Comparative vision: mid-level processing of form and motion in humans and pigeons

by

Jean-François Nankoo

A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Department of Psychology
University of Alberta

© Jean-François Nankoo, 2015

Abstract

The ability to perceive and act upon the external world is fundamental to every organism. For species such as humans and pigeons, vision is a dominant modality that allows interaction with the world. In this dissertation I examine the similarities and differences between humans and pigeons, two distantly related species that share the common problem of perceiving an object-filled world. Specifically, results are presented from a series of studies examining how form and motion interact and how they contribute to object perception at the intermediate level of visual processing. The similarities and differences in form and motion perception in humans and pigeons are discussed with respect to similarities and differences in neuroanatomy and with respect to evolutionary adaptation. The research presented in this dissertation provides evidence to further the current understanding of the general principles of object perception and vision in general.

Preface

This thesis is an original work by Jean-François Nankoo. The research project, of which this dissertation is a part, received research ethics approval from the University of Alberta Research Ethics Board, Project Name "Cognitive Processes in Pigeons", No. Pro 00000074, June 25, 2015 and Project Name "Investigations into memory for locations, objects and rewards in adults" No. Pro 00017020, June 25, 2015.

Chapter 2 of this thesis has been published as J. -F. Nankoo, C. R. Madan, M. L. Spetch, and D. R. Wylie, "Perception of dynamic Glass patterns", Vision Research, 72, 55-62. I was responsible for the data collection and analysis as well as the manuscript composition. C. R. Madan was involved with concept formation and assisted with data collection. M. L. Spetch and D. R. Wylie were involved with concept formation and manuscript composition.

Chapter 3 of this thesis has been published as J. -F. Nankoo, C. R. Madan, M. L. Spetch, and D. R. Wylie, "Temporal summation of global form signals in dynamic Glass patterns," Vision Research, 107, 30-35. I was responsible for the data collection and analysis as well as the manuscript composition. C. R. Madan was involved with concept formation and assisted with data collection. M. L. Spetch and D. R. Wylie were involved with concept formation and manuscript composition.

Chapter 4 of this thesis has been published as J. -F. Nankoo, C. R. Madan, M. L. Spetch, and D. R. Wylie, "erception of complex motion in humans and pigeons (*Columba livia*)," Experimental Brain Research, 232, 1843-1853. I was responsible for the data collection and analysis as well as the manuscript composition. C. R. Madan was involved with concept formation and assisted with data collection. M. L. Spetch and D. R. Wylie were involved with concept formation and manuscript composition.

Chapter 5 of this thesis has been published as J. -F. Nankoo, C. R. Madan, M. L. Spetch, and D. R. Wylie, "Re-evaluating birds' ability to detect Glass patterns," Animal Cognition, 18, 945-952. I was responsible for the data collection and analysis as well as the manuscript composition. C. R. Madan was involved with concept formation and assisted with data collection. M. L. Spetch and D. R. Wylie were involved with concept formation and manuscript composition.

Acknowledgements

I would sincerely like to thank my supervisor, Dr. Marcia Spetch, and my supervisory committee, which consisted of Drs. Marcia Spetch ,Douglas Wylie, and Weimin Mou. I am grateful for their guidance, patience and support throughout my Ph.D. I would also like to thank my examining committee, Drs. Craig Chapman, Anthony Singhal, and Robert Cook (Tufts University). Special thanks also to Dr. Christopher Madan (Boston College) without whom the work presented in this dissertation would not be possible.

I would like to thank all of those who have contributed to my overall Ph.D. experience; Drs. Alinda Friedman, Eric Legge, and Quoc Vuong (Newcastle University). Thank you also to Dr. Suzanne MacDonald for all her support. Last but not least, I would also like to thank my amazing parents, Cyril and Nöellette Nankoo, and my wonderful partner, Naheed E. Hosan for their endless support.

Sincerely,
Jean-François Nankoo

Table of Contents

List of Tables

List of Figures

List of abbreviations

ANOVA	Analysis of variance
AOS	Accessory optic system
c/deg	Cycles per degree
CFF	Critical flicker fusion
CI	Confidence interval
dLGN	Dorsal lateral geniculate nucleus
GP	Glass pattern
hMT+	Human motion complex
IT	Inferior temporal cortex
LM	Nucleus lentiformis mesencephali
LOC	Lateral occipital complex
MST	Medial superior temporal
MT	Middle temporal
MT+	Middle temporal complex
MTN	Medial terminal nucleus
nBOR	Nucleus of the basal optic root
NOT	Nucleus of the optic tract
nRT	Nucleus rotundus
PI	Performance index
RDS	Random dot stimuli
RMSD	Root mean square deviation
S-	Negative stimulus
S+	Positive stimulus
SEM	Standard error of the mean
V1	Primary visual cortex
V2	Secondary visual cortex
V5	Visual area MT

Chapter 1

Introduction

Comparative vision: mid-level processing of form and motion in humans and pigeons

1. Introduction

The goal of the present work is to investigate form and motion at the intermediate level of visual processing (i.e., mid-level vision) in both the humans and the pigeons. To begin, I will discuss several topics on the background necessary to understand the rationale and implications of the work presented in this dissertation. These topics are as follows: the importance of mid-level vision, an introduction to comparative vision, form perception, motion perception, and interaction of form and motion. Following a discussion of these topics, I will present five studies that provide a comprehensive psychophysical investigation of form and motion processing in humans and pigeons, and their influence on object perception. The results of these studies have important implications for understanding the general principles that guide object recognition and vision in general.

1.1 The importance of mid-level vision

The ability to perceive and recognize objects in the environment is essential for survival in many species, and even though object perception may seem effortless, it is quite a complex process. For instance, the visual system has to derive complex three-dimensional (3D) objects that we perceive from two upside down two-dimensional (2D) images on the retina. As shown in Figure 1.1, because the retinal image is 2D, different objects can project similar images on the retina, creating what is known as the inverse projection problem (Pizlo, 2001). In addition, the retinal image is unstable because the eyes moves frequently (i.e., saccades), and is heterogeneous because of the non-uniform distribution of cells in the retina. Yet, our perceptual world is very different from the retinal images; rather we perceive a stable homogenous world filled with objects.

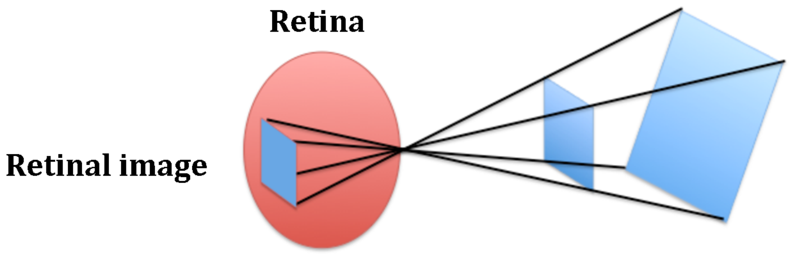


Figure 1.1 When we see an object, it creates a projection on the retina. Because the retinal image is in 2D, objects of different sizes and shapes can project the same image on the retina. For example, a rectangular shape has the same retinal image as a bigger rectangle that is further away and is tilted.

The mammalian visual system is thought to be hierarchical, and the stages of visual processing are built with information gathered from previous stages (Riesenhuber & Poggio, 1999; Marr, 1982; Giese & Poggio, 2003). The early stage (referred to as low-level vision) involves the extraction of local features from the retinal image. For example, cells in the primary visual cortex (V1) can be thought of as local feature detectors as they have small receptive fields and respond to oriented edges and bars (Hubel & Wiesel, 1962; see Carandini et al., 2005, for review). In contrast, the final stage of visual processing (i.e., referred to as high-level vision) entails recognition of complex objects such as faces (Desimone et al., 1984; Kanwisher et al., 1997; Tsao et al., 2006). Most of what is known about the visual system fall into one of these two stages. However, to fully understand how the perceptual world is built from retinal images, we need to have an understanding of all the stages involved, including the intermediate stage (i.e., mid-level vision) that bridges the gap between low level and high level vision (Marr, 1982).

Nakayama, He and Shimojo, (1995) proposed that the function of mid-level vision is to extract surfaces from the environment by pooling information gathered by the feature detectors. Objects in a scene are defined by their surfaces that can be identified based on a multitude of cues such as reflectance, texture, and contours. Identifying surfaces in a visual scene can often be problematic. For example, often surfaces are occluded by other surfaces. And yet in spite of the fact that occluded portions of surfaces are not registered by the low-level stage, we are able to perceptually complete the surface. Gestalt psychologists recognized the importance of surface perception and proposed that the visual system uses simple heuristics (i.e., the Gestalt principles) to extract surfaces within a scene (Wertheimer, 1923/1938; Köhler, 1940; Koffka, 1935). These heuristics allow the visual system to organize information by segregating and grouping surfaces, using properties such as texture, shape, and color; the visual system is able to achieve this in spite of limited retinal input (Nakayama, 1999; Anderson, 1999). In this dissertation, I will focus specifically on form and motion as surface properties (i.e., the perception of global form and motion).

1.2 Comparative vision

Vision is the primary sensory modality for a variety of animals with different neural organization and eyes that enable species to cope with the specific demands of their environment. The evolution of vision is likely to have played an important role in shaping the extant biodiversity, and has even been argued to be the catalyst for the Cambrian explosion, a period around 543 million years ago during which all animal forms known today emerged (Parker, 2003; but see Trestman, 2013). Comparative vision aims to probe how these different visual systems solve the problem of seeing and perceiving within a specific environment (Soto & Wasserman, 2010). Comparative psychologists have generally taken two approaches in their research: the *general processes* approach and the *adaptive specialization* approach (Riley & Langley, 1993; Shettleworth, 2010). Briefly, a general processes approach aims to identify the general principles of cognitive processes that are found in multiple species and are used under various environmental conditions. In other words, this approach aims to identify common solutions to similar computational problems, such as the problem of seeing objects (Papini, 2002). In contrast, with the adaptive specialization approach, researchers aim to identify species-specific solutions to solve computational problems specific to a particular environment (Shettleworth, 1993, 2000). These approaches are not mutually exclusive. For instance, certain species-specific mechanisms may consist of sub-components that are widespread. In the studies described in this dissertation, a general processes approach is taken, by comparing two distantly related species (i.e., humans and pigeons), to identify general principles of object perception. However, comparisons between the two systems can provide important insights, not only into the general principles of object perception but into the specific adaptations. Overall, such comparisons are important for understanding the adaptation and evolution of the sensory system of all vertebrates (Shimizu & Karten, 1991; Walls, 1942).

1.3 Why birds?

1.3.1 Spatial and Temporal acuity

As is the case for most primates, many birds are highly dependent on vision for their survival. Indeed of all vertebrate classes, birds are likely the most reliant on vision for their survival. Birds have relatively large eyes, and a considerable portion of their brain is devoted to processing visual information (see Gunturkun, 2000 and Cook, 2001 for reviews). For these reasons, birds are ideal organisms to compare with mammals, in particular primates. Indeed, the statement from Rochon-Duvigneaud (1943), that pigeons are nothing but two eyes with wings appears to be an apt reflection of the importance of vision, and is true of many birds. Furthermore, birds represent an interesting organism for comparative vision given that they, unlike primates, have evolved to deal with the constraints of flight. That is, flying birds have evolved to process complex visual stimuli while keeping their overall size, including brain size, to a minimum.

Research has shown that birds' visual capabilities on basic psychophysical tasks (i.e., at low level) are similar, and sometimes even better than those of humans (see Hodos, 2012 for review). For example, the critical flicker frequency (CFF) of some birds has been shown to be considerably higher than that of humans. The CFF is the frequency at which a flickering light can no longer be resolved and thus appears as continuous. The CFF is a behavioural measure of the visual system's temporal acuity, and is likely related to the detection of motion. Research shows that pigeons (*Columba livia*) and chickens (*Gallus gallus*) have an estimated CFF of 75 Hz and 105 Hz while humans have a CFF of 58.2 Hz (Jarvis et al., 2002; Hendricks, 1966; Nuboer et al., 1992; Hodos, 2012). In addition it has been shown that the CFF of chickens is even higher in the presence of UV light (Rubene et al., 2010). Another often-used measure of visual performance is the ability to resolve fine details in static stimuli, referred to as spatial acuity. Humans are known to have exceptionally high spatial acuity (i.e., 30 c/deg based on behavioural measures) under photopic conditions. In comparison, spatial acuity in birds varies from 6-8 c/deg in nocturnal birds, to 12-18 c/deg in pigeons, to 120-143 c/deg for eagles (Fite, 1973; Martin & Gordon, 1974; Porciatti et al., 1989; Ghim & Hodos, 2006; Hodos et al., 1976; Hahmann & Gunturkun, 1993; Schlaer, 1972; Reymond, 1985; see Hodos, 2012 for review).

1.3.2 Organization of the visual system

All vertebrates have three major visual pathways: the thalamofugal pathway, the tectofugal pathway and the accessory optic system (see Figure 1.2). In the avian brain, information from the retina travels mostly along the tectofugal pathway (pulvinar pathway in mammals). In pigeons for instance, about 75% - 95% of ganglion cells project to the optic tectum (superior colliculus in mammals), the retinal recipient of the tectofugal system (Remy & Gunturkun, 1991). In contrast, in the mammalian brain, the thalamofugal pathway (geniculate-striate pathway in mammals) is the dominant visual pathway (Butler & Hodos, 2005). Lesions to the thalamofugal pathway in humans and macaque monkeys have been shown to cause severe disruptions for colour perception, spatial resolution and can even result in "blindness" (Milner & Goodale, 1995; Ungerleider & Mishkin, 1982). In pigeons however, lesions to the thalamofugal pathway have been shown to result in little to no deficit on visual discrimination tasks involving color, form or intensity (Hodos, Karten, & Bonbright, 1973). In contrast, lesions to the pigeon tectofugal pathway result in deficits that are similar to the deficits found after lesions in the thalamofugal pathway of primates (Chaves, Hodos, & Gunturkun, 1993; Hodos, Karten, & Bonbright, 1973). In spite of these differences, the avian tectofugal and mammalian thalamofugal pathway have a similar modular organization (Shimizu et al., 2010). For example, both systems process form and motion information in parallel and appear to have a feed-forward hierarchical organization whereby information at higher levels is built from the information gathered at the lower stages (Cook, 2001).

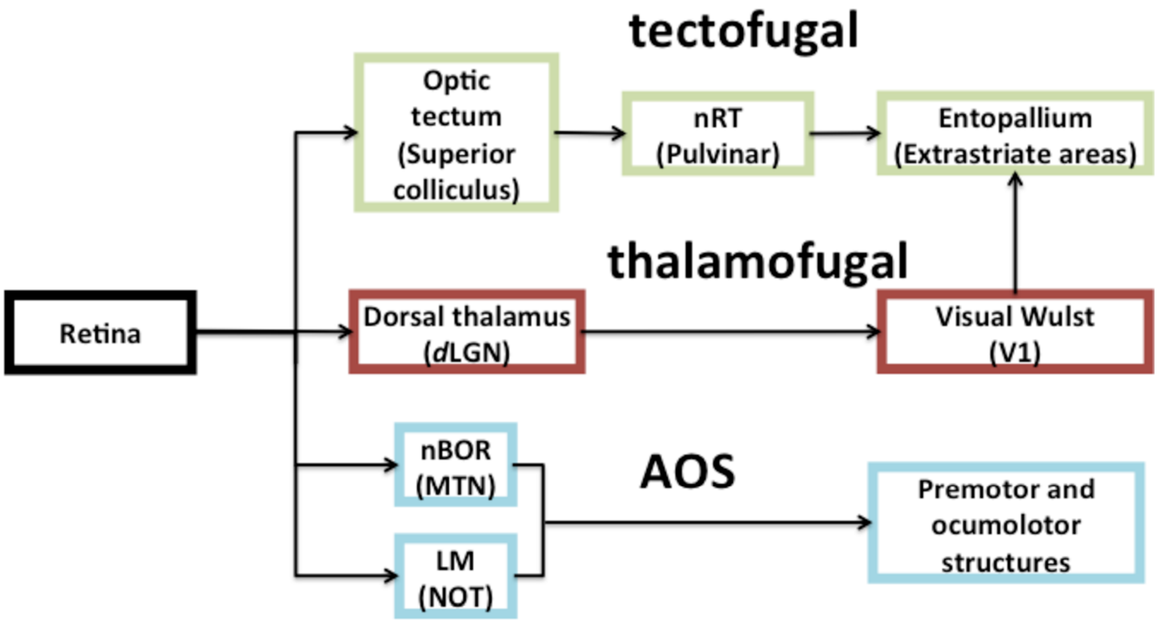


Figure 1.2 Simplified schematic of the three major pathways in birds and reptiles. In parentheses are the mammalian structures. AOS = accessory optic system; dLGN = dorsal lateral geniculate nucleus; LM = nucleus lentiformis mesencephali; MTN = medial terminal nucleus; nBOR = nucleus of the basal optic root; NOT = nucleus of the optic tract; V1 = primary visual cortex.

1.4 Global form pooling

Humans and pigeons exhibit complex visual abilities such as the ability to identify faces, scenes, emotional expressions, gender, and even the ability to categorize paintings from different artists (Herrnstein & Loveland, 1964; Troje et al., 1999; Huber et al., 2000; Watanabe et al., 1995;Watanabe, 2001; Kirkpatrick et al., 2014; Jitsumori and Yoshihara, 1997). As mentioned previously, an important stage in the processing of visual information is the extraction of surfaces from the visual scene. Surfaces can consist of form cues, and motion cues that are processed in parallel by the form pathway and the motion pathway (Mishkin, Ungerleider, & Macko, 1983; Livingstone & Hubel, 1988). In the form pathway, local featural information extracted by cells in V1/V2 is pooled to derive more complex global features or object surfaces (Riesenhuber & Poggio, 1999).

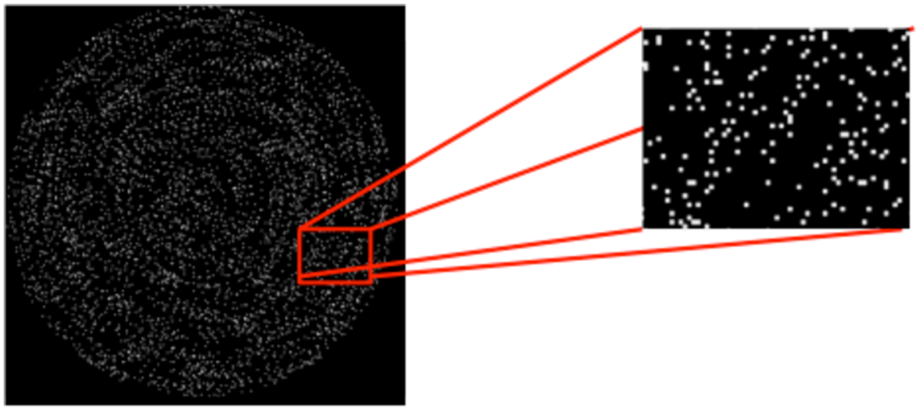


Figure 1.3 As illustrated in the enlarged image of a subsection section of a concentric Glass pattern (red box), the local cues present in Glass patterns provide a weak signal (as might be registered by local filters in V1). This is because each pair of dots is embedded in a noisy and random background comprising of other dot pairs. Nevertheless, a strong percept of global form arises from these weak local signals.

Psychophysicists have devised several stimuli to investigate this global pooling of V1 information, with Glass patterns being one of the most extensively used class of stimuli (Glass, 1969). Glass patterns are static moiré patterns that contain a global structure generated by aligning an array of randomly positioned dot pairs (i.e, dipoles) along contours of the desired global structure (Figure 1.3). As demonstrated by Smith, Kohn, and Movshon (2007) and Smith, Bair and Movshon (2002), the dipoles within Glass patterns provide weak local cues at the level of V1 and V2 as they are embedded in noise created by other dipoles. Yet, the global signal is strong and it can be perceived even when less than 20% percent of the dipoles are aligned in the correct orientations (Wilson & Wilkinson, 1998). These results suggest that the perception of Glass patterns consists of two stages; the initial stage consist of the detection of local cues, and the second consist of the pooling of these local cues to derive the global percept. Wilson and Wilkinson (1998) proposed that a likely candidate for the intermediate level of form processing is area V4 (see Loffler, 2013 for review). Neurons in V4 have receptive fields about four to seven time larger than V1 cells' receptive fields and electrophysiology in V4 shows greater activation for concentric radial and hyperbolic stimuli (i.e., non-Cartesian) when compared to parallel stimuli (i.e., Cartesian) (Desimone & Schein, 1987; Gallant et al., 1993). The preference of V4 for non-cartesian form has been confirmed through fMRI in humans (Dumoulin & Hess, 2007; Wilkinson et al., 2000; Ostwald et al., 2008). Furthermore, Gallant, Shoup, and Mazer (2000) reported deficiencies in processing concentric shape in a patient with lesion around V4.

1.5 Motion perception

Just as with the processes that leads to form perception, in the mammalian visual system, motion is processed in a feed-forward system. At the level of V1, local motion signals are extracted and are sent to the medial temporal area (MT), and subsequently to the medial superior temporal area (MST). In MT and MST, the local motion signals are pooled to create the percept of global motion (see Burr & Thompson, 2011 for review). To study the pooling mechanisms of motion, researchers often use random dots stimuli (RDS), a stimulus class that is in many ways similar to the previously mentioned Glass patterns. RDS consist of an array of randomly placed dots moving coherently (signal dots) intermingled with dot moving randomly (noise). Random dot stimuli allow researchers to examine the mechanisms of global motion without any confounds. For instance, many researchers (e.g., Watson & Turano, 1995) use gabor patches to study motion, however, these stimuli are confounded with orientation given that the stimulus can only move in directions perpendicular to their orientation and therefore cannot be used for global motion. Newsome and Pare (1988) used RDS to measure the coherence (i.e., signal to noise ratio) threshold in monkeys and reported that behavioural measures were equivalent to neural threshold of individual neurons in areas MT. These results have been substantiated in humans; Braddick et al., (2001) found activation in V5 (human homologue of MT) in response to coherent motion compared to random noise, but no such activity were found in V1. Electrophysiological studies in monkeys also suggest that MST is specialized in processing complex global motion (Duffy & Wurtz, 1991; Graziano, Andersen, & Snowden, 1994; Tanaka & Saito, 1989). While MT appears to respond to translational motion, evidence suggests that MST respond best to rotational and radial global motion.

1.6 Interaction form and motion

Although it has been established that at the mid-level stage of processing, form and motion in the mammalian brain are processed in parallel through distinct modules, accumulating evidence now suggest that form and motion do interact at the intermediate stage of visual processing (see Mather et al., 2013 for review). One example of form and motion interaction comes from the Gestalt principle of common fate in which an invisible form becomes visible the moment the elements of the form move together in a coherent fashion. Similarly, form information has been shown to generate the perception of coherent motion. For instance, observers report a salient percept of coherent motion when a series of independently generated Glass patterns is shown in rapid succession (termed dynamic Glass patterns) in spite of the fact that no coherent motion information is available in Glass patterns (Ross, Badcock, & Hayes, 2000). As mentioned previous, Glass patterns are stimuli that contain only form information (Glass, 1969). Currently little is known about the mechanisms that result in the global coherent motion percept from dynamic Glass patterns. Chapters 2 and 3 address this topic and aim to reconcile the perception of implied motion with the known distinction of form and motion at the mid-level stage of visual processing. Form and motion are processed by distinct units within the avian visual system, as is the case for the mammalian visual system (Shimizu et al., 2010). However, it is unknown whether pigeons perceive implied motion from dynamic Glass patterns as humans do. Chapters 4 and 5 attempts to address the question of whether pigeons perceive implied motion from dynamic Glass patterns in a similar way to humans.

Most of what is known about the interaction of form and motion at mid and high level processing is based on rigid motion information. Non-rigid motion involves movement of the object with no deformation. However, most if not all biological movement in nature involves motion with deformation (i.e., non-rigid motion). Thus, in chapter 6 I present a study on the use of form and non-rigid for object perception in humans and pigeons, and discuss hypotheses to link the perception of non-rigid motion with the known properties of mid-level vision.

1.7 Reference

Anderson, B. (1999). Surface perception. In R. A. Wilson, F. C. Keil (Eds.), *The MIT encylopedia of the cognitive sciences*. Cambridge: MIT Press

Braddick, O. J., O'Brien, J. M., Wattam-Bell, J., Atkinson, J., Hartley, T., & Turner, R. (2001). Brain areas sensitive to coherent visual motion. *Perception-London*, *30*(1), 61-72.

Butler, A. B. & Hodos, W. (2005). *Comparative vertebrate neuroanatomy: evolution and adaptation* (2nd ed.). New York: Wiley-Liss.

Burr, D., & Thompson, P. (2011). Motion psychophysics: 1985–2010. *Vision research*, *51*(13), 1431-1456.

Chaves, L. M., Hodos, W., & Güntürkün, O. (1993). Color-reversal learning: effects after lesions of thalamic visual structures in pigeons. *Visual neuroscience*, *10*(06), 1099-1107.

Carandini, M., Demb, J. B., Mante, V., Tolhurst, D. J., Dan, Y., Olshausen, B. A., Gallant, J. L., & Rust, N. C. (2005). Do we know what the early visual system does?. *The Journal of Neuroscience*, *25*(46), 10577-10597.

Cook R. G. (2001). Hierarchical stimulus processing in pigeons. In R. G. Cook (Ed.), *Avian visual cognition*. http://www.pigeon.psy.tufts.edu/avc/cook/

Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *The Journal of Neuroscience*, *4*(8), 2051-2062.

Desimone, R., & Schein, S. J. (1987). Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form. *Journal of neurophysiology*, *57*(3), 835-868.

Duffy, C. J., & Wurtz, R. H. (1991). Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *Journal of neurophysiology*, *65*(6), 1329-1345.

Dumoulin, S. O., & Hess, R. F. (2007). Cortical specialization for concentric shape processing. *Vision Research*, *47*(12), 1608–1613

Fite, K. V. (1973). Anatomical and behavioral correlates of visual acuity in the great horned owl. *Vision research*, *13*(2), 219-IN2.

Gallant, J. L., Braun, J., & Vanessen, D. C. (1993, January 1). Selectivity for polar, hyperbolic, and cartesian gratings in macaque visual-cortex. *Science*, *259*(5091), 100–103.

Gallant, J. L., Shoup, R. E., & Mazer, J. A. (2000). A human extrastriate area functionally homologous to macaque V4. *Neuron*, *27*(2), 227-235.

Ghim, M. M., & Hodos, W. (2006). Spatial contrast sensitivity of birds. *Journal of Comparative Physiology A*, *192*(5), 523-534.

Glass, L. (1969). Moire effect from random dots. *Nature*, *223*(5206), 578-580.

Giese, M. A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience*, *4*(3), 179-192.

Graziano, M. S., Andersen, R. A., & Snowden, R. J. (1994). Tuning of MST neurons to spiral motions. *The Journal of neuroscience*, *14*(1), 54-67.

Güntürkün, O. (2000). Sensory Physiology: Vision. In G. C., Whittow (Ed.), *Sturkie's avian physiology*, (pp. 1-19). Orlando: Academic Press.

Hahmann, U., & Güntürkün, O. (1993). The visual acuity for the lateral visual field of the pigeon (Columba livia). *Vision research*, *33*(12), 1659-1664.

Hendricks, J. (1966). Flickerthresholds as determined by a modified conditioned suppression procedure. *Journal of the Experimental Analysis of Behavior*, *9*(5), 501-506.

Herrnstein, R. J., and Loveland,D. H. (1964).Complex visual concept in the pigeon. *Science 146*, 549–551. doi: 10.1126/science.146.3643.549

Hodos, W., Karten, H. J., & Bonbright, J. C. (1973). Visual intensity and pattern discrimination after lesions of the thalamofugal visual pathway in pigeons. *Journal of Comparative Neurology*, *148*(4), 447-467.

Hodos, W., Leibowitz, R. W., & Bonbright, J. C. (1976). Near-field visual acuity of pigeons: effects of head location and stimulus luminance. *Journal of the Experimental Analysis of Behavior*, *25*(2), 129-141.

Hodos W (2012) What Birds See and What They Don't: Luminance, contrast, and spatial and temporal resolution. In O. F. Lazareva, T. Shimizu, E. A., Wasserman (Eds.), *How animals see the world: Behavior, biology, and evolution of vision* (pp. 5-25). London: Oxford University Press.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of physiology*, *160*(1), 106.

Huber, L., Troje, N. F., Loidolt, M., Aust, U., and Grass, D. (2000). Natural categorization through multiple feature learning in pigeons. Q. J. Exp. Psychol. B 53B, 341–357. doi: 10.1080/027249900750001347

Jarvis, J. R., Taylor, N. R., Prescott, N. B., Meeks, I., & Wathes, C. M. (2002). Measuring and modelling the photopic flicker sensitivity of the chicken (Gallus g. domesticus). *Vision research*, *42*(1), 99-106.

Jitsumori, M., and Yoshihara, M. (1997). Categorical discrimination of human facial expressions by pigeons: a test of the linear feature model. Q. J. Exp. Psychol. 50, 253–268

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, *17*(11), 4302-4311.

Kirkpatrick, K., Bilton, T., Hansen, B. C., and Loschky, L. C. (2014). Scene gist categorization by pigeons. J. Exp. Psychol. Anim. Behav. Process. Available online at: http://psycnet.apa.org/psycinfo/2013-44235-001/

Koffka, K. (1935). *Principles of Gestalt Psychology.* New York: Harcourt Brace.

Köhler, W. (1940). *Dynamics in Psychology.* New York: Liveright Publishing Corp.

Loffler, G. (2008). Perception of contours and shapes: Low and intermediate stage mechanisms. *Vision Research*, *48*(20), 2106–2127

Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*, *240*(4853), 740-749.

Martin, G. R., & Gordon, I. E. (1974). Visual acuity in the tawny owl (Strix aluco). *Vision Research*, *14*(12), 1393-1397.

Marr, D. (1982). *Vision: A computational investigation into the human representation and processing of visual information*. San Francisco: W. H. Freeman

Mather, G., Pavan, A., Marotti, R. B., Campana, G., & Casco, C. (2013). Interactions between motion and form processing in the human visual system. *Frontiers in computational neuroscience*, *7*.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: two cortical pathways. *Trends in neurosciences*, *6*, 414-417.

Nakayama, K. (1999). Mid-level vision. In R. A. Wilson, F. C. Keil (Eds.), *The MIT encyclopedia of the cognitive science*s. Cambridge: MIT Press.

Nakayama, K. & He, Z. J. (1995). Attention to surfaces: beyond a Cartesian understanding of visual attention. In T. V. Papathomas, C. Chubb, A. Gorea, E. Kowler (Eds), *Early Vision and Beyond*, (pp. 181-188). Cambridge: M.I.T. Press, Cambridge.

Newsome, W. T., & Pare, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual layer. *Journal of Neuroscience*, *8*(6), 2201–2211.

Nuboer, J. F. W., Coemans, M. A. J. M., & Vos, J. J. (1992). Artificial lighting in poultry houses: do hens perceive the modulation of fluorescent lamps as flicker?. *British poultry science*, *33*(1), 123-133.

Ostwald, D., Lam, J. M., Li, S., & Kourtzi, Z. (2008). Neural coding of global form in the human visual cortex. *Journal of Neurophysiology*, *99*(5), 2456–69. doi:10.1152/jn.01307.2007

Porciatti, V., Fontanesi, G., & Bagnoli, P. (1989). The electroretinogram of the little owl (Athene noctua). *Vision Research*, *29*(12), 1693-1698.

Papini, M. R. (2002). Pattern and process in the evolution of learning. *Psychological Review*, *109*, 186–201. doi:10.1037/0033- 295X.109.1.186.

Parker, A. (2003). *In the blink of an eye: How vision sparked the big bang of evolution*. New York: Perseus Publishing.

Pizlo, Z. (2001). Perception viewed as an inverse problem. *Vision Research*, *41*(24), 3145-3161.

Remy, M., & Güntürkün, O. (1991). Retinal afferents to the tectum opticum and the nucleus opticus principalis thalami in the pigeon. *Journal of Comparative Neurology*, *305*(1), 57-70.

Reymond, L. (1985). Spatial visual acuity of the eagle Aquila audax: a behavioural, optical and anatomical investigation. *Vision research*, *25*(10), 1477-1491.

Ross, J., Badcock, D. R., & Hayes, A. (2000). Coherent global motion in the absence of coherent velocity signals. Current Biology, 10, 679–682.

Riley, D. A., & Langley, C. M. (1993). The logic of species comparisons. *Psychological*

Science, 4, 185–189

Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature neuroscience*, *2*(11), 1019-1025.

Rochon-Duvigneaud, A. (1943). *Les yeux et la vision des vertébrés*. Paris: Masson.

Rubene, D., Håstad, O., Tauson, R., Wall, H., & Ödeen, A. (2010). The presence of UV wavelengths improves the temporal resolution of the avian visual system. *The Journal of experimental biology*, *213*(19), 3357-3363.

Shlaer, R. (1972). An eagle's eye: quality of the retinal image. *Science*, *176*(4037), 920-922.

Shettleworth, S. J. (1993). Where is the comparison in comparative cognition? Alternative research programs. *Psychological Science*, *4*, 179–184.

Shettleworth, S. J. (2000). Modularity and the evolution of cognition. In C. M. Heyes & L. Huber (Eds.), the evolution of cognition (pp. 43–60). Cambridge, MA: MIT Press.

Shettleworth, S. J. (2010). *Cognition, evolution, and behavior*. New York: York: Oxford University Press.

