence ratings on each trial. The stimulus duration was 600 ms, either in clockwise or counter-clockwise global motion. Observers made their response following stimulus offset by pressing one of two labelled keys on a standard computer keyboard. Following the direction response, four buttons labelled, 0, 1, 2, and 3 appeared on the display. Observers rated the perceived coherence of the immediately preceding trial. Participants completed 72 occluder-present trials and 72 occluder-absent trials. The discrimination task lasted approximately 15 minutes.

Results

Average phase error is reported in the adjustment task, and proportion correct is reported in the discrimination task. Coherence ratings in both tasks were transformed from a four point scale to scores ranging from 0 to 1. The distributions of all of the data are shown in Figure 3.14. Statistical analyses were performed in R (R Core Team, 2017). Either adjusted R-squared (R^2_{adj}) or Cohen's *d* are reported as a measure of association strength and effect size.

Adjustment Task

Results from the adjustment task from four representative observers are displayed in Figure 3.12. Average phase errors in the occluder present and absent conditions are shown in Figure 3.14a. Mean phase error in the occluder present ($M = 0.239$) and occluder absent ($M = 0.371$) conditions differed significantly ($t(18) = 2.51$, $p = .0220$, $d = 0.575$).

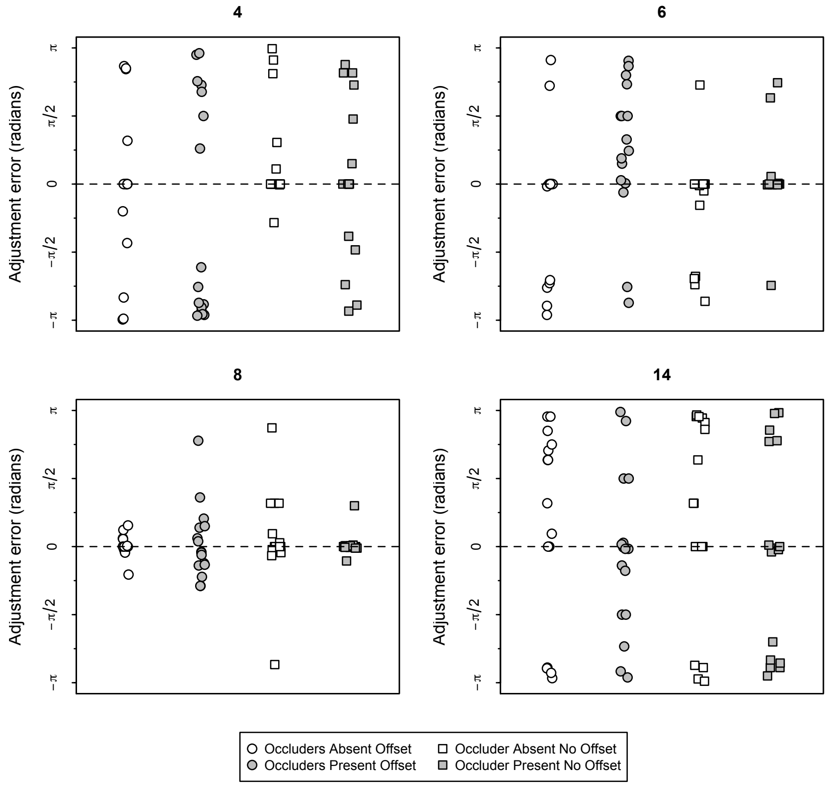


Figure 3.12 – Phase adjustment data from four representative observers in Experiment 4. Each symbol corresponds to a phase setting from a single trial. Results from occluder present and occluder absent trials are represented by filled and unfilled symbols, respectively. The square and circle symbols indicate results from trial in which the initial global motion was in the correct direction (i.e., no offset; relative phase was -90 or 90 deg) or was in an ambiguous direction (i.e., offset; relative phase was 0 or 180 deg).

Discrimination Task

The average proportions of correct responses in the discrimination task are shown in Figure 3.14c. The difference between response accuracy in the occluder present ($M = 0.789$) and occluder absent ($M = 0.561$) conditions was significant ($t(18) = 4.079$, $p < .001$, $d = 0.936$).

Relating Adjustment Responses & Discrimination Accuracy

Figure 3.13 displays the data and regression line comparing the results of each observer in both tasks in Experiment 4. Regressing direction discrimination accuracy onto average phase error in the adjustment task yielded a significant relationship on occluder present trials, ($b = -0.593$, $t(18) = -7.268$, $p =< .0001$, $R^2_{\text{adj}} = 0.7422$) and not occluder absent trials ($b = -0.178$, $t(18) = -1.227$, $p = 0.237$, $R^2_{\text{adj}} = 0.0273$).

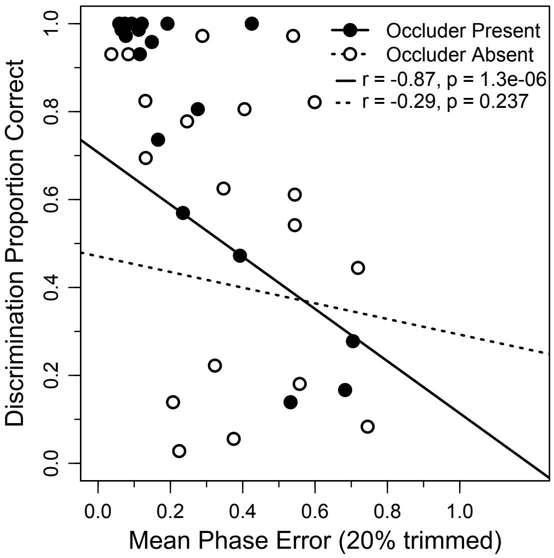


Figure 3.13 – Relationship between response accuracy in the discrimination task and the average phase error in the adjustment task for Experiment 4. Pearson's r and p values for each regression are shown in the top right corner of the plot.

Below-Chance Performance

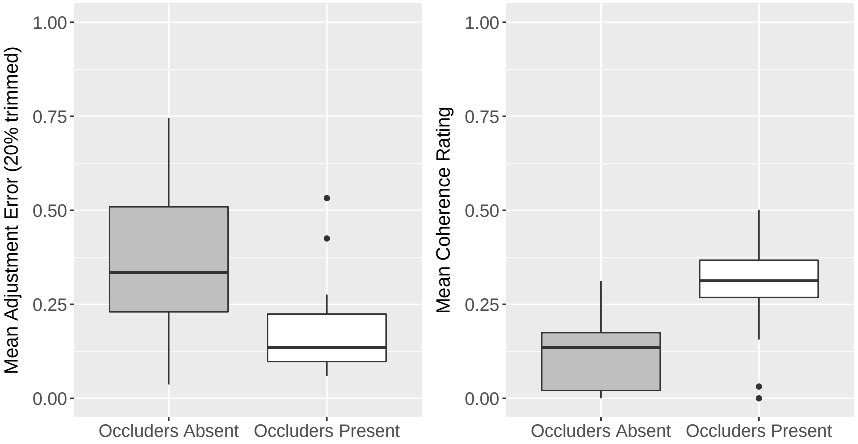
One goal of Experiment 4 was to test whether the illusion of opposite orbital motion obtained with the Lorenceau stimulus could be seen with a different stimulus. However, on average, performance in all four conditions in the adjustment and discrimination tasks is above chance levels (see Figure 3.14). The means of both occluder present ($t(18) = 5.44$, $p =< .0001$, $d = 1.25$, $mean = 0.24$) and occluder absent ($t(18) = 2.64$, $p = 0.017$, $d = 0.61$, $mean = 0.37$) were significantly below 0.5π phase error in the adjustment task. Similarly, the means of both occluder present ($t(18) = 4.11$, $p < 0.001$ $d = 0.94$, $mean = 0.79$) and occluder absent ($t(18) = 0.79$, $p = 0.446$, $d = 0.18$, $mean = 0.56$) were significantly above 0.5 proportion correct in the discrimination task.

Although observers did not display below-chance performance in either task on average, we tested whether performance was significantly below chance in the discrimination task in individual observers, using Bonferroni-corrected ($\alpha_{FW} = .01$) binomial tests. Using a Bonferroni-corrected ($\alpha_{FW} = .01$) binomial test, we found that proportion correct in the discrimination task was significantly less than 0.5 in six observers (mean accuracy = 0.11) when occluders were absent, and remained below chance in three of these observers (mean accuracy = 0.19) when occluders were present.

Coherence Ratings

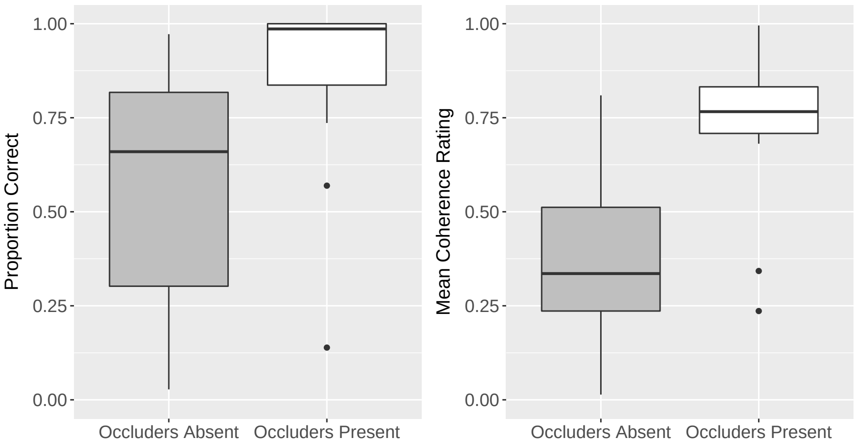
Average motion coherence ratings were analyzed in a 2 (Task) x 2 (Occluder present vs. absent) Analysis of variance (ANOVA). Results of this analysis are displayed in Table 3.2.

There was a significant main effect of occluder, reflecting the fact that coherence ratings were higher in the occluder present condition. There also was a significant main effect of task, indicating that coherence ratings were higher in the discrimination task than the adjustment task. Finally, there was a significant occluder × task interaction. To interpret this interaction, we conducted t tests comparing coherence ratings in the occluder-present and occluder-absent conditions in each task. Although the effect of the occluder was larger in the discrimination task, coherence ratings were significantly higher in the occluder-present condition both in the discrimination task ($t(18) = 4.718$, $p = .0002$, $d = 1.082$), and the adjustment task ($t(18) = 3.818$, $p = .0013$, $d = 0.876$).



(a) Adjustment error

(b) Adjustment task coherence rating



(c) Discrimination accuracy

(d) Discrimination task: coherence

Figure 3.14 – Boxplots illustrating results of Experiment 4. In the occluders present condition the stimulus was surrounded by the outline of a square, in the occluders absent condition that square was absent. a) The distributions of average (i.e., 20% trimmed mean) phase error across observers in the adjustment task. Perfect performance corresponds to 0 phase error. Phase error of 1 corresponds to the wrong direction of global motion. b) The distribution of mean coherence ratings in the adjustment task. c) The distribution of proportion correct in the discrimination task. d) The distribution of mean coherence rating in the discrimination task.

Effect	**df**	**MSE**	**F**	η^2_P	p_{adj}
Occluder	1, 18	0.04	25.24	.58	<.0001
Task	1, 18	0.03	59.28	.77	<.0001
Occluder × Task	1, 18	0.01	7.91	.31	.01

Table 3.2 – Experiment 4 ANOVA of Rated Coherence

Relating Coherence and Phase Error

The relationship between coherence and phase adjustment error was evaluated with an ordinal logistic mixed model regression using the Ordinal package in R (Christensen, R. H. B. , 2019a; R Core Team, 2017). Statistical significance was assessed with p values estimated using adaptive Gauss-Hermite quadrature approximation with 10 quadrature points, as recommended in (Christensen, R. H. B. , 2019b). The model included adjustment error as a continuous predictor, occluder (absent or present) as a categorical predictor, an adjustment × occluder interaction, and subjects as a random effect. The model was reasonably well defined (Condition number of Hessian: 259.35). The interaction between adjustment error and occluder was significant, indicating the the slopes of the regression lines in the occluder present and absent conditions differed significantly ($b = -2.043$, $z = -4.785$, $p < .0001$). The intercepts of the regression lines also differed significantly between the occluder present and absent conditions ($b = 1.306$, $z = 6.894$, $p < .0001$). Therefore, we fit separate models data from the occluder present and absent conditions. We found that there was a significant association between rated coherence and adjustment error in the occluder present condition ($b = -1.727$, $z = -4.787$, $p < .0001$) but not in the occluder absent condition ($b = -0.237$, $z = -0.772$, $p = .4403$). These analyses suggest that the relation between rated coherence and phase adjustment error are different depending on whether occluders are present or absent. For occluder present trials there is a relationship between coherence and phase adjustment error, but that relationship does not exist in occluder absent trials.

Discussion

Experiment 4 compared subjective and objective measures using performance in an adjustment and discrimination task and rated coherence to stimuli in each task. There were three goals in Experiment 4: 1) to explore perception of ambiguous motion in a different stimulus, 2) to examine whether observers experience illusory motion in this stimulus, and 3) to compare the objective measures used in the prior experiments in the current paper with subjective experience of perceived coherence.

To address goals one and two, we conducted analyses on the present data mirroring those used in Experiments 1, 2, and 3b. We found that the main findings of Experiments 1, 2, and 3b extend to the stimulus used in Experiment 4. On average, occluder present stimuli produced more accurate performance than occluder absent both in the adjustment and discrimination tasks. There was a significant relationship between adjustment and discrimination performance in occluder present stimuli. Unlike the prior experiments, the average discrimination and adjustment performance measures for occluder absent stimuli were above chance. However, several observers exhibited performance significantly below chance in both tasks, suggesting that at least some observers experienced illusory motion.

The final goal of Experiment 4 concerned ratings of perceived coherence. Occluder present stimuli were rated more coherent on average than occluder absent stimuli. In the adjustment task, we were able to look at whether coherence rating on each trial could be predicted by phase error on that trial. In occluder present stimuli, phase error was indeed related to coherence rating, where lower phase error occurred when coherence was rated higher. However, in occluder absent stimuli this relationship did not exist. This suggests that although on average rated coherence seems to be related to performance measures, on a trial-by-trial basis this relationship only exists for some stimuli (here: occluder present) and not others (here: occluder absent).