Shimizu, T. & Karten, H. J. (1991). Central visual pathways in reptiles and birds: Evolution of the visual system. In J. Cronly-Dillon & R. Gregory (Eds.), *Vision and visual dysfunction, vol. 2: Evolution of the eye and visual system*. (pp. 421-441). London: Macmillan Press

Shimizu, T., Patton, T. B., & Husband, S. A. (2010). Avian visual behavior and the organization of the telencephalon. *Brain, behavior and evolution*, *75*(3), 204-217.

Smith, M. A., Bair, W., & Movshon, J. A. (2002). Signals in macaque striate cortical neurons that support the perception of glass patterns. *Journal of Neuroscience, 22*, 8334–8345.

Smith, M. A., Kohn, A., & Movshson, J. A. (2007). Glass pattern responses in macaque V2 neurons. *Journal of Vision*, *7*, 1–15.

Soto, F., & Wasserman, E. (2010). Comparative Vision Science: Seeing Eye to Eye. *Comparative Cognition & Behavior Reviews*, *5*, 148–154. doi:10.3819/ccbr.2010.50011

Tanaka, K., & Saito, H. A. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology*, *62*(3), 626-641.

Trestman, M. (2013). The Cambrian explosion and the origins of embodied cognition. *Biological Theory*, *8*(1), 80-92.

Tsao, D. Y., Freiwald, W. A., Tootell, R. B., & Livingstone, M. S. (2006). A cortical region consisting entirely of face-selective cells. *Science*, *311*(5761), 670-674.

Troje, N. F., Huber, L., Loidolt, M., Aust, U., & Fieder, M. (1999). Categorical learning in pigeons: the role of texture and shape in complex static stimuli. *Vision research*, *39*(2), 353-366.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge: MIT Press.

Walls, G. L. (1942). *The vertebrate eye and its adaptive radiation*. Oxford, England: Cranbrook Institute of Science.

Watanabe, S. (2001). Van Gogh, Chagall and pigeons: picture discrimination in pigeons and humans. *Animal Cognition*, *4*(3-4), 147-151.

Watanabe, S., Sakamoto, J., & Wakita, M. (1995). Pigeons' discrimination of paintings by Monet and Picasso. *Journal of the experimental analysis of behavior*, *63*(2), 165.

Watson, A. B., & Turano, K. (1995). The optimal motion stimulus. *Vision research*, *35*(3), 325-336.

Wertheimer, M. (1923). Untersuchungen zur Lehre von der Gestalt, II. *Psychologische Forschung* 4:301-350. Condensed translation published as Laws of organization in perceptual forms, in W. D. Ellis (1938), *A Sourcebook of Gestalt Psychology* (pp. 71 - 88). New York: Harcourt, Brace.

Wilkinson, F., James, T. W., Wilson, H. R., Gati, J. S., Menon,R. S., &Goodale,M.A. (2000). An fMRI study of the selective activation of human extrastriate form vision areas by radial and concentric gratings. *Current Biology*, *10*(22), 1455–1458.

Wilson, H. R., & Wilkinson, F. (1998). Detection of global structure in Glass patterns: implications for form vision. *Vision research*, *38*(19), 2933-2947.

Chapter 2

Perception of dynamic Glass patterns

2.1 Abstract

In the mammalian brain, form and motion are processed through two distinct pathways at early stages of visual processing. However, recent evidence suggests that these two pathways may interact. Here we used dynamic Glass patterns, which have been previously shown to create the perception of coherent motion in humans, despite containing no motion coherence. Glass patterns are static stimuli that consist of randomly positioned dot pairs that are integrated spatially to create the perception of a global form, whereas dynamic Glass patterns consist of several independently generated static Glass patterns presented sequentially. In the current study, we measured the detection threshold of five types of dynamic Glass patterns and compared the rank order of the detection thresholds with those found for static Glass patterns and real motion patterns (using random dot stimuli). With both the static Glass patterns and dynamic Glass patterns, detection thresholds were lowest for concentric and radial patterns and highest for horizontal patterns. We also found that vertical patterns were better detected than horizontal patterns, consistent with prior evidence of a ‘‘horizontal effect’’ in the perception of natural scene images. With real motion, detection thresholds were equivalent across all patterns, with the exception of higher thresholds for spiral patterns. Our results suggest that dynamic Glass patterns are processed primarily as form prior to input into the motion system.

2.2 Introduction

Visual processing of form and motion is thought to be carried out independently by distinct neural substrates in the cortex of the mammalian brain (Braddick et al., 2000; Livingstone & Hubel, 1988; Milner & Goodale, 1995; Mishkin, Ungerleider, & Macko,1983). Form information is processed in the ventral pathway, where information from V1 is carried to V4 and the inferior temporal cortex (IT). In contrast, motion information is processed by the dorsal pathway, where information from V1 is carried to the middle temporal area (MT) and to the parietal cortex. Support for this two-pathway hypothesis has come from numerous monkey and human lesion studies that have demonstrated that damage to the ventral pathway results in impairment of object recognition, whereas damage to the dorsal pathway results in impairment of motion processing (Livingstone & Hubel, 1988; Ungerleider & Mishkin, 1982). For instance, patient L.M., who had bilateral damage to the dorsal pathway, was found to exhibit an impairment in detecting visual motion but no impairment to other visual functions (e.g., object and face recognition; Zihl, Cramon, & Mai, 1983).

Despite the apparent segregation at the cortical level, psychophysical evidence suggests that there is an interaction of form and motion processing (see Kourtzi, Krekelberg, and van Wezel (2008) for review). For instance, 2D motion can provide 3D shape information, a phenomenon called structure-from-motion (Siegel & Andersen, 1988). Similarly, form information can also influence motion perception. As one example, trailing lines, i.e., motion streaks, behind fast moving objects have been shown to influence the perception of motion direction (Geisler, 1999). Further evidence that form influences motion processing was shown by Ross, Badcock, and Hayes (2000), who demonstrated that humans perceive coherent motion (termed ‘‘implied motion’’ by Krekelberg et al., 2003) when shown a rapid sequence of independently generated Glass patterns, termed ‘‘dynamic Glass pattern’’. Importantly, this occurs in spite of the fact that no coherent motion information is available in these patterns. A Glass pattern is a pattern that consists of an array of randomly placed dots that are each paired with a second dot oriented along a common rule (Glass, 1969; see Figure 2.1). Given that each Glass pattern is generated based on an array of randomly placed dots, when a sequence of independently generated Glass patterns is shown, no coherent motion is present in the sequence. Ross, Badcock, and Hayes (2000) suggest that orientation information provided by the dipoles in Glass patterns influences motion perception in a similar way to motion streaks. Furthermore, Smith, Bair, and Movshon (2002) and Smith and Kohn (2007) showed that cells in V1 and V2 respond selectively to dipoles’ orientation.

Krekelberg et al. (2003) and Krekelberg, Vatakis, and Kourtzi (2005) investigated the neural basis of dynamic Glass patterns in monkeys and humans. Using single-unit recordings, Krekelberg et al. (2003) found that a subpopulation of motion selective cells in medial temporal (MT) and medial superior temporal (MST) areas of macaque monkeys did not differentiate between real coherent motion and dynamic Glass patterns. Krekelberg, Vatakis, and Kourtzi (2005) adapted this task into a human fMRI study and found similar results in the human visual cortex.

A **B**

Concentric
100% coherence

Concentric
60% coherence

C **D**

Radial
100% coherence

Horizontal
100% coherence

E **F**

Spiral
100% coherence

Vertical
100% coherence

Figure 2.1 Types of Glass patterns used in this study. Coherence (proportion of signal dots) was varied as illustrated with the concentric pattern at 60% coherence in panel B. In the real motion condition, each frame appeared as a random array of dots but the global motion pattern followed the same pattern as those of the Glass patterns.

Specifically, they found that the human motion complex (hMT+/V5) contains a subpopulation of cells that are selective to both implied motion (from dynamic Glass patterns) and real motion with the same pattern structure. In other words, these cells did not differentiate between real and implied motion. Krekelberg, Vatakis, and Kourtzi (2005) suggest that this overlap is why humans perceive coherent motion from the dynamic Glass patterns. Both implied and real motion have also been shown to be correlated with neural activation in the ventral pathway. However, in contrast to the areas in the dorsal pathway, in the ventral pathway, specifically in V4 and the lateral occipital complex (LOC), neurons that respond to implied motion patterns do not respond to real motion patterns and neurons that respond to real motion patterns do not respond to implied motion patterns.

Glass patterns are often used to investigate the processing of global form information because the shape of the patterns can only be determined by pooling the local information (Wilson & Wilkinson, 1998). Prior results have found that humans have different detection thresholds for different types of static Glass patterns, suggesting that the pooling mechanism is more efficient for certain types (Anderson & Swettenham, 2006; Aspell, Wattam-Bell, & Braddick, 2006; Kelly et al., 2001; Pei, Pettet, & Vildavski, 2005; Seu & Ferrera, 2001; Swettenham, Anderson, & Thai, 2010; Wilson & Wilkinson, 1998). Specifically, humans are usually more sensitive to concentric and radial forms (see Figure 2.1A–C), as compared to horizontal, vertical, and spiral forms (Figure 2.1D–F). There is some debate over these results because Dakin and Bex (2002) observed an effect of the shape of the stimulus window on threshold, with sensitivity for concentric patterns being reduced when a square stimulus window is used. Other studies, however, have found greater sensitivity to concentric and radial over translational patterns even with a square window (Anderson & Swettenham, 2006; Kelly et al., 2001), suggesting that the window cannot account for the entire advantage shown by concentric or radial patterns. It is believed that form processing of translational patterns (i.e., horizontal and vertical patterns) likely occur at a local level whereas radial, concentric, and spiral are processed at a global level. In contrast, when using random dot motion stimuli (i.e., dots are coherently shifted across frames) to assess the thresholds for different types global coherent motion, humans do not show differential thresholds for radial, concentric, or translational motion (Blake & Aiba, 1998; Morrone, Burr, & Vaina, 1995). However, humans do exhibit a higher threshold for spiral motion (Morrone et al., 1999). It should be noted that recently Lee and Lu (2010) found that thresholds were lower for radial and circular compared to translational motion by using a multiple aperture stimulus using arrays of randomly oriented drifting Gabor elements. Lee and Lu (2010) suggest that the difference between their results and those using random dot stimuli may be a due to correspondence noise found in the random dot stimuli.

Currently it is known that people have a lower threshold for dynamic compared to static Glass patterns. Burr and Ross (2006) and Or, Khuu, and Hayes (2007) have reported that thresholds for concentric and translational dynamic Glass patterns were lower than the thresholds of equivalent static Glass patterns. However it is currently unclear whether detection thresholds for dynamic Glass patterns are lower because of their similarity to real motion patterns, and thus potentially reliant on motion-related processes, or whether the detection of dynamic Glass patterns is driven by the same mechanisms as static Glass patterns. In order to address this issue, we sought to measure the thresholds for different types of dynamic Glass patterns to determine whether the relative performance on each pattern type is similar to static Glass patterns or similar to real motion patterns. In the present study we measured the thresholds for five types of patterns (Figure 2.1) and manipulated the presence or type of motion cue in three conditions: static Glass patterns, dynamic Glass patterns, and random dot stimuli that moved according to the types of pattern. In particular, the relative ranking of performance on each of the five patterns, across the three conditions, will indicate whether dynamic Glass patterns are encoded more similarly to real motion or to static forms. This is in turn will inform the research on form and motion interaction at an intermediate-level of visual processing.

2.3 Method

Participants

Seven adults with normal or corrected-to-normal vision participated in the static and dynamic Glass pattern conditions of this study (*n* = 7). This included all four authors, and three graduate students from the University of Alberta who had only cursory knowledge of the purpose of the experiment. Real motion consisted of the same participants with the exception of one author (*n* = 6). Prior to the actual experimental testing, the participants were given multiple training sessions and were therefore deemed to be experts in all three conditions.

Apparatus

Stimuli were displayed on a 19-in. Samsung SyncMaster 940BF monitor (resolution: 1280 x 1024 pixels; refresh rate: 60 Hz). Participants were seated comfortably at a viewing distance of 45 cm to the monitor, with the center of the monitor positioned at eye-level. Participants' head position was fixed with a chin rest.

Stimuli were generated in MATLAB (The MathWorks, Natick, MA) and saved as bitmap images. E-Prime version 2.0 (Psychology Software Tools Inc., Sharpsburg, PA) was used to present the stimuli and record responses.

Stimuli and design

Each stimulus was presented for a total duration of 167 ms. Five types of patterns were used in all the conditions (see Figure 2.1). Each stimulus consisted of 10 frames of Glass patterns or random dot stimuli, each of which was updated at every monitor refresh (16.7 ms per frame). The method of constant stimuli was used to present the stimuli.

It should be noted that the dipole orientation for spiral Glass patterns was randomly angled to be either at 45° or 135°, midway between dipole orientations for radial (0°) and concentric (90°) patterns. For real motion, the angular displacement of signal dots for spiral motion was also randomly either 45° or 135°.

Static Glass patterns

Each Glass pattern subtended a visual angle of 11.16° and consisted of square dots with an angular size of 0.04° x 0.04°. The density of dots within each pattern was set at 6% and the dot separation was 0.26°. The 10 frames for this condition were identical Glass patterns, thus giving the appearance of being static. The coherence level was varied by changing the ratio of signal-to-noise dots within a pattern. The signal was defined as the amount of dipoles in the Glass pattern. Thus at 50%, only half of the dots in the Glass pattern were part of a dipole. A total of eight coherence levels were used: 0%, 20%, 30%, 40%, 50%, 60%, 80%, and 100%.

In addition to the five types of patterns, we included a control random pattern (Wilson & Wilkinson, 1998). The control random patterns consisted of dipoles oriented randomly (i.e., there was no global form). The coherence level of the control random pattern was also varied to match those of the other patterns by adjusting the number of dipoles.

Dynamic Glass patterns

These were the same as static Glass patterns with the exception that for each frame we presented a new independently generated Glass pattern (following from the same global rule).

In the case of spiral Glass patterns, all frames in a given trial consisted of the same type of spiral pattern (i.e., angular displacements of either 45° or 135°).

Real motion

The stimuli consisted of randomly placed dots in a circular display of the same size as the Glass patterns. The size and density of the dots were also the same as those of the Glass patterns. Each dot moved at a speed of 15.67°/s (i.e., the distance each dot shifted across frames was equivalent to the separation of Glass pattern dipoles, 0.26°, given that our image update rate was 60 Hz). Dots were removed when their position on the current frame reached the edge of the circular aperture. New dots were generated following from Gaussian probability functions, such that dots were most likely to be generated near the center of the circular aperture for spiral and radial patterns, but would be most likely to be generated near the starting edge of the motion for horizontal and vertical patterns (e.g., the top edge of the aperture for vertical patterns with downward motion). Note that in the concentric pattern, dots never exceeded the edge of the aperture and thus were never removed. Patterns were generated such that the density of the pattern was consistently at 6%.

The image update rate, number of frames, and duration of stimuli were the same as those of static and dynamic Glass patterns. Five types of coherent motion were tested: concentric, radial, spiral, vertical and horizontal. Thus the motion patterns mimicked the form patterns used in static and dynamic Glass patterns conditions. Coherence level was varied by changing the likelihood that a dot was a signal dot in each frame (i.e., we used a limited lifetime algorithm; Scase, Braddick, & Raymond, 1996). Signal dots moved in the coherent direction, whereas noise dots moved randomly (distance and direction). At 100% coherence, each dot has a 100% chance of being chosen as a signal dot, and therefore all the dots move coherently.

However, at 50% coherence, on each frame each dot has a 50% chance of being a signal dot. The coherence levels in this condition were 0%, 20%, 30%, 40%, 50%, 60%, 80%, and 100%. However, due to the fact that motion was easily detected for all patterns except for spiral (i.e., performance was near-ceiling at coherences of 20%), we conducted an additional session using coherence levels of 0%, 4%, 6%, 8%, 10%, 12%, 16%, and 20% to obtain more precise threshold estimates.

The direction of motion within a trial remained consistent across frames, but was counterbalanced within the session. For radial patterns, the direction of motion moved inward (i.e., contraction) on half of the trials and outward (i.e., expansion) on half of the trials. These motion patterns were pre-generated such that dots always moved outwards (i.e., expansion). To create motion patterns where dots moved inwards (i.e., contraction), frame sequences were simply presented in the reverse order relative to how they were initially generated. Concentric patterns rotated either clockwise or counterclockwise; horizontal patterns moved left or right; vertical patterns moved up or down; spiral patterns rotated inward-clockwise or outward-counterclockwise.

Procedure

At the beginning of each block of trials, participants were told which type of pattern they would be trying to detect. As illustrated in Figure 2.2, the participants began the trial by clicking a yellow start stimulus. The stimulus display was then presented, followed by the appearance of two response circles. The green response circle always appeared on the left side of the screen, along with the word ‘‘Pattern’’, while the red circle always appeared on the right side of the screen, along with the words ‘‘No Pattern’’. Participants selected the green circle with the computer mouse if they perceived a coherent pattern, otherwise they selected the red circle. After the participant responded, there was a 250 ms delay before the yellow start stimulus appeared to begin the next trial.

Testing was carried out in five blocks: one block for each type of pattern. In each condition, a total of 20 trials per coherence level were presented for both the given pattern and the random control. This yielded a total of 320 trials within a block. Participants were allowed to take a brief break between blocks but were required to complete all five blocks in a single day.

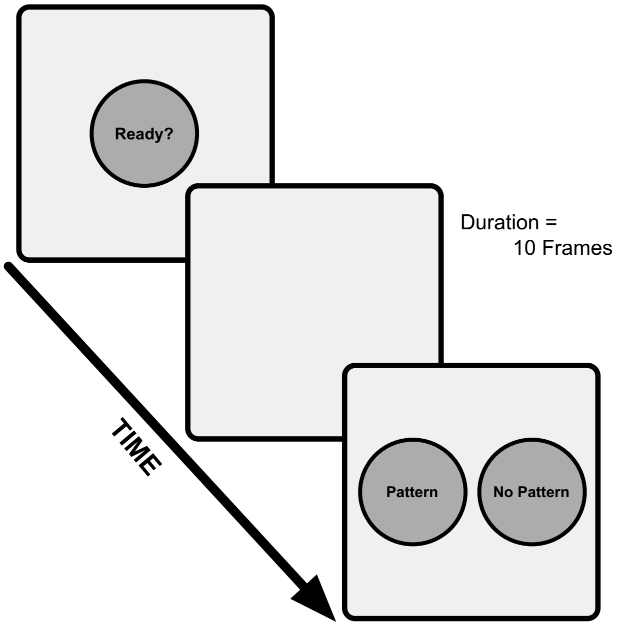


Figure 2.2 Illustration of a single trial. Polarity of the pattern is reversed for illustrative purposes only. In the experiment the participants viewed white dots on a black background, as in Figure 2.1.

Data analysis

To analyze the data, we first calculated the proportion of responses for which the participant detected a pattern at each coherence level (i.e., hits), for each block. We also calculated the proportion of responses for which the participant detected a pattern for random stimuli at each coherence level (i.e., false alarms).

We then calculated *d′*, following from standard signal-detection analyses (Green & Swets, 1966), by finding the difference of the *Z*-transformed values for hits and false alarms. We then plotted the d0 values as a function of coherence level (Figure 2.3). Participants' coherence threshold for each pattern was estimated using a three-parameter cumulative Weibull function (Weibull, 1951), *F*(*c*), of the following form:

$$F(c) = \alpha(1 - e^{-(c/\beta)^{\gamma}})$$

where *c* is the coherence level, and a, b, and c are the asymptote, spread, and shape parameters, respectively. The Weibull function was fit to data for each pattern, for each participant, by means of the Nelder and Mead (1965) simplex algorithm set to minimize the root-mean-squared-deviation (RMSD) between the function's estimation and the data. This procedure was repeated for 1000 iterations to ensure the global minima was found. The threshold was then calculated as the coherence level corresponding to *d′* = 1.5, using the best-fitting parameters.

All statistical analyses were conducted using SigmaPlot (Systat Software Inc., Chicago, IL) and MATLAB (The MathWorks Inc., Natick, MA). Effects were considered significant based on an alpha level of .05. One-way repeated-measures ANOVAs and Tukey post hoc pairwise analyses were conducted on the log-transformed threshold coherence levels of the different patterns. If the data violated the assumptions for parametric tests, a non-parametric test (Kruskal–Wallis) was performed instead, with pairwise comparisons conducted using Dunn's method. We then calculated the standard error for each pattern across participants before exponentially transforming the threshold back for reporting.

2.4. Results

Static Glass patterns

The mean *d'* for each pattern is plotted as a function of coherence level in Figure 2.3A. Figure 2.3B shows the mean coherence threshold of each pattern. A one-way repeated-measures ANOVA yielded a significant effect of pattern type, $F(4, 24) = 21.72$, $p < .001$. Tukey post hoc analyses demonstrated that the thresholds for concentric and radial patterns were significantly lower than the thresholds of the other patterns (all *p*s < .05) but did not differ from each other ($p > .1$). The threshold for spiral patterns was significantly lower than for horizontal patterns ($p < .01$) but not different from the threshold for vertical patterns ($p > .1$). Finally, the threshold for vertical patterns was significantly lower than the threshold for horizontal patterns ($p < .05$).

Dynamic Glass patterns

The mean *d'* for each pattern was plotted as a function of coherence level and is shown in Figure 2.3C. Figure 2.3D shows the mean threshold estimates for each pattern. As with the static Glass patterns, a one-way repeated-measures ANOVA

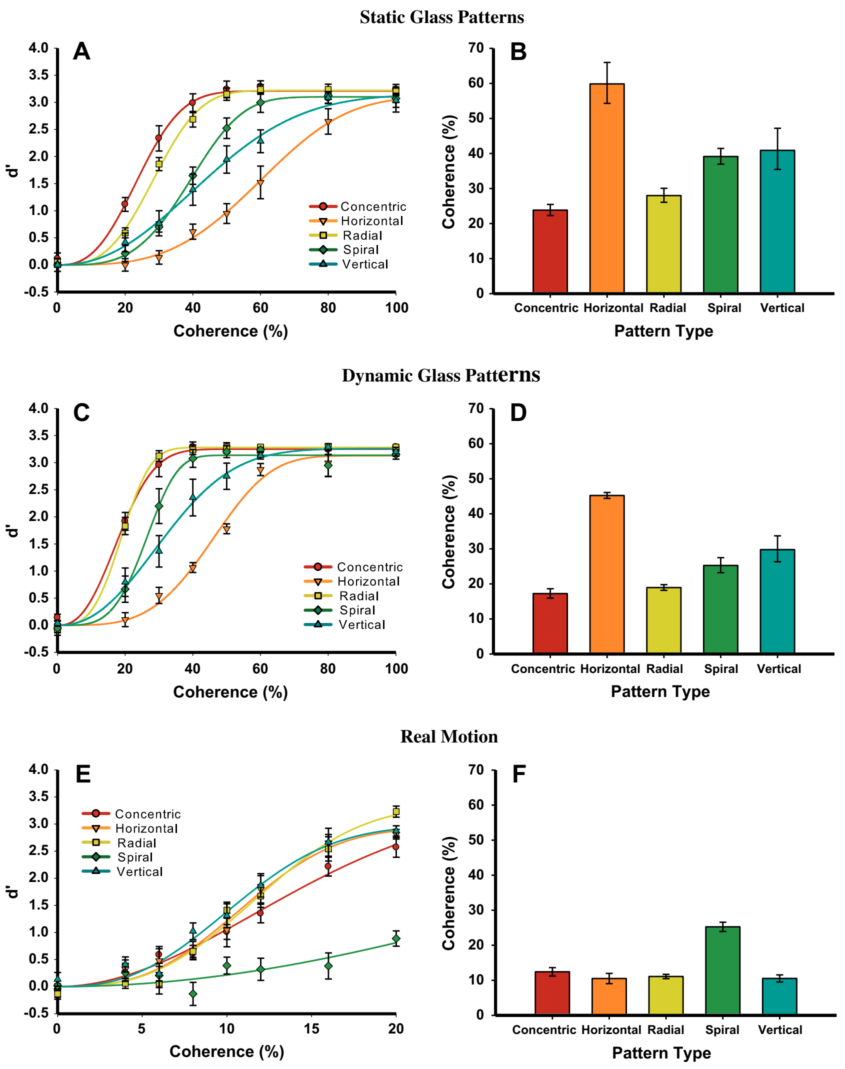


Figure 2.3 Panels A, C, and E represent the *d'* as a function of coherence level for each pattern type, within each condition. Lines represent the Weibull function fit for each pattern type; markers represent the observed *d'*. Panels B, D, and F represent the threshold (coherence level corresponding to a *d'* of 1.5) for each pattern type, within each condition. Error bars represent the standard error of the mean.

revealed a significant effect of pattern type, $F(4, 24) = 21.75$, $p < .001$. Tukey post hoc analyses found that thresholds for concentric and radial patterns did not differ from each other ($p > .1$) but were significantly lower than the thresholds for vertical and horizontal patterns (all *p*s < .05). The threshold for concentric patterns was lower than for spiral ($p < .05$); the threshold for radial did not differ to that for spiral ($p > .1$). The threshold for spiral pattern was also not different from the threshold for vertical patterns ($p > .1$), but was significantly lower than for horizontal patterns ($p < .001$). The threshold for vertical patterns was also found to be significantly lower than for horizontal ($p < .01$).

In addition to the above results, it should be noted that none of the participants reported seeing a reversal of directions within a trial.

Real motion

The mean *d'* for each pattern was plotted as a function of coherence level and is shown in Figure 2.3E. Figure 2.3F shows the mean threshold estimates for each pattern of motion. The results of a one-way repeated-measures ANOVA showed a significant effect of pattern type, $F(4,20) = 30.55$, $p < .001$. Tukey post hoc analyses revealed that there were no significant differences in threshold for concentric, radial, vertical, and horizontal motion (all *p*s > .05). However, the threshold for spiral motion was significantly higher than for each of the other patterns (all *p*s < .001).

Paired t-tests were used to compare the log-transformed thresholds between the two directions of motion in each pattern (e.g., radial motion: inward vs. outward, vertical: up vs. down). We found no significant difference in thresholds between motion directions for radial, concentric, horizontal, and vertical (all *p*s > .05; Bonefferoni corrected). However, this difference was significant for spiral, with participants detecting inward-clockwise motion with lower thresholds than outward-counterclockwise motion ($p < .05$; Bonefferoni corrected).

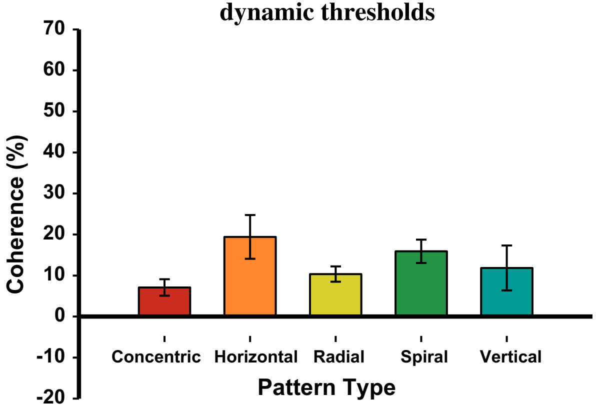
Effect of motion

There was a significant difference in the general performance (i.e., mean log-transformed threshold across patterns) between static Glass patterns (median = 3.53), dynamic Glass patterns (median = 3.14), and real motion (median = 2.49), $H(2) = 50.26$, $p < .001$. Pairwise analyses revealed that performance in real motion was significantly better than performance in for both static Glass patterns and the dynamic Glass patterns (both *p*s < .05). Performance in the dynamic Glass patterns was also found to be significantly better compared to performance in the static Glass patterns ($p < .05$) (see Figure 2.4).

2.5. Discussion

Coherence thresholds for different patterns of implied motion (i.e., motion coherence generated by form cues) were determined using dynamic Glass patterns and then contrasted with thresholds for comparable static Glass patterns and patterns of real motion (using random dot stimuli). We found that even though humans perceive dynamic Glass patterns as coherent motion (also see Ross, Badcock, & Hayes, 2000), dynamic Glass patterns appear to be processed more

(A) Difference between static and dynamic thresholds



(B) Difference between dynamic and real motion thresholds

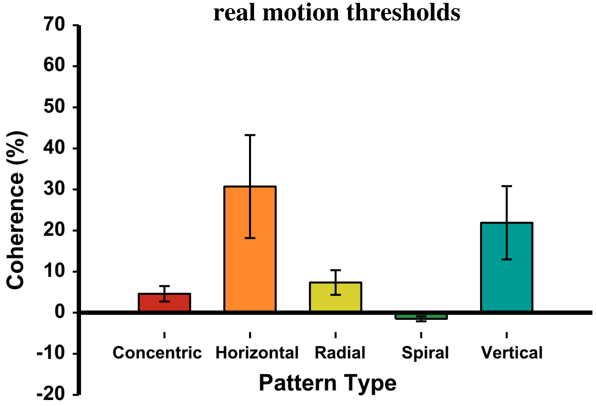


Figure 2.4 Panel A shows the mean difference between the threshold for each pattern in the static Glass pattern condition and the dynamic Glass pattern condition. Panel B shows the mean difference between the threshold for each pattern in the dynamic Glass pattern condition and the real motion condition.

similarly to static Glass patterns than to real motion. Specifically, we found that with both static and dynamic Glass patterns, our participants were more sensitive to concentric and radial patterns than to the other patterns. Furthermore, we found that our participants were better at detecting vertical patterns compared to horizontal patterns with both dynamic and static Glass patterns. In contrast, with real motion we found no significant differences in participants' ability to detect concentric, radial, vertical, and horizontal patterns, consistent with previous findings (Morrone, Burr, & Vaina, 1995; but see Lee & Lu, 2010). Additionally, participants were worst at detecting spiral motion pattern in real motion (also see Morrone et al., 1999), despite detecting spiral patterns relatively well in both static and dynamic Glass patterns.

The consistent detection threshold rankings across the patterns for dynamic and static Glass patterns suggests that in both cases participants may have been engaging in a form detection task (i.e., they based their decision on individual frames). However, given that thresholds were significantly lower for dynamic Glass patterns than for static patterns, it seems unlikely that participants simply based their judgement on the static form of one particular frame in the implied motion condition. If this were the case, the detection thresholds, in addition to the threshold ranking across patterns, should be equivalent in dynamic and static Glass patterns. Instead, our findings indicate that the detection of dynamic Glass patterns likely relies on a summation process where stimulus information is integrated across the ten frames of independent Glass patterns. That is, the signal in dynamic Glass pattern may be amplified due to summation across the ten independent Glass patterns. This potential temporal summation in the form areas then strongly influences the coherence thresholds in implied motion. It should be noted that given the lower detection thresholds across all pattern types, our results serve as evidence of a local-level summation process. However, our results do not exclude the possibility that summation also occurs at the level of global detectors.

The results of our study suggest that the improved performance observed in dynamic Glass patterns may be due to the fact that multiple signals (form cues) were being presented. The improved performance that we observed in the dynamic Glass pattern conditions is reminiscent of improved behavioral performance due to repetition of images with complementary parts (i.e., perceptual priming) (Biederman & Cooper, 1991; see Grill-Spector, Henson, & Martin, 2006; Wiggs & Martin, 1998; Henson, 2003 for reviews on perceptual priming). Moreover, our results are also in congruence with the findings from Beintema and Lappe (2002), who found that people are able to identify biological motion from a sequence of positional cues. In this study, Beintema and Lappe eliminated the role of motion signals by positioning the light points on the limbs rather than the joints and randomly relocating them on each frame. This result is also supported by studies finding that patients with lesioned motion areas are still able to perceive biological motion (Mcleod et al., 1996; Vaina et al.,1990). In a quantitative model of biological motion, Giese and Poggio (2003) suggest that ‘‘snapshot’’ neurons in the ventral pathway code for body shapes, and subsequently motion pattern neurons summate sequences of body shapes from the activity of these snapshot neurons. Our results suggest that a similar process likely occurs in the perception of dynamic Glass patterns, where form information from multiple frames can temporally summate in the absence of real motion cues.

Furthermore, we observed a difference in the ranking of the thresholds between dynamic Glass patterns and real motion patterns. This difference, along with the similarity between the ranking of the threshold between dynamic and static Glass patterns, indicates that dynamic Glass patterns are processed for their global form and then subsequently processed in the motion system. Supporting this conclusion, Krekelberg, Vatakis, and Kourtzi (2005) found that the same subpopulations of neurons are selective for implied and real motion patterns in hMT+/V5 (prototypical motion area). If implied motion was processed by MT+/V5 independently of global form areas, thresholds for implied motion should match those found with real motion. However, even when we lowered the coherence levels for real motion, this was not the case. Thus, it is likely that V4 and the LOC (areas suggested to be involved in extracting global form; Gallant, Shoup, & Mazer, 2000; Krekelberg, Vatakis, & Kourtzi, 2005; Ostwald et al., 2008) extract form information from dynamic Glass patterns and pass these signals to MT+/V5. This notion is further supported by Krekelberg, Vatakis, and Kourtzi's (2005) finding that neurons responsive for real motion were not selective for implied motion in the ventral pathway. Taken together, our findings, in conjunction with those from Krekelberg, Vatakis, and Kourtzi (2005), suggest that global form may be fully processed and subsequently influence activation in motion regions.