General Discussion

Experiment 1 examined how accurately young adults perceived the direction of global motion using adjustment and discrimination tasks. With both tasks, we found that observers accurately perceived global motion when the stimulus contained local dynamic noise, but consistently misperceived the direction of global motion when the stimulus did not contain noise. Furthermore, performance in both tasks was strongly correlated, which suggests that the failure to correctly perceive the direction of global motion was related to an inability to properly encode the relative phase of the two motion components. Experiment 2 replicated the main results of Experiment 1 using a lower amplitude local motion noise.

Experiment 3a replicated the effects of stimulus duration and the presence/absence of local noise found previously in younger adults (Lorenceau 1996, Chapter 1) in a group of older adult observers. Specifically, discrimination accuracy increased as a function of stimulus duration when noise was present, and decreased as a function of stimulus duration when noise was absent.

Experiment 3b focused on relating phase adjustment and discrimination performance and found below-chance performance with both tasks for zero-noise stimuli and above-chance performance for high-noise stimuli. However, older adults were more variable in their responses in the adjustment task, and performed worse on high-noise stimuli in the discrimination task compared to the younger adults of Experiment 1. This is unsurprising, given the prediction that older observers would perform more poorly and produce more variable data due to age-related differences in spontaneous noise in the system, which has been reported to increase with age (Pardhan, 2004; Schmolesky et al., 2000), and calculation efficiency, which has been reported to decrease with age (Bennett et al., 1999; Pardhan et al., 1996). Although it is still debated which of these effects is responsible for decrements to perception with aging, this type of change to the visual system can explain the general increase in participant variability. Various measures used to track variability of response are reported in the Appendix.

The age difference that we observed in the high-noise condition in Experiment 3b may be related to age-related deficits in temporal integration (Arena et al., 2012; Snowden and Kavanagh, 2006) and direction discrimination (Bocheva et al., 2013). However, it is interesting to note that we observed significant age differences in mean accuracy in the discrimination task but not in mean phase error in the adjustment task. The lack of an age difference in the adjustment task may be related to aspects of the task that are separate from motion integration *per se*. For example, the stimulus duration was considerably longer in the adjustment task than the discrimination task. Bennett et al. (2007) demonstrated that older adults can identify direction of global motion of random dot kinematograms as accurately as younger adults if given longer stimulus durations. The stimulus duration is fixed in the discrimination task, but not the adjustment task, which may explain the discrepancy in the age-difference in the discrimination task, but not the adjustment task. Older adults indeed took 24.49 seconds longer per trial on average (see Appendix for adjustment trial details).

Experiment 4 demonstrated that the effects reported in the current paper are not stimulus specific, and instead probably depend predominately on the requirement to integrate sinusoidal motion across separate pieces of the stimulus, which is common to all stimuli used in the current paper. In Experiment 4, we measure perceived coherence along with phase bias and discrimination ability. In general, larger phase errors were associated with reduced discrimination accuracy and lower perceived coherence. However, this relationship was found on a trial-by-trial basis in the adjustment task only in the occluder-present condition. From this analysis we can conclude that if the correspondence between performance and coherence exists for many types of stimuli, it is at least stronger in some stimuli than others.

Studies of motion integration have used a variety of methods to assess successful, coherent integration. Studies that use stimuli that are structured such that there is a definitive correct or incorrect response can use objective measures of performance in which the participant presumably either answers correctly on each trial if they perceive the coherent, integrated stimulus (Smith et al., 1999; Shiffrar et al., 1995; Tang et al., 2015). Studies that use stimuli that are inherently ambiguous (Adelson and Movshon, 1982; Anstis and Kim, 2011; Welch, 1989) typically use subjective measures of an observer's perception of motion. Objective measures are sometimes preferred to subjective measures because it is thought that they may be more reliable and less biased. However, objective measures may be only indirectly related to the phenomenon of interest, namely the perceived coherence of motion. In the current experiments, we were interested in whether an observer perceived one or two motion elements, but instead asked the observer to report the integrated motion direction. These tasks measured the extent to which observers can combine motion components, but do not measure the percept of the observer. To combat this weakness, in Experiment 4 of the current paper we ask observers to report their subjective experiences. In sum, we used several tasks, both objective and subjective, to characterize the perceptual experience of observers with this class of stimulus. We suggest that using several measures is a strategy to overcome the weaknesses of each method, and allows for a richer understanding of the experimental results. This added information fortunately comes with a very small added cost to the data collection and analysis process, and so it is an effort that is likely worthwhile for many researchers to undertake.

A large body of work focuses on the specific conditions that lead to grouping or segmentation. Typically, these studies vary the stimulus to determine which stimulus configurations lead to better grouping. The types of stimulus perturbations studied include varying local noise (Lorenceau, 1996), stimulus contrast and eccentricity

(Takeuchi, 1998), the presence and absence of occluders and terminators (McDermott and Adelson, 2004; Vallortigara and Bressan, 1991; Lorenceau and Shiffrar, 1992), notches or features that disambiguate motion (Castet and Wuerger, 1997), and the number of sides of the shape (Tang et al., 2015). In the current paper, we do not address the subject of ambiguous motion from this perspective. Instead, we are concerned with the perceptual consequences of not grouping the stimulus: i.e., what does the observer perceive in this stimulus when there is no noise in the dots (Experiments 1, 2, 3a, and 3b) or when the occluder is absent (Experiment 4). In the current paper, we have shown that misperception occurs in situations that do not lead to global grouping.

Our results suggest that the misperception of global motion is associated with a failure to accurately encode the relative phase of the horizontal and vertical motion components in our stimulus. Why might observers fail to encode phase accurately? One possibility is that the visual system fails to efficiently sample the motion stimulus. Recent studies suggest that rhythmic electrical responses in the brain are associated with moment-to-moment fluctuations in attention (e.g., Fries et al., 2008; Busch et al., 2009). Although often studied in detection tasks, the idea that the visual system samples from the environment in a rhythmic fashion has been implicated in motion integration tasks as well. In the current study, it is possible that observers are misrepresenting the phase of one or both elements when attempting to combine them, in a process similar to rhythmic visual aliasing. This misrepresentation may lead to a combination that more closely represents the opposite direction percept, and therefore produces performance that is below chance. Interestingly, if this explanation were true, it would imply that aliasing can occur under some conditions (i.e., the stimulus is segmented) and not under other conditions (i.e., the stimulus is grouped). It is also worth noting that the frequency of the motion components in the current stimulus is 0.83 Hz, which is quite low compared to the alpha-band frequencies typically studied in the rhythmic perception research, which range from 8-11 Hz. The aliasing literature therefore provides an interesting interpretation of the current results, but does not fully explain the phenomenon studied here.

Across all four experiments, there was a relationship between phase adjustment error and discrimination accuracy, and observers consistently misperceived the direction of global orbital motion when the stimulus did not contain local noise. We measured the magnitude of phase adjustment error in each observer, which was consistently high in stimuli that were typically misperceived. Our results support the conclusion that observers misperceive the direction of global motion when the stimulus does not contain local noise amplitude because their representation of relative phase of motion in these types of stimuli is systematically biased.

References

Adelson, E. H. and Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature*, 300(9):523–525.

Anstis, S. (2007). The flash-lag effect during illusory chopstick rotation. *Perception*, 36(7):1043–1048.

Anstis, S. and Kim, J. (2011). Local versus global perception of ambiguous motion displays. *Journal of Vision*, 11(3):1–13.

Arena, A., Hutchinson, C. V., and Shimozaki, S. S. (2012). The effects of age on the spatial and temporal integration of global motion. *Vision Research*, 58:27–32.

Ball, K. and Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research*, 27(6):953–965.

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

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

Bocheva, N., Angelova, D., and Stefanova, M. (2013). Age-related changes in fine motion direction discriminations. *Experimental Brain Research*, 228(3):257–278.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4):433–436.

Busch, N. a., Dubois, J., and VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. *The Journal of Neuroscience*, 29(24):7869–7876.

Castet, E. and Wuerger, S. (1997). Perception of moving lines: Interactions between local perpendicular signals and 2D motion signals. *Vision Research*, 37(6):705–720.

Christensen, R. H. B. (2019a). *ordinal—Regression Models for Ordinal Data* . R Foundation for Statistical Computing. R package version 2019.3-9.

Christensen, R. H. B. (2019b). *A Tutorial on fitting Cumulative Link Mixed Models with clmm2 from the ordinal Package.*

Fries, P., Womelsdorf, T., Oostenveld, R., and Desimone, R. (2008). The Effects of Visual Stimulation and Selective Visual Attention on Rhythmic Neuronal Synchronization in Macaque Area V4. *Journal of Neuroscience*, 28(18):4823–4835.

Hutchinson, C. V., Arena, A., Allen, H. a., and Ledgeway, T. (2012). Psychophysical correlates of global motion processing in the aging visual system: A critical review. *Neuroscience and Biobehavioral Reviews*, 36(4):1266–1272.

Lorenceau, J. (1996). Motion integration with dot patterns: Effects of motion noise and structural information. *Vision Research*, 36(21):3415–3427.

Lorenceau, J. and Alais, D. (2001). Form constraints in motion binding. *Nature Neuroscience*, 4(7):745–751.

Lorenceau, J. and Shiffrar, M. (1992). The influence of terminators on motion integration across space. *Vision Research*, 32(2):263–273.

McDermott, J. and Adelson, E. H. (2004). The geometry of the occluding contour and its effect on motion interpretation. *Journal of Visionsion*, 4(10):944–954.

Murray, R. F., Sekuler, A. B., and Bennett, P. J. (2001). Time course of amodal completion revealed by a shape discrimination task. *Psychonomic Bulletin & Review*, 8(4):713–720.

Pardhan, S. (2004). Contrast sensitivity loss with aging: sampling efficiency and equivalent noise at different spatial frequencies. *Journal of the Optical Society of America. A, Optics, image science, and vision*, 21(2):169–175.

Pardhan, S., Gilchrist, J., Elliott, D. B., and Beh, G. K. (1996). A comparison of sampling efficiency and internal noise level in young and old subjects. *Vision Research*, 36(11):1641–1648.

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

R Core Team (2017). *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria.

Roudaia, E., Bennett, P. J., Sekuler, A. B., and Pilz, K. S. (2010). Spatiotemporal properties of apparent motion perception and aging. *Journal of Vision*, 10(14):1–15.

Schmolesky, M. T., Wang, Y., Pu, M., and Leventhal, A. G. (2000). Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. *Nature Neuroscience*, 3(4):384–90.

Shiffrar, M., Li, X., and Lorenceau, J. (1995). Motion integration across differing image features. *Vision Research*, 35(15):2137–2146.

Shiffrar, M. and Pavel, M. (1991). Percepts of rigid motion within and across apertures. *Journal of Experimental Psychology: Human Perception and Performance*, 17(3):749–761.

Smith, A. T., Curran, W., and Braddick, O. J. (1999). What motion distributions yield global transparency and spatial segmentation? *Vision Research*, 39(6):1121–1132.

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

Stoner, G. R. and Albright, T. D. (1996). The Interpretation of Visual-Motion - Evidence for Surface Segmentation Mechanisms. *Vision Research*, 36(9):1291–1310.

Takeuchi, T. (1998). Effect of contrast on the perception of moving multiple Gabor patterns. *Vision Research*, 38(20):3069–3082.

Tang, M. F., Dickinson, J. E., Visser, T. A. W., Edwards, M., and Badcock, D. R. (2015). Role of form information in motion pooling and segmentation. *Journal of Vision*, 15(2015):1–18.

Vallortigara, G. and Bressan, P. (1991). Occlusion and the perception of coherent motion. *Vision Research*, 31(11):1967–1978.

Welch, L. (1989). The perception of moving plaids reveals two motion-processing stages. *Nature*, 337(6209):734–736.

Appendix

Table 1, 2, and 3 report multiple characteristics of individual observer performance meant to provide information about how each observer completed the task. These values are used to make sure that observers are adjusting the dial at least some amount on every trial, and exploring all possible arrangements of the stimulus. Four measures are reported in each table. The first of these measures is the total value of adjustments made, in radians. This represents the total amount of radians adjusted by the observers on the average trial. During the experiment, the dial was checked for movement every 700 ms. Column two of Table 1 reports the number of 700 ms increments in which an adjustment is made. This information is useful to combine with the total radians adjusted on average, and the trial length to understand how consistently observers adjusted the stimulus throughout the trial. Finally, we report trial length in seconds. This also represented the stimulus duration, as the stimulus was on screen until the observer was satisfied with their adjustment decision.

These control measures can help identify observers who did not adjust the dial during the trial, or made a very poor effort at the task by adjusting the dial by the same amount each trial. These types of behaviour indicate failure to properly attempt to complete the task. We did not exclude any participants from our analyses, but include these values to add information to our overall findings. Mainly, the differences between observers in these values indicate different methods of completing the task, despite similar instructions. It is important to note that many tasks likely have variations in performance such as this, but do not have access to this information due to the structure of the task.

Table 1: Experiment 1

Observer Number	Total radians adjusted		Number of intervals with adjustment		Trial duration (seconds)	
	mean	sd	mean	sd	mean	sd
1	41.67	4.26	29.62	3.12	9.65	12.00
2	35.25	23.75	24.50	11.76	17.81	11.12
3	26.61	13.85	27.62	10.08	25.78	16.96
4	10.43	10.67	19.68	10.72	27.40	16.97
5	10.99	4.82	20.12	12.92	24.35	27.32
6	25.73	15.57	23.49	17.61	21.37	16.58
7	40.52	11.12	24.13	6.28	14.19	16.43
8	41.45	20.24	15.49	11.10	13.51	9.67
9	10.33	2.90	30.02	5.66	11.85	12.26
10	23.67	14.08	30.76	15.25	23.61	18.63
11	24.34	9.08	46.17	16.23	29.96	22.14
12	46.99	14.51	29.63	3.40	15.48	16.01
13	148.39	47.63	24.53	6.73	18.29	19.87
14	104.23	28.20	47.29	27.82	32.34	21.64
15	8.01	4.53	5.06	2.23	9.23	6.35
16	49.86	18.81	39.05	17.35	20.70	19.79
17	9.42	2.74	18.66	8.84	15.95	11.06
18	37.10	17.08	30.03	20.28	12.77	12.73
19	31.95	13.38	20.8	7.48	17.07	12.72
20	41.50	16.98	37.50	11.67	48.38	27.54
21	6.87	5.83	33.12	12.51	14.84	16.61
22	5.78	1.93	32.10	11.78	16.11	12.91
23	51.77	22.42	26.15	15.24	19.32	12.43
24	15.35	7.18	21.93	11.29	24.88	10.06
25	30.77	4.40	66.59	16.23	25.21	26.09
26	71.75	36.85	55.15	23.65	50.42	41.26
27	127.09	19.82	74.31	25.92	43.03	38.98
28	131.47	6.37	65.48	14.63	18.15	27.99
29	54.82	22.76	90.48	21.94	23.56	24.91
30	52.00	22.89	60.55	12.41	21.85	19.56

Table 2: Experiment 2

Observer Number	Total radians adjusted		Number of intervals with adjustment		Trial duration (seconds)	
	mean	sd	mean	sd	mean	sd
1	23.09	6.77	105.98	31.51	35.38	37.30
2	2.33	1.26	16.39	8.21	19.62	15.71
3	11.75	4.71	33.34	10.16	19.84	19.46
4	5.38	1.39	80.63	14.55	21.59	16.68
5	15.38	7.92	47.01	10.75	24.29	25.60
6	25.54	16.62	58.26	21.10	29.83	23.02
7	19.37	9.35	24.09	10.03	21.71	11.24
8	36.81	5.46	20.04	8.06	12.45	10.33
9	16.07	9.22	37.25	33.23	23.61	14.61
10	53.64	15.79	54.27	17.69	27.92	25.39
11	26.70	12.66	72.35	16.18	19.01	22.37
12	33.04	12.07	38.14	8.80	18.09	15.64
13	18.59	5.95	30.20	9.19	26.66	23.37
14	5.35	.99	54.38	20.26	22.57	14.30
15	268.94	80.73	109.35	30.42	34.73	33.94

c

Table 3: Experiment 3b

Observer Number	Total radians adjusted		Number of intervals with adjustment		Trial duration (seconds)	
	mean	sd	mean	sd	mean	sd
1	5.47	1.16	38.30	5.54	8.50	4.59
2	54.61	28.79	50.41	25.60	45.00	34.20
3	16.01	6.46	42.48	20.84	52.86	28.50
4	40.87	13.54	197.00	49.69	88.75	66.24
5	12.41	1.92	96.82	40.98	59.97	36.40
6	29.21	16.84	85.58	32.20	67.81	38.01
7	12.73	7.89	59.03	30.05	118.25	71.31
8	181.23	38.18	164.39	40.63	48.84	32.43
9	25.71	19.80	12.93	7.92	45.76	26.48
10	37.48	12.67	14.50	4.90	26.59	12.47
11	15.48	10.19	48.87	24.78	33.57	22.13
12	12.56	4.68	19.62	15.69	33.58	9.98
13	2.77	2.60	15.93	6.19	20.65	12.67
14	5.83	0.59	24.17	4.65	22.02	15.33
15	8.86	7.57	27.39	11.74	27.19	14.98

Chapter 4

Visual completion in younger and older adults: Comparing judgements of aspect ratio and size over time

4.1 Abstract

Size and aspect ratio are attributes of two-dimensional shapes that are hypothesized to be encoded by mid-level visual areas, and are thought to be important for shape perception. Shape perception is affected by aging, although the nature of these changes are relatively unexplored. We measured the extent and time course of completion for younger and older adults using three shape discrimination tasks. In Experiment 1, sensitivity to aspect ratio is measured to the outline of a rectangle in three configurations. The configurations were: complete, with the entire outline of the rectangle visible; fragmented, with corners of the rectangle deleted; or occluded, resembling the fragmented condition, except with corners occluded by opaque squares. We measured the extent to which perceptual completion occurred by comparing aspect ratio discrimination thresholds in the three stimulus configurations at various stimulus durations. In all conditions, discrimination thresholds declined with increasing stimulus duration until they reached a lower asymptote and remained approximately constant at longer durations. Compared to younger observers, older adults took more time to reach minimum threshold for occluded and fragmented stimuli. In older adults, performance reached an asymptote in complete rectangles first, followed by occluded, and then fragmented. In Experiments 2 and 3, older and younger adults judged the size of the outline of squares and rectangles in each of the above stimulus configurations. In these experiments, stimulus configuration did not affect performance, leading to the conclusion that completion is not relevant to the judgement of size. Consistent with prior research, we conclude that judgements of aspect ratio and size may be different from one another. Complete and incomplete objects may be processed differently based on the information to be extracted (i.e., the shape's aspect ratio or its size).

Introduction

The Gestalt principles of grouping describe the stimulus factors that influence our ability to perceive visual scenes as organized patterns and objects. In many situations, parts of objects are occluded or obstructed from view; however, those partly-occluded objects are perceptually completed so that the representations of that object include the visually occluded area. Hence, object completion is important for creating an maintaining veridical representations of the environment. The current paper addresses how perceptual completion affects the ability to extract stimulus properties (i.e., aspect ratio and size) and how this changes with age.

The current experiments used a stimulus that comprised an outline of a rectangle in one of three configurations: complete, occluded and fragmented. In the complete condition the entire outline of the rectangle is shown. In the occluded condition, occluders are placed over the corners of the object and, consistent with the Gestalt principles of continuity and closure, observers typically perceive the figure as the outline of a rectangle whose corners are simply masked by the occluders. In other words, the rectangle is amodally completed behind the occluder. In the fragmented condition, the occluders are set to the same luminance as the background and therefore are invisible. Although the four visible contours are the same as those visible in the occluded condition, the resulting percept is very different: most observers perceive the contours as four unconnected contours. In the fragmented and occluded conditions, the same amount of the rectangle stimulus is visible, and so comparisons between these conditions provide information on how the visual system perceptually completes objects in different cases.

Occluded, complete and fragmented stimuli of many different shapes are used frequently to study the process of perceptual completion. Performance on a specific task may be better or worse for occluded than complete objects based on whether the representation of a complete object helps or hurts the task. Perceptually completing an object may make it easier to extract various features of that object, such as the angular orientation of Kanizsian figures (Ringach and Shapley, 1996). Alternatively, observers are slower to locate fragmented targets in visual search tasks (Rauschenberger and Yantis, 2001) and less accurate in visual working memory tasks (Chen et al., 2016) when a fragmented target is placed adjacent to an occluder.

Perceptual completion has been shown to enhance shape discrimination (Murray et al., 2001; Ringach and Shapley, 1996), such that conditions where perceptual completion is likely to occur also lead to better shape discrimination. Indeed, Gold et al. (2000) demonstrated that parts of a stimulus that lie along illusory boundaries are used in shape discrimination tasks. Although illusory or occluded boundaries contain no visible information, they are useful in shape discrimination. However, EEG evidence suggests that the neural processes involved in shape discrimination and perceptual completion may be distinct from one another (Murray, 2004), meaning that although perceptual completion can help shape discrimination, they are not the same process.

The present study compares perceptual completion in older and younger adults. Many aspects of visual perception change during healthy aging (see Owsley, 2011; Faubert, 2002, for reviews). Some of the deficits in aging hypothesized to occur in mid-level visual processing are relevant to the current study, such as integration of spatial and temporal information (Roudaia et al., 2010; Blake et al., 2008). However, shape discrimination has been shown to be largely unaffected by healthy aging (Wang, 2001; Habak et al., 2009). What remains unclear is whether shape discrimination in the context of perceptual completion is affected by aging.

In this paper, we explore how the ability to make judgements of aspect ratio (Experiment 1) and size (Experiments 2 and 3) changes with stimulus duration, stimulus configuration, and across the adult lifespan. Specifically, we measure discrimination thresholds for changes in aspect ratio and size in complete, occluded, and fragmented stimuli. We then model the relationship between threshold and stimulus duration.

Experiment 1

Method

Observers

Fifteen younger adults (9 female, M = 20.5 years, range = 18-33 years) and 15 older adults (9 female, M = 71.3 years, range=60-84 years) participated in the experiment. One additional younger observer participated and was subsequently replaced because average proportion correct throughout the experiment was equal to 0.40 and did not vary systematically across stimulus conditions. All observers were compensated $10 per hour or received partial course credit for participating. Older observers completed both the Montreal Cognitive Assessment and the Mini Mental State exam prior to participation in this experiment. All of the older participants had normal scores on both tests. Each participant provided informed consent prior to the start of the experiment, and all experimental protocols were approved by the McMaster Research Ethics Board.

Apparatus

Stimuli were displayed on an NEC MultiSync monitor displaying 640 × 480 pixels at 67 Hz and an average luminance of 25.58 cd/m^2. Stimuli were generated on an Apple PowerPC computer using MATLAB software and Psychophysics and Video Toolbox (Brainard, 1997; Pelli, 1997). The height and width of the viewable screen were 24 and 33 cm, respectively (20 pixels/cm). Viewing was binocular through natural pupils from a viewing distance of 114 cm. Viewing position was stabilized with a chin and forehead rest. The display was the only source of illumination in the test room.

Stimuli

The stimulus was a white, outlined rectangle, which took three forms (Figure 4.1). In the complete configuration the complete outline of the rectangle was shown. In the occluded configuration the rectangle's corners were covered by grey occluders. In the fragmented configuration the rectangle's corners were obscured by occluders that were the same colour and luminance as the background and therefore the stimulus appeared to consist of four unconnected contours. Eight stimulus durations were used:

15, 30, 45, 60, 75, 105, 165, and 210 ms. The three stimulus configurations (complete, occluded, and fragmented) were crossed with the eight stimulus durations to create 24 different stimulus conditions.

The stimulus background was grey, with a luminance of 25.57 cd/m^2. The contours comprising the rectangle were 0.1° thick and had a luminance of 82.13 cd/m^2 for a Weber contrast of 2.21. The sides of the rectangle varied in length between 1.8° and 2.2°, and on average were 2°. The occluders were square (2.6° per side) and positioned so that 0.8° of the rectangle was visible between the occluders. In the occluder condition, the occluders were dark grey (luminance = 13.95 cd/m^2). In the fragmented condition the occluders were the same colour and luminance as the background and therefore were not visible.

A small white fixation dot (0.05°, luminance = 25.57 cd/m^2) appeared in the centre of the display at the start of each trial and was present until the stimulus disappeared. The stimulus rectangle was presented at a fixed orientation while it orbited around the fixation point at a radius of 0.20° and a frequency of 2 Hz. The occluders remained stationary; only the outline of the rectangle was in motion. The starting position and direction of motion of the rectangle was randomized. The 15 ms stimulus duration represented a single frame and therefore the rectangle was stationary in that condition. A $h° \times v°$ high-contrast (power spectral density = $5.6x10^{-4°}$) white noise mask followed the display of the stimulus and remained on the screen until the observer's response. In the occluded condition, the occluders appeared on the screen with the onset of the fixation point and remained on screen until the mask was shown. This display sequence was used to encourage the perception of a complete rectangle appearing behind the occluders.

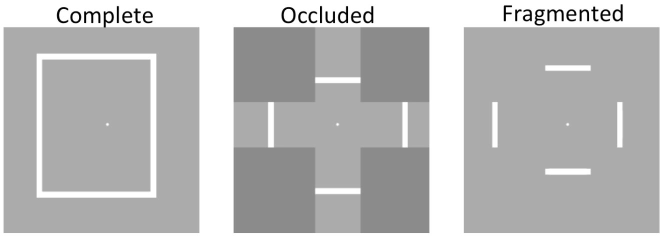


Figure 4.1 – Depiction of the stimulus configurations used in all three experiments. Pictured illustration is a cropped image of a single frame. In occluded condition, occluders were equally sized.

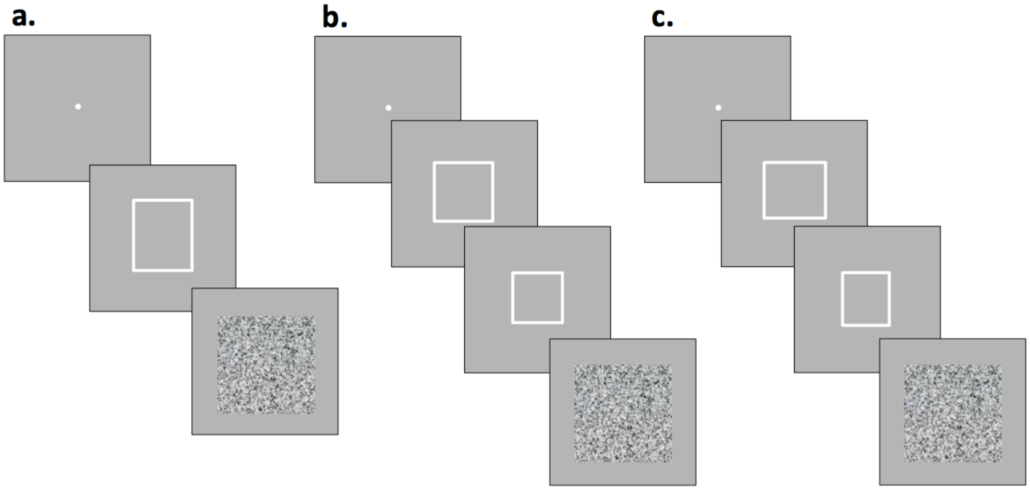


Figure 4.2 – Depiction of a single trial in each of the experiments presented currently. The stimulus was displayed for one of eight stimulus durations, in one of the three stimulus formations shown in Figure 4.1. A noise mask replaced the stimulus during the response period. a) Experiment 1: Aspect ratio task. Observers choose whether the stimulus is longer vertically or horizontally. b) Experiment 2: Size ratio task. The task contains two intervals, a reference and test stimulus. Observers choose whether the test stimulus is larger or smaller than the reference. Both stimuli had an aspect ratio of 1. c) Experiment 3: Area ratio task. The task contains two intervals, a reference and test stimulus. Observers choose whether the test stimulus is larger or smaller in total area than the reference. On every trial one of the two stimuli was always longer vertically, the other stimulus was longer horizontally.