We additionally found that the sensitivity to vertical Glass patterns was significantly greater than that to horizontal Glass pattern, not only for static stimuli but also for dynamic Glass patterns. This difference has previously been reported in the detection of static Glass patterns (Kelly et al., 2001). This anisotropy may be due to what is known as the horizontal effect (Essock et al., 2003). The horizontal effect is found in broadband stimuli where observers are relatively worse at perceiving horizontal stimuli than vertical and oblique stimuli. Hansen and Essock (2004) suggest that the horizontal effect is the result of the visual system discounting orientation information that is more dominant in natural images, most notably horizontally oriented information. Supporting the generalization of this effect to Glass patterns, Wilson et al. (2001) found that humans have a lower threshold for oblique Glass patterns compared to horizontal and vertical Glass patterns. Given that oblique contents are less prevalent compared to horizontal and vertical in natural scenes (Hansen & Essock, 2004) these results provide further support for the hypothesis of a horizontal effect in complex stimuli. It should also be noted that the differences between horizontal and vertical stimuli are also supported by recent fMRI results that found that an array of horizontal and vertical line segments activate different cortical areas beyond V1 (Aspell et al., 2010). Importantly, the results of the current study are the first evidence of this difference in the detection of dynamic Glass patterns.

2.6 Conclusion

In conclusion, we have found that the ranking of thresholds for different types of implied motion generated by dynamic Glass patterns are similar to those found for static Glass patterns. This suggests that in spite of a strong coherent motion illusion, dynamic Glass pattern appear to be processed first primarily as form information prior to being input into the motion system. This hypothesis is further strengthened by the result of a horizontal effect in both static and dynamic Glass pattern, but not with real motion.

2.7 Acknowledgements

This research was supported by grants from the National Science and Engineering Research Council (NSERC) of Canada to M.L.S and D.R.W. We are grateful to Alinda Friedman and Quoc Vuong for their feedback, as well as three graduate students at the University of Alberta who were participants in the experiment (M.K.M., N.E.H., Y.Y.C.).

2.8 References

Anderson, S. J., & Swettenham, J. B. (2006). Neuroimaging in human amblyopia. *Strabismus*, *14*(1), 21-35.

Aspell, J. E., Wattam-Bell, J., Atkinson, J., & Braddick, O. J. (2010). Differential human brain activation by vertical and horizontal global visual textures. *Experimental brain research*, *202*(3), 669-679.

Aspell, J. E., Wattam-Bell, J., & Braddick, O. (2006). Interaction of spatial and temporal integration in global form processing. *Vision research*, *46*(18), 2834-2841.

Beintema, J. A., & Lappe, M. (2002). Perception of biological motion without local image motion. *Proceedings of the National Academy of Sciences*, *99*(8), 5661-5663.

Biederman, I., & Cooper, E. E. (1991). Priming contour-deleted images: Evidence for intermediate representations in visual object recognition. *Cognitive psychology*, *23*(3), 393-419.

Blake, R., & Aiba, T. S. (1998). Detection and discrimination of optical flow components. *Japanese Psychological Research*, *40*(1), 19-30.

Braddick, O. J., O'Brien, J. M. D., Wattam-Bell, J., Atkinson, J., & Turner, R. (2000). Form and motion coherence activate independent, but not dorsal/ventral segregated, networks in the human brain. *Current Biology*, *10*(12), 731-734.

Burr, D., & Ross, J. (2006). The effects of opposite-polarity dipoles on the detection of Glass patterns. *Vision Research*, *46*(6), 1139-1144.

Dakin, S. C., & Bex, P. J. (2002). Summation of concentric orientation structure: seeing the Glass or the window?. *Vision Research*, *42*(16), 2013-2020.

Essock, E. A., DeFord, J. K., Hansen, B. C., & Sinai, M. J. (2003). Oblique stimuli are seen best (not worst!) in naturalistic broad-band stimuli: A horizontal effect. *Vision research*, *43*(12), 1329-1335.

Gallant, J. L., Shoup, R. E., & Mazer, J. A. (2000). A human extrastriate area functionally homologous to macaque V4. *Neuron*, *27*(2), 227-235.

Geisler, W. S. (1999). Motion streaks provide a spatial code for motion direction. *Nature*, *400*(6739), 65-69

Giese, M. A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience*, *4*(3), 179-192.

Glass, L. (1969). Moire effect from random dots. *Nature*, *223*(5206), 578-580.

Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends in cognitive sciences*, *10*(1), 14-23.

Hansen, B. C., & Essock, E. A. (2004). A horizontal bias in human visual processing of orientation and its correspondence to the structural components of natural scenes. *Journal of Vision*, *4*(12), 5.

Henson, R. N. A. (2003). Neuroimaging studies of priming. *Progress in neurobiology*, *70*(1), 53-81.

Kelly, D. M., Bischof, W. F., Wong-Wylie, D. R., & Spetch, M. L. (2001). Detection of glass patterns by pigeons and humans: implications for differences in higher-level processing. *Psychological Science*, *12*(4), 338-342.

Kourtzi, Z., Krekelberg, B., & Van Wezel, R. J. (2008). Linking form and motion in the primate brain. *Trends in cognitive sciences*, *12*(6), 230-236.

Krekelberg, B., Dannenberg, S., Hoffmann, K. P., Bremmer, F., & Ross, J. (2003). Neural correlates of implied motion. *Nature*, *424*(6949), 674-677.

Krekelberg, B., Vatakis, A., & Kourtzi, Z. (2005). Implied motion from form in the human visual cortex. *Journal of Neurophysiology*, *94*(6), 4373-4386.

Lee, A. L., & Lu, H. (2010). A comparison of global motion perception using a multiple-aperture stimulus. *Journal of Vision*, *10*(4), 9.

Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*, *240*(4853), 740-749.

McLeod, P. (1996). Preserved and Impaired Detection of Structure From Motion by a “Motion-blind" Patient. *Visual Cognition*, *3*(4), 363-392.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: two cortical pathways. *Trends in neurosciences*, *6*, 414-417.

Morrone, M. C., Burr, D. C., Di Pietro, S., & Stefanelli, M. A. (1999). Cardinal directions for visual optic flow. *Current Biology*, *9*(14), 763-766.

Morrone, M. C., Burr, D. C., & Vaina, L. M. (1995). 2 Stages of Visual Processing for Radial and Circular Motion. *Nature*, *376*(6540), 507-509.

Nelder, J. A., & Mead, R. (1965). A simplex method for function minimization. *The computer journal*, *7*(4), 308-313.

Or, C. C. F., Khuu, S. K., & Hayes, A. (2007). The role of luminance contrast in the detection of global structure in static and dynamic, same-and opposite-polarity, Glass patterns. *Vision Research*, *47*(2), 253-259.

Ostwald, D., Lam, J. M., Li, S., & Kourtzi, Z. (2008). Neural coding of global form in the human visual cortex. *Journal of Neurophysiology*, *99*(5), 2456-2469.

Pei, F., Pettet, M. W., Vildavski, V. Y., & Norcia, A. M. (2005). Event-related potentials show configural specificity of global form processing. *Neuroreport*, *16*(13), 1427-1430.

Ross, J., Badcock, D. R., & Hayes, A. (2000). Coherent global motion in the absence of coherent velocity signals. *Current Biology*, *10*(11), 679-682.

Scase, M. O., Braddick, O. J., & Raymond, J. E. (1996). What is noise for the motion system?. *Vision research*, *36*(16), 2579-2586.

Seu, L., & Ferrera, V. P. (2001). Detection thresholds for spiral Glass patterns. *Vision Research*, *41*(28), 3785-3790.

Siegel, R. M., & Andersen, R. A. (1988). Perception of three-dimensional structure from motion in monkey and man. *Nature*, *331*, 259-261.

Smith, M. A., Bair, W., & Movshon, J. A. (2002). Signals in macaque striate cortical neurons that support the perception of glass patterns. *The Journal of neuroscience*, *22*(18), 8334-8345.

Smith, M. A., Kohn, A., & Movshon, J. A. (2007). Glass pattern responses in macaque V2 neurons. *Journal of Vision*, *7*(3), 5.

Swettenham, J. B., Anderson, S. J., & Thai, N. J. (2010). MEG responses to the perception of global structure within glass patterns.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge: MIT Press.

Vaina, L. M., Lemay, M., Bienfang, D. C., Choi, A. Y., & Nakayama, K. (1990). Intact "biological motion" and "structure from motion" perception in a patient with impaired motion mechanisms: A case study. *Visual neuroscience*, *5*(04), 353-369.

Weibull, W. (1951). A Statistical Distribution Function of Wide Applicability. *Journal of Applied Mechanics*, *13*, 293-297.

Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current opinion in neurobiology*, *8*(2), 227-233.

Wilson, H. R., Loffler, G., Wilkinson, F., & Thistlethwaite, W. A. (2001). An inverse oblique effect in human vision. *Vision research*, *41*(14), 1749-1753.

Wilson, H. R., & Wilkinson, F. (1998). Detection of global structure in Glass patterns: implications for form vision. *Vision research*, *38*(19), 2933-2947.

.

Zihl, J., Von Cramon, D., & Mai, N. (1983). Selective disturbance of movement vision after bilateral brain damage. *Brain*, *106*(2), 313-340.

Chapter 3

Temporal summation of global form signals in dynamic Glass patterns

3.1 Abstract

The ability to perceive complex objects in the environment requires that the visual system integrate local form information into global shapes. Glass patterns (GPs) are stimuli that are commonly used to study this integration process. GPs consist of randomly positioned dot-pairs oriented in a coherent way to create a global form. When multiple GPs are presented sequentially, observers report a percept of illusory coherent motion and have lower detection thresholds relative to a single presentation GPs. The percept of illusory motion has been attributed to the visual system interpreting the dot-pairs in GPs as motion streaks. However, it remains unclear why dynamic GPs are detected at lower thresholds than static GPs. Two main differences exist between static and dynamic GPs: (a) dynamic GPs contain multiple presentations of global form signals compared to a single presentation in static GPs and (b) dynamic GPs have a greater temporal frequency than static GPs. Here we investigated which of these two factors contributed to the heightened sensitivities for dynamic GPs. We systematically varied the number of unique GPs and the rate at which each unique frame is presented (i.e., temporal frequency). The results show that, within the range of temporal frequency used, the primary influence on detection thresholds was the number of unique frames. These results

suggest that the improved detection sensitivities can be driven by a mechanism of temporal summation of global form.

3.2 Introduction

Researchers have long established that the mammalian visual system is organized in a modular fashion, whereby different areas are specialized for processing particular types of information (Calabretta & Parisi, 2005). Consistent with this idea, form and motion information are processed by distinct neural pathways at the lower levels of the visual system (Braddick et al., 2000; Livingstone & Hubel, 1988; Milner & Goodale, 1995; Ungerleider & Mishkin, 1982; Van Essen &Gallant, 1994). However, recent psychophysical and neurophysiological studies have demonstrated interactions between the form and motion pathways (see Kourtzi, Krekelberg, & van Wezel, 2008, for review). For instance, in the phenomenon known as structure-from-motion, two-dimensional motion information provides information about the three-dimensional structure of objects (Siegel & Andersen, 1988). In a similar way, form signals have been shown to influence motion perception (Geisler, 1999). For example, Ross, Badcock, and Hayes (2000) have shown that form information constrains incoherent motion to generate the appearance of coherent global motion when multiple independently-generated Glass patterns are presented in rapid succession.

A Glass pattern is a type of static stimulus that consists of an array of randomly-positioned dot-pairs (i.e., dipoles) that are oriented in a way to provide the percept of a global shape (Figure. 3.1A; Glass, 1969). Glass patterns are commonly used to study how the visual system pools local orientation information to allow us to perceive the global form of objects in the environment, in the same way that random-dot stimuli are used to investigate global pooling of local motion signals (Williams & Sekuler, 1984; Wilson & Wilkinson, 1998). Ross, Badcock, and Hayes (2000) have shown that if a series of independently-generated Glass patterns, with the same global form, are shown in rapid succession, termed dynamic Glass patterns (dynamic GPs), observers perceive a salient illusion of coherent motion. They considered this to be ‘‘implied motion’’ and noted that their participants could not differentiate implied motion from real motion. Furthermore, Krekelberg et al. (2003) and Krekelberg, Vatakis, and Kourtzi (2005) found that cells in the prototypical motion areas of monkeys and humans (medial temporal area [MT] and medial temporal complex [MT+], respectively) do not differentiate between real motion and implied motion. Thus, the results from Krekelberg and colleagues and those of Ross, Badcock, and Hayes (2000) provide evidence of an interaction between form and motion, whereby the motion system of the mammalian visual system translates global form information into coherent global motion information.

Various research groups have reported that the detection thresholds for dynamic Glass patterns are significantly lower than the detection thresholds for static Glass patterns (e.g., Burr & Ross, 2006; Or, Khuu, & Hayes, 2007). Because thresholds for real global motion are generally lower than those for global form, the lower thresholds for dynamic GPs relative to static GPs suggest that dynamic GPs are processed in a similar way to real motion. However, based on psychophysical evidence, Nankoo et al. (2012) have suggested that the decrease in thresholds with dynamic GPs is likely related to the form system (e.g., V4). Nankoo et al. (2012) measured the detection threshold for concentric, radial, spiral, horizontal and vertical static GPs, dynamic GPs, and real global motion. They showed that even though thresholds for both dynamic GPs and real motion were significantly lower than static GPs, the relative performance in each of the patterns suggests that the low thresholds of dynamic GPs and real motion are based on different mechanism. In particular, with real motion, detection thresholds were equivalent for all patterns except for higher thresholds for spiral motion (see also Morrone, Burr, & Vaina, 1995). In contrast, with dynamic GPs, participants were best at detecting concentric and radial patterns, and worst at vertical and horizontal patterns, with spiral at an intermediate detection threshold. The relative ranking of the thresholds for dynamic GPs were identical to the relative ranking of the thresholds for static GPs (see also Wilson & Wilkinson, 1998). Nankoo et al. (2012) argue that this suggests that the decrease in threshold found in dynamic GPs is driven by the same or similar form-related processes that drive the detection of GPs, as opposed to motionrelated processes.

Recently, Day and Palomares (2014) reported a negative linear relationship between temporal frequency and coherence threshold in dynamic GPs; as temporal frequency was increased, threshold decreased (see also Edwards & Crane, 2007). Day and Palomares (2014) argued that their result is consistent with the idea that the dynamic GPs are processed by the ‘motion streak’ system (Ross, 2004; Ross, Badcock, & Hayes, 2000). The motion streak model is based on the finding that fast-moving objects leave a trailing blur due to temporal integration (Geisler, 1999). At high velocities, the visual system appears to utilize the form from the trailing blur (i.e., streak) to disambiguate direction information (Burr & Ross, 2002). Day and Palomares suggested that if dynamic GPs are interpreted as motion streaks by the visual system, it follows that increasing the temporal frequency would increase sensitivity. However, while Day and Palomares' study showed the importance of temporal frequency, it does not rule out the possibility that lower detection thresholds for dynamic GPs are also due to the additional form signals present in dynamic GPs. The increase in temporal frequency also means that there is an increase in the number of unique frames presented. Thus, it is unclear whether the increased sensitivity of dynamic GPs relative to static GPs is due to the summation of multiple global form signals.

In the current study we tested the hypothesis that the lower thresholds observed for dynamic GPs are due to a summation of the form signals. Given that dynamic GPs consist of multiple independent static GPs, and thus contain multiple presentations of unique global form signals relative to static GPs, we measured the detection thresholds of our participants for static GPs (one GPs frame), dynamic GPs (12 GPs frames), and intermediate stimuli containing two, four, and six unique GPs frames, presented in different types of frame alternation sequences to also manipulate temporal frequency (see Table 3.1). If the lower thresholds observed for dynamic GPs are due to the summation of multiple form signals, we can expect a linear decrease in threshold as the number of unique frames increases. In addition, each GPs in dynamic GPs is presented for a short duration relative to one GPs in static GPs (i.e., temporal frequency). In order to account for this factor, we measured the thresholds for stimuli that contained blocks of unique GPs (Table 3.1).

3.3 Method

Nine adults with normal or corrected-to-normal vision participated in this study (*n* = 9). This sample included three of the authors, two graduate students, and four undergraduate students from the University of Alberta. All the participants were naïve to the purpose of the experiment, except for the three authors. The experiment was conducted in accord with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

3.3.1 Apparatus

The stimuli were displayed on a 2200 Viewsonic VX2268wm FuHzion LCD monitor (resolution: 1680 x 1050 pixels; refresh rate: 120 Hz). Participants were seated comfortably at a viewing distance of 45 cm to the monitor, with the center of the monitor positioned at eye-level. Participants' head position was fixed with a chin rest. Stimuli were generated using in-house MATLAB code and presented using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997).

3.3.2. Stimuli and design

Each stimulus was presented for a total duration of 200.00 ms (12 frames, 60 Hz image update rate). Each GPs subtended a visual angle of 10.7° (diameter of aperture), and each square dot within the stimulus subtended 0.04° x 0.04°. The density of dots within each pattern was set at 6% and the dot separation was 0.25°. The dipoles were oriented to generate a percept of vertical structure (Figure. 3.1). We chose vertical GPs because Nankoo et al. (2012) have previously shown that the improvement in the detection threshold between static GPs and dynamic GPs is largest for vertical patterns relative to other orientations such as concentric or horizontal, and thus would provide us with the greatest statistical sensitivity for the current study.

A temporal two-alternative forced-choice design was used, whereby the participants were presented with two consecutive patterns; one pattern that contained form signals (i.e., GPs) and one that contained a noise pattern (i.e., randomly-oriented dipoles). The participants' task was to identify which pattern contained the signal. The order of the signal stimulus and the noise stimulus was pseudo randomly counterbalanced across trials. Detection thresholds were determined using the QUEST adaptive staircase method (Watson & Pelli, 1983). In this method, coherence (the % of dipoles aligned in the pattern) was systematically increased or decreased depending on the participant's performance. In each trial, a psychometric function is fit to all the data collected, and an estimate of the threshold is derived.

3.3.3. Presentation sequence

As shown in Table 3.1, the number of unique GPs (i.e., unique frames) used was 2, 4, and 6, in addition to the static and dynamic GPs condition (i.e., 1 and 12 unique frames, respectively). The unique frames were presented in two ways. In one presentation format, the unique frames were presented in an alternating sequence whereby a sequence of unique frames was repeated for a total of 12 frames per

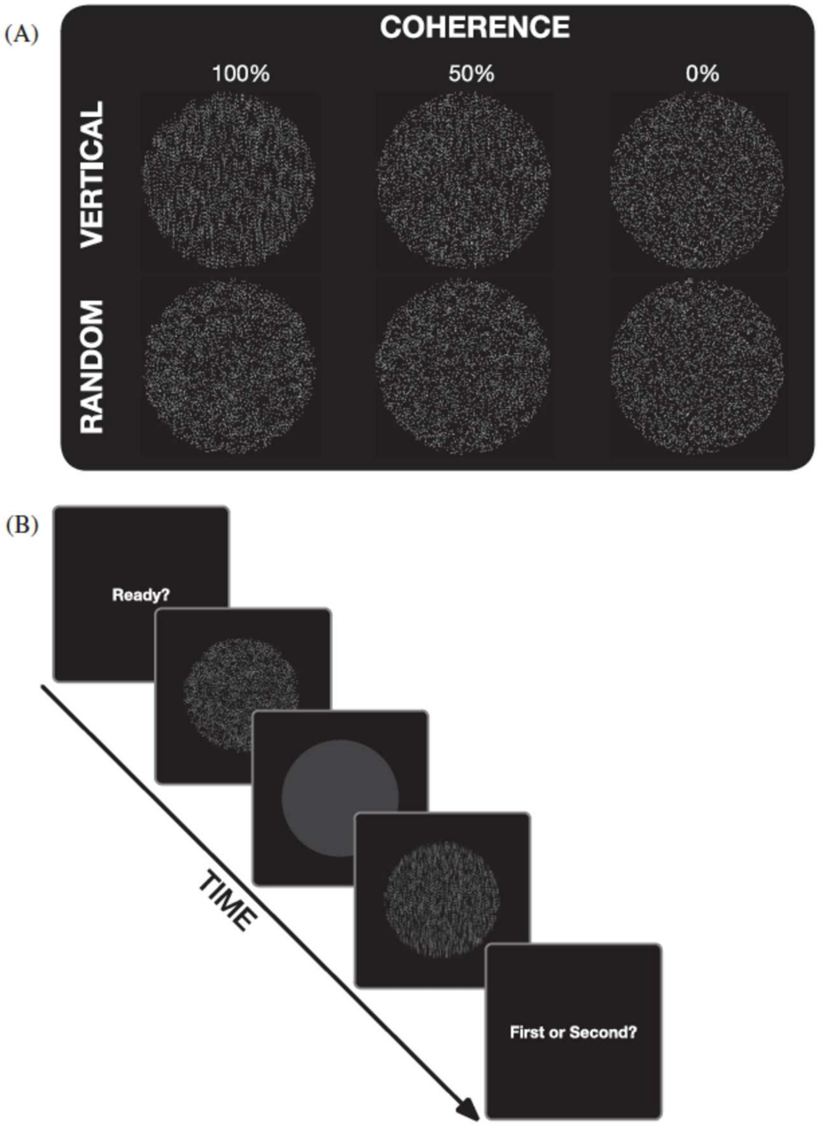


Figure 3.1 Panel A shows examples of vertical and random Glass patterns with 100%, 50%, and 0% coherence. Panel B shows an illustration of a single trial.

CONDITION	FRAME SEQUENCE	NUMBER OF UNIQUE FRAMES	TEMPORAL FREQUENCY (HZ)
STATIC (1-0)	AAAAAAAAAAAA	1	1
DYNAMIC (12-60)	ABCDEFGHIJKL	12	60
2-10	AAAAAABBBBBB	2	10
2-20	AAABBBAAABBB	2	20
2-60	ABABABABABAB	2	60
4-20	AAABBBCCCDDD	4	20
4-60	ABCDABCDABCD	4	60
6-30	AABBCCDDEEFF	6	30
6-60	ABCDEFABCDEF	6	60

Table 3.1 Details on each condition. Each condition name consists of two numbers corresponding to the number of unique frames and the temporal frequency used. For the frame sequence, each unique letter represents an independent Glass pattern, and each letter position represents a frame at 60 Hz. Frames denoted with sequential letters have no relation (e.g., frames A and B are independent).

stimulus. For example, in patterns with two unique frames (''A'' and ''B''), the pattern would consist of a repeating sequence of the two unique frames (i.e., frame A → frame A → frame B → frame B; Table 3.1) until 12 frames have been presented. For these alternating sequences, the temporal frequency was kept at 60 Hz given that the image is updated with a new frame every 16.67 ms. In the other presentation format, the unique frames were presented in a blocked sequence where we manipulated the rate at which each unique frame was presented (i.e., temporal frequency). Relative to the alternating sequences, with the blocked sequences all identical frames are shown consecutively (i.e., a block) before the next block of a new unique frame is shown (e.g., frame A → frame A → frame B → frame B; Table 3.1). The block arrangement and number of unique frames resulted in temporal frequencies of 20 Hz, 30 Hz, and 40 Hz.

3.3.4. Procedure

Prior to each session, the participants were reminded of the global pattern that they were to detect (vertical). On each trial, the participants were presented sequentially with two stimuli, one containing the pattern signals of varying coherence (based on the QUEST estimates), and one containing only randomly-oriented dipoles (i.e., 0% coherence). The stimuli were presented centrally, and were temporally separated by 500 ms (Figure. 3.1B). A message then prompted the participant to press the key ‘‘A’’ if the pattern containing the signal was presented first, or press the key ‘‘L’’ if the pattern containing the signal was the second stimulus presented. No feedback was provided. After a 2 s inter-trial interval, the next trial began.

Each session consisted of all eight conditions presented in a random order. Participants completed 45 trials per condition, which yielded a total of 405 trials per session. Testing was carried out over three sessions, all conducted within one week..

3.3.5. Data analysis

The detection thresholds were determined by a maximum likelihood procedure using the QUEST adaptive staircase procedure (Watson & Pelli, 1983). In the QUEST procedure, the participant's psychometric function is assumed to follow a Weibull distribution (Weibull, 1951) and coherence levels are based on responses in previous trials.

To more conclusively measure the amount of unique variance explained by each factor, we statistically tested the relationship between both the number of unique frames and temporal frequency with the detection threshold, controlling for the other factor, using a partial correlation analysis. These partial correlations were conducted within each subject and then aggregated using Fisher's transform (see Corey, Dunlap, & Burke, 1998). Both correlations reported in the results section are partial correlations aggregated using Fisher's transform.

To improve the reliability of our detection threshold estimates, we had participants complete three sessions. Our task required considerable effort to maintain attention, and occasional lapses in attention could decrease the accuracy of an adaptive method from converging on the participant's actual detection threshold.

For each participant we therefore used the two estimates for each condition that had the lowest SD, and we averaged these two estimates for our measure of each participant's detection threshold in each condition. Because our selection was based on SD and not on threshold, and because it was applied equally to all conditions, it would not distort the comparison between conditions.

All statistical analyses were conducted using MATLAB (The MathWorks Inc., Natick, MA). Effects were considered significant based on an alpha level of .05.

3.4 Results

Figure. 3.2 shows the detection thresholds in terms of coherence level for all nine conditions. As with previous studies (e.g., Nankoo et al., 2012), participants' thresholds were significantly lower at detecting dynamic GPs (*mean* = 21%; SD = 0.10%) compared to static GPs (*mean* = 36%; SD = 0.08%), $t(8) = 6.89$, $p < .001$. A repeated-measures ANOVA revealed a significant effect across the remaining conditions ($F(6,48) = 4.52$, $p = .001$; Figure. 3.2). As visible in Figure. 3.3A, the detection thresholds of the remaining conditions decreased as a function of the number of unique frames. Indeed, the partial correlations confirmed a significant correlation between the number of unique frames and the detection thresholds [$r_{\text{p-pop}}(8) = -.44$, $p = .043$]. In contrast, as shown in Figure. 3.3B, the correlation between temporal frequency and detection threshold was not significant [$r_{\text{p-pop}}(8) = \_.27$, $p = .13$]. Thus, the results suggest that the addition of new form signals (i.e., more unique frames) in dynamic Glass patterns is the dominant factor in the detection advantage for dynamic versus static Glass patterns.

3.5 Discussion

In the current study, we investigated the mechanisms behind the detection of dynamic GPs by measuring the detection thresholds for vertical GPs as a function of both temporal frequency and the number of unique form signals. Detection thresholds were higher for the static GPs, which contained only one unique frame and a temporal frequency of 1 Hz, than for the dynamic GPs, which

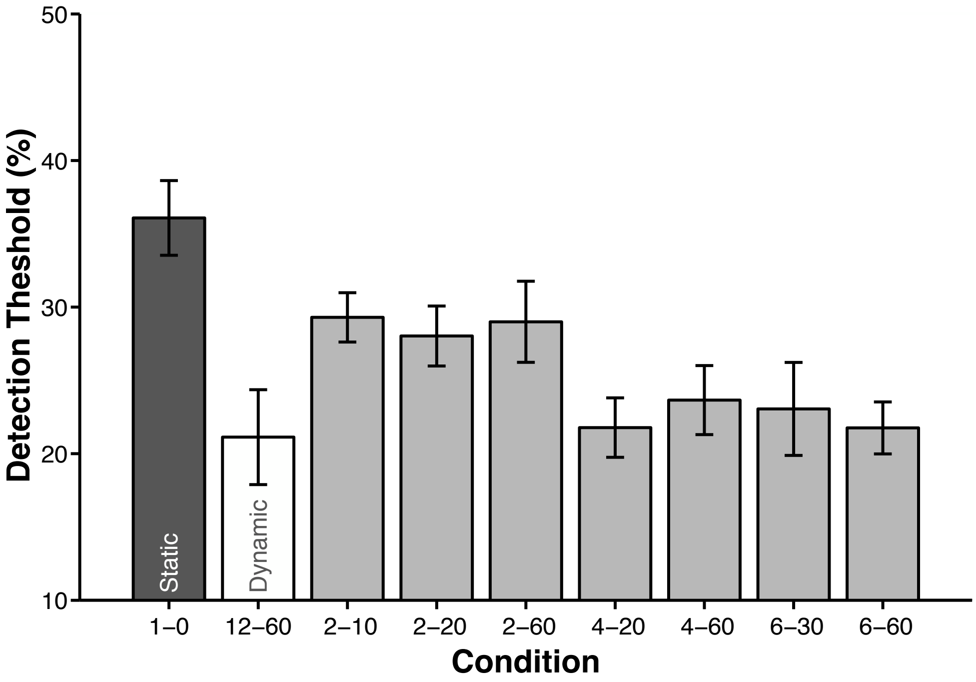


Figure 3.2Mean detection thresholds for each condition. Error bars represent the standard error of the mean.

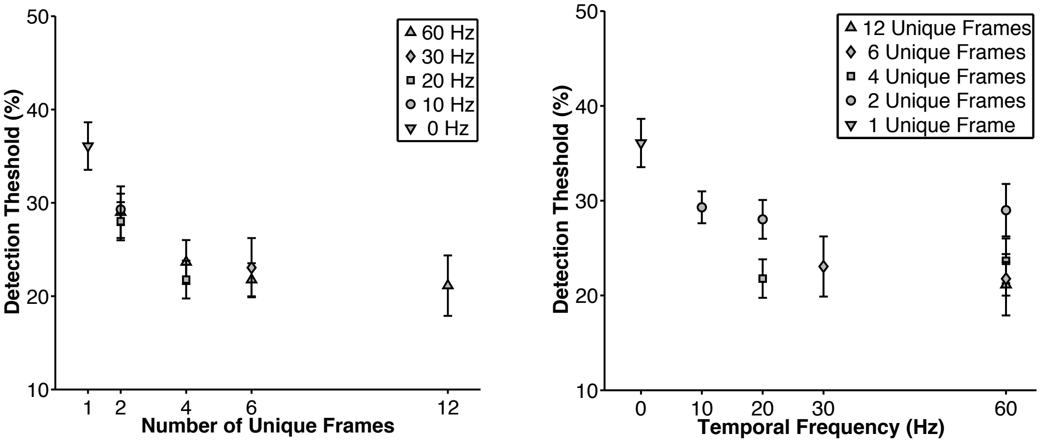


Figure 3.3 Panel A shows the mean detection thresholds as a function of the number of unique frames. Panel B shows the mean detection thresholds as a function of the temporal frequency. Error bars represent the standard error of the mean.

contained 12 unique frames and a temporal frequency of 60 Hz. These results are consistent with previous studies (e.g., Nankoo et al., 2012), and served as a control to allow us to examine the intermediate levels of both factors. Similar to Day and Palomares (2014), we found that an increase in temporal frequency lowered detection thresholds, but we also found that the contribution of this factor was minor relative to the contribution of unique global form signals. Therefore, our results suggest that the addition of unique form signals is a dominant factor for the improved sensitivity in dynamic GPs.

Some researchers have suggested that the illusory coherent motion perceived with dynamic GPs is the result of activation of the 'motion streak' sensors (Burr & Ross, 2002; Geisler, 1999; Ross, Badcock, & Hayes, 2000). At high velocities, movement of an object across the retina leaves a trail of blur that is parallel to the axis of motion. Geisler (1999) has shown that the visual system is able to use the streak, a form signal, to aid motion direction detection (Mather et al., 2013). Geisler's model of motion streak suggests that motion signals are summated with parallel orientation signals at early cortical levels. Evidence from imaging studies supports the existence of a motion streak system at the level of V2 (Apthorp et al., 2013). Given that the dipoles in Glass patterns are known to activate orientation detectors in V1/V2 (Smith, Bair, & Movshon, 2002; Smith, Kohn, & Movshon, 2007), it has been suggested that the perceived coherent motion and the lower thresholds for dynamic GPs, relative to static GPs, are the result of the motion streak sensors interpreting the dipoles as streaks (Day & Palomares, 2014; Ross, Badcock, & Hayes, 2000). Even though it is plausible that the illusory coherent motion perceived with dynamic GPs is mediated by the motion streak system, current evidence does not exclude alternative hypotheses for the reduction in threshold relative to static GPs.

A major difference between static GPs and dynamic GPs is that dynamic GPs consist of multiple presentations of the global form signals relative to the single signal present in static GPs. Our result indicated that the increased sensitivity is primarily due to the additional form signals present in dynamic GPs. It is known that under certain circumstances, stimulus repetition results in lower neural activity in various brain regions and more importantly, improves performance (i.e., priming; Grill-Spector, Henson, & Martin, 2006). Dynamic GPs consist of multiple presentations of static GPs, and can be interpreted as a case of stimulus repetition. Bar and Biederman (1998) provided evidence of priming in V4 using stimuli presented at 65 ms. Given that current evidence suggests that Glass patterns are processed at the intermediate levels of visual processing (e.g., V4), it is possible the improvement of the detection thresholds of dynamic GPs relative to static GPs is a consequence of the multiple instances of global form signals akin to priming mechanisms. This hypothesis would suggest that the more global form information is present in the stimulus, the lower the threshold will be. Our findings support this prediction, suggesting a potential temporal summation of global form signals.

3.6 Conclusion

Studies have shown that dipoles within Glass patterns activate orientation detectors at the level of V1 and V2, and it has been argued that the motion streak sensors also utilize information from orientation detectors within these areas to disambiguate motion direction (Smith, Bair, & Movshon, 2002; Smith, Kohn &

Movshon, 2007). For these reasons, the percept of illusory coherent motion with dynamic GPs has been attributed to the motion streak system. However, the motion streak hypothesis does not adequately explain the lower thresholds of dynamic GPs relative to static GPs, and the differences between dynamic GPs and real motion (Nankoo et al., 2012). Although our results do not exclude the contribution of a motion-based mechanism (Day & Palomares, 2014), we showed that the amount of unique global form signals is an important factor in reducing thresholds in dynamic Glass patterns. It is likely that the global form signals are summated in a similar way to the proposed ‘‘snapshot’’ neuron model of biological motion that summates form information across frames (Giese & Poggio, 2003).

3.7 Acknowledgements

This research was supported by grants from the National Science and Engineering Research Council (NSERC) of Canada to M.L.S. and D.R.W., and by an NSERC Alexander Graham Bell Canada Graduate Scholarship (Doctoral level) to C.R.M.

3.8 References

Apthorp, D., Schwarzkopf, D. S., Kaul, C., Bahrami, B., Alais, D., & Rees, G. (2013). Direct evidence for encoding of motion streaks in human visual cortex. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*(1752), 20122339.

Bar, M., & Biederman, I. (1998). Subliminal visual priming. *Psychological Science*, *9*(6), 464-468.

Braddick, O. J., O'Brien, J. M. D., Wattam-Bell, J., Atkinson, J., & Turner, R. (2000). Form and motion coherence activate independent, but not dorsal/ventral segregated, networks in the human brain. *Current Biology*, *10*(12), 731-734.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial vision*, *10*, 433-436.

Burr, D. C., & Ross, J. (2002). Direct evidence that "speedlines" influence motion mechanisms. *The Journal of Neuroscience*, *22*(19), 8661-8664.

Burr, D., & Ross, J. (2006). The effects of opposite-polarity dipoles on the detection of Glass patterns. *Vision Research*, *46*(6), 1139-1144.

Calabretta, R., & Parisi, D. (2005). Evolutionary connectionism and mind/brain modularity. In W. Callebaut & D. Rasskin-Gutman (Eds.), Modularity. Understanding the development and evolution of complex natural systems (pp. 309–330). Cambridge, MA: MIT Press.

Corey, D. M., Dunlap, W. P., & Burke, M. J. (1998). Averaging correlations: Expected values and bias in combined Pearson rs and Fisher's z transformations. *The Journal of general psychology*, *125*(3), 245-261.

Day, A. M., & Palomares, M. (2014). How temporal frequency affects global form coherence in Glass patterns. *Vision research*, *95*, 18-22.

Edwards, M., & Crane, M. F. (2007). Motion streaks improve motion detection. *Vision research*, *47*(6), 828-833.

Geisler, W. S. (1999). Motion streaks provide a spatial code for motion direction. *Nature*, *400*(6739), 65-69.

Giese, M. A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience*, *4*(3), 179-192.

Glass, L. (1969). Moire effect from random dots. *Nature*, *223*(5206), 578-580.

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends in cognitive sciences*, *10*(1), 14-23.

Kourtzi, Z., Krekelberg, B., & Van Wezel, R. J. (2008). Linking form and motion in the primate brain. *Trends in cognitive sciences*, *12*(6), 230-236.

Krekelberg, B., Dannenberg, S., Hoffmann, K. P., Bremmer, F., & Ross, J. (2003). Neural correlates of implied motion. *Nature*, *424*(6949), 674-677.

Krekelberg, B., Vatakis, A., & Kourtzi, Z. (2005). Implied motion from form in the human visual cortex. *Journal of Neurophysiology*, *94*(6), 4373-4386.

Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*, *240*(4853), 740-749.

Mather, G., Pavan, A., Marotti, R. B., Campana, G., & Casco, C. (2013). Interactions between motion and form processing in the human visual system. *Frontiers in computational neuroscience*, *7*.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.

Morrone, M. C., Burr, D. C., & Vaina, L. M. (1995). Two stages of visual processing for radial and circular motion. *Nature*, *376*(6540), 507.

Nankoo, J. F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2012). Perception of dynamic Glass patterns. *Vision research*, *72*, 55-62.

Or, C. C. F., Khuu, S. K., & Hayes, A. (2007). The role of luminance contrast in the detection of global structure in static and dynamic, same-and opposite-polarity, Glass patterns. *Vision Research*, *47*(2), 253-259.

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

Ross, J. (2004). The perceived direction and speed of global motion in Glass pattern sequences. *Vision Research*, *44*, 441–448.

Ross, J., Badcock, D. R., & Hayes, A. (2000). Coherent global motion in the absence of coherent velocity signals. Current Biology, 10, 679–682.

Siegel, R., & Andersen, R. (1988). Perception of three-dimensional structure from motion in monkey and man. Nature, 331, 259–261.

Smith, M. A., Bair, W., & Movshon, J. A. (2002). Signals in macaque striate cortical neurons that support the perception of glass patterns. *Journal of Neuroscience, 22*, 8334–8345.

Smith, M. A., Kohn, A., & Movshson, J. A. (2007). Glass pattern responses in macaque V2 neurons. *Journal of Vision*, *7*, 1–15.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge: MIT Press.

Van Essen, D. C., & Gallant, J. L. (1994). Neural mechanisms of form and motion processing in the primate visual system. *Neuron*, *13*, 1–10.

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics*, *33*(2), 113–120.

Weibull, W. (1951). A statistical distribution function of wide applicability. *Journal of Applied Mechanics*, *18*, 292–297.

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

Wilson, H. R., & Wilkinson, F. (1998). Detection of global structure in Glass patterns: Implications for form vision. *Vision Research*, *38*, 2933–2947.

Chapter 4

Perception of complex motion in humans and pigeons (*Columba livia*)

4.1 Abstract

In the primate visual system, local motion signals are pooled to create a global motion percept. Like primates, many birds are highly dependent on vision for their survival, yet relatively little is known about motion perception in birds. We used random-dot stimuli to investigate pigeons' ability to detect complex motion (radial, rotation, and spiral) compared to humans. Our human participants had a significantly lower threshold for rotational and radial motion when compared to spiral motion. The data from the pigeons, however, showed that the pigeons were most sensitive to rotational motion and least sensitive to radial motion, while sensitivity for spiral motion was intermediate. We followed up the pigeon results with an investigation of the effect of display aperture shape for rotational motion and velocity gradient for radial motion. We found no effect of shape of the aperture on thresholds, but did observe that radial motion containing accelerating dots improved thresholds. However, this improvement did not reach the thresholds levels observed for rotational motion. In sum, our experiments demonstrate that the pooling mechanism in the pigeon motion system is most efficient for rotation.

4.2 Introduction

The ability to perceive motion is critical for survival for mobile organisms as it serves several functions such as detection of prey/predators, perception of self-motion, and separation of figure from ground (Nakayama, 1985). In the mammalian visual system, motion is processed hierarchically in a feed-forward system that first extracts local signals at the lower cortical areas (e.g., primary visual cortex [V1]) and pools those signals at a higher cortical level (e.g., medial temporal area [MT+]) to create the percept of global motion (see Burr & Thompson 2011, for review). Neurophysiological studies have shown that in the monkey medial superior temporal area (MST), cells are selective for global translation motion and global complex motion (e.g., radial and rotational motion; Britten & van Wezel, 1998; Duffy & Wurtz 1991; Saito et al. 1986; Tanaka & Saito, 1989). These results from animal models have been substantiated by brain imagining studies that have found increased BOLD activity in the human V5/MT+ (homologue of MT/MST) in response to complex motion patterns (Morrone et al. 2000; Wall et al. 2008).

Physically, the difference among complex motion patterns is quantitative, in that it is based solely on the deviation in trajectory of the elements in the pattern (see Figure 4.1 in Morrone et al. 1999). For example, if the local vectors in a radial pattern (Figure 4.1a) were to be deviated by 45°, this would result in a spiral motion (Figure 4.1b), whereas a deviation of 90° would result in a rotational motion (Figure 4.1c). Morrone et al. (1999) and Burr et al. (2001) have shown that humans have lower detection thresholds for expansion/ contraction (i.e., radial) and rotational motion (clockwise/counterclockwise rotation) relative to spiral motion. They suggest that this is evidence that specialized global detectors are tuned specifically to the cardinal directions, that is deviations of 0° (i.e., radial expansion), 90° (clockwise rotation), 180° (radial contraction), and 270° (counterclockwise rotation) of complex motion. However, others have suggested the alternative hypothesis that there are spiral detectors that could simply be less responsive compared to radial and rotational detectors (e.g., Meese and Anderson 2002; Meese and Harris 2001; Snowden and Milne 1996). Some physiological studies with non-human primates have indeed identified neurons tuned to spiral motion in MST (Geesaman & Andersen 1996; Graziano et al. 1994). Regardless of whether there are spiral detectors, the evidence suggests that in primates, motion integration of local signals is more efficient for rotational and radial motion.

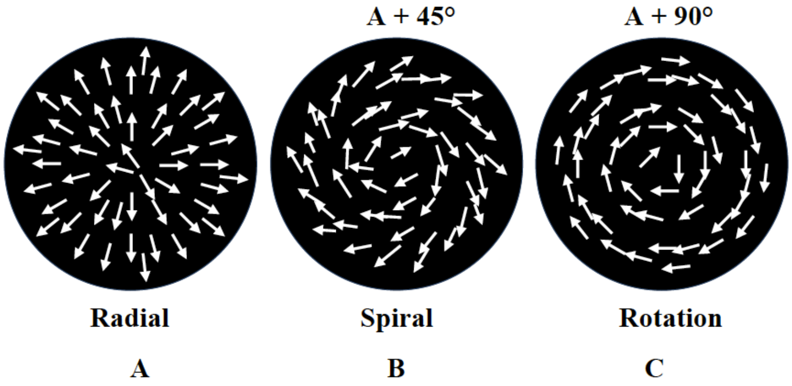


Figure 4.1 Types of motion patterns used in this study. Each pattern differs from the other solely based on the direction of the local vectors. **a** Shows radial motion, **b** shows spiral motion, and **c** shows rotational motion.

As is the case for primates, many birds are predominantly dependent on vision for their survival, but unlike the primate visual system, relatively little is known about the higher telencephalic areas of the avian visual system (Husband and Shimizu 2001). All vertebrates have three major visual pathways: the thalamofugal pathway (i.e., the retino-collicular pathway), the tectofugal pathway (i.e., the retino-thalamostriate pathway), and the accessory optic system (AOS). In the mammalian brain, 90 % of the ganglion cells from the retina travel along the thalamofugal pathway. However, in the avian brain, most axons leaving the retina travel along the tectofugal pathway (Butler & Hodos, 2005). Lesions to the thalamofugal pathway in humans and macaque monkeys have been shown to disrupt color perception, spatial resolution, and can even result in "blindness" (Milner & Goodale, 1995; Ungerleider & Mishkin, 1982). In contrast, lesions to the thalamofugal pathway have little to no deficit on visual discrimination tasks involving color, form, or intensity in pigeons. Lesions to the pigeon tectofugal pathway, however, result in deficits that are similar to the deficits found after lesions in the thalamofugal pathway of primates (Chaves et al., 1993). The organization of visual information in the pigeon tectofugal pathway is reminiscent of the organization in the mammalian extrastriate cortex as it is functionally segregated (Shimizu et al., 2010). For instance, the entopallium, a telencephalic structure that is part of the tectofugal pathway, is segregated such that the rostral caudal region processes motion information (Nguyen et al., 2004; Shimizu et al., 2010).

Given that most birds and primates are visually dependent, comparative research between birds and primates provides an opportunity to investigate how two different visual systems solve similar problems (i.e., the problem of seeing and perceiving). Currently, there is little information on the psychophysical properties of low- and mid-level vision in birds, especially with respect to the motion integration (Lazareva et al., 2012). Bischof et al. (1999) used random dot stimuli to investigate global motion by comparing coherent motion to random motion in pigeons and humans. They found that the pigeon visual system was much less tolerant of dynamic noise compared to the human visual system. It should also be noted that Bischof et al. (1999) used planar motion (specifically up, down, left and right global motion) and they did not observe any differences in performance based on direction of motion. In this study, we investigate whether the pigeon visual system is more sensitive to certain complex motion patterns relative to others by measuring the detection of complex motion embedded in noise (Pelli & Farell 1999) using similar patterns to those used by Morrone et al. (1999). We also measured the detection thresholds in humans to allow a direct comparison of the psychophysical properties of the motion system in the primate and avian visual systems.

4.3 Experiment 1

4.3.1 Methods

Participants

Six adults with normal or corrected-to-normal vision participated in the experiment. Participants included three authors and three graduate students from the University of Alberta who had only cursory knowledge of the purpose of the experiment.

Six pigeons with previous unrelated touch screen experience served as subjects. The birds were housed in individual cages under a 12-h light/dark cycle (light onset at 6:00 a.m.). All birds were maintained at approximately 85 % of their free-feeding weights. Water and grit were available adlib in the home cages.

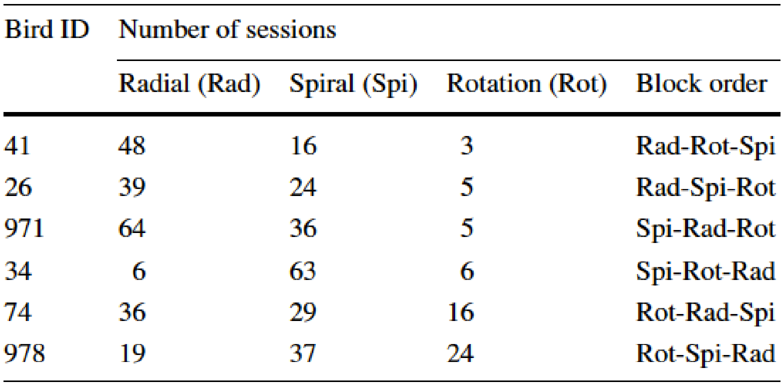
Apparatus

For both humans and pigeons, stimuli were displayed on a 22″ Viewsonic VX2268wm FuHzion LCD computer monitor (resolution: 1,680 x 1,050 pixels; refresh rate: 120 Hz). Participants' head position was fixed with a chin rest. For pigeons, the experiment was conducted in touch screen operant chambers. The monitor was equipped with a 17″ Carroll Touch infrared touch frame. Each chamber contained two solenoid-type bird feeders on the side walls of the chamber. Lamps located within each feeder illuminated feeder presentations, and photocells measured the duration of head entries into the hoppers to limit feeding durations to 1 s per food presentation. The chambers were connected to computers located in an adjacent room. These computers controlled all of the experimental contingencies and recorded the responses.

Stimuli and design

The stimuli consisted of randomly placed dots in a circular aperture that subtended 39.81° in diameter. The dots were white and subtended a visual angle of 0.36° x 0.36°. The white dots were presented on a black background. The dot density in the display was 3 %. In one condition (i.e., radial), each dot moved 0.72° per frame, which means that the speed was 42.93°/s. In the two remaining conditions (i.e., Rotation and Spiral), dots closer to the center of the pattern moved at a slower speed, while the dots closer to the edges moved at a higher speed in order to maintain rigidity of the motion pattern. However, the average velocities in these two conditions were matched to that of the radial condition. We used a lifetime of five frames, and each frame was updated on every second monitor refresh (16.7 ms per frame; image update rate: 60 Hz). Viewing distance was set at 45 cm for human participants, whereas for pigeons, we scaled down the physical measurements of the stimuli (including dot size) by a factor of 5 to account for viewing distance in the operant box (Bischof et al., 1999). Dots were removed when their position on the current frame reached the edge of the circular aperture or if they reached their lifetime limit. New dots were generated following Gaussian probability functions (SD = 4.22°), such that dots were most likely to be generated near the center of the circular aperture for spiral and radial patterns. Note that in the rotation pattern, dots never exceeded the edge of the aperture and thus were only removed if they reached the lifetime limit.

Three types of global complex motion were used: radial, spiral, and rotation (Figure 4.1). The three conditions were counterbalanced across participants (see Block Order in Table 4.1). The coherence level was varied by changing the ratio of signal-to-noise dots within a pattern. Signal dots moved in the coherent direction, whereas noise dots moved in a randomly assigned direction (Scase et al., 1996). We used the method of constant stimuli to present the different coherence levels. A total of 11 coherence levels were used. For pigeons, we used: 0, 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100 %. For humans, we used: 0, 1, 2, 4, 6, 8, 10, 15, 20, 25, and 30 %. The use of different levels of coherence for pigeons and humans are based on the findings of Bischof et al. (1999) who found that motion integration in pigeons were poor relative to humans. For radial patterns, the direction of motion moved inward (i.e., contraction) or outward (i.e., expansion). Likewise, rotation patterns rotated either clockwise or counterclockwise and spiral patterns rotated inward clockwise or outward counterclockwise. The direction of motion within a trial remained consistent across frames, but was counterbalanced within the session.



Bird ID	Number of sessions			
	Radial (Rad)	Spiral (Spi)	Rotation (Rot)	Block order
41	48	16	3	Rad-Rot-Spi
26	39	24	5	Rad-Spi-Rot
971	64	36	5	Spi-Rad-Rot
34	6	63	6	Spi-Rot-Rad
74	36	29	16	Rot-Rad-Spi
978	19	37	24	Rot-Spi-Rad

Table 4.1 Number of training sessions required to reach criterion for each motion pattern in Experiment 1

Procedure

Participants were tested using a two-alternative forced choice paradigm. At the beginning of each block of trials, participants were told which type of pattern they would be trying to detect. As illustrated in Figure 4.2, participants began the trial by “clicking” a gray start stimulus (i.e., moving the mouse cursor over the stimulus and depressing the left mouse button). Thereafter, the S+ (motion containing coherence motion) and S− (noise pattern; identical to 0 % coherence) were presented simultaneously. The participants were then required to click on the S+. No feedback was given. The left/right position of the S+ and S− was counterbalanced.

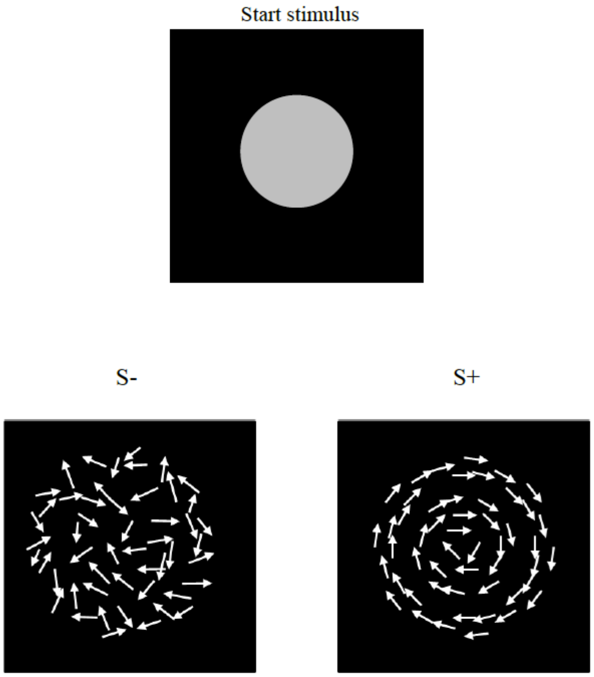


Figure 4.2 Illustration of the stimulus presentation protocol. First, the start stimulus is presented. After a peck (or mouse click for humans), two motion patterns are shown: one with coherent motion (S+) and one with no coherence (S−). In this example, the coherence is at 100 %, meaning that all the dots moved in the same direction

Testing was carried out in three blocks: one block for each type of motion pattern. In each condition, a total of 40 trials per coherence level and 20 trials per direction were presented for both the given pattern and the random control. This yielded a total of 440 trials within a block. Participants were allowed to take a brief break between blocks.

The procedure for the pigeons was similar to that described above, but with a few modifications. Prior to testing, the birds were trained to discriminate between the S+ (at 100 % coherence level) and S− (0 % coherence level). Pigeons responded by pecking at the pattern. The criterion for moving on to the testing phase was 85 % correct responses over three consecutive days. Testing was carried out in three blocks: one block for each type of pattern. Pigeons were trained and tested on one motion pattern before moving on to the next pattern. One session was carried out per day and each session lasted 45 min. The pigeons were allowed to complete as many trials as possible within the session. Testing was carried over a 10-day period. In each condition, across all sessions, the pigeons completed an average of 144 trials per coherence. If the birds' performance at 100 % coherence was below the training criterion for 2 days in a row, they were put back on training until they reach the training criterion. Thereafter they resumed testing.

Data Analysis

To analyze the data, we calculated the percent correct for each coherence level, for each motion pattern. Participants' coherence threshold for each motion pattern was estimated using a four-parameter cumulative Weibull function (Weibull, 1951) of the following form:

$$F(c) = \alpha(1 - e^{-(c/\beta)^{\gamma}}) + \delta$$

where c is the coherence level, and α, β, and γ are the asymptote, spread, and shape parameters of the Weibull function, respectively. δ is the y-intercept, to account for the guessing rate. The Weibull function was chosen as it provides a good approximation to the psychometric function (May and Solomon 2013; Quick 1974). The Weibull function was fit to data for each pattern, for each participant, by means of the Nelder and Mead (1965) simplex algorithm set to minimize the root-mean-squared-deviation (RMSD) between the function's estimation and the data. This procedure was repeated for 1,000 iterations to ensure the global minima was found. The threshold was then calculated as the coherence levels corresponding to 75 % accuracy using the best-fitting parameters.

All statistical analyses were conducted using SigmaPlot (Systat Software Inc., Chicago, IL) and MATLAB (The MathWorks Inc., Natick, MA). Effects were considered significant based on an alpha level of 0.05. One-way repeated-measures ANOVAs and post hoc pairwise analyses, using Holm-Sidak method, were conducted on the threshold coherence levels of the different motion patterns.

4.3.2 Results and discussion

Accuracy for each pattern is plotted as a function of coherence level in Figure 4.3a. Figure 4.3b shows the mean detection threshold of each motion pattern. A one-way repeated measures ANOVA yielded a significant main effect of motion pattern, $F(2, 10) = 103.08$, $p < .001$. Holm-Sidak post hoc pairwise comparisons demonstrated that the thresholds for rotation and radial patterns were significantly lower than the threshold for spiral motion [$t(5)$rotation vs spiral = 12.88; $t(5)$radial vs spiral = 11.94; all ps < .001] but did not differ from each other [$t(5)$rotation vs

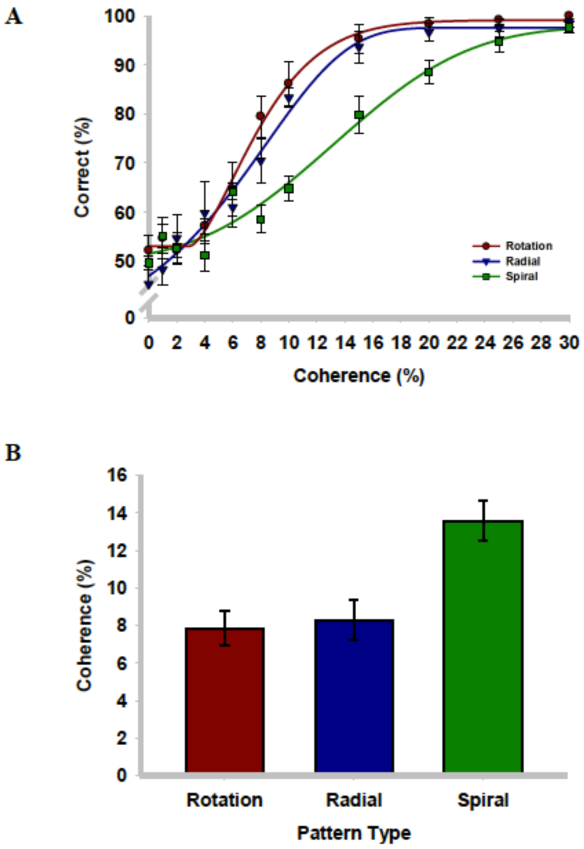


Figure 4.3 **a** Represents the percent correct as a function of coherence level for each motion pattern type for the human participants. *Lines* represent the Weibull function fit for each pattern type; *markers* represent the observed mean percentage correct. **b** Represents the estimated threshold (coherence level corresponding to 75 % correct) for each motion pattern for the human participants. *Error bars* represent the standard error of the mean

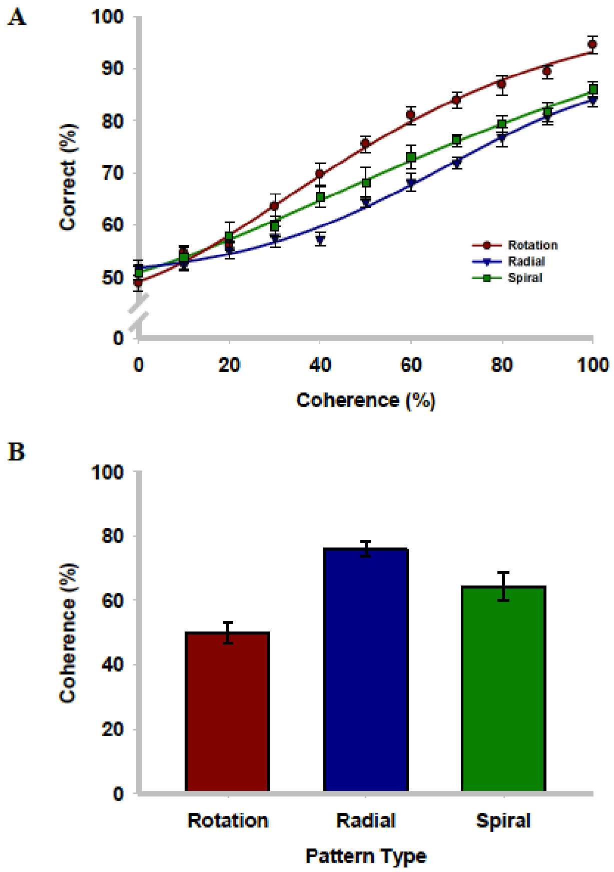


Figure 4.4 **a** Represents the percent correct as a function of coherence level for each motion pattern type for the pigeons. Lines represent the Weibull function fit for each pattern type; markers represent the observed mean percentage correct. **b** Represents the estimated threshold (coherence level corresponding to 75 % correct) for each motion pattern for the pigeons. Error bars represent the standard error of the mean

radial = 0.94; *p* = .37]. Paired *t* test revealed that there were no differences between clockwise and counterclockwise rotational motion [*t*(5) = 2.37; *p* = .06]. However, the threshold for contraction in the radial motion condition was significantly lower than the threshold for expansion [*t*(5) = 4.62; *p* = .006], as was the threshold for clockwise contraction spiral motion compared to counter-clockwise expansion spiral motion [*t*(5) = 2.73, *p* = .04; Figure 4.4].

Pigeons

Accuracy for each motion pattern is plotted as a function of coherence level in Figure 4a. Figure 4b shows the mean detection threshold of each motion pattern. A one-way repeated-measures ANOVA yielded a significant main effect of motion pattern, *F*(2, 10) = 13.51, *p* < .001. The results of Holm-Sidak post hoc pairwise comparisons revealed that the thresholds for each motion pattern differed significantly from each other. The threshold for rotational motion was significantly lower than those of radial [*t*(5) = 5.19; *p* < .001] and spiral motion [*t*(5) = 2.87; *p* = .01]. The threshold for spiral motion was also found to be significantly lower than the threshold for radial motion [*t*(5) = 2.32; *p* = .04]. Paired *t* tests revealed that there were no differences between clockwise and counterclockwise rotational motion [*t*(5) = 0.42; *p* = .70], clockwise contraction and counter-clockwise expansion spiral motion [*t*(5) = 0.23; *p* = .83], or expansion and contraction radial motion [*t*(5) = 1.18; *p* = .29] (Figure 4.5).

The number of training sessions required to reach criterion varied among motion patterns and individual birds. In particular, the pigeons reached criterion on rotational motion faster than for the other two patterns (M ± S D = 9.83 ± 8.33 sessions). Both radial (M = 35.33 ± 20.61 sessions) and spiral motion (M = 34.18 ± 16.14 sessions) required similar number of sessions to reach criterion. Shown in Table 4.1, four out of the six birds learned the task in the rotational motion condition within 6 days, providing further evidence that birds were much more sensitive to rotational motion. The differences, however, were not significant (F(2, 10) = 3.60, p = .07).

The results from the human data are congruent with the reported literature (e.g., Nankoo et al. 2012) in that we found that our participants were more sensitive to rotation and radial motion compared to spiral motion. With respect to the direction of radial motion, we found that our participants were more sensitive to contraction as opposed to expansion. This result is consistent with previous studies on radial motion detection (Edwards & Badcock, 1993; Edwards & Ibbotson, 2007; Shirai et al., 2006). We also noted lower thresholds for clockwise contraction spiral motion compared to counter-clockwise expansion spiral motion. In contrast, pigeons were most sensitive to rotational motion but least sensitive to radial motion, with detection of spiral motion at an intermediate level. The higher sensitivity to rotational motion in pigeons was corroborated by the smaller number of sessions required to reach criterion in the rotation condition relative to both spiral and radial conditions. No differences due to the direction of motion were found.

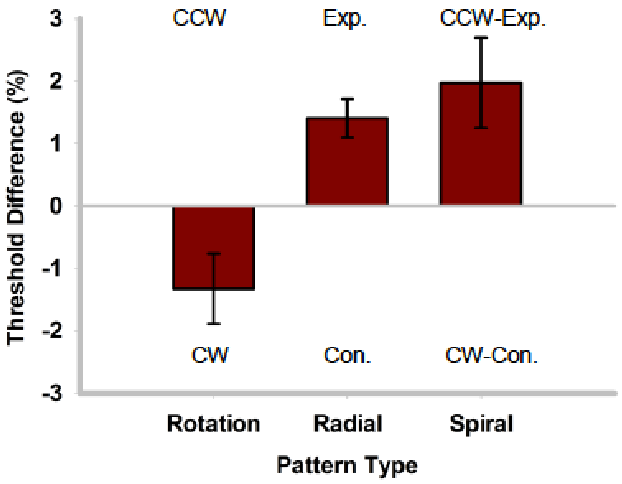


Figure 4.5 Shows the difference in estimated threshold (coherence level corresponding to 75 % correct) between the direction of motion in each of the three conditions for the human participants. For the rotation condition, the *bar* represents the difference between counterclockwise and clockwise motion. For the radial condition, the *bar* represents the difference between expansion and contraction motion. For the spiral condition, the *bar* represents the difference between counter-clockwise expansion and clockwise contraction motion. *Error bars* represent the standard error of the mean

In the global form literature, an aperture artifact has been suggested to facilitate perception of concentric form, shown with Glass patterns (Dakin and Bex 2002; Glass 1969). Glass patterns are stimuli considered to be equivalent to random-dot motion for studying global form perception given that the local signals in these patterns consist of dots pairs whose orientations are summated to identify the global structure. Wilson and Wilkinson (1998) have reported that human adults were better at detecting concentric form from noise compared to translation form from noise. However, Wilson and Wilkinson (1998) used a circular stimulus window. Dakin and Bex (2002) have shown that windowing Glass patterns in a square window abolish the advantage of concentric patterns relative to translation.

They note that translation and noise patterns windowed in a circular aperture cause the pattern to be less dense at the edge because the dot pairs are perpendicular to the edge. This artifact is not found in concentric Glass patterns because the dot pairs align with the edge orientation (which makes the edge more defined than in translation or random). Dakin and Bex (2002) suggest that the more defined edge of concentric form relative to noise is what explains the concentric advantage found in the literature. Similarly, because both translation and noise have less defined edges, participants cannot use edge integrity to identify the pattern from the noise as easily as in the concentric condition. Given the effect of shape aperture in Glass patterns, it is unclear whether the lower thresholds for rotational motion found with the pigeons were also an artifact of the shape of the stimulus display. Because we used a circular display aperture, no dots would cross the edge of the display compared to radial and spiral motion, but also compared to the random motion. Thus, the rotation patterns had fewer flickers as fewer dots disappeared at the edges. This may have facilitated discrimination of rotational motion from random motion. To address this concern, we carried out Experiment2, in which we compared the thresholds of the pigeons for rotational motion within a circular display aperture to rotational motion within a square aperture.

4.4 Experiment 2

4.4.1 Methods

Four pigeons with previous unrelated touch screen experience served as subjects for Experiment 2. Housing and feeding protocols were the same as in Experiment 1.

Apparatus, stimuli, and design

The apparatus was the same as in Experiment 1. In the circular aperture condition, the stimuli consisted of dots in a circular aperture with a diameter of 39.81°. In the square aperture condition, the dots (white dots on black background) were placed in a square aperture that subtended 36.62° x 36.62°. The areas of both apertures were identical. Both stimuli contained 326 dots. The dots in the square and circular aperture moved on average 0.72° per frame, which means that the average speed was 42.93°/s, similar to the stimuli in Experiment 1. The stimuli and design were similar to Experiment 1 in every other aspect.

Procedure

The procedure for the pigeons was identical to Experiment 1 except that we only used rotational motion, and the manipulated variable was the shape of the aperture: circular or square (Figure 4.6). The order of the two conditions was counterbalanced across birds.