Procedure

All observers completed a practice session before the start of the experiment. The practice session consisted of 7 trials in each of the three conditions; the stimulus duration was 1000 ms and the rectangle's aspect ratio was 1:1.2. Observers then completed 24 blocks of trials, one for each stimulus condition. Block order was randomized. There were 5 practice trials at the beginning of each block. The practice trials at the start of each block closely resembled the experimental trials in the following block. A message appeared on the screen to let observers know when practice and experimental trials began and ended. On each trial, the fixation point was displayed alone or with occluders (in the occluded condition) for 1000 ms. The stimulus then appeared for the specified duration followed by the mask. Participants then indicated whether the stimulus rectangle was longer horizontally or vertically by pressing one of two keys labelled "wide" and "tall" on a standard computer keyboard. Participants were given an opportunity to take an unconstrained break between each block. The entire experiment took between 90 and 120 minutes to complete.

Within each block of trials, the aspect ratio of the rectangle was varied with a single 2-down/1-up staircase. Each staircase began with an aspect ratio of 1:1.40 and ended following 3 reversals or 50 trials, whichever occurred first. Each block also contained several trials in which the aspect ratio of the rectangle was 1:1.60 or 1:1.01, which were designed to yield response accuracies that were high and near chance, respectively. These trials were randomly intermixed with trials in which the aspect ratio was set by the adaptive staircase, and occurred on approximately 30% of the trials in each block. Each block therefore included no more than 65 trials. The responses from all trials in each block were used to estimate psychometric functions, as described below.

Results

Statistical analyses were conducted with R (R Core Team, 2013). Aspect ratio is reported as the quotient of the longer side divided by the shorter side, regardless of whether the stimulus was longer horizontally or vertically.

Psychometric functions modelled log aspect ratio, and were estimated for each observer and each condition using the *quickpsy* R package (Linares and López-Moliner, 2016). Psychometric curves were cumulative normal curves with lower asymptotes set to 0.5; the mean, standard deviations, and lapse rate were estimated using a maximum likelihood procedure with differential evolution optimization. Figure 4.3 displays the data and psychometric curves for one representative younger observer.

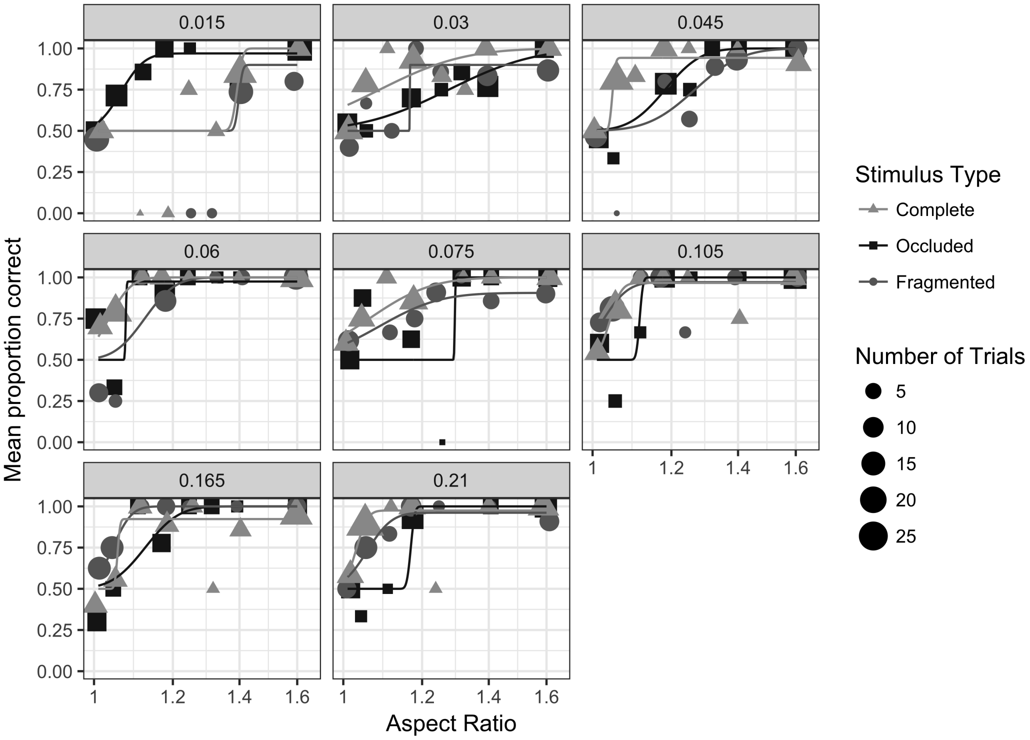


Figure 4.3 – Experiment 1: Data from a representative young observer and corresponding fitted psychometric curves.

The psychometric functions were used to estimate discrimination thresholds, which were defined as the aspect ratio that corresponded to a response accuracy of 70%. The 70% threshold was identified from each experimental condition for each observer, but in approximately 5% cases, the psychometric functions did not reach an accuracy of 70% in the range of aspect ratio values tested. In those cases, thresholds were set to 2.08, which was 30% greater than the maximum aspect ratio used in the experiment (i.e., 1.60). The choice to set these thresholds to 2.08 is somewhat arbitrary, but necessary for the following analysis of threshold by stimulus duration. The analyses presented throughout the paper were repeated using several values ranging between 1.60 and 2.60. The results of these variants produced the same pattern of results as those presented here.

Figure 4.4 displays the average thresholds in each condition, ignoring stimulus

	Complete	Occluded	Fragmented
Younger Adult	0	0	7
Older Adults	3	7	18

Table 4.1 – Experiment 1: Frequency of NA thresholds. A total of 120 thresholds were estimated in each condition.

duration, for Experiment 1. Data were analyzed using a linear mixed-effects model of square-root transformed thresholds that included Age and Stimulus configuration as factors. Thresholds that were set to 2.08 were excluded from this analysis. We report the output of the ANOVA of this model. The Kenward-Roger method (Kenward and Roger, 1997) was used to approximate the degrees of freedom, as this method better approximates F-distributions for linear mixed models (Judd et al., 2012). There was a significant main effect of Age ($F(1, 28) = 12.93$, $p = .001$), indicating that thresholds were, on average, higher in older adults than younger adults. There also was a significant main effect of Stimulus Configuration ($F(2, 652) = 44.13$, $p < .0001$). The Age × Stimulus Configuration interaction was significant ($F(2, 652) = 3.13$, $p = .044$). Additional linear mixed-effects models were used to compare stimulus configurations in each of the two age groups. In younger adults adults, thresholds in the fragmented condition were higher than in the complete condition ($F(1, 217) = 31.86$, $p < .0001$), and thresholds in the occluded condition were higher than thresholds in the complete condition ($F(1, 224) = 53.54$, $p < .0001$). Thresholds in the fragmented and occluded conditions did not differ significantly ($F(1, 217) = 0.17$, $p = .679$). In older adults, thresholds in the fragmented condition were higher than in the complete condition ($F(1, 204) = 41.54$, $p < .0001$), and thresholds in the occluded condition were higher than thresholds in the complete condition ($F(1, 214) = 30.36$, $p < .0001$). Unlike younger adults, thresholds in the fragmented condition were higher than in the occluded condition ($F(1, 200) = 4.37$, $p = .038$). Table 4.1 displays the amount of NA thresholds in each condition. A disproportionate amount of NA values are in the fragmented condition in both younger and older adults.

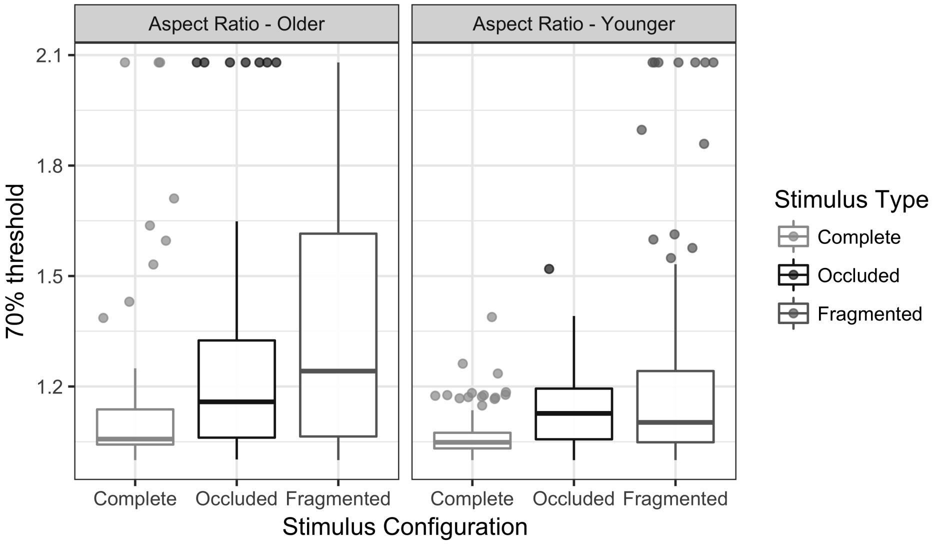


Figure 4.4 – Experiment 1: 70% thresholds, ignoring stimulus duration.

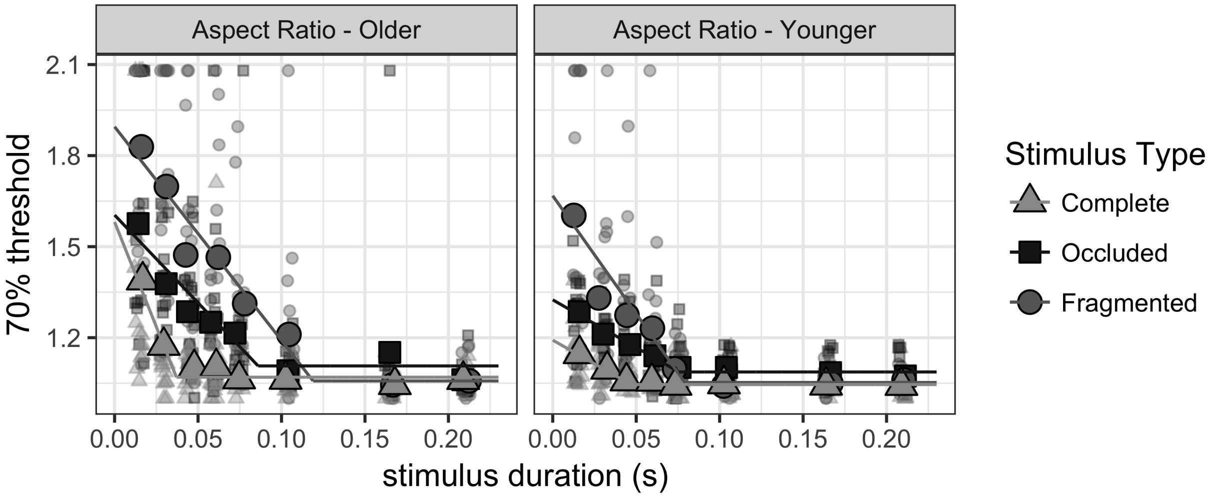


Figure 4.5 – Experiment 1: Thresholds plotted against stimulus duration for each stimulus duration and age group. Small symbols show thresholds from individual observers; large symbols show group means. The solid lines are the best-fitting bilinear functions (Eq 4.1) that were estimated with the bootstrap procedure described in the text.

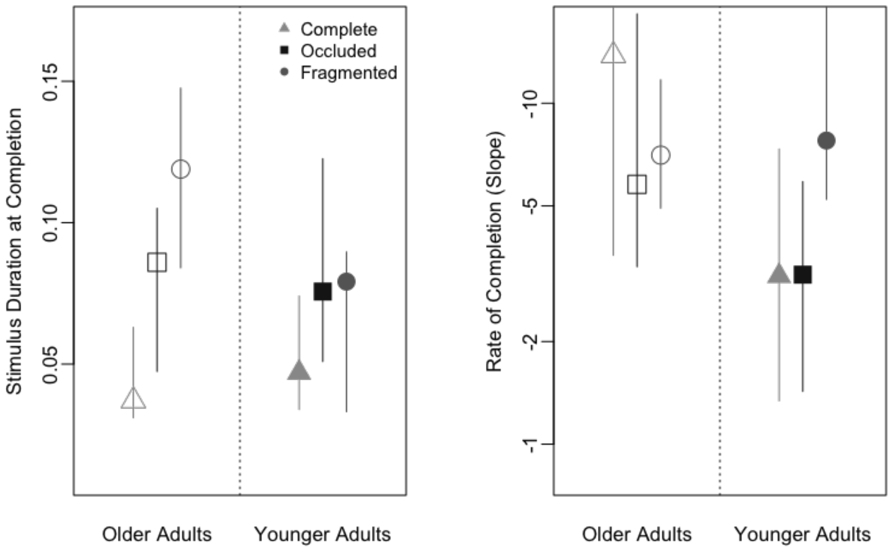
Threshold-vs.-Duration Functions

We were interested in how shape discrimination thresholds varied with stimulus duration. We hypothesized that thresholds would decrease as a function of stimulus duration until some critical duration beyond which thresholds would remain constant. We therefore modelled the threshold-vs.-duration function with a bilinear function that consisted of an initial line with a negative slope followed by a second line with a slope of zero. The bilinear function was defined as

$$T = \begin{cases} ad + b, & \text{for } d \in [0, k]. \\ h, & \text{for } d > k. \end{cases} \tag{4.1}$$

where T is threshold, d is stimulus duration, a and b are the slope and intercept of the descending line, h is the lower asymptote of the function, and k is the critical stimulus duration that separates the descending and constant parts of the curve. Parameter a, which was used as an estimate of the rate of visual completion, was constrained to be less than zero and greater than -71, which is the maximum slope that is possible given the range of thresholds (2.08 to 1.01) and the difference between the two shortest stimulus durations (15 and 30 ms). Parameter k was used as an estimate of the time needed to visually complete the rectangle. We found that variability across conditions made it difficult to obtain stable estimates of the threshold-vs.-duration function for individual participants. We therefore computed maximum likelihood estimates of the best-fitting parameters for average thresholds within each condition and age group. Equation 4.1 was fit to the mean thresholds for 1500 bootstrapped samples of participants from each age group. For each parameter, the bootstrapped distributions were then used to calculate the mean value and the 95% percentile-bootstrap confidence interval.

Figure 4.5 plots thresholds against stimulus duration and the best-fitting threshold-vs.-duration functions. Inspection of the figure indicates that Equation 4.1 provided reasonably good fits to the average thresholds in each condition and both age groups. The figure also shows that thresholds were generally higher in older than younger adults at short stimulus durations, but that thresholds were similar in the two age groups at long durations. Hence, older and younger adults performed equally well when stimulus duration was longer than ≈ 100 ms. Also, in both age groups thresholds for short duration stimuli were lowest in the complete condition and highest the fragmented condition, but the slopes of the descending portion of the curves (i.e., parameter a in Eq 4.1) were similar across conditions. As a result, the kink point in the bilinear curves (i.e., parameter k in Eq 4.1) appeared to vary systematically across conditions. These points are illustrated more clearly in Figure 4.6a, which shows the mean values and 95% confidence intervals for parameters k and a. In older adults k was lowest in the complete condition, highest in the fragmented condition, and intermediate in the occluded condition. In younger adults, k was lowest in the complete condition and similar in the occluded and fragmented conditions. On average, a was higher in older than younger adults but did not appear to vary systematically across stimulus conditions: In younger adults the rate of completion was slightly higher in the fragmented condition, but a was was nearly constant across conditions in older adults.



(a) Stimulus duration at completion **(b)** Rate of completion

Figure 4.6 – Experiment 1: The mean values of parameters k and a from Equation 4.1 and displayed in Figure 4.5. Panel a represent parameter k in Equation 4.1 and panel b represents parameter a in Equation 4.1.

Discussion

Experiment 1 measured shape discrimination thresholds in older and younger adults as a function of stimulus duration. Mean thresholds in both age groups were well-fit by a bilinear threshold-vs.-duration function: thresholds decreased with increasing stimulus duration up to a critical duration (k in Eq 4.1) and then remained constant (Figure 4.5). In both age groups, k varied systematically with stimulus condition (Figure 4.6a), being shortest in the complete condition and longest in the fragmented condition. We interpret this result as showing that visual completion takes time (Murray et al., 2001), and that completion helps the judgement of the aspect ratio of rectangles. Importantly, the value of k in the complete condition was approximately the same in younger ($M = 0.043$, $\mathrm{CI}_{95\%} = [0.033,\ 0.075]$) and older ($M = 0.050$, $\mathrm{CI}_{95\%} = [0.032,\ 0.081]$) adults, suggesting that age differences in the occluded and fragmented stimulus configurations represent a change in rate of visual completion rather than generalized slowing (Salthouse, 2000).

We also found that the *rate* of completion (a in Eq 4.1) was greater in older adults than younger adults (Figure 4.6b), indicating that performance in older adults was more strongly affected by stimulus duration. On the other hand, the rate of completion did not vary systematically across stimulus conditions. We hypothesized that in both age groups the rate of completion would be greatest in the fragmented condition, least in the complete condition, and intermediate in the occluded condition, but there is little evidence for such an effect.

We hypothesized that thresholds would be highest for the fragmented condition, lower in the occluded condition, and lowest in the complete condition. The predicted pattern was found in older adults, but there was no significant difference between thresholds in the occluded and fragmented conditions in younger adults. Due to the constraints of the experiment, the psychometric curve did not reach 70% correct in all conditions for all observers. The proportion of missing thresholds was higher in the fragmented condition for both age groups. Drawing across these two findings, we suggest that discrimination of aspect ratio is likely different for younger observers in the occluded and fragmented conditions, although we failed to find that difference in this experiment.

Experiment 1 explored completion in younger and older adults while they were judging aspect ratio. As demonstrated, perceptual completion assists extraction of aspect ratio in this task. We sought to explore whether completion would aid in perception of other shape features, and so in Experiment 2 we test whether perceptual completion affects judgements of size.

Experiment 2

Method

Observers

Fifteen younger adults (7 female, M = 20.0 years, range = 18-26 years) and 15 older adults (8 female, M = 70.4 years, range = 60-79 years) participated in the experiment. All observers were compensated $10 per hour and/or received partial course credit for participating. As in Experiment 1, older observers completed both the Montreal Cognitive Assessment and the Mini Mental State exam prior to participation in this experiment, and all of the participants had normal scores on both exams. Each participant provided informed consent prior to the start of the experiment, and the experimental protocols were approved by the McMaster Research Ethics Board.

Apparatus & Stimuli

The apparatus used in Experiment 2 was identical to that of Experiment 1. The stimuli used in Experiment 2 were outlines of squares that varied in size, and the contours comprising the squares had the same size, luminance, and motion as the contours used to construct the rectangles used in Experiment 1. As in Experiment 1, stimuli were displayed in complete, occluded, and fragmented configurations. Each stimulus did not vary in aspect ratio, and were always perfectly square.

Procedure

Each trial consisted of the presentation of a reference stimulus followed by a test stimulus. The duration of the reference stimulus was 300 ms, the inter-stimulus interval was 500 ms, and the duration of the test stimulus was one of eight values (15, 30, 45, 60, 75, 105, 165, 210 ms) that varied across conditions. As in Experiment 1, the offset of the test stimulus was followed immediately by a white noise mask. When occluders were present, they appeared on screen with the fixation point, and remained visible until the presentation of the mask at the end of a trial. The observer's task was to determine if the test stimulus was larger or smaller than the reference stimulus on each trial by pressing one of two labelled keys on a standard computer keyboard.

There were three stimulus configurations and eight test stimulus durations for a total of 24 conditions. As in Experiment 1, i) the conditions were blocked and presented in a random order; ii) there were practice trials at the beginning of the experiment and prior to each block; and iii) observers were allowed to take a break at the end of each block. The experiment took approximately 90 to 120 minutes to complete.

Results

Analyses are conducted using R statistical software (R Core Team, 2013). Size ratio is reported as the quotient of the larger square divided by the smaller square, regardless of whether the test stimulus was larger or smaller than the reference.

Psychometric functions modelled log size ratio, and were estimated for each observer and each condition using the *quickpsy* R package (Linares and López-Moliner, 2016). As in Experiment 1, psychometric curves were cumulative normal curves with lower asymptotes set to 0.5; the mean, standard deviations, and lapse rate were estimated using a maximum likelihood procedure with differential evolution optimization. Figure 4.7 displays the data and psychometric curves for one representative younger observer. Again, for some observers the psychometric curve for a particular condition did not reach 70% accuracy, and in those cases, thresholds were set to 2.08. This occurred in approximately 0.7% of the data.

Figure 4.8 displays the average thresholds in each stimulus configuration, ignoring stimulus duration, for Experiment 2. Thresholds were analyzed using a linear mixed-effects model of square-root transformed thresholds that included Age and Stimulus Configuration as factors. Thresholds that were set to 2.08 were excluded from this analysis. Degrees of freedom were approximated with the Kenward-Roger method.

There was a significant main effect of age ($F(1, 28) = 5.40$, $p = .028$), where thresholds were higher for older adults than younger adults. There was a main effect of stimulus configuration ($F(2, 681) = 4.34$, $p = .013$). The age by stimulus configuration interaction was not significant ($F(2, 681) = 1.87$, $p = .154$). Three additional mixed-effects models were conducted to compare between stimulus configurations. Thresholds for occluded stimuli were significantly higher than thresholds for fragmented stimuli

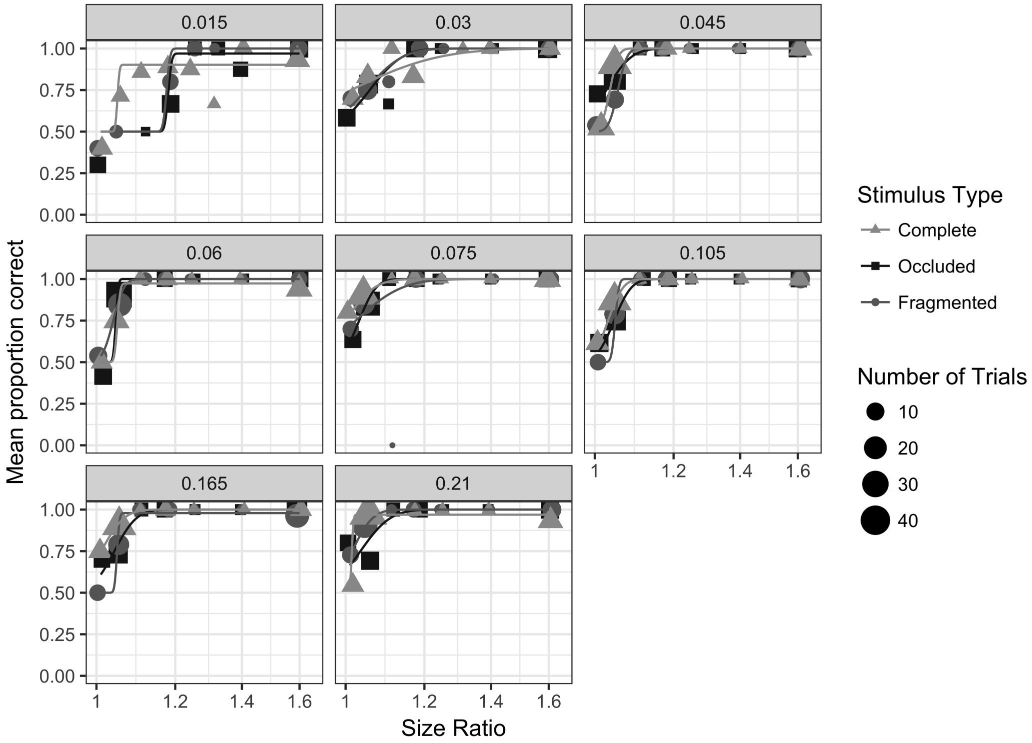


Figure 4.7 – Experiment 2: Data from a representative young observer and corresponding fitted psychometric curves.

	Complete	Occluded	Fragmented
Younger Adult	0	1	0
Older Adults	2	2	0

Table 4.2 – Experiment 2: Frequency of NA thresholds. A total of 120 thresholds were estimated in each condition.

($F(1, 446) = 6.78$, $p = .009$), and thresholds for occluded stimuli were significantly higher than thresholds for complete stimuli ($F(444) = 5.90$, $p = .015$) Thresholds for fragmented and complete stimuli did not differ significantly ($F(1, 447) = 0.00$, $p = .946$). Table 4.2 displays the amount of NA thresholds in each condition. There does not seem to be a clear pattern of NA values and conditions.

Threshold-vs.-Duration

As in Experiment 1, we again modelled the association between discrimination thresholds and stimulus duration using a bilinear function (see Equation 4.1). Figure 4.9 plots thresholds against stimulus duration and the best-fitting threshold-vs.-duration functions. In general, thresholds were lower in Experiment 2 compared to Experiment 1. Again, older adults had higher thresholds than younger adults at short stimulus durations, and this age difference disappeared at stimulus durations greater than 100 ms.

Figure 4.10 illustrates the mean values and 95% percentile confidence intervals for parameters k and a. Unlike in Experiment 1, the estimates of parameters of the threshold-vs.-duration functions were not reliable: the confidence intervals for each parameter span a wide range in both older and younger adults. There is no clear pattern in parameter a, the rate of completion, in both age groups. In older adults, parameter k appears to vary across stimulus configurations, but the pattern of variation is opposite to the predicted pattern of results.

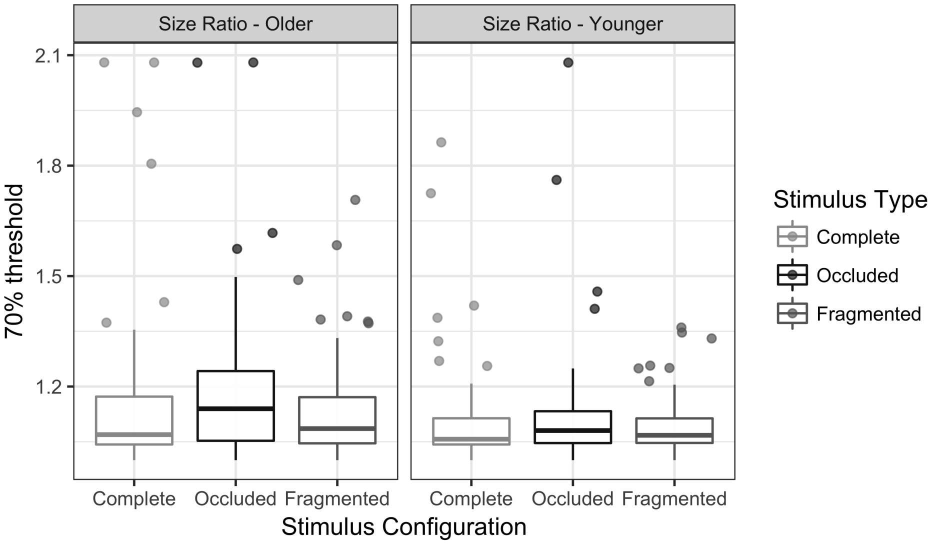


Figure 4.8 – Experiment 2: 70% thresholds, ignoring stimulus duration.