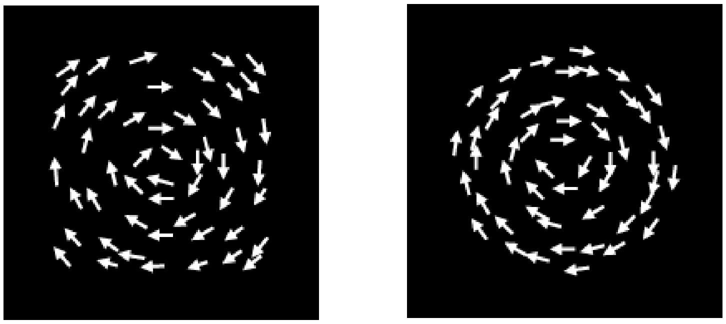


Figure 4.6 Illustration of the stimulus used in Experiment 2. **a** Shows the square display aperture and **b** shows the circular display aperture. The areas of both apertures in the actual experiment were identical. Note that this is not an exact reproduction

4.4.2 Results and discussion for Experiment 2

Figure 4.7a shows the mean percentage correct for each aperture shape plotted as a function of coherence level. Figure 4.7b shows the mean detection threshold of each motion pattern. A paired t test revealed that the difference in performance between the two aperture shapes did not differ significantly [$t(3) = 1.48$, $p = .23$]. The result from Experiment 2 suggests that the greater sensitivity of pigeons to rotational motion was not due to an artifact of the shape of the aperture. While Experiment 2 controlled the shape of the aperture to address the higher sensitivity of rotational motion, it is unclear whether the lower sensitivity of pigeons to radial motion, relative to rotation, is due to the characteristics of the rotational and radial motion patterns. The rotational motion used in Experiment 1 is a motion pattern that can be generated by rotational optic flow from self-motion or by object motion in the environment. However, the radial motion from Experiment 1 (i.e., radial motion with constant linear velocity) cannot be generated by self-motion or object motion. To control for this difference, we conducted Experiment 3 to investigate whether the lower sensitivity of the pigeons for radial motion in Experiment 1 was not due to the fact that the animal never encounters radial motion with constant linear velocity. The radial motion from Experiment 3 used an increasing linear velocity (in expansion; decreasing in contraction), akin to what an animal would encounter in nature (Gibson, 1954).

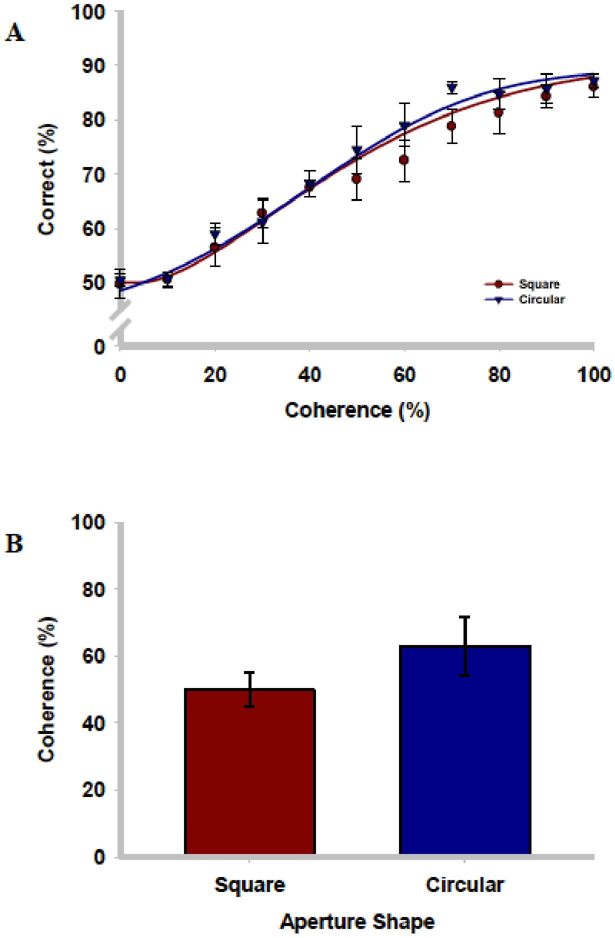


Figure 4.7 **a** Represents the percent correct as a function of coherence level for each aperture shape. *Lines* represent the Weibull function fit for each pattern type; *markers* represent the observed mean percentage correct. **b** Represents the estimated threshold (coherence level corresponding to 75 % correct) for each aperture shape. *Error bars* represent the standard error of the mean

4.5 Experiment 3

4.5.1 Methods

Four pigeons with previous unrelated touch screen experience served as subjects for Experiment 3. Housing and feeding protocols were the same as in Experiments 1 and 2. The apparatus was the same as in Experiment 1. In one condition, the stimuli consisted of radial motion with dots moving at a constant linear velocity of 42.93°/s. In the second condition, we used radial motion with dots increasing speed with eccentricity. Here dots moved at a curvilinear speed such that as dots moved further from the origin, speed increased. Importantly, the average speed of the dots was equal that of the constant linear velocity condition.

4.5.2 Results and discussion for Experiment 3

Figure 4.8a shows the accuracy for each condition plotted as a function of coherence level. Figure 4.8b shows the mean detection threshold of each radial motion condition. A paired *t* test found that the pigeons performed better on the radial motion with accelerating dots as opposed to radial motion with constant linear velocity, $t(3) = 3.28$, $p = 0.046$ (Figure 4.8). The result of Experiment 3 shows that the pigeons are more sensitive to radial motion when there is a nonlinear acceleration as opposed to a constant velocity. This may be because optic flow consists of elements that move with a nonlinear acceleration as the animals move in the environment (Gibson, 1954). Thus, the pigeon visual system may be more sensitive to this naturalistic motion pattern. However, it should be noted that Edwards and Ibbotson (2007) showed that humans have lower thresholds for radial motion when there is a constant velocity. Nonetheless, even with the accelerating dots, the thresholds of the pigeons did not match those found for rotational motion.

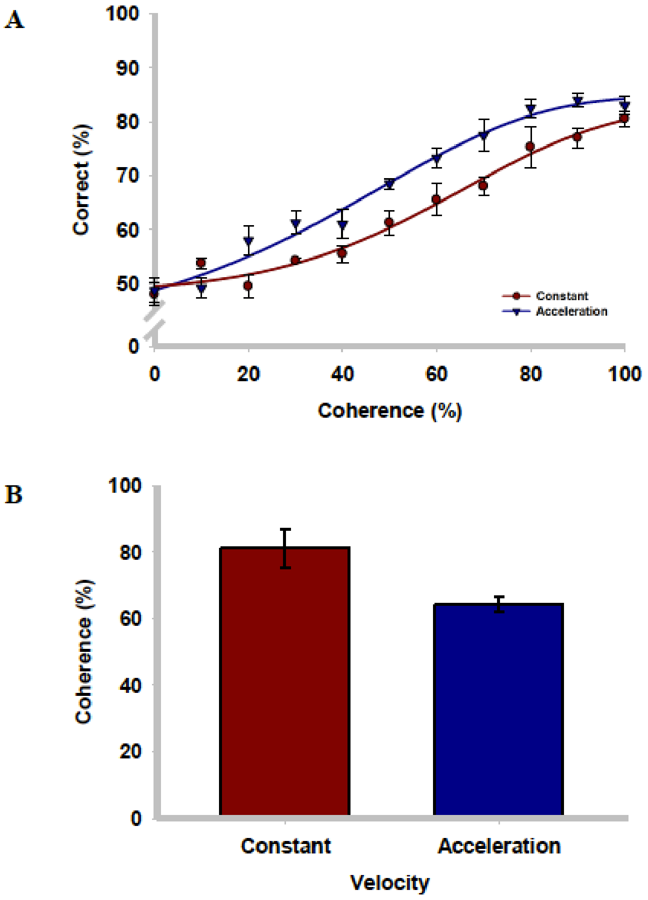


Figure 4.8 **a** Represents the percent correct as a function of coherence level for each velocity types. *Lines* represent the Weibull function fit for each pattern type; *markers* represent the observed mean percentage correct. **b** Represents the estimated threshold (coherence level corresponding to 75 % correct) for each velocity types. *Error bars* represent the standard error of the mean

As shown in Figure 4.9, they instead were comparable to those of spiral motion in Experiment 1.

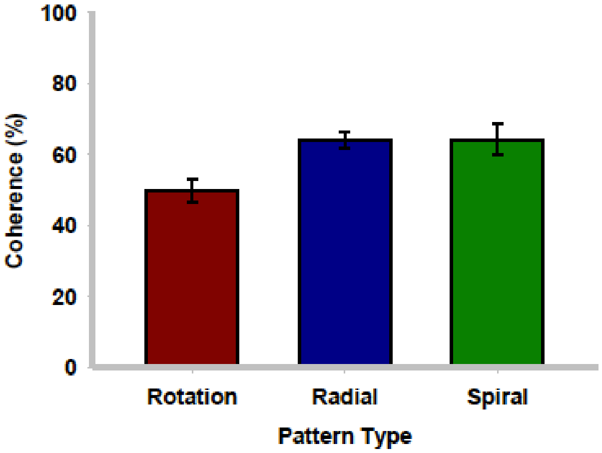


Figure 4.9 The estimated threshold (coherence level corresponding to 75 % correct) for rotational and spiral motion from Experiment 1, and radial motion with accelerating velocity from Experiment 3 are shown. *Error bars* represent the standard error of the mean

4.6 General discussion

Our results indicate that humans and pigeons differ in their ability to detect complex motion. Specifically, we found that pigeons were more sensitive to rotational motion than to radial or spiral motion. Humans, on the other hand, were more sensitive to both radial and rotational motion than to spiral motion. We also noted a higher sensitivity for contraction compared to expansion in the radial motion condition and to clockwise contraction compared to counter-clockwise expansion in the spiral motion. Experiment 2 demonstrated that the superior detection for rotational motion by pigeons was not an artifact of the shape of the display aperture. In Experiment 3, we found that pigeons were better at detecting radial motion that contained elements moving with a nonlinear acceleration, although the thresholds did not reach the levels found for rotational motion.

Neuroimaging studies have shown that the human homologue of MT/MST, respond to complex motion (Huk et al., 2002; Morrone et al., 2000; Pitzalis et al., 2010). Furthermore, Morrone et al. (1999) and Burr et al. (2001) demonstrated that humans are more sensitive to rotational and radial motion relative to spiral motion. These findings show that the primate visual system has the neural equipment to process complex motion, and it is most efficient at pooling signals along either a rotational or radial trajectory.

While there are many studies that probe the primate motion system, relatively little is known about the avian motion system, especially with respect to motion integration. Here, we provide evidence that the avian visual system is particularly sensitive to global rotation, but not radial and spiral motion. In other words, the pooling mechanism in the pigeon visual system is most efficient for motion along a rotational trajectory. This fundamental difference in global motion sensitivity is interesting as it raises the question as to why this difference exists. Global radial motion is generated during translational movement of the organism and is used to estimate heading (Gibson, 1954; Warren, 2004). Thus, radial pattern from optic flow is an important cue for visually dependent mobile animals. Optic flow components (i.e., radial, rotation, and translation) are processed in the AOS, a subcortical visual pathway found in all vertebrates (Simpson, 1984). In the primate visual system, there are multiple connections between the AOS and MT/MST (Boussaoud et al., 1992; Distler & Hoffmann, 2001), which suggests that the complex motion detectors in MST are involved in processing optic flow patterns. In the pigeon brain, cells in the AOS respond to radial optic flow as well as rotation optic flow (for recent reviews, see Wylie 2013, and Wylie & Iwaniuk, 2012). Thus, it is surprising that the pigeon visual system is less sensitive to radial motion given the importance of radial motion as a self-motion cue and given that the mechanisms are in place for the pigeon visual system to process both radial and rotation global motion. However, one explanation for this is that our stimuli did not engage the AOS because our stimuli were of higher velocities to the preferred speed (i.e., 0.05–5°/s) of cells in the AOS. The AOS is specialized for large field slow moving motion resulting from self-motion (Frost, 1985), although there are some cells responsive to higher velocities (Crowder & Wylie, 2001; Wylie & Crowder, 2000). Therefore, it is possible that our stimuli were interpreted as moving objects, as opposed to optic flow. The higher sensitivity for rotational motion may be specific to movement of objects in the environment as opposed to optic flow resulting from self-motion.

One interesting line of research has shown that circular trajectories of local motion are an important cue for identifying point-light walkers (see Troje & Chang, 2013 for a review). Specifically, the research shows that humans may use the circular motion of the feet (termed rolling wheel), to identify biological movement, and provide facing direction. While Troje and Aust (2013) have noted that pigeons do not appear to use this local rolling wheel cue, it does highlight the functional advantages of having specialized complex motion detectors that are independent from the optic flow system. Thus, one can hypothesize that the sensitivity to global circular motion in pigeons may serve critical functions such as identifying body direction of other flying animals with respect to gravity.

Object motion in pigeons is processed primarily in the tectofugal pathway, where information from the retina is sent to the optic tectum before reaching the nucleus rotundus (nRT) and finally the entopallium (see Hellmann et al., 2004; Wylie & Iwaniuk, 2012, for review). Information in the nRT is segregated into regions containing neurons that are responsive to luminance, color, 2D motion, and motion in depth. Cells responsive for motion are found in the ventral, central, and caudal nRT (Wang et al., 1993). The projections from the nRT to entopallium, a telencephalic structure that some researchers have likened to the mammalian extrastriate cortices (Shimizu & Bowers, 1999; Shimizu et al., 2010), are topographical. Neurons in the caudal entopallium respond to motion, and lesions to this area cause a deficit in the detection of global translation motion (Nguyen et al. 2004). Cells in the entopallium have a large receptive field and respond to stimuli moving at high velocities of 16–128°/s (Gu et al., 2002). In addition, the entopallium receives input from the visual Wulst, a telencephalic structure that is part of the thalamofugal pathway and that has been shown to respond to local components within plaid patterns but not to the global direction of the pattern (Baron et al., 2007). For these reasons, the entopallium appear to be a likely candidate for motion integration and processing of complex motion and where the rotation sensitivity stems from. Furthermore, the caudal entopallium contains cells that are responsive to looming stimuli (Xiao et al., 2006; Xiao & Frost, 2009). Looming stimuli result from approaching objects, whether through movement of the object or through self-motion, as opposed to radial motion which is solely a result of self-motion. This again suggests the specialization of this system for object motion and may also explain the relatively low sensitivity to radial motion that we observed.

The thresholds of the pigeons for radial and spiral motion are also telling. If we assume that these motion patterns were activating the rotation global detectors, we should have observed a higher sensitivity for spiral motion relative to radial motion, as spiral motion is physically more closely related to rotational motion than the radial motion from Experiment 1. Although the results from Experiment 1 suggest that this is the case, it is likely that the reduced sensitivity was due to the fact that radial motion in Experiment 1 consisted of dots moving at a constant linear velocity. However, the radial motion in Experiment 3 contained accelerating dots and was therefore more similar to spiral and rotational motion from Experiment 1 given that the speed of the dots within these patterns were also dependent on the distance from the center of the pattern. Thresholds for radial motion with accelerating dots in Experiment 3 remained higher than for rotation but were similar to the spiral motion. Therefore, we can surmise that there are other non-rotational detectors that are perhaps less efficient at pooling the local motion signals or fewer in numbers relative to rotation detectors.

Finally, our results also show that in general, pigeons perform poorly, relative to humans, on motion detection tasks. This is congruent with previous research on motion detection (e.g., Bischof et al., 1999). The validity of these results, however, is contentious given that the lack of psychophysical data on stimulus parameters necessary for optimal performance on motion tasks in pigeons. Furthermore, as shown by various researchers (Loidolt et al., 2006; Rubene et al., 2010), the apparatus used to present stimuli has a significant impact on birds' performance in tasks that rely on motion. Therefore, we should be cautious when interpreting the lower overall sensitivity of pigeons relative to humans in motion detection tasks.

It should be noted that Martinoya et al. (1983) reported behavioral data that suggest that there are differences in motion sensitivities when stimuli are presented in the lateral versus the frontal field in pigeons. These differences have been argued to reflect a difference in the anatomy of the pigeon retina (See Güntürkün, 2000 for a review). The pigeon retina has two distinct areas: the red field and the yellow field. The red field is located dorsotemporal retina and contains an area of high ganglion cells density known as the area dorealis. The rest of the retina is part of the yellow field and contains the fovea. It has often been argued that the yellow field and the red field subserve different functions. The yellow field is often linked to the detection of motion (e.g., approaching predator), whereas the red field is associated with feeding behavior (e.g., pecking at the ground) (Maldonado et al., 1988; Nye, 1973). In our study, the pigeons' movement was not restricted, and given the size of our stimuli, we argue that it is unlikely that the red field was specifically engaged during the task. In addition, the stimuli in our study were presented in the frontal plane, which means that the birds would need to tilt their head backwards to allow the image to project onto the red field. Based on video recordings of the birds, we did not observe any backward head tilts during the experiments.

Here, we have reported that the avian motion system is most sensitive to rotational motion, suggestive of a more efficient pooling mechanism. Furthermore, the bias for rotational motion suggests the presence of global detectors tuned to rotational motion in the pigeon visual system. In addition, based on the evidence, it appears that the rotation global detectors were not involved in processing radial and spiral global motion. Additionally, it is unlikely that these detectors are involved in processing optic flow as has been hypothesized for the detectors in the primate brain.

4.7 Acknowledgements

We would like to thank J.P., A.N.S. and M.K.M. for participating in our study. We would also like to thank Isaac Lank, Jeffrey Pisklak, and Jason Long for their help with technical issues and for running the pigeons in the experiments. This research was supported by grants from the National Science and Engineering Research Council (NSERC) of Canada to M.L.S. and D.R.W., and by an NSERC Alexander Graham Bell Canada Graduate Scholarship (Doctoral level) to C.R.M

4.8 Reference

Baron, J., Pinto, L., Dias, M. O., Lima, B., & Neuenschwander, S. (2007). Directional responses of visual wulst neurones to grating and plaid patterns in the awake owl. *European Journal of Neuroscience*, *26*(7), 1950-1968.

Bischof, W. E., Reid, S. L., Wylie, D. R., & Spetch, M. L. (1999). Perception of coherent motion in random dot displays by pigeons and humans. *Perception & psychophysics*, *61*(6), 1089-1101.

Boussaoud, D., Desimone, R., & Ungerleider, L. G. (1992). Subcortical connections of visual areas MST and FST in macaques. *Visual neuroscience*, *9*(3-4), 291-302.

Britten, K. H., & van Wezel, R. J. (1998). Electrical microstimulation of cortical area MST biases heading perception in monkeys. *Nature neuroscience*, *1*(1), 59-63.

Burr, D., & Thompson, P. (2011). Motion psychophysics: 1985–2010. *Vision research*, *51*(13), 1431-1456.

Burr, D. C., Badcock, D. R., & Ross, J. (2001). Cardinal axes for radial and circular motion, revealed by summation and by masking. *Vision research*, *41*(4), 473-481.

Chaves, L. M., Hodos, W., & Güntürkün, O. (1993). Color-reversal learning: effects after lesions of thalamic visual structures in pigeons. *Visual neuroscience*, *10*(06), 1099-1107.

Crowder, N. A., & Wylie, D. R. (2001). Fast and slow neurons in the nucleus of the basal optic root in pigeons. *Neuroscience letters*, *304*(3), 133-136.

Dakin, S. C., & Bex, P. J. (2002). Summation of concentric orientation structure: seeing the Glass or the window?. *Vision Research*, *42*(16), 2013-2020.

Distler, C., & Hoffmann, K. P. (2001). Cortical input to the nucleus of the optic tract and dorsal terminal nucleus (NOT-DTN) in macaques: a retrograde tracing study. *Cerebral Cortex*, *11*(6), 572-580.

Duffy, C. J., & Wurtz, R. H. (1991). Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *Journal of neurophysiology*, *65*(6), 1329-1345.

Edwards, M., & Badcock, D. R. (1993). Asymmetries in the sensitivity to motion in depth: A centripetal bias. *PERCEPTION-LONDON-*, *22*, 1013-1013.

Edwards, M., & Ibbotson, M. R. (2007). Relative sensitivities to large-field optic-flow patterns varying in direction and speed. *PERCEPTION-LONDON-*, *36*(1), 113.

Frost, B. J. (1985). Neural mechanisms for detecting object motion and figure–ground boundaries contrasted with self-motion detecting systems. In D. Ingle, M. Jeannerod, D. Lee (Eds.), *Brain mechanisms and spatial vision*, (pp. 415-419). Dordrecht: Martinus Nijhoff Publishers.

Geesaman, B. J., & Andersen, R. A. (1996). The analysis of complex motion patterns by form/cue invariant MSTd neurons. *The Journal of Neuroscience*, *16*(15), 4716-4732.

Gibson, J. J. (1954). The visual perception of objective motion and subjective movement. *Psychological Review*, *61*(5), 304.

Glass, L. (1969). Moire effect from random dots. *Nature*, *223*(5206), 578-580.

Graziano, M. S., Andersen, R. A., & Snowden, R. J. (1994). Tuning of MST neurons to spiral motions. *The Journal of neuroscience*, *14*(1), 54-67.

Gu, Y., Wang, Y., Zhang, T., & Wang, S. R. (2002). Stimulus size selectivity and receptive field organization of ectostriatal neurons in the pigeon. *Journal of Comparative Physiology A*, *188*(3), 173-178.

Güntürkün, O. (2000). Sensory Physiology: Vision. In G. C., Whittow (Ed.), *Sturkie's avian physiology*, (pp. 1-19). Orlando: Academic Press.

Hellmann, B., Güntürkün, O., & Manns, M. (2004). Tectal mosaic: organization of the descending tectal projections in comparison to the ascending tectofugal pathway in the pigeon. *Journal of Comparative Neurology*, *472*(4), 395-410.

Huk, A. C., Dougherty, R. F., & Heeger, D. J. (2002). Retinotopy and functional subdivision of human areas MT and MST. *The Journal of Neuroscience*, *22*(16), 7195-7205.

Husband, S. & Shimizu, T. (2001). Evolution of the avian visual system. In R. G. Cook (Ed.), *Avian visual cognition*. www.pigeon.psy.tufts.edu/avc/husband/

Lazareva, O. F., Shimizu, T., & Wasserman, E. A. (2012). *How animals see the world: comparative behavior, biology, and evolution of vision*. London: Oxford University Press.

Loidolt, M., Aust, U., Steurer, M., Troje, N. F., & Huber, L. (2006). Limits of dynamic object perception in pigeons: Dynamic stimulus presentation does not enhance perception and discrimination of complex shape. *Learning & behavior*, *34*(1), 71-85.

Maldonado, P. E., Maturana, H., & Varela, F. J. (1988). Frontal and lateral visual system in birds. *Brain, Behavior and Evolution*, *32*(1), 57-62.

Martinoya, C., Rivaud, S., & Bloch, S. (1983). Comparing frontal and lateral viewing in the pigeon. II. Velocity thresholds for movement discrimination. *Behavioural brain research*, *8*(3), 375-385.

May, K. A., & Solomon, J. A. (2013). Four theorems on the psychometric function. *PloS one*, *8*(10), e74815.

Meese, T. S., & Anderson, S. J. (2001). Spiral mechanisms are required to account for summation of complex motion components. *Journal of Vision*, *1*(3), 160-160.

Meese, T. S., & Harris, M. G. (2001). Independent detectors for expansion and rotation, and for orthogonal components of deformation. *PERCEPTION-LONDON-*, *30*(10), 1189-1202.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.

Morrone, M. C., Burr, D. C., Di Pietro, S., & Stefanelli, M. A. (1999). Cardinal directions for visual optic flow. *Current Biology*, *9*(14), 763-766.

Morrone, M. C., Tosetti, M., Montanaro, D., Fiorentini, A., Cioni, G., & Burr, D. C. (2000). A cortical area that responds specifically to optic flow, revealed by fMRI. *Nature neuroscience*, *3*(12), 1322-1328.

Nakayama, K. (1985). Biological image motion processing: a review. *Vision research*, *25*(5), 625-660.

Nankoo, J. F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2012). Perception of dynamic Glass patterns. *Vision research*, *72*, 55-62.

Nelder, J. A., & Mead, R. (1965). A simplex method for function minimization. *The computer journal*, *7*(4), 308-313.

Nguyen, A. P., Spetch, M. L., Crowder, N. A., Winship, I. R., Hurd, P. L., & Wylie, D. R. (2004). A dissociation of motion and spatial-pattern vision in the avian telencephalon: implications for the evolution of “visual streams”. *The Journal of neuroscience*, *24*(21), 4962-4970.

Nye, P. W. (1973). On the functional differences between frontal and lateral visual fields of the pigeon. *Vision Research*, *13*(3), 559-574.

Pelli, D. G., & Farell, B. (1999). Why use noise?. *JOSA A*, *16*(3), 647-653.

Pitzalis, S., Sereno, M. I., Committeri, G., Fattori, P., Galati, G., Patria, F., & Galletti, C. (2010). Human V6: the medial motion area. *Cerebral Cortex*, *20*(2), 411-424.

Quick Jr, R. F. (1974). A vector-magnitude model of contrast detection. *Kybernetik*, *16*(2), 65-67.

Rubene, D., Håstad, O., Tauson, R., Wall, H., & Ödeen, A. (2010). The presence of UV wavelengths improves the temporal resolution of the avian visual system. *The Journal of experimental biology*, *213*(19), 3357-3363.

Saito, H. A., Yukie, M., Tanaka, K., Hikosaka, K., Fukada, Y., & Iwai, E. (1986). Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *The Journal of Neuroscience*, *6*(1), 145-157.

Scase, M. O., Braddick, O. J., & Raymond, J. E. (1996). What is noise for the motion system?. *Vision research*, *36*(16), 2579-2586.

Shimizu, T., & Bowers, A. N. (1999). Visual circuits of the avian telencephalon: evolutionary implications. *Behavioural brain research*, *98*(2), 183-191.

Shimizu, T., Patton, T. B., & Husband, S. A. (2010). Avian visual behavior and the organization of the telencephalon. *Brain, behavior and evolution*, *75*(3), 204-217.

Shirai, N., Kanazawa, S., & Yamaguchi, M. K. (2006). Anisotropic motion coherence sensitivities to expansion/contraction motion in early infancy. *Infant Behavior and Development*, *29*(2), 204-209.

Simpson, J. I. (1984). The accessory optic system. *Annual review of neuroscience*, *7*(1), 13-41.

Snowden, R. J., & Milne, A. B. (1996). The effects of adapting to complex motions: position invariance and tuning to spiral motions. *Journal of Cognitive Neuroscience*, *8*(5), 435-452.

Tanaka, K., & Saito, H. A. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology*, *62*(3), 626-641.

Troje, N. F., & Aust, U. (2013). What do you mean with “direction”? Local and global cues to biological motion perception in pigeons. *Vision research*, *79*, 47-55.

Troje, N. F., & Chang, D. H. F. (2013) Shape-independent processes in biological motion perception. In K. L. Johnson & Shiffrar, M. (Eds.), *People Watching:*

Social, Perceptual, and Neurophysiological Studies of Body Perception (pp. 82-100). London: Oxford University Press.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge: MIT Press.

Wall, M. B., Lingnau, A., Ashida, H., & Smith, A. T. (2008). Selective visual responses to expansion and rotation in the human MT complex revealed by functional magnetic resonance imaging adaptation. *EuropeanjJournal of neuroscience*, *27*(10), 2747-2757.

Wang, Y. C., Jiang, S., & Frost, B. J. (1993). Visual processing in pigeon nucleus rotundus: luminance, color, motion, and looming subdivisions. *Visual neuroscience*, *10*(01), 21-30.

Warren, W. (2004). Optic flow. In L. Chalupa & J. Werner (Eds.), *The visual Neurosciences*, (pp 1391–1401). Boston: MIT Press.

Weibull, W. (1951). Wide applicability. *Journal of applied mechanics*, *103*.

Wilson, H. R., & Wilkinson, F. (1998). Detection of global structure in Glass patterns: implications for form vision. *Vision research*, *38*(19), 2933-2947.

Wylie, D. R. (2013). Processing of visual signals related to self-motion in the cerebellum of pigeons. *Frontiers in behavioral neuroscience*, *7*.

Wylie, D. R., & Crowder, N. A. (2000). Spatiotemporal properties of fast and slow neurons in the pretectal nucleus lentiformis mesencephali in pigeons. *Journal of neurophysiology*, *84*(5), 2529-2540.

Wylie D. R., & Iwaniuk, A. N. (2012). Neural mechanisms underlying visual motion detection in birds. In O. F. Lazareva, T. Shimizu, E. A., Wasserman (Eds.), *How animals see the world: Behavior, biology, and evolution of vision* (pp. 289–318). London: Oxford University Press.

Xiao, Q., & Frost, B. J. (2009). Looming responses of telencephalic neurons in the pigeon are modulated by optic flow. *Brain research*, *1305*, 40-46.

Xiao, Q., Li, D. P., & Wang, S. R. (2006). Looming-sensitive responses and receptive field organization of telencephalic neurons in the pigeon. *Brain research bulletin*, *68*(5), 322-328.

Chapter 5

Re-evaluating birds' ability to detect Glass patterns

5.1 Abstract

Glass patterns (GPs) are static stimuli that consist of randomly positioned dot-pairs that are spatially integrated to create the perception of a global form. However, when multiple independently generated static GPs are presented sequentially (termed 'dynamic' GP), observers report a percept of coherent motion, and data show an improvement in sensitivity. This increased sensitivity has been attributed to a summation of the form signals provided by the individual GPs. In Experiment 1, we tested whether pigeons also show a heightened sensitivity to dynamic GPs. Our results show that pigeons are significantly better at learning to discriminate dynamic GPs from noise compared with static GPs. However, in contrast to previous research, we found that pigeons did not perform well enough with our static GPs to extract sensitivity measurements. In Experiment 2, we compared our static GPs to those that have been used previously. We show that the difference in the comparison noise patterns is important. We used dipole noise patterns, while previous studies used uniform noise patterns that differ in mean dot spacing to the S+. We argue that prior findings from the use of GPs in pigeons should be re-evaluated using dynamic GP stimuli with noise that consist of dipoles.

5.2 Introduction

To perceive an object-filled scene, the visual system organizes the multitude of incoming signals through a process of integration and segregation of information. For instance, the analysis of complex shapes in the primate brain involves an integration stage in which local orientation signals from V1 neurons are pooled at higher cortical levels to derive global complex form of objects in the environment (Riesenhuber & Poggio, 1999, 2000). To study the pooling mechanisms of the form signals, researchers frequently use Glass patterns (GPs) (Glass, 1969). GPs are static moire´ patterns that consist of randomly placed dot pairs (dipoles) that are oriented in specific ways to generate different types of global forms. Orientation detectors in V1 and V2 respond to the dipoles in GPs, and the orientation information is pooled at higher cortical levels (e.g., V4) (Smith et al., 2002; Smith & Kohn, 2007; Wilson & Wilkinson, 1998). Thus, GPs are useful for studying the pooling mechanisms that ultimately extract complex shapes.

When presented with a rapid sequence of independently generated GPs with the same global form, termed 'dynamic' GPs, human observers report a salient percept of coherent motion (Ross et al., 2000). This occurs in spite of the fact that no coherent motion signals are present in the GPs. In addition, human observers appear to be significantly more sensitive in the detection of those dynamic GPs compared to static GPs (Nankoo et al., 2012; Burr & Ross, 2006; Or et al., 2007). The mechanisms responsible for the perception of dynamic GPs remain a subject of investigation, but two possible explanations have been put forth. First, it has been suggested that the illusory coherent motion in dynamic GPs is the result of motion streak sensors interpreting dipoles as streaks that result from high velocity movement of objects across the retina (Day & Palomares, 2014; Geisler, 1999; Ross et al., 2000). Second, the improved sensitivity observed with dynamic GPs may be a consequence of summation of the greater number of unique global form signals present in dynamic GPs (Nankoo et al., 2012; 2015). Nankoo et al. (2012) showed that the relative detection thresholds of concentric, radial, vertical, horizontal, and spiral dynamic GPs are similar to those of static GPs and different from those of real motion (see Figure 3 in Nankoo et al., 2012). Nankoo et al. (2015) provided evidence suggesting that the number of unique GPs frames is a more dominant factor than motion streak in facilitating the perception of form from dynamic GPs.

Birds, like mammals, appear to see and act upon an object-filled environment (Cook, 2000). Indeed, evidence suggests that some birds have similar (and sometimes superior) visual capabilities compared to the most visually dependent mammals, primates (see Hodos, 2012 for review). Several studies have demonstrated that pigeons, a common model organism for studies of avian vision, have the ability to see complex objects within a scene in a similar way to humans (e.g., Cavoto & Cook 2006; see Lazareva et al., 2012 for review). The capability of pigeons to perceive complex objects raises the question of whether a similar integration of form signals to that found in primates is present in the avian brain. Kelly et al. (2001) attempted to probe this question by comparing the detection thresholds for static GPs of different global forms (i.e., concentric, radial, vertical, horizontal, and spiral) in pigeons and humans. Kelly et al. (2001) reported that pigeons did not show any differential sensitivity to the types of GPs used. In contrast to birds, multiple studies, including Kelly et al. (2001), have shown that humans have a heightened sensitivity to concentric and radial GPs (Wilson & Wilkinson, 1998; Anderson & Swettenham, 2006; Nankoo et al. 2012; although see Dakin & Bex, 2002). It has been suggested that the heightened sensitivity for concentric GPs in humans is due to the presence of specialized concentric detectors that feed into higher-level cortical areas, and is related to face perception (Wilson & Wilkinson, 1998; Wilson et al., 1997; Fecko et al., 2014). Kelly et al. (2001) suggested that their results reflect the propensity for pigeons to rely more on local information than humans, and that unlike humans, they do not possess a specialized pooling mechanism for concentric form as they tend to use local cues for recognition of conspecifics (Cavoto & Cook, 2001). A recent study by Qadri and Cook (2014) found similar results in starlings, suggesting that perhaps the bias for concentric and radial superiority is unique to primates (or mammals in general).