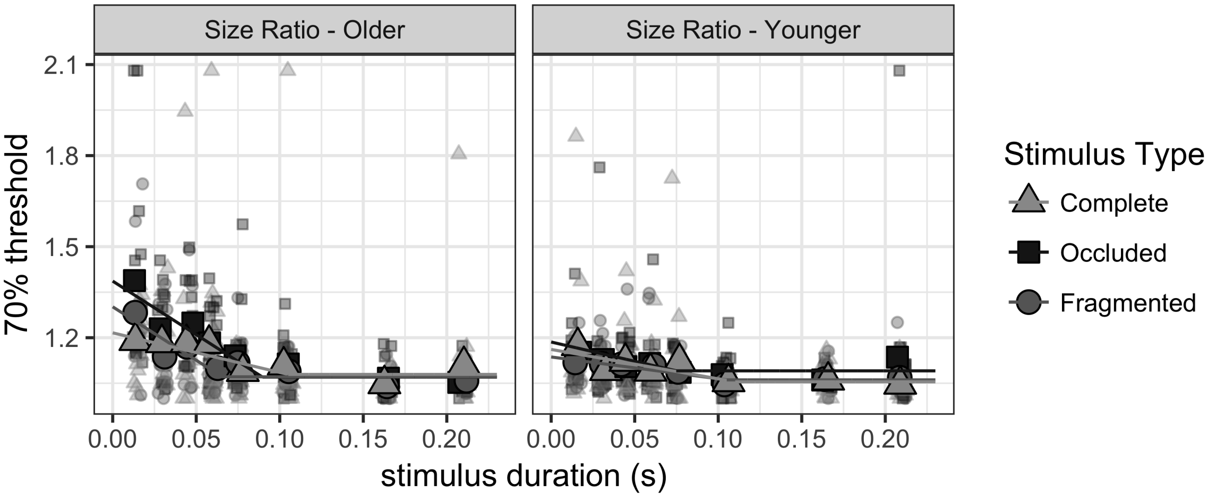
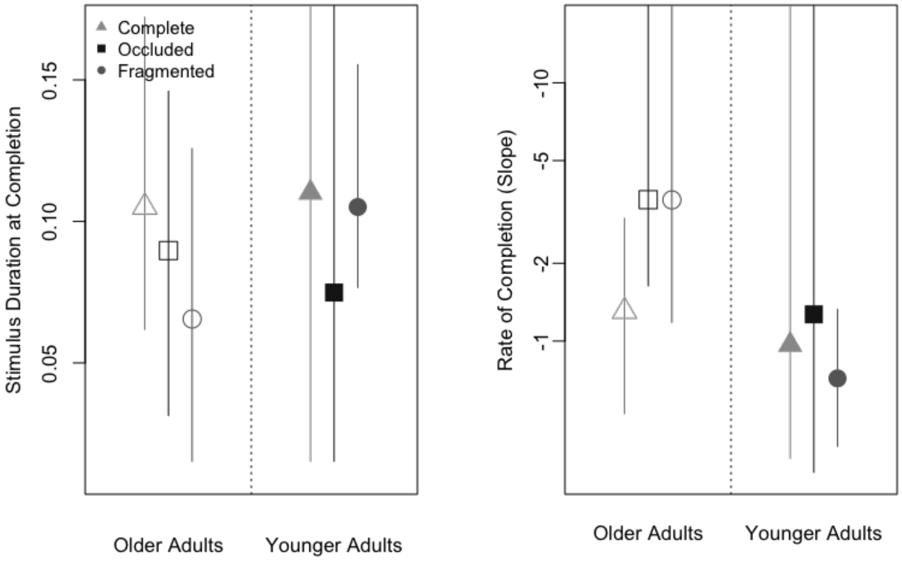


Figure 4.9 – Experiment 2: Thresholds plotted against stimulus duration for each stimulus duration and age group. Small symbols show thresholds from individual observers; large symbols show group means. The solid lines are the best-fitting bilinear functions (Eq 4.1) that were estimated with the bootstrap procedure described in the text.



(a) Stimulus duration at completion **(b)** Rate of completion

Figure 4.10 – Experiment 2: Parameters and 95% bootstrapped percentile confidence interval of bilinear line shown in Equation 4.1 and displayed in Figure 4.9. Panel a represents parameter k in Equation 4.1 and panel b represents parameter a in Equation 4.1.

Discussion

Experiment 2 demonstrated that size discrimination thresholds, unlike aspect ratio discrimination thresholds, were not strongly dependent on the degree of completion and stimulus duration. Similar to Experiment 1, we hypothesized that the stimulus duration at completion would be shortest for complete stimuli, longer for occluded, and longest for fragmented stimuli. We found no clear evidence of this pattern. Further, there does not seem to be any clear pattern between the stimulus configurations and rate of completion in either younger or older adults. In Experiment 1, there was some evidence that slopes were steeper for older adults than younger adults. In the current experiment, there was some evidence that slopes were steeper for older adults than younger adults, given that estimates for slope in older adults are all smaller than -1. However, the unreliability of the estimates of all of the slope parameters makes this a weakly supported conclusion.

We conclude that the bilinear model of the relationship between stimulus duration and thresholds is likely not a good model for these data. It is unclear if performance benefits from increases in stimulus duration for this task. Furthermore, it does not seem like performance in this tasks varies between the three stimulus configurations, suggesting that perceiving a complete figure might not aid in judgements of size.

In this experiment, observers had to compare the size of the reference and test stimulus on each trial. However, since they were always shown a square, they did not have to compute the area of the test and reference stimuli, and instead could make their size judgements exclusively on either the length or the width of the stimuli. Therefore, compared to Experiment 1, which required estimation of the size of both the length and width at once, Experiment 2 required only estimation of one dimension of the test and reference stimuli. A potential concern is that the size task in Experiment 2 may be easier than Experiment 1 not due to differences in size or aspect ratio judgements, but instead due to the amount of calculations required of the observer. To control for this possibility, Experiment 3 was conducted to again require judgements of size in a task similar to Experiment 2, but where the aspect ratio of the test and reference stimulus changes on every trial, and observers base their judgements of size on area, and not simply on the length or width of the stimuli.

Experiment 3

Method

Observers

Fifteen younger adults (10 female, M = 19.9, range=18-25 years) and 15 older adults (8 female, M = 71.8, range=62-81 years) participated in each experiment. All observers were compensated $10 per hour and/or received partial course credit for participating. The experiment lasted between 90 and 120 minutes. As in Experiment 1 and 2, older observers completed both the Montreal Cognitive Assessment and the Mini Mental State exam prior to participation in this experiment. All of the older participants had normal scores on both tests. Each participant provided informed consent prior to the start of the experiment, and all experimental protocols were approved by the McMaster Research Ethics Board.

Apparatus, Stimuli and Procedure

The apparatus used in Experiment 3 was identical to that of Experiments 1 and 2. The stimuli used in Experiment 3 were outlines of rectangles that varied in size, and the contours comprising the rectangles had the same size, luminance, and motion as the contours used to construct the rectangles used in Experiments 1 and 2. As in Experiments 1 and 2, stimuli were displayed in complete, occluded, and fragmented configurations. On each trial the aspect ratio of both the reference stimulus and the test stimulus were randomly jittered between 0.9:1 and 1:1.11. The area of the reference rectangle was randomly shifted between 3.24 and 4.84 degrees of visual angle, which corresponded with the average area of the reference in Experiment 2. The ratio of the areas of the test and reference stimuli was varied trial-to-trial according to the staircase procedure outlined in Experiment 1. The observer's task was to determine if the area of the test stimulus was larger or smaller than the area of the reference stimulus. Due to the aspect ratio manipulation, only the total area of both the reference and the test stimulus was useful for the task, as neither the length nor width by itself was a reliable cue to area.

There were three stimulus configurations and eight test stimulus durations creating a total of 24 conditions. As in Experiments 1 and 2, the conditions were blocked and presented in random order, there were practice trials at the beginning of the experiment prior to each block, and observers were given a break at the end of each block. The experiment took approximately 90 to 120 minutes to complete.

Results

Analyses are conducted using R statistical software (R Core Team, 2013). Area ratio is reported as the quotient of the larger rectangle divided by the smaller rectangle, regardless of whether the test stimulus was larger or smaller than the reference, and regardless of the aspect ratio of either stimulus.

Psychometric functions relating response accuracy to log area ratio were used to estimate discrimination threshold. A psychometric function was estimated for each observer in each condition using the *quickpsy* R package (Linares and López-Moliner, 2016). The fitting procedure was identical to Experiments 1 and 2. Figure 4.11 displays all data and psychometric curves from one representative young observer. The psychometric curves were used to estimate the 70% threshold for each observer in each experimental condition. As in Experiments 1 and 2, the psychometric functions did not reach 70% correct for some observers in some conditions, and therefore a discrimination threshold could not be estimated reliably in those conditions. In those cases, thresholds were set to 2.08. This occurred in approximately 1% of the data.

Average thresholds in each stimulus configuration, ignoring stimulus duration are displayed in Figure 4.12. Square-root transformed thresholds were analyzed with a linear mixed-effects model that included age and stimulus configuration as categorical predictor variables. Thresholds set to 2.08 were excluded from the analysis. Degrees of freedom were approximated using the Kenward-Roger method. There was a significant main effect of stimulus configuration ($F(2, 676) = 5.69$, $p = .003$). The main effect of age was not significant ($F(1, 28) = 2.52$), $p < .123$). The age by stimulus configuration interaction was not significant ($F(2, 690) = 0.80$, $p = .449$). Three additional linear mixed-effects models were used to evaluate differences between stimulus configurations. Thresholds in the occluded condition were significantly greater than thresholds in the fragmented condition ($F(1, 443) = 8.73$, $p = .003$), and thresholds in the complete condition ($F(1, 439) = 7.52$, $p = .006$). Thresholds in the fragmented and complete conditions did not differ significantly ($F(1, 445) = 0.00$, $p = .958$). Table 4.3 displays the amount of NA thresholds in each condition. There does not seem to be a clear pattern of NA values among conditions.

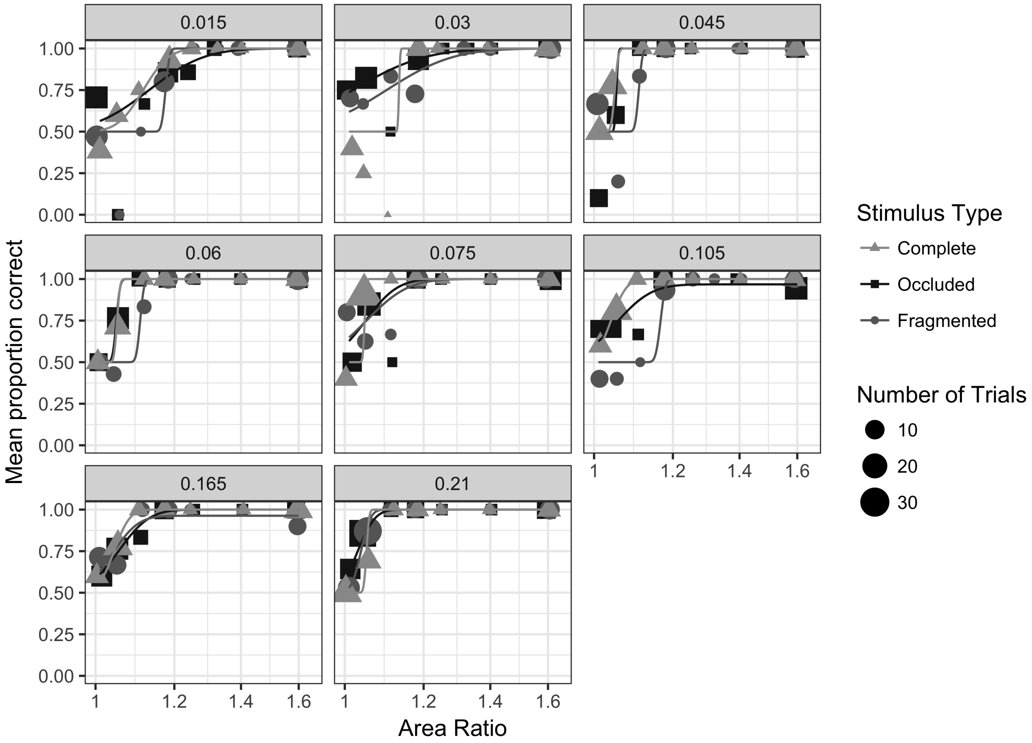


Figure 4.11 – Experiment 3: Data from a representative young observer and corresponding fitted psychometric curves.

	Complete	Occluded	Fragmented
Younger Adult	2	1	0
Older Adults	2	5	0

Table 4.3 – Experiment 3: Frequency of NA thresholds. A total of 120 thresholds were estimated in each condition.

One goal of Experiment 3 was to control for potential differences in task difficulty between Experiments 1 and 2. To address this goal we compared average thresholds across the three experiments in each age group. Square-root transformed thresholds were analyzed with a linear mixed-effects model that included age and experiment as categorical predictor variables. Thresholds set to 2.08 were excluded from the analysis. Degrees of freedom were approximated using the Kenward-Roger method. There was a significant main effect of age ($F(1, 84) = 18.27$, $p < .0001$) indicating that older adults had higher thresholds than younger adults. There was also a significant main effect of experiment ($F(2, 84) = 9.43$, $p < .001$). The age by experiment interaction was not significant ($F(2, 84) = 0.94$, $p = .396$). Three additional linear mixed-effects models were conducted to evaluate the differences between experiments. Thresholds in Experiment 1 were higher than in Experiment 2 ($F(1, 58) = 7.24$, $p = .009$) and thresholds in Experiment 1 were higher than in Experiment 3($F(1, 58) = 14.66$, $p < .001$). Thresholds in Experiments 2 and 3 did not differ significantly ($F(1, 58) = 1.14$, $p = .291$).

Threshold-vs.-Duration

As in Experiments 1 and 2, the relation between discrimination threshold and stimulus duration was modelled with a bilinear function (see Equation 4.1). The 70% thresholds for all observers and the best-fitting threshold-vs.-duration functions are displayed in Figure 4.13. The figure indicates that thresholds generally were lower in younger than older adults at the brief stimulus durations, but were similar in both age groups at stimulus durations greater than approximately 100 ms. As in Experiment 2, thresholds-vs.-duration functions did not depend noticeably on stimulus configuration.

Figure 4.14 illustrates the parameters from older and younger observers for each stimulus configuration, with their 95% bootstrapped percentile confidence intervals. A key motivation for this experiment was to determine whether varying the aspect ratios of the reference and test stimuli would increase task difficulty and allow for more reliable modelling of the parameters of the bilinear function. However, as was found in Experiment 2, the best-fitting parameters of Equation 1 had very wide confidence intervals and did not differ systematically across conditions or age groups.

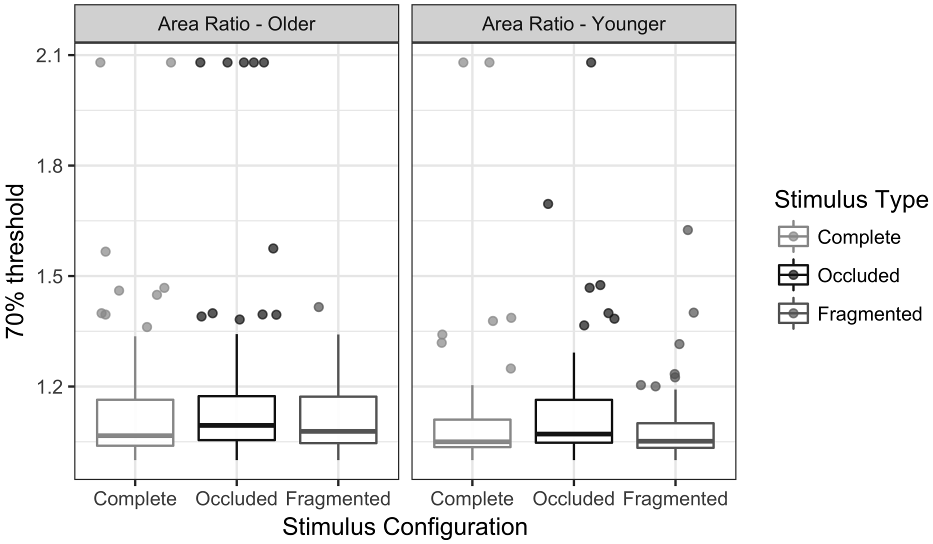


Figure 4.12 – Experiment 3: 70% thresholds, ignoring stimulus duration.