In order to further examine the potential differences in global form processes between the avian and mammalian visual system, we investigated the detection of dynamic GPs in pigeons. We initially aimed to compare the detection threshold of pigeons for concentric patterns of dynamic and static GPs. However, this was not possible as the majority of birds failed to reach a sufficient level of performance with static GPs to estimate thresholds. Thus, we instead analyzed acquisition of the discrimination to assess whether the birds were better able to discriminate global form from noise for dynamic or static GPs. Better performance in the dynamic GPs condition might suggest that the avian visual system processes dynamic GPs in a similar way to the primate visual system. That is, better performance with dynamic

GPs might suggest that a form-summation mechanism, as suggested by Nankoo et al. (2012) for humans, is present in the avian visual system.

5.3 Experiment 1

5.3.1 Methods

Six pigeons with previous unrelated touch screen experience served as subjects. Three birds were assigned to the dynamic GP group, and three birds were assigned to the static GP group. The birds were housed in individual cages under a 12-h light/dark cycle (light onset at 6:00 a.m.). All birds were maintained at approximately 85 % of their free-feeding weights. Water and grit were available adlib in the home cages.

Apparatus

The stimuli were displayed on a 2200 Viewsonic VX2268wm FuHzion LCD computer monitor (resolution 1680 x 1050 pixels; refresh rate 120 Hz). The experiment was conducted in touch screen operant chambers. The monitor was equipped with a 1700 Carroll Touch infrared touch frame. Each chamber contained two solenoid-type bird feeders on the sidewalls of the chamber. Lamps located within each feeder illuminated feeder presentations, and photocells measured the duration of head entries into the hoppers to limit feeding durations to 1 s per food presentation. The chambers were connected to computers located in an adjacent room. These computers controlled all of the experimental contingencies and recorded the responses.

Stimuli and design

Each stimulus was presented for two minutes or until the birds made a choice. Concentric patterns were used in both the static and dynamic conditions (see Figure 5.1). Each stimulus consisted of multiple frames of GPs, each of which was updated at every second monitor refresh (image update rate 60 Hz). For the dynamic GP condition, each frame was a unique and independently generated GP, whereas in the static condition, each frame within a trial was identical, thus giving the impression of a static image; a sample dynamic GP is included as electronic supplementary material to the present paper.

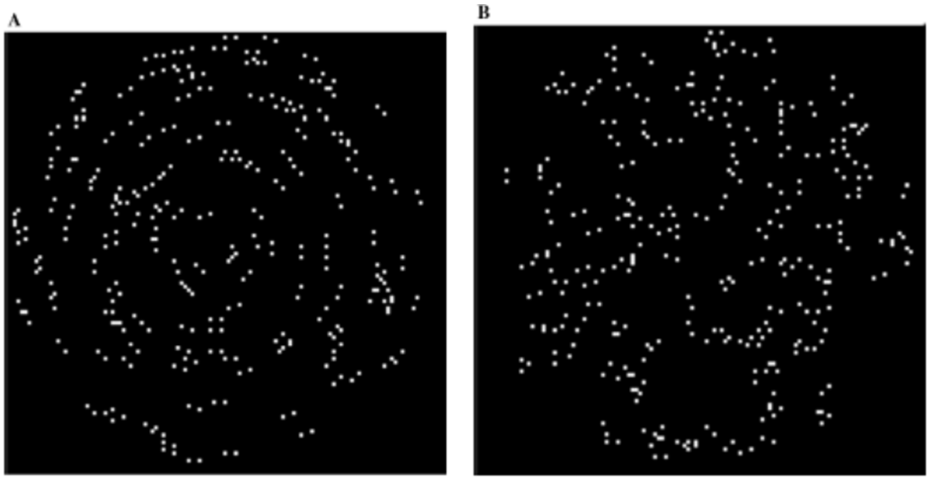


Figure 5.1 Types of stimuli used in Experiment 1. a A concentric Glass pattern (100 % coherence) and b the noise pattern (0 % coherence)

Assuming an estimated 9 cm viewing distance (Bischof et al., 1999; also see Nankoo et al., 2014), each individual GP subtended a visual angle of 39.8° (232 pixels) and consisted of white square dots with an angular size of 0.36° x 0.36° (2 x 2 pixels) on a black background. The density of dots within each pattern was set at 3

%, and the dot separation was 1.07° (6 pixels). As shown in Figure 5.1, the S+ pattern contained only signal dipoles (100 % coherence), whereas the S- pattern contained only randomly oriented dipoles (0 % coherence). Thus, there was no global form in the S-, but the distribution of dots in both the S+ and S- were equivalent.

Procedure

Pigeons were tested using a simultaneous two-alternative forced choice paradigm. The S+ and S- stimuli were presented simultaneously. The left–right location of the S+ and S- on the screen was randomized across trials. Each trial began when the birds pecked a gray start stimulus. Thereafter, a peck to the S+ resulted in access to food for one second. A peck to the S- resulted in no food reward. The birds completed as many trials as possible within 45-min sessions. In our data, this resulted in a minimum of 55 trials per session and an average of 150 trials per session. The criterion for completing the training was a mean of 75 % correct responses over three consecutive sessions. The performance for each session was calculated using a simple moving average of three sessions. A maximum of 45 training sessions were conducted

Data analysis

Statistical analyses, using a binomial-sign test, were conducted for each session in order to establish whether the birds performed significantly better than chance. The accuracy measure was based on a moving average of three sessions.

Analysis of the overall performance of each bird was done by deriving a performance index (PI). The PI consisted of dividing the percent correct of the last session by the total number of sessions in order to account for the differences in number of sessions performed by the birds. Thus, a larger PI equates to better performance, incorporating both accuracy and speed of acquisition. Thereafter, analyses using independent t tests were conducted on the reciprocals of the PIs to avoid violating parametric assumptions (Fowler & Cohen, 1990).

Effects were considered significant based on an alpha level of 0.05 on all statistical tests. All statistical analyses were conducted using SigmaPlot (Systat Software Inc., Chicago, IL).

5.3.2 Results and discussion

As shown in Figure 5.2a, all three birds in the dynamic GP group reached criterion within 45 sessions (bird 1 = 11 sessions; bird 2 = 16 sessions; bird 3 = 32 sessions); in contrast, in the static group, all three birds failed to reach criterion within 45 sessions. Based on one-tailed binomial tests, all three birds in the dynamic GP group performed significantly greater than chance within nine sessions, whereas in the static GP group, the birds required a minimum of 11 sessions to perform better than chance (Figure 5.2b). Finally, the performance of the birds based on PI was found to be significantly higher in the dynamic GP condition (t (4) = 4.51, p = 0.011; see Figure 5.2c).

While the results from Experiment 1 shows that pigeons learn to discriminate dynamic GPs from noise more readily than static GPs from noise, it is

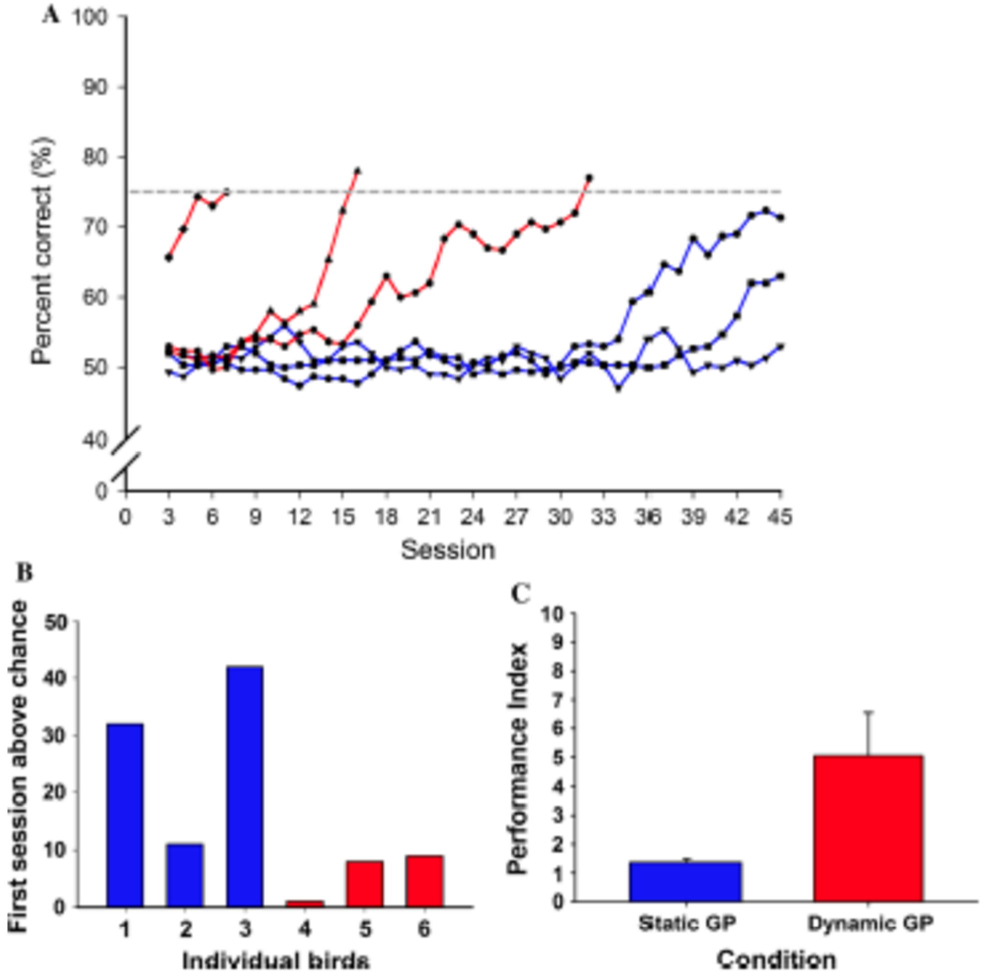


Figure 5.2 **a** Mean performance of the birds in the dynamic GPs (in red) and the static GPs condition (in blue) as a function of session. **b** Number of sessions that each bird required to perform significantly above chance. c The mean PI for both the static and dynamic GPs. Error bars = SEM

unclear why our birds performed better with dynamic GPs. For instance, while it could be due to summation of the form signals as has been suggested by Nankoo et al. (2012, 2015), it is also possible that the performance increase should be attributed to other factors, such as dynamic GPs being attended to more because they 'moved' (i.e., changed rapidly over time). However, regardless of the mechanisms, the results suggest that dynamic GPs may be a more suitable stimulus to probe the avian global form mechanisms.

Our results from the static GP condition seem surprising in light of the discrimination of static GPs by pigeons and starlings in previous studies (Kelly et al., 2001; Qadri & Cook, 2014). For example, Kelly et al. found that seven out of 11 birds were successful in learning the discrimination task. We therefore conducted a follow-up experiment to test whether the difficulty in learning the static GPs in our study could be due to our stimuli parameters. Specifically, two noteworthy differences exist between the GPs used in Kelly et al. and ours (Figure 5.1). First, Kelly et al. used black dots on a white background, whereas our GPs consisted of white dots on a black background. Second, the type of noise used in Kelly et al. consisted of randomly positioned single dots, whereas ours consisted of randomly oriented dipoles (e.g., Wilson & Wilkinson, 1998).

In Experiment 2, we trained pigeons to discriminate between static GPs and randomly positioned single dots (Random-Uniform condition) as this was the type of noise used in Kelly et al. (2001), as well as between static GPs and dipole noise (Random-Dipole condition), as was done in our Experiment 1 (Figure 5.3). Both conditions used black dots on a white background, eliminating dot polarity as a potential confound.

5.4 Experiment 2

5.4.1 Methods

Four pigeons with previous unrelated touch screen experience served as subjects for Experiment 2. Housing and feeding protocols were the same as in Experiment 1.

Figure 5.3 Types of stimulus used in Experiment 2. **a** A concentric Glass pattern (100 % coherence) and **b** a dipole noise pattern (0 % coherence). **c** A uniform noise pattern

Apparatus, stimuli, and design

The apparatus was the same as in Experiment 1 except for the following differences: For both the Random-Dipole condition and the Random-Uniform condition, the dots were black, and the background was white. The Random-Dipole condition was identical to the static GP condition in Experiment 1 in every other aspect. That is, the S- consisted of randomly oriented dipoles (Figure 5.3b). In the

Random-Uniform condition, the S- (noise pattern) consisted of random dots (single dots) instead of randomly oriented dipoles (Figure 5.3c). The stimuli, design, and procedure were similar to Experiment 1 in every other aspect. Unlike Experiment 1, we used a within subject design whereby the birds completed both conditions sequentially. The condition order was counterbalanced across birds. Birds 1 and 2 completed the Random-Uniform condition first, while birds 3 and 4 completed Random-Dipole condition first. A paired samples *t* test was used to test for differences between the two conditions.

5.4.2 Results and discussion

The same performance index and accuracy criteria as Experiment 1 were used for analysis. As can be seen in Figure 5.4a, three out of four birds passed the criterion for the discrimination between static GPs and uniform noise patterns within 45 sessions (bird 1 = 30 sessions; bird 2 = 14 sessions; bird 3 = 6 sessions; bird 4 = did not reach criterion). In contrast, none of the birds tested were able to reach criterion for the discrimination between GPs and dipole noise patterns. As shown in Figure 5.4b, all the birds achieved a performance that was significantly higher than chance within 21 sessions (one-tailed binomial test, all *p*s < .05) in the Random-Uniform condition. These birds required, on average, 25 more sessions (SD = 7.38) to perform significantly above chance in the Random-Dipole condition.

The performance of the birds based on PI was significantly higher in the Random-Uniform condition ($t(3) = 5.37$; $p = .013$; see Figure 5.4c).

Our results support the hypothesis that the difficulty of our birds to learn the discrimination between GPs of 100 % coherence and 0 % coherence in Experiment

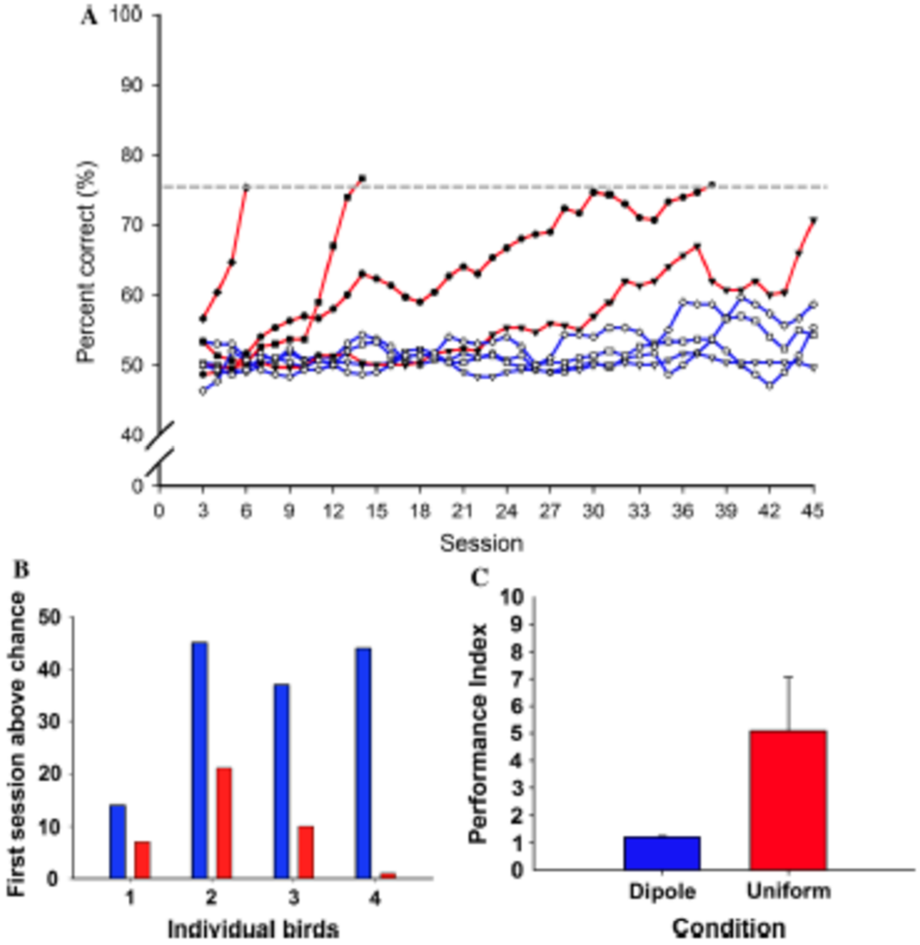


Figure 5.4 **a** Mean performance of the birds in the Random-Uniform condition (in red) and the Random-Dipole condition (in blue) as a function of session. Each unique symbol represents a unique bird. **b** Number of sessions that each bird required to perform significantly above chance. **c** The mean PI for both the static and dynamic GPs. Error bars = SEM

1 is likely to be due to difficulty resolving the global structure of GPs. Kelly et al. (2001) and Qadri and Cook (2014) reported that pigeons and starlings were able to discriminate GPSs from noise. However, it is clear that the use of random-uniform noise facilitates detection of the coherent GPs. The intention in using random dipole noise, rather than random uniform noise, is that the mean dot spacing should be matched to the coherent pattern. In Figure 5.5, we show this quantitatively, by plotting the cumulative distribution function (CDF) of the distance of each dot to its nearest neighbor. As evident in this figure, for approximately 30 % of the dots, there is no difference in this distance between the two types of random patterns. However, for the concentric GPs and random-dipole noise, over half of the dots have

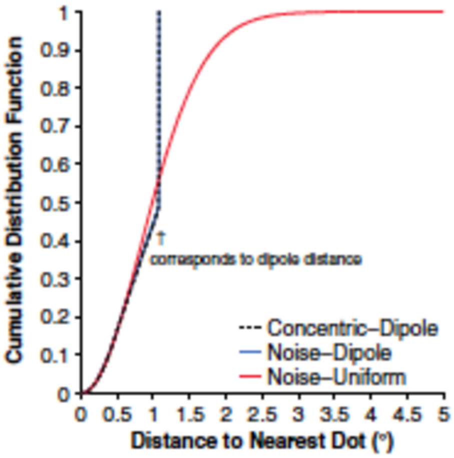


Figure 5.5 Cumulative distribution function of distance to nearest dot for concentric, noise-dipole, and noise-uniform Glass patterns. Distributions calculated based on 1000 Glass patterns generated of each pattern type. Note that concentric and noise-dipole almost completely overlap

their dipole partner as their nearest neighbor, whereas the sigmoid function simply continues to fall off for the random-uniform noise. This difference in distributions clearly illustrates a local statistic that random-dipoles control for, as well as the strategy that could be used by pigeons to differentiate coherent versus random-uniform GPs instead of relying on global form processing. Thus, it is likely that the birds learned the potentially less demanding task of discriminating between dot distributions, as opposed to attempting to resolve the global structure of the patterns.

5.5 General discussion

The results from our study revealed two important aspects of investigating global pooling mechanisms for form perception in birds. In Experiment 1, we show that pigeons learn to discriminate dynamic GPs from noise better than static GPs from noise. This is congruent with the results from Nankoo et al. (2012) who showed that thresholds for dynamic GPs were lower than static GPs in humans (also see Burr & Ross, 2006; Or et al., 2007). This result suggests that the use of dynamic GPs may be a more effective probe to investigate the global pooling of form information in pigeons and other species. Second, and perhaps more importantly, we found that our pigeons had difficulty discriminating globally coherent structured static GPs from globally incoherent static GPs. In contrast, the birds readily discriminated coherent static GPs from uniform noise, which provided an additional statistic of the mean dot spacing of the patterns that could be used to learn the discrimination. It therefore seems likely that our pigeons used the spatial distribution of the dots in the patterns to make their choice. We are not suggesting that the birds were unable to extract the global form of the patterns; rather that reliance on local strategy may be the favoured strategy.

Nankoo et al. (2012) showed that for humans, the relative ranking of thresholds with different dynamic GPs parallels the relative ranking of the thresholds for static GPs, and albeit thresholds were better with dynamic GPs across all patterns: In both dynamic and static GP conditions, the observers were best at detecting concentric, followed by radial, spiral, vertical, and were worst at horizontal. These relative rankings of thresholds differ from those observed when using random dot kinematograms (i.e., global motion), suggesting that global form mechanisms are dominant in the detection of dynamic GPs (see also Nankoo et al., 2015). Given that our birds exhibited a heightened performance for dynamic GPs relative to static GPs, it is possible that our birds' performance in the dynamic GPs condition is due to the greater amount of global form information as each frame consists of a unique static GP. In other words, the performance of the birds in the dynamic GPs condition may have been due to a summation mechanism of the global form signals.

The perception of global and local form has been extensively studied in birds (see Cook 2001 for review), and often local and global stimuli are put in conflict in order to extract the biases of birds. While these studies have shown that general birds are more likely to use local cues (at least given the stimuli and parameters tested) compared to humans, they also show that birds are clearly able to process stimuli globally (Cook, 2001; Fremouw et al., 2003). Kelly et al. (2001) used GPs to investigate whether the avian global mechanism was similar to the human mechanism. However, they found that unlike humans, birds did not show a preference for concentric GPs. Indeed, performances of the birds with all patterns used were equivalent. More recently, Qadri and Cook (2014) have shown a similar set of results using starlings. However, both these studies used noise patterns that differed from the signal not only in global structure but also in dot distribution, as demonstrated in Figure 5.5. Given the known bias to processing local information, it is likely that the birds in both studies ignored the global structure and made their choices based on the local information. Indeed, such a strategy would result in equivalent performance regardless of global structure. Here, we have shown that when the mean dot spacing of the noise were controlled to be the same as the signal patterns, the birds were significantly poorer at discriminating signal from noise. This finding reinforces the argument that the birds in Kelly et al. (2001) and Qadri and Cook (2014) may have attended to the differences at the local level as there was no need to globally integrate the orientation signals to solve the task, an alternative strategy noted in the discussion section of both of these papers.

5.6 Conclusions

GPs are useful for investigating the global mechanisms of form perception as they allow for control of local and global cues independently. Here, we found that birds can learn to discriminate between dynamic GPs and noise of equivalent mean dot spacing more readily than static GPs. The results of Experiment 2 showed that when the static GPs (S+) and the noise pattern (S-) differed in mean dot spacing, pigeons performed significantly better than when controlling for mean dot spacing, thus suggesting that birds in previous studies using static GPs may have been using a local strategy rather than relying on the global structure of the GPs. It is, however, unclear whether a summation of global form signals, like those suggested for human data (Nankoo et al., 2012), is responsible for the enhanced performance with dynamic GPs or whether this is due to an attention effect. For instance, Franconeri and Simons (2003) reported that translation and looming motion capture attention in a visual search task in humans. The effect of motion on attention was present even when the stimulus is not novel. Regardless, our results indicate that investigating the pooling mechanisms of form perception with static GPs in birds may be challenging. Our findings suggest that dynamic GPs are a suitable alternative to static GPs to investigate global form perception in birds.

5.7 Acknowledgements

This research was supported by grants from the National Science and Engineering Research Council (NSERC) of Canada to M.L.S. and D.R.W., and by an NSERC Alexander Graham Bell Canada Graduate Scholarship (Doctoral-level) to C.R.M. All research was conducted in accordance with Canadian Council on Animal Care guidelines and with approval from the University of Alberta Animal Welfare Policy Committee.

5.8 Reference

Anderson, S. J., & Swettenham, J. B. (2006). Neuroimaging in human amblyopia. *Strabismus*, *14*(1), 21-35.

Bischof, W. E., Reid, S. L., Wylie, D. R., & Spetch, M. L. (1999). Perception of coherent motion in random dot displays by pigeons and humans. *Perception & psychophysics*, *61*(6), 1089-1101.

Burr, D., & Ross, J. (2006). The effects of opposite-polarity dipoles on the detection of Glass patterns. *Vision Research*, *46*(6), 1139-1144.

Cavoto, K. K., & Cook, R. G. (2001). Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *27*(1), 3.

Cavoto, B. R., & Cook, R. G. (2006). The contribution of monocular depth cues to scene perception by pigeons. *Psychological Science*, *17*(7), 628-634.

Cook, R. G. (2000). The comparative psychology of avian visual cognition. *Current Directions in Psychological Science*, *9*(3), 83-89.

Cook R. G. (2001). Hierarchical stimulus processing in pigeons. In R. G. Cook (Ed.), *Avian visual cognition*. http://www.pigeon.psy.tufts.edu/avc/cook/

Dakin, S. C., & Bex, P. J. (2002). Summation of concentric orientation structure: seeing the Glass or the window?. *Vision Research*, *42*(16), 2013-2020.

Day, A. M., & Palomares, M. (2014). How temporal frequency affects global form coherence in Glass patterns. *Vision research*, *95*, 18-22.

Feczko, E., Shulman, G. L., Petersen, S. E., & Pruett, J. R. (2014). Interactions between concentric form-from-structure and face perception revealed by visual masking but not adaptation. *Journal of vision*, *14*(2), 15.

Fowler J, Cohen L (1990) Practical statistics for field biology. Wiley, England

Franconeri, S. L., & Simons, D. J. (2003). Moving and looming stimuli capture attention. *Perception & psychophysics*, *65*(7), 999-1010.

Fremouw, T., Herbranson, W. T., & Shimp, C. P. (2002). Dynamic shifts of pigeon local/global attention. *Animal Cognition*, *5*(4), 233-243.

Geisler, W. S. (1999). Motion streaks provide a spatial code for motion direction. *Nature*, *400*(6739), 65-69.

Glass, L. (1969). Moire effect from random dots. *Nature*, *223*(5206), 578-580.

Hodos W (2012) What Birds See and What They Don't: Luminance, contrast, and spatial and temporal resolution. In O. F. Lazareva, T. Shimizu, E. A., Wasserman (Eds.), *How animals see the world: Behavior, biology, and evolution of vision* (pp. 5-25). London: Oxford University Press.

Kelly, D. M., Bischof, W. F., Wong-Wylie, D. R., & Spetch, M. L. (2001). Detection of glass patterns by pigeons and humans: implications for differences in higher level processing. *Psychological Science*, *12*(4), 338-342.

Lazareva, O. F., Shimizu, T., & Wasserman, E. A. (2012). *How animals see the world: comparative behavior, biology, and evolution of vision*. London: Oxford University Press.

Nankoo, J. F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2012). Perception of dynamic Glass patterns. *Vision research*, *72*, 55-62.

Nankoo, J. F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2014). Perception of complex motion in humans and pigeons (Columba livia). *Experimental brain research*, *232*(6), 1843-1853.

Nankoo, J. F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2015). Temporal summation of global form signals in dynamic Glass patterns. *Vision research*, *107*, 30-35.

Or, C. C. F., Khuu, S. K., & Hayes, A. (2007). The role of luminance contrast in the detection of global structure in static and dynamic, same-and opposite-polarity, Glass patterns. *Vision Research*, *47*(2), 253-259.

Qadri, M. A., & Cook, R. G. (2014). The perception of Glass patterns by starlings (Sturnus vulgaris). *Psychonomic bulletin & review*, *22*(3), 687-693.

Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature neuroscience*, *2*(11), 1019-1025.

Riesenhuber, M., & Poggio, T. (2000). Models of object recognition. *Nature neuroscience*, *3*, 1199-1204.

Ross, J., Badcock, D. R., & Hayes, A. (2000). Coherent global motion in the absence of coherent velocity signals. *Current Biology*, *10*(11), 679-682.

Smith, M. A., Kohn, A., & Movshon, J. A. (2007). Glass pattern responses in macaque

V2 neurons. *Journal of Vision*, *7*(3), 5.

Smith, M. A., Bair, W., & Movshon, J. A. (2002). Signals in macaque striate cortical neurons that support the perception of glass patterns. *The Journal of neuroscience*, *22*(18), 8334-8345.

Wilson, H. R., & Wilkinson, F. (1998). Detection of global structure in Glass patterns: implications for form vision. *Vision research*, *38*(19), 2933-2947.

Wilson, H. R., Wilkinson, F., & Asaad, W. (1997). Concentric orientation summation in human form vision. *Vision research*, *37*(17), 2325-2330.

Chapter 6

A comparative study of the contribution of non-rigid motion and shape information to object perception.

6.1 Abstract

The ability to perceive and recognize objects is essential to many animals, including humans. The prevailing notion has been that the most important aspect of object perception is its static properties. However, recent research has demonstrated that motion information plays an important role in object perception. Most studies, however, have only focused on rigid motion, yet non-rigid motion characteristics of objects, such as the slithering motion of a snake, can also provide valuable information to aid object perception and recognition. Here we investigated the relative contributions of non-rigid motion and static form to object perception. In addition, we compared the contribution of non-rigid motion and form in humans and pigeons, two species that rely extensively on vision. We found that both humans and pigeons are able to use form and non-rigid motion information independently in order to identity complex objects. Specifically, we found that humans and pigeons perform equally well whether form-only, non-rigid motion-only or both form and non-rigid motion were informative. Given that both humans and pigeons showed similar results, we argue that the use of non-rigid motion for object perception is

evolutionarily important and should be considered in general theories of vision, at least with respect to visually sophisticated animals.

6.2 Introduction

For most animals, the ability to manoeuvre within, and interact with their environment is critical for survival. Fundamental to this is the ability to perceive and recognize objects within the environment. Indeed, visually dependent animals such as humans and pigeons recognize objects with ease within seconds (Potter, 1976; Thorpe et al., 1996). It is thought that the ability to perceive and recognize an object is based mainly on static properties of the object. As such, prevalent models of object perception primarily describe how static properties such as shape contribute to object recognition (Marr, 1982; Biederman, 1987; Bülthoff & Edelman, 1992; Tarr & Bülthoff, 1995; Edelman & Bülthoff, 1992; Lawson & Humphreys, 1996). Yet, objects are rarely completely static in nature; whether it is through movement of the observer or movement of the object being observed, motion is often seen in conjunction with static properties of objects. Thus, researchers have begun to investigate the role of motion in object perception (e.g. Friedman, Vuong, & Spetch, 2009; Newell, Wallraven, & Huber, 2004; Stone, 1998).

Contrary to the prevailing assumption that motion only serves to aid the recovery of shape for object perception (Marr & Nishihara, 1978), recent evidence indicate that motion, independent from static information, contributes to object recognition. This was found to be true not only for humans, but also in non-human animals (see Spetch & Friedman, 2006 and Cook & Murphy, 2012 for reviews). For instance, Spetch, Friedman and Vuong (2006) investigated the role of motion for object recognition by training both humans and pigeons to respond to 3D objects rotating in depth motion. This type of motion (i.e., rotation or translation on a Euclidian plane) is most often associated with inanimate objects and is referred to as rigid motion, as there is no deformation of shape (Aggarwal, Cai, Liao, & Sabata, 1998). Spetch, Friedman, and Vuong (2006) found that accuracy for both humans and pigeons decreased when the motion of a target object was reversed or different from the learned motion even though the shape of the object remained the same (see also Vuong & Tarr 2004). It is however worth noting that while there was a reduction in accuracy when motion was changed, humans were less affected by this change relative to pigeons. Although humans appear to be less reliant on motion compared to pigeons, these results do show that both species use motion for object recognition (Spetch, Friedman, & Vuong 2006; see Spetch & Friedman, 2006 for review). In addition, Nankoo et al., (2014, 2015) have shown that humans and pigeons also differ in their ability to perceive global form and global motion (a process critical for object perception). Specifically, they showed that while pigeons are able to integrate local motion information to extract a global motion pattern, the pigeon visual system struggles to integrate of local orientation signals (as found in Glass patterns) information. Therefore, given that organisms with distinct ecological and biological constraints, such as humans and pigeons, rely of motion to identify objects, this suggests that motion is an important cue for solving the problem of object recognition.

While studies on rigid motion, such as Spetch, Friedman, and Vuong (2006), have been informative as to the involvement of motion in object recognition, objects encountered in nature do not only move rigidly but often also move in a non-rigid fashion (Aggarwal, Cai, Liao, & Sabata, 1994). For instance, the characteristic movement of a snake or butterfly causes a deformation of the 3D shape and is thus classified as non-rigid motion. Studies show that non-rigid motion can contribute to object recognition. For example, studies suggest that non-rigid facial movement has a facilitative effect on face recognition, a phenomenon termed the “facial movement beneficial effect” (O’Toole et al., 2002; Xiao, Perrotta, Quinn, Wang, Sun, & Lee, 2014). Motion of body parts (i.e., articulated motion) has also been shown to carry identity information that can readily be extracted by humans (Setti & Newell, 2010). Using point-light displays that mimic joint movements (i.e., biological motion) during locomotion, research shows that humans can extract an array of information such as gender, emotion, and identity of the walker (see Troje & Chang, 2012, for review). In other words, articulated motion alone provides a multitude of information about object identity. Evidence on the contribution of articulated motion with non-human animals is more scarce, but nonetheless shows that non-human animals can also extract important information from the movement of body parts (Dittrich, Lea, Barrett, & Gurr, 1998). Qadri, Sayde, and Cook (2014) presented pigeons with video sequences of human models engaging in a dancing action or a martial arts action. They noted that articulated motion facilitated discrimination (which they termed dynamic superiority effect) when compared to static random presentation of the human model.

In spite of the prevalence of non-rigid motion in nature, relatively little is known about how non-rigid motion is utilized in conjunction with static information for object recognition in general. Recently, Vuong, Friedman and Read (2012) investigated the relative contribution of non-rigid motion and shape information for object recognition in human observers. Participants in Vuong, Friedman and Read (2012) were tasked to determine whether two objects were same or different. Using a parameter-based morphing technique, the shape and motion differences between the objects were systematically varied and the participants were told to use the shape cue (shape-only condition), motion cue (motion-only condition) or both cues (shape+motion condition) to distinguish between the objects. In the single cue conditions, participants were instructed to ignore the irrelevant cue (e.g., motion in the shape-only condition) regardless of whether they were the same or different. In contrast, in the shape+motion condition, the participants were required to base their decision on both cues; for instance, only when both shape and motion were different between the objects, they were to respond 'different'. In the shape-only and motion-only conditions, participants were able to distinguish between the objects, although shape was more difficult to ignore (i.e., motion-only condition). However, when both shape and motion were used, participants weighted shape more heavily than motion. That is, Vuong, Friedman and Read (2012) showed that humans are able to use either shape or non-rigid motion to differentiate between objects, but they show a shape bias when both cues are available.

Given the reported shape bias in the human visual system and the motion bias found at both at the intermediate and higher level of visual processing, it is essential to further examine whether these biases remain when using biologically relevant motion (i.e., non-rigid motion) for object perception. Therefore, in the current study, we investigated the contribution of non-rigid motion and shape for object perception in pigeons, and compared performance to human observers. We employ the same morphing technique as used by Vuong, Friedman and Read (2012), but modified the procedure so that the participants had to identify a 'correct' object (i.e. S+) from an 'incorrect' object (i.e., S-). This procedure was adopted to facilitate testing with the pigeons. By varying the values of the S+ on the shape continuum, the non-rigid motion continuum, and on both dimensions at the same time, we were able to ascertain whether pigeons and humans differ in their reliance on shape and non-rigid motion to discriminate one object from another.

6.3 Experiment 1

6.3.1 Methods

Participants

Six pigeons with previous unrelated touch-screen experience served as subjects. The birds were housed in individual cages under a 12-hr light:dark cycle (light onset at 6:00 a.m.). All birds were maintained at approximately 85% of their free-feeding weights. Water and grit were available ad lib in the home cages.

Apparatus

Stimuli were displayed on a 22" Viewsonic VX2268wm FuHzion LCD computer monitor (resolution: 1680 x 1050 pixels; refresh rate: 120 Hz). The experiment was conducted in touch-screen operant chambers. The monitor was equipped with a 17” Carroll Touch infrared touch frame. Each chamber contained two solenoid-type bird feeders on the side walls of the chamber. Lamps located within each feeder illuminated feeder presentations, and photocells measured the duration of head entries into the hoppers to limit feeding durations to 1 second per food presentation. The chambers were connected to computers located in an adjacent room. These computers controlled all of the experimental contingencies and recorded the responses.

Stimuli

The stimuli consisted of 3D objects rendered with a gray surface on a yellow background. The objects were sampled from a shape and motion stimulus space from which we manipulated the object’s three-dimensional shape and non-rigid motion independently (see Vuong, Friedman, & Read, 2012 for details). Figure 1 illustrates the shape and motion stimulus space used in the current study. On the shape dimension, shapes at both end of the shape continuum (i.e., prototypes) were “block shape” and “pyramid shape”. On the motion continuum, the motion prototypes were “bending motion” and “twisting motion”. The shape and motion ranged from 0% (S+) to 100% (S-) and intermediate morphs were derived by linear combinations of the prototypes. For example, as illustrated in Figure 6.1A, the S+ is a pyramid on the shape dimension, and twisting motion on the motion dimension (Figure 6.1B). Consequently, the S- is a block on the shape continuum, and bending on the motion dimension. Figure 6.2A shows all the possible combinations of S+ and S- using block and pyramid as the prototypes for shape, and twisting and bending for the motion prototypes. Figure 6.2B illustrates the shape+motion continuum, where the stimuli were varied on both shape and motion dimensions simultaneously, e.g., from a bending pyramid to a twisting block. The assignment of shape/motion properties to S+ vs. S- was counterbalanced across birds.

The stimuli consisted of 100 frames that were presented at 60 Hz. Note that the frames were looped through until a response was made, or for a maximum duration of 2 min. Based on an estimated distance of 9 cm (Bischof, Reid, Wylie, Spetch, 1999), the stimuli subtended an estimated 21.19° (160 pixels) x 34.36° (190 pixels) of visual angle. The experiment and stimulus presentation was controlled by a Windows PC computer running E-Prime (PST Software, Pittsburgh, PA).

Procedure

Training consisted of two phases. In Phase 1, only the S+ was shown on the display, and birds received a 1 s reward via a food dispenser if they pecked at the stimulus. Phase 2 was the discrimination-learning phase where the birds learned to discriminate one prototype (S+) from its opposite counterpart on the shape-motion space (Figure 6.2). Each bird was randomly assigned to one of four groups, each of which had a different S+ (Figure 6.2A). The birds responded by pecking at the stimulus. A peck to the S+ resulted in 1 sec reward via a food dispenser. A peck to the S- resulted in no reward. The birds were moved to the testing phase after they achieved an accuracy of 85% over three consecutive sessions. Testing consisted of three conditions: a shape-only condition in which the shape of the S+ was manipulated while the motion remained the same as the S+, a motion-only condition in which the motion of the S+ was manipulated while the shape remained the same as the S+, and a shape+motion condition in which both the shape and motion of the S+ were changed to the same degree. The S- from training remained unchanged during testing. A peck to the S+ resulted in a 1 sec food reward, whereas a peck to the S- resulted in no reward. Trials from all three conditions were presented randomly in each testing session.

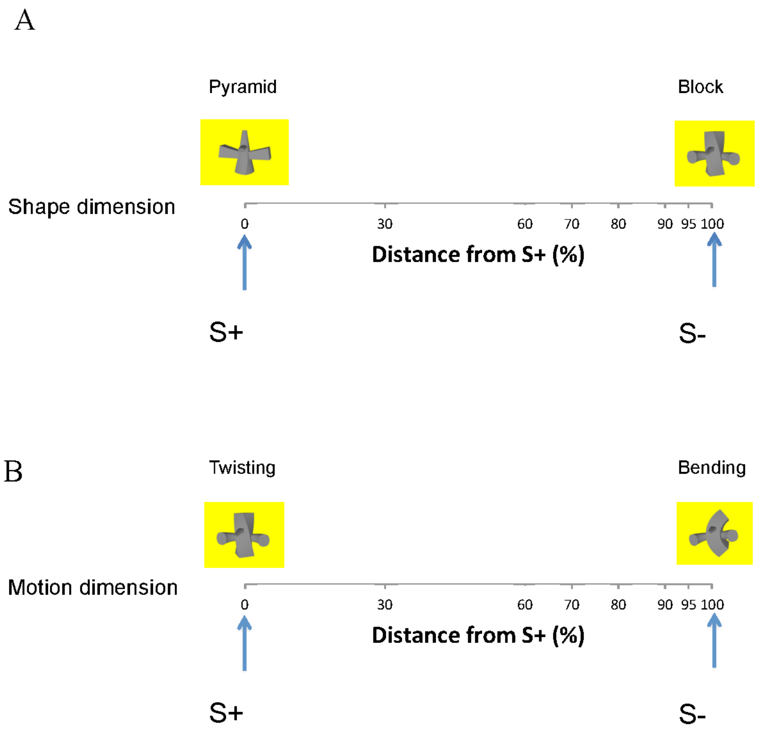


Figure 6.1 Panel A shows the shape dimension with the rewarded shape (S+) and the non-rewarded shape (S-) at the extreme of the dimension. Two types of shapes were used: pyramid and block. Either pyramid or block could be used as the S+, counterbalanced across birds. During testing, the S+ shape is morphed towards the S-. Panel B shows the motion dimension with the rewarded motion (S+) and the non-rewarded motion (S-) at the extreme of the dimension. Two types of motion were used: twisting and bending. Either twisting motion or bending motion could be used as the S+, counterbalanced across birds. During testing, the S+ motion is morphed towards the S-. The unit of morph is percentage of S- (or distance from S+).

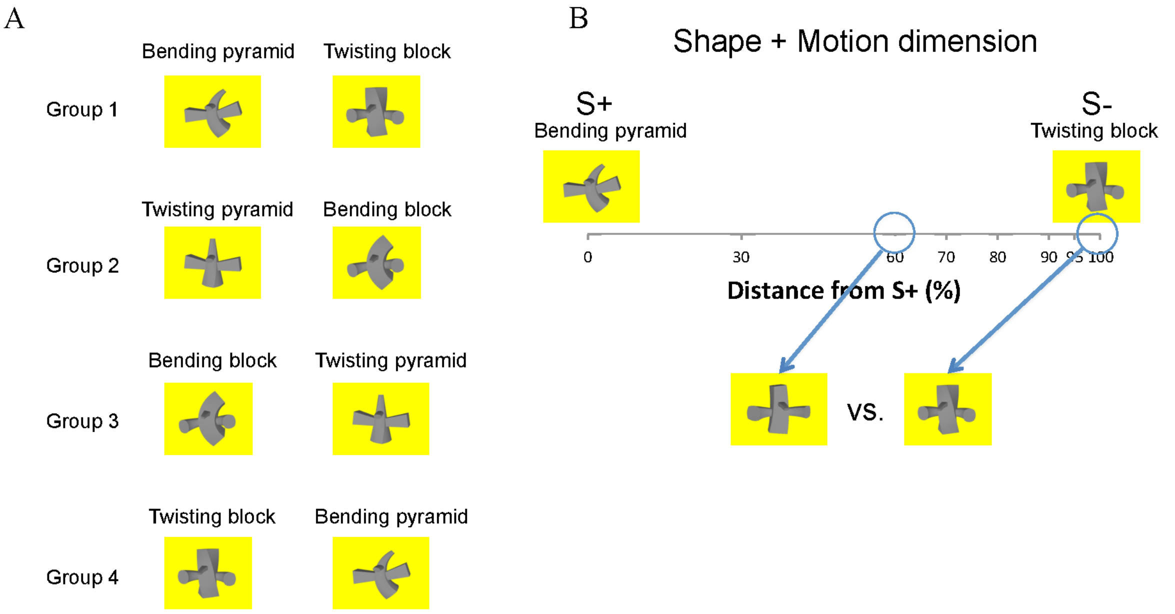


Figure 6.2 Panel A shows all combinations of S+ and S- prototypes used in this study. Panel B shows the shape motion dimension as single continuum. During testing, the S- remains identical to the S- seen during training. However, the S+ is morphed along the shape motion continuum.

Regardless of the S+ prototype, testing was carried out by changing the S+ shape and/or motion dimensions by 0% (i.e., S+), 30%, 60%, 70%, 80%, 90%, 95%, and 100% (i.e., S-). These values were chosen based on pilot data collected prior to this study. If the birds' performance in baseline trials (i.e., S+) in the testing phase was below the training criterion for two days in a row, they were put back on training until they reached the training criterion. Thereafter they resumed testing. In both training and testing sessions, birds were allowed to complete as many trials as possible for a duration of 45 min. Birds performed at least 120 trials for each level of each condition.

6.3.2 Results

The training data shows that the birds learned the task relatively quickly, with the fastest bird surpassing the criterion within four sessions, and the slowest bird taking 11 sessions. As shown in Figure 6.3A, the accuracy in both the shape-only and motion-only conditions remained relatively high regardless of the distance to S+ (M_{shape} = 91.08%, SD_{shape} = 3.42%; M_{motion} = 92.46%, SD_{motion} = 3.02%). A significant main effect of condition (i.e. Shape-only, Motion-only, and Shape+Motion) was found, $F(2, 70) = 52.20$, $p < .001$. This significant result was followed by a polynomial trend analysis in which we found a significant linear trend for both the Shape-only and motion-only conditions (*p*s $< .05$). However, for the Shape+Motion condition, performance followed a quadratic trend ($p < .05$).

To examine whether the results were influenced by the amount of testing that was done, we analyzed performance from the first five sessions. As shown in Figure 6.3B, accuracy in both shape-only and motion-only conditions remained high regardless of the distance to S+ (M_{shape} = 89.58%, SD_{shape} = 4.79%; M_{motion} = 91.56%, SD_{motion} = 2.56%). There again was a significant main effect of condition (i.e. shape-only, motion-only, and shape+motion), $F(2, 70) = 77.32$, $p < .001$. A trend analysis found a significant linear trend for both the Shape-only and motion-only conditions (*p*s $< .05$). And similarly to the analysis based on 23 sessions, for the Shape + Motion condition, performance followed a quadratic trend ($p < .05$).

6.4 Experiment 2

6.4.1 Methods

Participants

Twelve adults with normal or corrected-to-normal vision participated in the experiment. The participants were undergraduate students from the University of Alberta and were naive as to the purpose of the experiment. All participants provided informed consent.

Procedure.

Stimuli were displayed on a computer with the same specifications as Experiment 1. However, no touchscreen was used. Instead participants responded by clicking the mouse cursor on the stimulus. A chin rest was used to maintain the distance of the participant to the monitor at 47 cm.

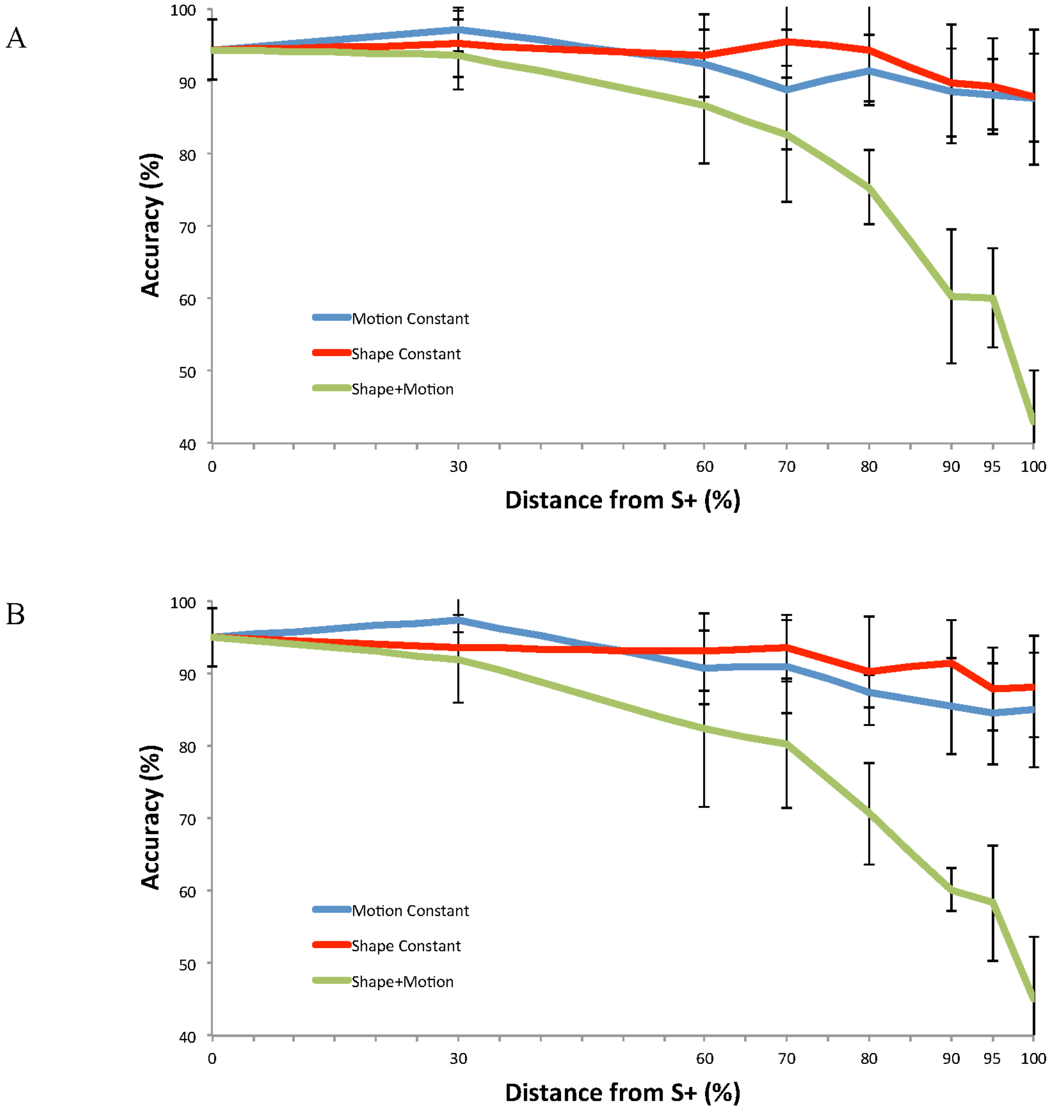


Figure 6.3 Panel A shows the accuracy of the pigeons in the shape-only, motion-only, and shape + motion conditions as a function of distance from S+ (i.e., percentage of S- motion and shape present) after 23 sessions. Error bars represent 95% CI. The figure in panel B is identical to panel A, except that panel B shows performance after 5 sessions.

The stimuli were exactly the same as used in Experiment 1, with the exception that the S+ was changed by 0%, 80%, 90%, 95%, and 100% on the shape and motion dimensions. These levels were chosen given that the levels used for pigeons were deemed too easy for human observers, based results from initial pilot participants. The stimuli subtended approximately 5.96° (160 pixels) x 7.08° (190 pixels) of visual angle.

Three participants were assigned to one of four groups, each of which had a different S+ (see Figure 2A). Prior to testing, the participants were given ten training trials to learn to discriminate between the S+ and S-. The training phase was similar to the training phase 2 in Experiment 1. A correct response resulted in visual feedback (i.e., the word 'correct' appeared on the screen), whereas an incorrect response resulted in no feedback and the trial ended. After the training trials the participants moved to the testing phase, and completed at least 30 trials per morph level.

6.4.2 Results

All participants responded correctly on at least eight trials in the training phase. Overall, the pattern of results was similar to the pigeons. As shown in Figure 6.4, the accuracy in both motion and shape condition remained high regardless of the distance to S+ ($Mean_{Shape}$ = 96.46%, SD_{Shape} = 2.21%; $Mean_{Motion}$ = 96.61%, SD_{Motio} = 0.61%). A significant main effect of condition (i.e. shape-only, motion-only, and shape + motion) was found, *F*(2, 56) = 78.81, $p < .001$. This significant result was followed by a trend analysis in which we found a significant linear trend for both the Shape-only and Motion-only conditions (*ps* < .05). However, for the Shape + Motion condition, performance followed a quadratic trend ($p < .05$).

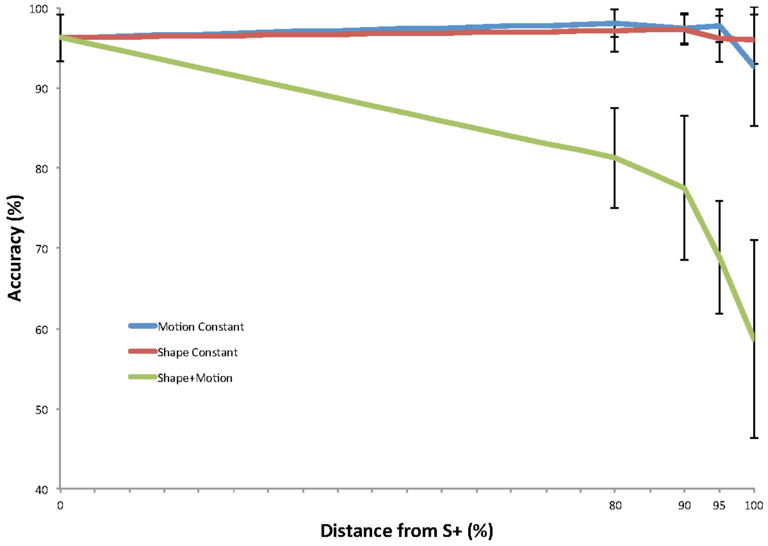


Figure 6.4 Shows the accuracy of human observers in the shape-only, motion-only, and shape + motion conditions as a function of distance from S+ (i.e., percentage of S- motion and shape present). Error bars represent 95% CI.

6.5 Discussion

The results from both experiments demonstrate the important role of non-rigid motion for object perception. Specifically, we found that both pigeons and humans can rely on non-rigid motion and shape information equally and independently. That is, when shape information is made more similar to the S- both species were able to reliably discriminate between the objects based on the learned non-rigid motion information. The opposite is also true in that when motion was made less informative to the discrimination, both pigeons and humans can rely on the shape information regardless of shape change. In other words both humans and pigeons were able to rely on the learned cues, and were able to discount either one and rely on the most informative cue. Only when both shape and motion information were changed did we observe a significant decline in performance as a function of the degree of change from the S+. These results suggest that both humans and pigeon weighed the non-rigid motion equally to the shape, and that they both can use both types of information independently.

Our finding that non-rigid motion is equally relied upon as shape information is in contrast to Vuong, Friedman and Read (2012). In their study, Vuong, Friedman and Read (2012) observed that humans have a shape bias in a same-different task, using similar stimuli (sampled from the same shape-motion stimulus space) as used in the current study. The most obvious explanation for this discrepancy is that the difference between our results and those of Vuong, Friedman and Read (2012) stems from the difference in the task performed by the participants. Specifically, Vuong, Friedman and Read (2012) used a same-different task in which the observers were asked determined whether two objects presented simultaneously were same or different while paying attention only to the shape or motion, or to both the shape and motion at the same time. In our study, participants learned to discriminate one object from another without any instructions relating the cues. Indeed, several studies have reported that the type of task does influence which cue is weighed more (Liu & Cooper, 2001; Mayer & Vuong, 2012; Newell et al., 2004; Setti & Newell, 2010). We argue that because we did not provide the participants with instructions relating to which cue to attend to, our result may be a more accurate reflection of the strategy used by humans and pigeons for object perception.

Previously, Qadri et al. (2014) and Asen and Cook (2012) have shown that pigeons are able to use non-rigid motion to discriminate between two objects of the same shape. Our study builds on their findings to investigate the contribution of non-rigid motion in combination with shape information for object perception. Specifically, in our study, both non-rigid motion and shape of objects was systematically manipulated to investigate their relative contribution to object perception. The finding that pigeons relied on both cues equally, as was the case for the human participants, is an important contribution. Until now, research has shown that pigeons in general exhibit a motion bias when shape and motion information are available for object recognition when compared to humans (Spetch et al., 2006). Indeed there are reports that at the lower levels of visual processing, the avian visual system is not as sensitive to shape information as it is for motion (Nankoo, Madan, Wylie, & Spetch, 2015). Yet, in our study we found no such bias. This is likely because most studies with pigeons used rigid motion, which is often associated with inanimate objects, whereas non-rigid motion tends to be associated with biological motion. Therefore, it is possible that the presence of biological-like motion may have facilitated shape perception in birds. In other words, because of the importance of identifying biological agents, the non-rigid motion may also signal to the birds to use the shape information. This hypothesis is supported by the relatively high performance from the pigeons throughout the experiment. Thus, it is possible that in the presence of a biological stimulus, birds use all the available cues to identify the object. It would be pertinent to test this hypothesis with multiple cues such as color, shape, rigid-, and non-rigid motion.

The independent use of shape and motion found for both humans and pigeons is consistent with the modular organization of the visual system in both species. In mammals, it is well known that motion and shape are processed by distinct neural pathways; the dorsal and ventral pathway respectively (Braddick et al., 2000; Livingstone & Hubel, 1988; Milner & Goodale, 1995; Ungerleider & Mishkin, 1982;Van Essen & Gallant, 1994). In addition, this independence of shape and motion found in our study is congruent with computational model for object processing by Giese and Poggio (2003). Similarly, the avian visual system also processes shape and motion through distinct pathways. For example, Nyguen and al. (2004), showed, with a lesion study, that the entopallium (putative equivalent to the mammalian extrastiate) is divided into several functional units, and includes the caudal entallium for motion processing and the rostral portion for shape processing. In spite of the apparent similarities in functional organization of the visual system, a major difference between the avian and the mammalian visual system is that the primary route for visual information in the avian brain is along the tectofugal pathway, whereas in the mammalian brain it is the thalamofugal pathway. In addition, humans and pigeon have different biological and ecological constraints, such as the need for smaller brain to cope with the demands of flight. Given these differences our results, in conjunction to neuroanatomical and neurophysiological data, suggest that the independent processing of shape and non-rigid motion is a general principle of object recognition.

6.6 Acknowledgements

This research was supported by grants from the National Science and Engineering Research Council (NSERC) of Canada to M.L.S. and D.R.W., and by an NSERC Alexander Graham Bell Canada Graduate Scholarship (Doctoral-level) to C.R.M. All research was conducted in accordance with Canadian Council on Animal Care guidelines and with approval from the University of Alberta Animal Welfare Policy Committee.

6.7 Reference

Aggarwal, J. K., Cai, Q., Liao, W., & Sabata, B. (1998). Nonrigid motion analysis: Articulated and elastic motion. *Computer Vision and Image Understanding*, *70*, 142–156.

Asen, Y., & Cook, R. G. (2012). Discrimination and categorization of actions by pigeons. *Psychological science*, *23*(6), 617-624.

Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review*, *94*, 115–147.

Bischof, W. E., Reid, S. L., Wylie, D. R., & Spetch, M. L. (1999). Perception of coherent motion in random dot displays by pigeons and humans. *Perception & psychophysics*, *61*(6), 1089-1101.

Braddick, O. J., O'Brien, J. M. D., Wattam-Bell, J., Atkinson, J., & Turner, R. (2000). Form and motion coherence activate independent, but not dorsal/ventral segregated, networks in the human brain. *Current Biology*, *10*(12), 731-734.

Bülthoff, H. H., & Edelman, S. (1992). Psychophysical support for a 2-dimensional view interpolation theory of object recognition. *Proceedings of the National Academy of Sciences of the U. S .A.*, *89*(1), 60-64.

Dittrich, W. H., Lea, S. E., Barrett, J., & Gurr, P. R. (1998). Categorization of natural movements by pigeons: Visual concept discrimination and biological motion. *Journal of the experimental analysis of behavior*, *70*(3), 281-299.

Edelman, S., & Bülthoff, H. H. (1992). Orientation dependence in the recognition of familiar and novel views of three-dimensional objects. *Vision Research*, *32*, 2385-2400.

Friedman, A., Vuong, Q. C., & Spetch, M. L. (2009). View combination in moving objects: The role of motion in discriminating between novel views of similar and distinctive objects by humans and pigeons. *Vision Research*, *49*(6), 594–607.

Giese, M. A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience*, *4*(3), 179-192.

Lawson, R., & Humphreys, G. W. (1996). View specificity in object processing: Evidence from picture matching. Journal of Experimental Psychology: *Human Perception and Performance*, *22*, 395-416.

Liu, T., & Cooper, L. a. (2001). The influence of task requirements on priming in object decision and matching. *Memory & Cognition*, *29*(6), 874–882.

Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*, *240*(4853), 740-749.

Marr, D. (1982). *Vision: A computational investigation into the human representation and processing of visual information*. San Francisco: W. H. Freeman

Mayer, K. M., & Vuong, Q. C. (2012). The influence of unattended features on object processing depends on task demand. *Vision Research*, *56*(2012), 20–27.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.

Nankoo, J.-F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2015). Re-evaluating birds' ability to detect Glass patterns. *Animal Cognition*, *18*, 945-952.

Newell, F. N., Wallraven, C., & Huber, S. (2004). The role of characteristic motion in object categorization. *Journal of Vision*, *4*(2), 118–129.

Cook, R. G., & Murphy, M. S. (2012) Avian visual processing of motion and objects. In O. F. Lazareva, T. Shimizu, E. A., Wasserman (Eds.), *How animals see the world: Behavior, biology, and evolution of vision* (pp. 271-288). London: Oxford University Press.

Nguyen, A. P., Spetch, M. L., Crowder, N. A., Winship, I. R., Hurd, P. L., & Wylie, D. R. (2004). A dissociation of motion and spatial-pattern vision in the avian telencephalon: implications for the evolution of “visual streams”. *The Journal of neuroscience*, *24*(21), 4962-4970.

O’Toole, A. J., Roark, D. a., & Abdi, H. (2002). Recognizing moving faces: A psychological and neural synthesis. *Trends in Cognitive Sciences*, *6*(6), 261–266.

Potter, M. C. (1976). Short-term conceptual memory for pictures. *Journal of experimental psychology: human learning and memory*, *2*(5), 509.

Qadri, M. A. J., Sayde, J. M., & Cook, R. G. (2014). Discrimination of Complex Human Behavior by Pigeons (Columba livia) and Humans. *PLoS ONE*, *9*(11), e112342.

Setti, A., & Newell, F. N. (2010). The effect of body and part-based motion on the recognition of unfamiliar objects. *Visual Cognition*, *18*(3), 456–480.

Spetch, M. L., Friedman, A., & Vuong, Q. C. (2006). Dynamic object recognition in pigeons and humans. *Learning & Behavior : A Psychonomic Society Publication*, *34*(3), 215–228.

Spetch, M. L., & Friedman, a. (2006). Comparative Cognition of Object Recognition. *Comparative Cognition & Behavior Reviews*, *1*, 12–35.

Stone, J. V. (1998). Object recognition using spatiotemporal signatures. *Vision Research*, *38*(7), 947–951.

Tarr, M. J., & Bülthoff, H. H. (1995). Is human object rec- ognition better described by geon structural descrip- tions or by multiple views? Comment on Biederman and Gerhardstein (1993). *Journal of Experimental Psychology: Human Perception and Performance*, *21*(6), 1494- 1505.

Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *nature*, *381*(6582), 520-522.

Troje, N. F., & Chang, D. H. F. (2013) Shape-independent processes in biological motion perception. In K. L. Johnson & Shiffrar, M. (Eds.), *People Watching: Social, Perceptual, and Neurophysiological Studies of Body Perception* (pp. 82-100). London: Oxford University Press.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M.A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge: MIT Press.

Van Essen, D. C., & Gallant, J. L. (1994). Neural mechanisms of form and motion processing in the primate visual system. *Neuron*, *13*(1), 1-10.

Vuong, Q. C., & Tarr, M. J. (2004). Rotation direction affects object recognition. *Vision Research*, *44*(14), 1717–1730.

Vuong, Q. C., Friedman, a., & Read, J. C. a. (2012). The relative weight of shape and non-rigid motion cues in object perception: A model of the parameters underlying dynamic object discrimination. *Journal of Vision*, *12*, 16–16.

Xiao, N. G., Perrotta, S., Quinn, P. C., Wang, Z., Sun, Y. H. P., & Lee, K. (2014). On the facilitative effects of face motion on face recognition and its development. *Frontiers in Psychology*, *5*(JUN), 1–16.

Chapter 7

General Discussion

The studies reported in this dissertation examine the interaction of form and motion at the intermediate level of visual processing in humans and pigeons. The results of these studies provide many insights into the psychophysical properties of mid-level vision that are critical for object perception, and ultimately further the current understanding of the general principles of object perception and recognition. In the studies reported, five main questions were addressed: 1) do humans process implied motion as real motion? 2) What is the mechanism of implied motion? 3) Is the pigeon visual system sensitive to complex motion in the same way as the human visual system? 4) Are pigeons, like humans, also more sensitive to implied motion (using dynamic Glass patterns) compared to global form (using static Glass patterns)? 5) Do pigeons and humans rely on non-rigid motion and form differently for object perception?

To investigate the intermediate stages of form and motion processing, I used two classes of stimuli, Glass patterns and RDS, that are specifically geared towards investigating the mid-level processes of form and motion respectively (Glass, 1969; Nakayama & Tyler, 1981). In chapter 2, I set out to characterize the psychophysical properties of implied motion (i.e., perception of coherent motion from dynamic Glass patterns) in order to determine whether the human visual system processes implied motion as real motion. Chapter 3 builds on the results from chapter 2, to test the hypothesis that the perception of implied motion is mainly driven by a temporal summation mechanism, similar to the snapshot neurons in Giese and Poggio’s (2003) neural model for the perception of biological motion in the form pathway. Given that the sensitivity of the avian motion system to complex motion is unknown, in chapter 4, I set out to investigate whether there is any evidence of specialized global motion detectors in pigeons as has been shown in humans. In chapter 5, I aimed to answer the question of whether birds perceived implied motion from dynamic Glass patterns, and whether the avian visual system employs similar algorithms to that of the human visual system. Finally, in chapter 6, an investigation of the use of form and non-rigid motion for object perception was carried out. This was done in order to determine whether the reliance on form and motion is different due to the use of non-rigid motion, and whether there is a difference between humans and pigeons.

7.1 Summary of Novel Findings

7.1.1 Summation of form signals

The results from the study presented in chapter 2 (published in Nankoo et al., 2012) suggest that the perception of implied motion from dynamic Glass patterns is likely processed in the form pathway. The data shows that the relative sensitivities of human observers to different types of dynamic Glass patterns are strikingly similar to those of static Glass patterns, although the thresholds for each pattern type was substantially lower with dynamic Glass patterns. With both dynamic and static Glass patterns, thresholds were lowest for concentric followed by radial, spiral, vertical and horizontal. This is in stark contrast to the relative sensitivities observed with real motion using RDS. With real motion, thresholds were equivalent for concentric (i.e., rotation), radial, vertical and horizontal. Observers performed significantly worse with spiral motion. Therefore, to answer the question of whether humans process implied motion as real motion, the results from chapter 2 suggest that this is not the case. Instead, the results suggest that the detection mechanisms for static and dynamic Glass patterns are fundamentally different from the detection mechanisms for real global motion. It should, however, be noted that these results only apply to the detection thresholds and do not indicate whether the perception of coherent motion from dynamic Glass patterns is generated solely from the form pathway. Nonetheless, the increased sensitivity observed with dynamic Glass patterns relative to static Glass patterns suggest that there may also be a temporal summation mechanism operating in the form pathway (Giese & Poggio, 2003; Gilaie-Dotan et al., 2013).