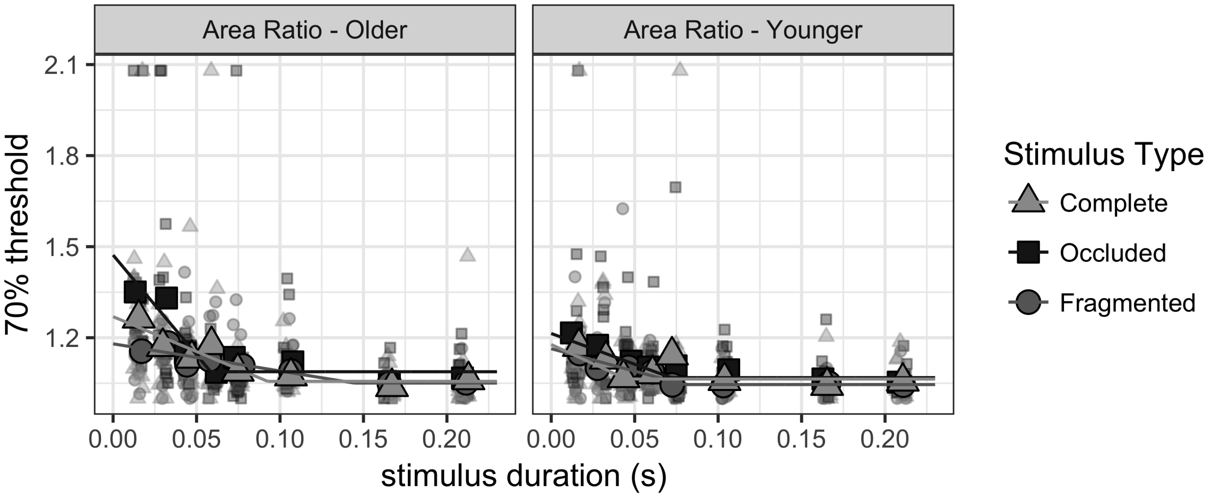
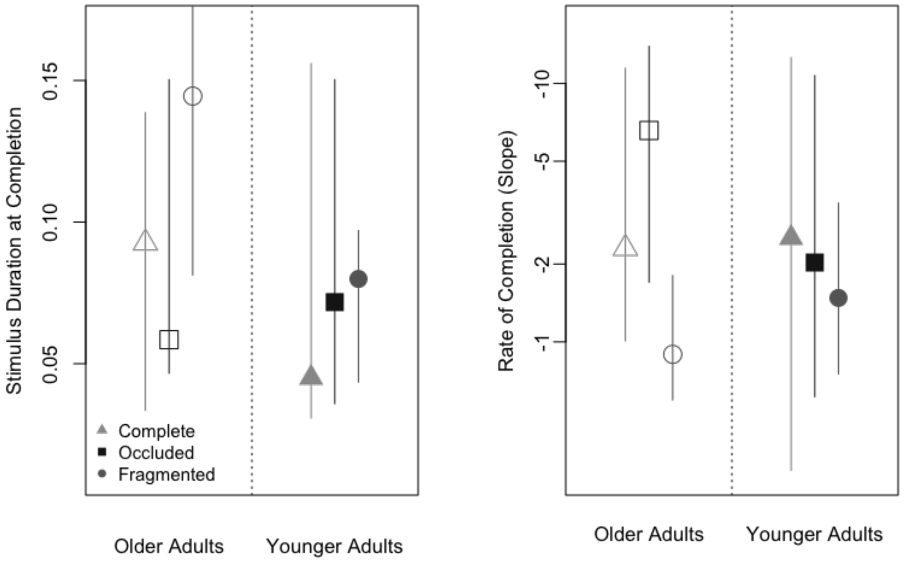


Figure 4.13 – Experiment 3: Thresholds plotted against stimulus duration for each stimulus duration and age group. Small symbols show thresholds from individual observers; large symbols show group means. The solid lines are the best-fitting bilinear functions (Eq 4.1) that were estimated with the bootstrap procedure described in the text.



(a) Stimulus duration at completion **(b)** Rate of completion

Figure 4.14 – Experiment 3: Parameters and 95% bootstrapped percentile confidence interval of bilinear line shown in Equation 4.1 and displayed in Figure 4.13. Panel a represent parameter k in Equation 4.1 and panel b represents parameter a in Equation 4.1.

Discussion

Experiment 3 examined the hypothesis that the different results obtained in Experiments 1 and 2 reflected differences in task difficulty rather than differences between aspect ratio and size discrimination. Despite modifications to the procedure between Experiments 2 and 3, average thresholds did not differ between the two experiments. In addition, the effects of age group and stimulus configuration on size discrimination were similar in the two experiments. The similarity in results between Experiments 2 and 3 suggests that the results of Experiment 2 were not simply related to task difficulty. Like Experiment 2, the current experiment did not find evidence that the stimulus-vs.-duration functions varied systematically with respect to stimulus configuration, and that the threshold-vs-duration functions were poorly fit to the data, and therefore likely do not represent a plausible model for this task. We conclude that these findings are caused by the requirement to judge the size of the stimuli, since this is common to Experiment 2 and 3, but absent from Experiment 1.

General Discussion

Three experiments measured discrimination thresholds in younger and older adults for changes in aspect ratio, size, and area as a function of stimulus duration and stimulus configuration.

Average thresholds were compared between stimulus configurations in each experiment. In Experiment 1, discrimination thresholds for changes in aspect ratio were larger for occluded stimuli than complete stimuli, and larger still for fragmented stimuli. This pattern of data suggests that aspect ratio judgements were more difficult as the stimulus contained less evidence for completion. This effect of stimulus configuration was not found in Experiments 2 and 3, which measured discrimination thresholds for changes in size and area. Instead, size and area discrimination thresholds were consistently higher in the occluded condition than the other two conditions. These results suggest that completion affects judgements of size and aspect ratio differently.

A bilinear model of threshold as a function of stimulus duration was fit in all three experiments. This bilinear model provided a good fit to aspect ratio discrimination thresholds (Experiment 1), and the parameters of the best-fitting function varied systematically, where the kink point in the bilinear curves occurred earliest for complete stimuli, and later for occluded and fragmented stimuli. However, the bilinear model did not provide good fits to the size and area discrimination thresholds measured in Experiments 2 and 3. Also, the parameters of the best-fitting functions had very wide confidence intervals and did not vary systematically across stimulus conditions or age groups. These modelling results are consistent with the suggestion that completion and aging have different effects on the perception of aspect ratio and size/area.

Some previous studies suggest that shape discrimination is unaffected by healthy aging (Wang, 2001; Habak et al., 2009); however how perceptual completion affects shape discrimination has not been studied in healthy aging. In the present study, older adults differed from younger adults in a few interesting ways. Average shape discrimination thresholds were larger for older than younger adults in Experiment 1 and 2. In Experiment 1, where thresholds could be reliably modelled as a function of stimulus duration, the stimulus duration at completion was similar for younger and older adults for complete objects, which corresponds with prior findings of no difference in shape perception across aging. However, older adults needed more time to extract aspect ratio from occluded and fragmented objects, which means that the difference seen in this experiment between age groups are likely due to the requirements for perceptual completion in this task. Overall, older adults produce similar patterns of data to younger adults, suggesting that the perceptual processes used to complete the tasks in the current paper are similar between younger and older adults.

Thresholds were lower on average in Experiments 2 and 3 than in Experiment 1. This result is consistent with prior research (Regan and Hamstra, 1992) that found better perceptual discrimination between figures of different sizes than aspect ratios. Regan and Hamstra also showed that size and aspect ratio judgements were similar for rectangles and ellipses, which suggests that the results of the current paper are likely to generalize to shapes that differ from the rectangles used presently.

Dickinson et al. (2017) suggested that size may be treated differently by the visual system than aspect ratio, specifically through separate information channels. Dickinson et al. (2017) arrived at this conclusion by comparing the nature of aftereffects of both attributes on subsequent judgement of aspect ratio or size of squares. The results of the current experiments are in line with this idea. Although both size and aspect ratio judgements involve measuring the length and width of the shape, it seems that completion and longer stimulus durations help in aspect ratio judgements but have no clear effect on size or area judgements.

Completion is thought to help shape perception (Murray et al., 2001; Ringach and Shapley, 1996). However the current experiments found evidence for an effect of completion on the perception of a shape's aspect ratio, not its size or area. It seems that completion can aid in shape perception, but only for certain shape judgements and not others. Hence, our results suggest that the degree to which completion aids shape perception depends on the information that is to be extracted from the shape. Aspect ratio and size may be different from one another, and as such, completion helps aspect ratio judgements, but not size.

References

Blake, R., Rizzo, M., and McEvoy, S. (2008). Aging and perception of visual form from temporal structure. *Psychology and Aging*, 23(1):181–189.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4):433–436.

Chen, S., Müller, H. J., and Conci, M. (2016). Amodal completion in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 42(9):1344–1353.

Dickinson, J. E., Morgan, S. K., Tang, M. F., and Badcock, D. R. (2017). Separate banks of information channels encode size and aspect-ratio. *Journal of Vision*, 17(3):1–20.

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

Gold, J. M., Murray, R. F., Bennett, P. J., and Sekuler, A. B. (2000). Deriving behavioural receptive fields for visually completed contours. *Current Biology*, 10(11):663–666.

Habak, C., Wilkinson, F., and Wilson, H. R. (2009). Preservation of shape discrimination in aging. *Journal of Vision*, 9(12):18–18.

Judd, C. M., Westfall, J., and Kenny, D. A. (2012). Treating stimuli as a random factor in social psychology: A new and comprehensive solution to a pervasive but largely ignored problem. *Journal of Personality and Social Psychology*, 103(1):54–69.

Kenward, M. G. . and Roger, J. H. . (1997). Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics*, 53(3):983–997.

Linares, D. and López-Moliner, J. (2016). quickpsy: An R Package to Fit Psychometric Functions for Multiple Groups. *The R Journal*, 8(1):122–131.

Murray, M. M. (2004). Setting Boundaries: Brain Dynamics of Modal and Amodal Illusory Shape Completion in Humans. *Journal of Neuroscience*, 24(31):6898–6903.

Murray, R. F., Sekuler, A. B., and Bennett, P. J. (2001). Time course of amodal completion revealed by a shape discrimination task. *Psychonomic Bulletin & Review*, 8(4):713–720.

Owsley, C. (2011). Aging and vision. *Vision Research*, 51(13):1610–1622.

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

R Core Team (2013). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rauschenberger, R. and Yantis, S. (2001). Masking unveils pre-amodal completion representation in visual search. *Nature*, 410(6826):369–372.

Regan, D. and Hamstra, S. J. (1992). Shape discrimination and the judgement of perfect symmetry: Dissociation of shape from size. *Vision Research*, 32(10):1845–1864.

Ringach, D. L. and Shapley, R. (1996). Spatial and temporal properties of illusory contours and amodal boundary completion. *Vision Research*, 36(19):3037–3050.

Roudaia, E., Pilz, K. S., Sekuler, a. B., and Bennett, P. J. (2010). Spatiotemporal properties of apparent-motion perception in aging. *Journal of Vision*, 9(8):695–695.

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

Wang, Y. Z. (2001). Effects of aging on shape discrimination. *Optometry and Vision Science*, 78(6):447–454.

Chapter 5

General discussion

The ability to quickly and accurately identify the sources of motion to parse a visual scene is fundamental to navigating the external environment, and so questions such as those investigated in the current dissertation are central to perceptual research. The present dissertation investigated the themes of grouping and shape completion in motion. Several experiments were conducted to characterize how younger and older observers perceive four-sided figures in various configurations, presented in orbital motion. The current chapter outlines the main findings, discusses the implications of the current work, and suggests avenues for future research in this area.

Summary of key results

The research described in Chapter 2 introduced an ambiguous motion integration task where local position noise of elements of the stimulus acts as a cue to global grouping. In the first experiment, evidence of illusory motion was found at low levels of noise and long stimulus durations. Experiments 1 and 2 explored the ambiguous motion task by varying stimulus duration, amount of stimulus noise, and background noise. In addition, Experiment 2 measured confidence responses from observers, and found that observers exhibited confidence in their errors when they show below-chance performance. Finally, the third experiment tested the hypothesis that illusory motion was caused by attending to a single motion component. No evidence was found for this hypothesis, and thus the chapter does not make strong conclusions about the origin of the illusory global motion.

Chapter 3 measured the magnitude of phase integration bias when a global grouping cue is present and absent. In this chapter, relative phase integration was measured in older adults. The effect of the local noise grouping cue was similar in younger and older adults, although older adults may be more susceptible to the illusion (Experiment 3a) or were more variable in their responses than younger adults (Experiment 3b). The final experiment of Chapter 3 compared rated perceived coherence with direction discrimination accuracy and phase adjustment accuracy to relate the current results with previous experiments that obtained subjective ratings of grouping, and found a general correspondence between tasks.

In Chapter 4, perceptual completion was investigated in aging by modelling how the ability to judge the aspect ratio or size of rectangles or squares differs between younger and older adults as a function of stimulus duration and stimulus configuration, specifically complete, occluded and fragmented shapes. We found that discrimination thresholds were higher in older adults than younger adults but the effects of stimulus duration and configuration were similar in the two age groups. Comparing the characteristics of the shapes, threshold of aspect ratio in each stimulus configuration followed a clear pattern of decreased thresholds as the stimulus configuration more closely resembled a complete rectangle. There was no such pattern in size or area judgements, leading to the conclusions that judgements of size and aspect ratio depend on different perceptual processes even though both characteristics depend on calculations of length and width.

Complete vs Incomplete Perceptual Grouping

The current dissertation has demonstrated that the binary classification of "grouped" and "ungrouped" does not fully represent the perceptual experience of all visual stimuli. In addressing this issue, we employed a variety of methods to characterize what an observer experiences when attempting to perceptually group spatially distant elements in motion. We demonstrated that probing perception using several behavioural measures is necessary to properly characterize an observer's experience.

The scope of the current dissertation was limited, so there are many avenues for future research. One goal of the dissertation was to explore phase integration and perceptual grouping in several contexts. The strength of the grouping cue typically was varied within an experiment, but we did not manipulate parameters of the motion or shape. Manipulations of the speed of motion, or the size and luminance of the stimulus are important to consider because the particular variants of the stimuli used in the current dissertation may be affecting experimental results. Tang et al. (2015) conducted similar experiments to those conducted in Chapter 2 composed of aligned patches of sinusoidal gratings, varying the number of sides of the shape (3-8) and the space between local contours. However, Tang et al. (2015) measured observer threshold and thus were unable to detect below-chance performance or other evidence of illusory motion. Several papers have investigated the characteristics of occluders or terminators (e.g., Lorenceau and Shiffrar, 1992; McDermott and Adelson, 2004), although we did not experimentally vary these attributes in the current work. Additional experiments are needed to bridge the topics of the current dissertation and the established literature.

Shape Completion

Chapter 4 focused on the ability to extract stimulus properties from complete and incomplete shapes. Specifically, the experiments of Chapter 4 measured whether the degree of shape completion affected an observer's ability to extract aspect ratio or size information. We found that aspect ratio estimates were affected by completion, but size estimates were not.

The methods used in Chapter 4 implicitly assume that visual completion is a gradual process. Thresholds of aspect ratio, size, and area declined as stimulus duration increased. Specifically for aspect ratio, we assumed that increasing stimulus duration allowed visual processing to perceptually complete the object, which in turn allowed the observer to extract more precise information about the shape of the stimulus. This assumption is consistent with results reported by Gold and Shubel (2006), who modelled the spatio-temporal properties of completion using classification images and find evidence for progress in completion over time. In Gold and Shubel (2006), the classification image was measured for 500 ms, but, similar to the current dissertation, the time between 100-200 ms was especially important for the completion process.

The stimuli in Chapter 4 were rectangles. Regan and Hamstra (1992) found that the shape discrimination accuracy of both aspect ratio and size were similar for rectangular and elliptical stimuli, suggesting that similar results would be found in Chapter 4 using elliptical stimuli. However, the predicted results of an experiment that extended the methods of Chapter 4 to complex shapes are not straightforward. The literature on perception of complex shapes outlines a number of rules that describe perception of these shapes. For example, the minima rule states that minima of curvatures form boundaries between parts. Similarly, the convex region of an ambiguous boarder will contain the figure, and the concave boarder contain the background (Hoffman and Singh, 1997). In this literature, it is typical to have observers categorize shapes made up of several superimposed ellipses to create complex shapes. It would be interesting to combine the methods of Chapter 4 with the literature of complex shapes to discover how exactly shape attributes can be estimated from shapes where the calculations are not defined by simple combinations of length and width. In comparison to the shape perception literature in general, the experiments of Chapter 4 are a fundamental and necessary first step to exploring how completion affect extraction of shape properties in general, and the work can hopefully be extended to more complex and irregular shapes.

Aging Visual System: Grouping and Shape Completion

There are many changes with aging and perceptual organization which would suggest that some functions of perceptual organization occur differently in the older and younger visual systems. Therefore experiments in Chapters 3 and 4 examined visual grouping and shape perception in healthy older adults.

Age-related changes in vision can be attributed to changes occurring at several levels of the visual processing hierarchy. At the earliest stages of vision, older adults experience changes in the optical components of the eye, such as thickening of the ocular media in the lens (Savage et al., 1993; Weale, 1988), that contribute to changes in vision that occur during aging. However, changes in optics cannot account for all of the effects of aging on vision. For example, age-related changes in acuity, spatial contrast sensitivity, orientation discrimination, and motion detection are all due, at least in part, to changes in neural processes (Atchley and Andersen, 1998; Spear, 1993; Betts et al., 2012; Roudaia et al., 2008).

Despite these changes in vision with age, many tests of perceptual organization and vision have found no difference between older and younger adults that cannot be accounted for by non-visual changes such as slower processing speed (Salthouse, 2000), slower reaction time (Fozard et al., 1994), deficits in divided attention (Verhaeghen and Cerella, 2002), or reduced hand dexterity (Carmeli et al., 2003). The present thesis also found little evidence for aging effects on perceptual organization. Chapter 3 demonstrated that older adults may be more susceptible to the illusion of opposite global motion than younger adults in some situations but not others. Comparing the results of younger adults (Chapter 2, Experiment 1) to older adults (Chapter 3, Experiment 3a), older adults may be more susceptible to the illusion of opposite global motion. However, in Chapter 3, Experiment 3b, older adults do not display lower accuracy than younger adults (in the comparable experiment in Chapter 3, Experiment 1), although their responses may be more variable. Experiments in Chapter 4 found that older adults require more time to reach younger adult levels of performance in the discrimination of aspect ratios, but the effects of stimulus configuration on performance was the same in both age groups in all three experiments. The results of the current dissertation demonstrate a common finding in the literature on perception in aging, which is that by and large older adults are often capable of the same perceptual abilities as younger adults, but may complete them in a different way, or may require more time (as in Chapter 4), or make more frequent errors and display less flexibility (as in Chapter 3) (Owsley, 2011).

We explored both perceptual grouping and perceptual completion in younger and older adults in Chapters 3 and 4. Our exploration of healthy aging as a special population expands upon the literature “baseline" of younger adult observers and provides unique information about the human perceptual system as a whole. It would be interesting to further extend the findings of the current dissertation to explore other special populations. In Autism spectrum disorder (ASD), both motion sensitivity (Bertone et al., 2003) and perceptual grouping (Brosnan et al., 2004; Farran and Brosnan, 2011) are altered compared to typically developing individuals. It is commonly found that the tendency to group globally is reduced in a variety of tasks for individuals with ASD compared to typically developing controls (Suzanne Scherf et al., 2008). It is unclear how these group differences will interact with the kinds of tasks presented in Chapters 2 and 3. On the surface, it might be expected that ASD participants would perform worse in these motion integration tasks because of the reduced ability to group globally. However, older adults often display a reduced ability to encode global motion (Hutchinson et al., 2012), yet the results of Chapter 3 point to similar performance between younger and older adults. It is therefore unclear how ASD participants would perform given this consideration.

The results of Chapter 4 are consistent with the notion that older adults display a deficit in shape processing (Roudaia et al., 2008; Andersen and Ni, 2008), and that that visual completion is worse in older adults (Salthouse and Prill, 1988). Andersen and Ni (2008) report that older adults are worse than younger adults at shape perception, but not motion. We confirm this finding of Andersen and Ni (2008), as older and younger adults perform worse on average in all experiments in Chapter 4, although all stimuli in the current dissertation were in motion, and as such motion and form are not separable. We chose to present the stimuli in Chapter 4 in motion to encourage the perception of the completed figure, but did not directly measure the effect of motion in older adults. Considering the results of Andersen and Ni (2008), this manipulation may have helped younger but not older adults to perceptually complete.

One potential criticism of the current research is that the method of studying aging in this paper is cross-sectional, and so the differences observed are not necessarily due to age, and could be due to many other confounds associated with each age group. The solution to this criticism is to conduct longitudinal or cross-sequential designs, which follow an individual observer to record how perception changes as that observer ages. Of course, longitudinal and cross-sequential designs are resource intensive, and so the findings of the current dissertation represent effects that could be later confirmed by a design which measures aging longitudinally. Additionally, we employed a number of methods to ensure that confounds were not responsible for the results. First, all of the older adults completed tests of cognitive decline. All of the older adults tested in the dissertation passed these tests. We similarly restricted observers to those without cataracts, glaucoma, and other visual conditions that occur more commonly in older adults that would affect performance in the tasks used in this dissertation. Finally, all of the experiments included practice sessions which allowed all participants to become familiar with the procedure before beginning the experimental trials, and were run by experimenters who are extensively experienced in both younger and older adult perceptual experiments, which allowed for standardized and clear experimental instructions.

Measurement in Perceptual Research

A constant theme throughout the dissertation has been the reliance of much of perceptual research on using certain tasks and measures as a proxy to the underlying concept of interest. Here, we employ several different methods to be able to measure the effects of interest. In several cases (Chapter 3, Chapter 4) we find that the conclusions made about perceptual organization ability changed depending on method.

In Chapter 3 we compared objective and subjective tasks. In every stimulus used in Chapters 2 and 3, it is possible for an observer to sum the motion of the two components while perceiving a disjointed figure, so performance on an objective task may not fully represent the observer's perceptual experience. Experiment 4 of Chapter 3 compared performance on an objective task, specifically direction discrimination and adjustment, and a subjective task where observers rated the perceived coherence of the stimulus. This experiment revealed that performance in the subjective and objective tasks corresponded on average in the presence and absence of a grouping cue, although only corresponded on a trial-by-trial basis in the presence of a grouping cue. In general, the comparison between tasks in Chapter 3 corresponded such that tasks lead to the same conclusions about perceptual abilities.

In Chapter 4 we compared several measures of shape completion, specifically comparing aspect ratio (Experiment 1) with judgments of size (either length as in Experiment 2 or area and in Experiment 3). In this chapter, we found that the ability to extract stimulus properties changed depending on the property that is estimated. Completion helped estimation of aspect ratio, but not size or area. Here, the conclusions made about stimulus duration and completion changed depending on which task was being used as a measurement of shape completion.

It is common to use indirect but objective measures of psychological constructs. It is somewhat less common to use subjective report of perception (but see (Castet and Wuerger, 1997; McDermott and Adelson, 2004)). Throughout the dissertation, we suggest that more than one measure is often necessary to properly characterize an effect, and to ensure that it an effect is generalizable to the psychological construct of interest and not specific to the task.

Conclusions

The function of perceptual organization is important for navigating the external environment. Motion and static grouping are aspects of perceptual organization that allow an observer to make sense of the often noisy, occluded, or incomplete information in a visual scene. Research in this dissertation demonstrated that although accurate interpretation may be possible when a stimulus contains cues to global grouping, in the absence of those cues, the perceptual consequences are quite different than expected: such as illusory motion direction (Chapter 2) or non-correspondence between subjective and objective perceptual tasks (Chapter 3). In general, the research of this dissertation points to the need for a general expansion in methods to ensure that the entire perceptual experience of observers is able to be measured.

References

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

Atchley, P. and Andersen, G. J. (1998). The effect of age, retinal eccentricity, and speed on the detection of optic flow components. *Psychology and Aging*, 13(2):297–308.

Bertone, A., Mottron, L., Jelenic, P., and Faubert, J. (2003). Motion perception in autism: A "complex" issue. *Journal of Cognitive Neuroscience*, 15(2):218–225.

Betts, L. R., Sekuler, A. B., and Bennett, P. J. (2012). Spatial characteristics of motion-sensitive mechanisms change with age and stimulus spatial frequency. *Vision Research*, 53(1):1–14.

Brosnan, M. J., Scott, F. J., Fox, S., and Pye, J. (2004). Gestalt processing in autism: Failure to process perceptual relationships and the implications for contextual understanding. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, 45(3):459–469.

Carmeli, E., Patish, H., and Coleman, R. (2003). The aging hand. *Journal of Gerontology*, 58A(2):146–152.

Castet, E. and Wuerger, S. (1997). Perception of moving lines: Interactions between local perpendicular signals and 2D motion signals. *Vision Research*, 37(6):705–720.

Farran, E. K. and Brosnan, M. J. (2011). Perceptual grouping abilities in individuals with autism spectrum disorder; Exploring patterns of ability in relation to grouping type and levels of development. *Autism Research*, 4(4):283–292.

Fozard, J. L., Vercruyssen, M., Reynolds, S. L., Hancock, P. A., and Quilter, R. E. (1994). Age differences and changes in reaction time: The Baltimore longitudinal study of aging. *Journals of Gerontology*, 49(4):179–189.

Gold, J. M. and Shubel, E. (2006). The spatiotemporal properties of visual completion measured by response classification. *Journal of Vision*, 6(4):356–365.

Hoffman, D. D. and Singh, M. (1997). Salience of visual parts. *Cognition*, 63(1):29–78.

Hutchinson, C. V., Arena, A., Allen, H. A., and Ledgeway, T. (2012). Psychophysical correlates of global motion processing in the aging visual system: A critical review. *Neuroscience and Biobehavioral Reviews*, 36(4):1266–1272.

Lorenceau, J. and Shiffrar, M. (1992). The influence of terminators on motion integration across space. *Vision Research*, 32(2):263–273.

McDermott, J. and Adelson, E. H. (2004). Junctions and cost functions in motion interpretation. *Journal of Vision*, 4(7):552–563.

Owsley, C. (2011). Aging and vision. *Vision Research*, 51(13):1610–1622.

Regan, D. and Hamstra, S. J. (1992). Shape discrimination and the judgement of perfect symmetry: Dissociation of shape from size. *Vision Research*, 32(10):1845–1864.

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

Salthouse, T. A. (2000). Aging and measures of processing speed. *Biological Psychology*, 54:35–54.

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

Savage, G. L., Haegerstrom-Portnoy, G., Adams, A. J., and Hewlett, S. E. (1993). Age changes in the optical density of human ocular media. *Clinical Vision Sciences*, 8(1):97–108.

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

Suzanne Scherf, K., Luna, B., Kimchi, R., Minshew, N., and Behrmann, M. (2008). Missing the big picture: Impaired development of global shape processing in autism. *Autism Research*, 1(2):114–129.

Tang, M. F., Dickinson, J. E., Visser, T. A. W., Edwards, M., and Badcock, D. R. (2015). Role of form information in motion pooling and segmentation. *Journal of Vision*, 15(2015):1–18.

Verhaeghen, P. and Cerella, J. (2002). Aging, executive control, and attention: A review of meta-analyses. *Neuroscience and Biobehavioral Reviews*, 26:1–9.

Weale, R. A. (1988). Age and the transmittance of the human crystalline lens. *The Journal of Physiology*, 395(1):577–587.