The study presented in chapter 3 (published in Nankoo et al., 2015) aimed to test the hypothesis that the reduced thresholds with dynamic Glass patterns relative to static Glass patterns reported in chapter 2 (see also Burr & Ross, 2006; Or, Khuu, & Hayes, 2007) is indeed due to a temporal summation of the form signals. Varying the number of unique static Glass patterns within dynamic Glass patterns was used to test this hypothesis. In agreement with the summation hypothesis, it was found that the more unique frames present in the dynamic Glass patterns, the lower the threshold. Indeed, partial correlations confirmed that the number of unique static Glass patterns is the dominant factor responsible for the lower thresholds observed with dynamic Glass patterns. Thus chapter 3 provides an answer as to the mechanism (i.e., summation of global form signals) for the perception of dynamic Glass patterns.

The evidence for a temporal summation mechanism of the global form signals noted in chapter 3 is reminiscent of the analysis carried out by snapshot neurons proposed in Giese and Poggio's (2003) neural model of biological motion. Specifically, Giese and Poggio (2003; see also Lange & Lappe, 2006) proposed that snapshot neurons in the form pathway code for static body shapes that are then summated upstream in the form pathway by motion pattern neurons. Thus, taken together, the results from chapters 2 and 3 show that implied motion in humans is likely processed in the form pathway through a mechanism that is similar to snapshot neurons.

7.1.2 Rotation bias in pigeons

In order to investigate the perception of implied motion in pigeons, it was essential to establish the sensitivity of the avian motion system to different types of complex motion in the same way as was done for humans in the study reported in chapter 2. In chapter 4, I present a study on the perception of complex motion in pigeons and humans (published in Nankoo et al., 2014). The results indicate that pigeons are significantly more sensitive to rotational motion relative to radial or spiral motion. It was also found that the pigeons' performance with radial motion was lower than with spiral motion. These results differ from those obtained with humans. Human observers' sensitivity was highest when detecting rotational and radial motion (i.e., cardinal directions) whereas they performed significantly poorer on spiral motion (intermediate on the complex motion continuum; see Figure 2 in Morrone, et al., 1999). The results from human studies suggest that humans have specialized detectors for complex motion in cardinal directions (Morrone, et al., 1999). Based on the data obtained from the study reported in chapter 4, it appears that the pigeon motion system may have a rotational motion detector and either pigeons do not have any other type of complex motion detectors, or have weaker radial and spiral detectors. Therefore, the answer to the question of whether the pigeon visual system is sensitive to complex motion in the same way as the human visual system is evidently no based on the results of chapter 4.

7.1.3 Perception of implied motion in pigeons

In chapter 5 I present a study on the perception of implied motion from dynamic Glass patterns in pigeons. Specifically, I aimed to investigate whether pigeons' performance when detecting static and dynamic Glass patterns are similar to those of humans (published in Nankoo et al., 2015). A lower threshold for dynamic Glass patterns in pigeons would suggest that a similar temporal summation mechanism to that suggested for humans in chapters 2 and 3. However, the pigeons, unexpectedly, were unable to learn the discriminate between static Glass pattern and static noise well enough (i.e., 80% correct over 3 sessions) to extract threshold measurement. In contrast, the pigeons were able to learn the discrimination between dynamic Glass patterns and noise. These results suggest there may indeed be a temporal summation mechanism at play in the perception of dynamic Glass patterns, although the study does not exclude other hypotheses such as the possibility that pigeons were more attentive to the dynamic Glass patterns due to motion (regardless of whether it was perceived as random or coherent). Further testing is required to establish stronger evidence based on thresholds measurements.

Given that previous studies have reported threshold measurements using static Glass patterns with pigeons (and starlings) (Kelly, Bischof, Wong-Wylie, & Spetch, 2001; Qadri, & Cook, 2014), a second experiment was carried in order to clarify why the birds in the study presented in chapter 5 were not able to perform at criterion. What was found was that the birds were able to easily learn the discrimination between 100% coherent Glass pattern and noise only when the noise consisted of randomly position dots rather than randomly oriented dipoles as was used in experiment 4.2. The density distribution of the dots in noise patterns containing randomly oriented and coherent Glass patterns are equivalent whereas in the noise pattern with randomly distributed dots (as used by Kelly, Bischof, Wong-Wylie, & Spetch, 2001; Qadri, & Cook, 2014), the density distribution of the dots is uniformly distributed (see Figure 5.5). Thus, birds in previous studies might have learned the task based on density distribution of the dots in the patterns rather than the global structure of the patterns.

7.1.4 Contribution of form and non-rigid motion to object perception

In chapter 6, I report a study in which I investigate the role of shape and non-rigid motion for the perception of complex 3D objects in order to understand the impact of the differences at the mid-level processing on higher-level object perception. In addition, because prior comparative studies have focused on use of rigid motion (although see Qadri, Sayde, & Cook, 2014), it is not known how birds process non-rigid motion in conjunction with form information for object perception. Using Vuong, Friedman, & Read's (2012) parametric morphing technique, shape and non-rigid motion dimensions were systematically varied independently along a continuum. Both pigeons and humans learned the task with ease and showed that they can rely on shape and non-rigid motion information independently to discriminate between objects. That is, for both pigeons and humans, performance with only one informative cue (regardless if that cues was form or non-rigid motion) was equivalent to performance when both cues were informative.

7.2 Future Directions

Given the relative dearth of information on mid-level vision across species (Lazareva, Shimizu, & Wasserman, 2012), the studies presented in this dissertation provide a good foundation for further investigations, with the ultimate goal of understanding general principles of vision. Here I briefly outline some avenues for further research that can build upon the investigations presented in this dissertation.

7.2.1 Probing the mechanisms of the perception of dynamic Glass patterns.

The main outcome from the studies in chapters 2 and 3 is that the increased sensitivity observed for implied motion using dynamic Glass patterns is primarily driven by a form mechanism that appear to summate global form signals (Nankoo et al., 2012; Nankoo et al., 2015). This summation of form signals is akin to the summation mechanism described by in Giese and Poggio's (2003) neural model of biological movement. Thus, hypothetically, the snapshot and motion pattern neurons from Giese and Poggio's model can also explain the perception of, and sensitivity to, implied motion as reported in this dissertation. In order to further our understanding of the perception of implied motion, future studies should build upon the results presented in chapters 2 and 3. For instance, does Giese and Poggio's (2003) model of snapshot and motion pattern neurons predict the behavioural data from dynamic Glass patterns? Such a question can be answered by comparing simulations to behavioural data.

However, another potential explanation for increased sensitivity with dynamic Glass patterns may be related to memory processes. Studies have shown that repeatedly presented stimuli tend to be perceived better and faster through a priming effect (Grill-Spector, Henson, & Martin, 2006; Bar & Biederman, 1998). The facilitative effect of priming has been argued to be due to a sharpening of cortical representation (Wiggs & Martin, 1998; Henson & Rugg, 2003), and is accompanied by suppression in neural activity, termed repetition suppression (Grill-Spector, Henson & Martin, 2006). Future studies should explore the role of priming and repetition suppression in the perception of implied motion from dynamic Glass patterns.

7.2.2 Rotational bias in the pigeon motion system.

In the study presented in chapter 4, the perception of complex motion between humans and pigeons was found to be different. Humans are most sensitive to complex motion in the cardinal directions (Morrone et al., 1999), suggesting that humans have rotational and radial motion detectors. In contrast, pigeons appear to be most sensitive to rotational complex motion and least sensitive to radial motion. Performance with spiral motion was poorer than with rotational motion, but better than radial motion. This pattern of performance would be predicted if the pigeon visual system contained only rotation motion detectors. Specifically, as the motion direction deviates from rotation towards radial, performance should also decrease linearly. This is indeed shown from the study in chapter 5 (Nankoo et al., 2014). It has been argued that the sensitivity to cardinal directions in humans is related to processing optic flow (Morrone et al., 1999). It is well known that pigeons have neurons that respond to rotational and radial optic flow (see Wylie, 2013 for review), and indeed it has been argued that flying animals tend to rely on optic more for navigation (Collett, Collett, & Srinivasan, 2006; Srinivasan, Zhang & Bidwell, 1997; Srinivasan et al., 1996; Bhagavatula et al., 2011). Given the previous research, the bias for rotation motion is indeed surprising. One potential explanation for this preference for rotational motion may be related to eye movements. In birds, torsional eye movements are much larger than in humans (Wallman & Letelier, 1993). As shown in Figure 7.2, torsional eye movements result in rotational optic flow. One potential way to isolate whether torsional eye movements are the reason for rotational motion detectors is to test birds with reduced eye movements such as owls (Steinbach & Angus, 1974). Other possible explanations for the sensitivity to rotational motion may be that it is related to the dynamic of flight. During flight it is essential for birds to monitor body pitch, yaw and roll to maintain stabilization (Taylor & Thomas, 2002). However, given that the parameters used in the RDS more closely relates to object motion as opposed to optic flow, it is likely that, if the rotational sensitivity is related to flight dynamics, it is to monitor flight patterns of conspecifics and predators during flight. Comparing flying birds such as pigeons to flightless birds such as chickens can test such a hypothesis.

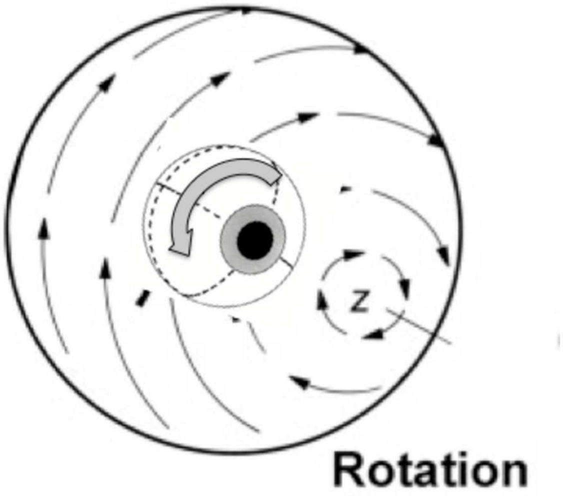


Figure 7.1 Illustration of anti-clockwise torsional eye movement (represented by the gray arrow) resulting clock-wise rotational optic flow about the *z*-axis.

The reduced sensitivity to radial motion in birds relative to humans is interesting and warrants further investigation. It is well known that flying animals rely extensively on optic flow to maneuver within the environment. However, as mentioned previously, the parameters of the RDS used likely relates more to object motion than optic flow. In the context of object motion, radial motion patterns are likely to occur with looming stimuli. Thus, it is possible that the reduced sensitivity observed suggest a heavier reliance on looming parameters (e.g. increase in size of the retinal image) in birds. Presenting both stimuli within the same display and varying speed parameters independently can test the contribution of looming stimuli and radial motion.

7.2.3 Motion from form in pigeons.

The results presented in chapters 5 suggest the possibility that the avian visual system may also summate form signals as is proposed for the mammalian system. However, due to the difficulty in obtaining threshold measurements with the pigeons, it is unclear whether pigeons' performance was simply because they paid more attention to the dynamic Glass patterns due to the motion capture or due to a summation mechanisms as described by Giese and Poggio (2003). A paradigm similar to that used in the study presented in chapter 3 would provide an adequate test for this question. This also leads to the question of whether the pigeons perceived a coherent motion or incoherent motion in the patterns.

7.2.4 Perception of static Glass patterns in birds.

Another outcome from the study presented in chapter 5 is that it became evident that the results from previous studies (Kelly, Bischof, Wong-Wylie, & Spetch, 2001; Qadri, & Cook, 2014) on global form perception using static Glass patterns in birds may be erroneous to some degree. It is also clear that using static Glass patterns with birds may be impractical because of the difficulty with learning the discrimination from static noise. Rather, based on the evidence presented in chapters 2 and 3 that perception of dynamic Glass patterns is similar to the perception of static Glass patterns, I suggest that studies such as Kelly, Bischof, Wong-Wylie, and Spetch, (2001) and Qadri and Cook (2014) be redone using dynamic Glass patterns. Such a study would allow us to ascertain whether that the avian visual system has any detection bias towards certain shapes as was found in humans (Wilson & Wilkinson, 1998). In other words, until such a study is carried out, it is unknown whether birds have detector units specialized for certain shapes.

7.2.5 Linking mid-level vision to non-rigid motion

Lastly in chapter 6 I take a look at how non-rigid motion in combination with form information is used for object perception. The results show that both humans and pigeons appear to use form and non-rigid motion independently, and can rely on either cue to make discriminations between objects. Given the differences between form and motion processing in humans and pigeons at the intermediate level, this is a surprising result. In addition, previous research on object perception has generally shown that pigeons tend to rely more on motion compared to humans (Peissig & Goode, 2012; Spetch & Freidman, 2006). Further research is required to investigate why the results using non-rigid motion differ from the results using rigid motion. For instance, because non-rigid motion is often associated with biological organisms, it is possible that both humans and pigeon make equal use of all available cues to identify biologically relevant agents. It is also important to bridge the gap between the mid-level and high-level processes of vision. The results of chapter 6 however do not appear to be congruent with the biases observed in chapters 2-5. Further studies should aim to manipulate the components of non-rigid motion, such as rotation, translation, strain, and dilatation. Using a parametric morphing technique, such as Vuong, Friedman and Read (2012), it would be feasible to manipulate these variables individually and investigate whether the biases observed in chapters 2-5 (e.g., pigeons bias to rotation motion) is still present at the higher level of object perception.

7.3 Summary

The ability to perceive objects in the world is essential to many animals across taxa. Thus, an understanding of the similarities and differences in perceptual organization is critical to understand the general principles of object perception and vision in general. Chapters 2 and 3 demonstrate that humans perceive implied motion more readily than static form, but both are processed by the same or similar mechanism (i.e. likely within the form pathway). Chapter 4 demonstrates that pigeons, unlike humans, may only have a global rotation detector whereas chapter 5 shows that pigeons, like humans, are better at perceiving implied motion compared to form. Finally, chapter 6 shows that both humans and pigeons can use form and non-rigid motion independently to identify objects. Taken together these studies highlight the need for better general theories of mid-level vision.

7.4 Reference

Bar, M., & Biederman, I. (1998). Subliminal visual priming. *Psychological Science*, *9*(6), 464-468.

Bhagavatula, P. S., Claudianos, C., Ibbotson, M. R., & Srinivasan, M. V. (2011). Optic flow cues guide flight in birds. *Current Biology*, *21*(21), 1794-1799.

Burr, D., & Ross, J. (2006). The effects of opposite-polarity dipoles on the detection of Glass patterns. *Vision Research*, *46*(6), 1139-1144.

Collett, M., Collett, T. S., & Srinivasan, M. V. (2006). Insect navigation: measuring travel distance across ground and through air. *Current biology*, *16*(20), R887-R890.

Glass, L. (1969). Moire effect from random dots. *Nature*, *223*(5206), 578-580.

Giese, M. A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience*, *4*(3), 179-192.

Gilaie-Dotan, S., Kanai, R., Bahrami, B., Rees, G., & Saygin, A. P. (2013). Neuroanatomical correlates of biological motion detection. *Neuropsychologia*, *51*(3), 457-463.

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends in cognitive sciences*, *10*(1), 14-23.

Henson, R. N. A., & Rugg, M. D. (2003). Neural response suppression, haemodynamic repetition effects, and behavioural priming. *Neuropsychologia*, *41*(3), 263-270.

Kelly, D. M., Bischof, W. F., Wong-Wylie, D. R., & Spetch, M. L. (2001). Detection of glass patterns by pigeons and humans: implications for differences in higher level processing. *Psychological Science*, *12*(4), 338-342.

Lange, J., & Lappe, M. (2006). A model of biological motion perception from configural form cues. *The Journal of Neuroscience*, *26*(11), 2894-2906.

Lazareva, O. F., Shimizu, T., & Wasserman, E. A. (2012). *How animals see the world: comparative behavior, biology, and evolution of vision*. London: Oxford University Press.

Morrone, M. C., Burr, D. C., Di Pietro, S., & Stefanelli, M. A. (1999). Cardinal directions for visual optic flow. *Current Biology*, *9*(14), 763-766.

Nakayama, K., & Tyler, C. W. (1981). Psychophysical isolation of movement sensitivity by removal of familiar position cues. *Vision research*, *21*(4), 427-433.

Nankoo, J. -F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2012). Perception of dynamic Glass patterns. *Vision research*, *72*, 55-62.

Nankoo, J. -F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2014). Perception of complex motion in humans and pigeons (Columba livia). *Experimental brain research*, *232*(6), 1843-1853.

Nankoo, J. -F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2015). Temporal summation of global form signals in dynamic Glass patterns. *Vision research*, *107*, 30-35.

Or, C. C. F., Khuu, S. K., & Hayes, A. (2007). The role of luminance contrast in the detection of global structure in static and dynamic, same-and opposite-polarity, Glass patterns. *Vision Research*, *47*(2), 253-259.

Peissig, J. J., & Goode, T. (2012). The recognition of rotated objects in animals. *How animals see the world: comparative behavior, biology, and evolution of vision* (pp, 233-246). Oxford University Press, New York.

Qadri, M. A., & Cook, R. G. (2014). The perception of Glass patterns by starlings (Sturnus vulgaris). *Psychonomic bulletin & review*, *22*(3), 687-693.

Spetch, M. & Friedman, A. (2006). Comparative cognition of object recognition. *Comparative Cognition Reviews, 1,* 12-35.

Srinivasan, M., Zhang, S., Lehrer, M., & Collett, T. (1996). Honeybee navigation en route to the goal: visual flight control and odometry. *The Journal of Experimental Biology*, *199*(1), 237-244.

Srinivasan, M., Zhang, S., & Bidwell, N. (1997). Visually mediated odometry in honeybees. *The Journal of Experimental Biology*, *200*(19), 2513-2522.

Steinbach, M. J., Angus, R. G., & Money, K. E. (1974). Torsional eye movements of the owl. *Vision research*, *14*(8), 745-746.

Taylor, G. K., & Thomas, A. L. R. (2002). Animal flight dynamics II. Longitudinal stability in flapping flight. *Journal of Theoretical Biology*, *214*(3), 351-370.

Vuong, Q. C., Friedman, A., & Read, J. C. (2012). The relative weight of shape and non-rigid motion cues in object perception: A model of the parameters underlying dynamic object discrimination. *Journal of vision*, *12*(3), 16.

Wallman, J. & Letelier, J. -C. (1993). Eye movements, head movements, and gaze stabilization in birds. In H. P. Zeigler, H. -J. Bischof (Eds), *Vision, brain, and behavior in birds* (pp. 245-263). Cambridge, MA, US: The MIT Press

Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current opinion in neurobiology*, *8*(2), 227-233.

Wilson, H. R., & Wilkinson, F. (1998). Detection of global structure in Glass patterns: implications for form vision. *Vision research*, *38*(19), 2933-2947.

Wylie, D. R. (2013). Processing of visual signals related to self-motion in the cerebellum of pigeons. *Frontiers in behavioral neuroscience*, *7*.

Work Cited

Aggarwal, J. K., Cai, Q., Liao, W., & Sabata, B. (1998). Nonrigid motion analysis: Articulated and elastic motion. *Computer Vision and Image Understanding*, *70*, 142–156.

Anderson, B. (1999). Surface perception. In R. A. Wilson, F. C. Keil (Eds.), *The MIT encylopedia of the cognitive sciences*. Cambridge: MIT Press

Anderson, S. J., & Swettenham, J. B. (2006). Neuroimaging in human amblyopia. *Strabismus*, *14*(1), 21-35.

Apthorp, D., Schwarzkopf, D. S., Kaul, C., Bahrami, B., Alais, D., & Rees, G. (2013). Direct evidence for encoding of motion streaks in human visual cortex. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*(1752), 20122339.

Asen, Y., & Cook, R. G. (2012). Discrimination and categorization of actions by pigeons. *Psychological science*, *23*(6), 617-624.

Aspell, J. E., Wattam-Bell, J., Atkinson, J., & Braddick, O. J. (2010). Differential human brain activation by vertical and horizontal global visual textures. *Experimental brain research*, *202*(3), 669-679.

Aspell, J. E., Wattam-Bell, J., & Braddick, O. (2006). Interaction of spatial and temporal integration in global form processing. *Vision research*, *46*(18), 2834-2841.

Baron, J., Pinto, L., Dias, M. O., Lima, B., & Neuenschwander, S. (2007). Directional responses of visual wulst neurones to grating and plaid patterns in the awake owl. *European Journal of Neuroscience*, *26*(7), 1950-1968.

Bar, M., & Biederman, I. (1998). Subliminal visual priming. *Psychological Science*, *9*(6), 464-468.

Beintema, J. A., & Lappe, M. (2002). Perception of biological motion without local image motion. *Proceedings of the National Academy of Sciences*, *99*(8), 5661-5663.

Biederman, I., & Cooper, E. E. (1991). Priming contour-deleted images: Evidence for intermediate representations in visual object recognition. *Cognitive psychology*, *23*(3), 393-419.

Blake, R., & Aiba, T. S. (1998). Detection and discrimination of optical flow components. *Japanese Psychological Research*, *40*(1), 19-30.

Braddick, O. J., O'Brien, J. M., Wattam-Bell, J., Atkinson, J., Hartley, T., & Turner, R. (2001). Brain areas sensitive to coherent visual motion. *Perception-London*, *30*(1), 61-72.

Braddick, O. J., O'Brien, J. M. D., Wattam-Bell, J., Atkinson, J., & Turner, R. (2000). Form and motion coherence activate independent, but not dorsal/ventral segregated, networks in the human brain. *Current Biology*, *10*(12), 731-734

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial vision*, *10*, 433-436.

Butler, A. B. & Hodos, W. (2005). *Comparative vertebrate neuroanatomy: evolution and adaptation* (2nd ed.). New York: Wiley-Liss.

Burr, D., & Thompson, P. (2011). Motion psychophysics: 1985–2010. *Vision research*, *51*(13), 1431-1456.

Burr, D., & Ross, J. (2006). The effects of opposite-polarity dipoles on the detection of Glass patterns. *Vision Research*, *46*(6), 1139-1144.

Burr, D. C., & Ross, J. (2002). Direct evidence that "speedlines" influence motion mechanisms. *The Journal of Neuroscience*, *22*(19), 8661-8664.

Bischof, W. E., Reid, S. L., Wylie, D. R., & Spetch, M. L. (1999). Perception of coherent motion in random dot displays by pigeons and humans. *Perception & psychophysics*, *61*(6), 1089-1101.

Boussaoud, D., Desimone, R., & Ungerleider, L. G. (1992). Subcortical connections of visual areas MST and FST in macaques. *Visual neuroscience*, *9*(3-4), 291-302.

Britten, K. H., & van Wezel, R. J. (1998). Electrical microstimulation of cortical area MST biases heading perception in monkeys. *Nature neuroscience*, *1*(1), 59-63.

Collett, M., Collett, T. S., & Srinivasan, M. V. (2006). Insect navigation: measuring travel distance across ground and through air. *Current biology*, *16*(20), R887-R890.

Calabretta, R., & Parisi, D. (2005). Evolutionary connectionism and mind/brain modularity. In W. Callebaut & D. Rasskin-Gutman (Eds.), Modularity. Understanding the development and evolution of complex natural systems (pp. 309–330). Cambridge, MA: MIT Press.

Corey, D. M., Dunlap, W. P., & Burke, M. J. (1998). Averaging correlations: Expected values and bias in combined Pearson rs and Fisher's z transformations. *The Journal of general psychology*, *125*(3), 245-261.

Cavoto, K. K., & Cook, R. G. (2001). Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *27*(1), 3.

Cavoto, B. R., & Cook, R. G. (2006). The contribution of monocular depth cues to scene perception by pigeons. *Psychological Science*, *17*(7), 628-634.

Carandini, M., Demb, J. B., Mante, V., Tolhurst, D. J., Dan, Y., Olshausen, B. A., Gallant, J. L., & Rust, N. C. (2005). Do we know what the early visual system does?. *The Journal of Neuroscience*, *25*(46), 10577-10597.

Chaves, L. M., Hodos, W., & Güntürkün, O. (1993). Color-reversal learning: effects after lesions of thalamic visual structures in pigeons. *Visual neuroscience*, *10*(06), 1099-1107.

Cook, R. G. (2000). The comparative psychology of avian visual cognition. *Current Directions in Psychological Science*, *9*(3), 83-89.

Cook R. G. (2001). Hierarchical stimulus processing in pigeons. In R. G. Cook (Ed.), *Avian visual cognition*. http://www.pigeon.psy.tufts.edu/avc/cook/

Crowder, N. A., & Wylie, D. R. (2001). Fast and slow neurons in the nucleus of the basal optic root in pigeons. *Neuroscience letters*, *304*(3), 133-136.

Distler, C., & Hoffmann, K. P. (2001). Cortical input to the nucleus of the optic tract and dorsal terminal nucleus (NOT-DTN) in macaques: a retrograde tracing study. *Cerebral Cortex*, *11*(6), 572-580.

Day, A. M., & Palomares, M. (2014). How temporal frequency affects global form coherence in Glass patterns. *Vision research*, *95*, 18-22.

Dakin, S. C., & Bex, P. J. (2002). Summation of concentric orientation structure: seeing the Glass or the window?. *Vision Research*, *42*(16), 2013-2020.

Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *The Journal of Neuroscience*, *4*(8), 2051-2062.

Desimone, R., & Schein, S. J. (1987). Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form. *Journal of neurophysiology*, *57*(3), 835-868.

Duffy, C. J., & Wurtz, R. H. (1991). Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *Journal of neurophysiology*, *65*(6), 1329-1345.

Dumoulin, S. O., & Hess, R. F. (2007). Cortical specialization for concentric shape processing. *Vision Research*, *47*(12), 1608–1613

Edwards, M., & Badcock, D. R. (1993). Asymmetries in the sensitivity to motion in depth: A centripetal bias. *PERCEPTION-LONDON-*, *22*, 1013-1013.

Edwards, M., & Ibbotson, M. R. (2007). Relative sensitivities to large-field optic-flow patterns varying in direction and speed. *PERCEPTION-LONDON-*, *36*(1), 113.

Edwards, M., & Crane, M. F. (2007). Motion streaks improve motion detection. *Vision research*, *47*(6), 828-833.

Essock, E. A., DeFord, J. K., Hansen, B. C., & Sinai, M. J. (2003). Oblique stimuli are seen best (not worst!) in naturalistic broad-band stimuli: A horizontal effect. *Vision research*, *43*(12), 1329-1335.

Fite, K. V. (1973). Anatomical and behavioral correlates of visual acuity in the great horned owl. *Vision research*, *13*(2), 219-IN2.

Frost, B. J. (1985). Neural mechanisms for detecting object motion and figure–ground boundaries contrasted with self-motion detecting systems. In D. Ingle, M. Jeannerod, D. Lee (Eds.), *Brain mechanisms and spatial vision*, (pp. 415-419). Dordrecht: Martinus Nijhoff Publishers.

Gallant, J. L., Braun, J., & Vanessen, D. C. (1993, January 1). Selectivity for polar, hyperbolic, and cartesian gratings in macaque visual-cortex. *Science*, *259*(5091), 100–103.

Gallant, J. L., Shoup, R. E., & Mazer, J. A. (2000). A human extrastriate area functionally homologous to macaque V4. *Neuron*, *27*(2), 227-235.

Geisler, W. S. (1999). Motion streaks provide a spatial code for motion direction. *Nature*, *400*(6739), 65-69

Ghim, M. M., & Hodos, W. (2006). Spatial contrast sensitivity of birds. *Journal of Comparative Physiology A*, *192*(5), 523-534.

Glass, L. (1969). Moire effect from random dots. *Nature*, *223*(5206), 578-580.

Giese, M. A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience*, *4*(3), 179-192.

Graziano, M. S., Andersen, R. A., & Snowden, R. J. (1994). Tuning of MST neurons to spiral motions. *The Journal of neuroscience*, *14*(1), 54-67.

Güntürkün, O. (2000). Sensory Physiology: Vision. In G. C., Whittow (Ed.), *Sturkie's avian physiology*, (pp. 1-19). Orlando: Academic Press.

Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.

Geesaman, B. J., & Andersen, R. A. (1996). The analysis of complex motion patterns by form/cue invariant MSTd neurons. *The Journal of Neuroscience*, *16*(15), 4716-4732.

Gibson, J. J. (1954). The visual perception of objective motion and subjective movement. *Psychological Review*, *61*(5), 304.

Graziano, M. S., Andersen, R. A., & Snowden, R. J. (1994). Tuning of MST neurons to spiral motions. *The Journal of neuroscience*, *14*(1), 54-67.

Gu, Y., Wang, Y., Zhang, T., & Wang, S. R. (2002). Stimulus size selectivity and receptive field organization of ectostriatal neurons in the pigeon. *Journal of Comparative Physiology A*, *188*(3), 173-178.

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends in cognitive sciences*, *10*(1), 14-23.

Hansen, B. C., & Essock, E. A. (2004). A horizontal bias in human visual processing of orientation and its correspondence to the structural components of natural scenes. *Journal of Vision*, *4*(12), 5.

Hahmann, U., & Güntürkün, O. (1993). The visual acuity for the lateral visual field of the pigeon (Columba livia). *Vision research*, *33*(12), 1659-1664.

Hendricks, J. (1966). Flickerthresholds as determined by a modified conditioned suppression procedure. *Journal of the Experimental Analysis of Behavior*, *9*(5), 501-506.

Henson, R. N. A. (2003). Neuroimaging studies of priming. *Progress in neurobiology*, *70*(1), 53-81.

Herrnstein, R. J., and Loveland,D. H. (1964).Complex visual concept in the pigeon. *Science 146*, 549–551. doi: 10.1126/science.146.3643.549

Hodos, W., Karten, H. J., & Bonbright, J. C. (1973). Visual intensity and pattern discrimination after lesions of the thalamofugal visual pathway in pigeons. *Journal of Comparative Neurology*, *148*(4), 447-467.

Hodos, W., Leibowitz, R. W., & Bonbright, J. C. (1976). Near-field visual acuity of pigeons: effects of head location and stimulus luminance. *Journal of the Experimental Analysis of Behavior*, *25*(2), 129-141.

Hodos W (2012) What Birds See and What They Don't: Luminance, contrast, and spatial and temporal resolution. In O. F. Lazareva, T. Shimizu, E. A., Wasserman (Eds.), *How animals see the world: Behavior, biology, and evolution of vision* (pp. 5-25). London: Oxford University Press.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of physiology*, *160*(1), 106.

Huber, L., Troje, N. F., Loidolt, M., Aust, U., and Grass, D. (2000). Natural categorization through multiple feature learning in pigeons. Q. J. Exp. Psychol. B 53B, 341–357. doi: 10.1080/027249900750001347

Hellmann, B., Güntürkün, O., & Manns, M. (2004). Tectal mosaic: organization of the descending tectal projections in comparison to the ascending tectofugal pathway in the pigeon. *Journal of Comparative Neurology*, *472*(4), 395-410.

Huk, A. C., Dougherty, R. F., & Heeger, D. J. (2002). Retinotopy and functional subdivision of human areas MT and MST. *The Journal of Neuroscience*, *22*(16), 7195-7205.

Husband, S. & Shimizu, T. (2001). Evolution of the avian visual system. In R. G. Cook (Ed.), *Avian visual cognition*. www.pigeon.psy.tufts.edu/avc/husband/

Jarvis, J. R., Taylor, N. R., Prescott, N. B., Meeks, I., & Wathes, C. M. (2002). Measuring and modelling the photopic flicker sensitivity of the chicken (Gallus g. domesticus). *Vision research*, *42*(1), 99-106.

Jitsumori, M., and Yoshihara, M. (1997). Categorical discrimination of human facial expressions by pigeons: a test of the linear feature model. Q. J. Exp. Psychol. 50, 253–268

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, *17*(11), 4302-4311.

Kelly, D. M., Bischof, W. F., Wong-Wylie, D. R., & Spetch, M. L. (2001). Detection of glass patterns by pigeons and humans: implications for differences in higher-level processing. *Psychological Science*, *12*(4), 338-342.

Kirkpatrick, K., Bilton, T., Hansen, B. C., and Loschky, L. C. (2014). Scene gist categorization by pigeons. J. Exp. Psychol. Anim. Behav. Process. Available online at: http://psycnet.apa.org/psycinfo/2013-44235-001/

Koffka, K. (1935). *Principles of Gestalt Psychology.* New York: Harcourt Brace.

Köhler, W. (1940). *Dynamics in Psychology.* New York: Liveright Publishing Corp.

Kourtzi, Z., Krekelberg, B., & Van Wezel, R. J. (2008). Linking form and motion in the primate brain. *Trends in cognitive sciences*, *12*(6), 230-236.

Krekelberg, B., Dannenberg, S., Hoffmann, K. P., Bremmer, F., & Ross, J. (2003). Neural correlates of implied motion. *Nature*, *424*(6949), 674-677.

Krekelberg, B., Vatakis, A., & Kourtzi, Z. (2005). Implied motion from form in the human visual cortex. *Journal of Neurophysiology*, *94*(6), 4373-4386.

Krekelberg, B., Dannenberg, S., Hoffmann, K. P., Bremmer, F., & Ross, J. (2003). Neural correlates of implied motion. *Nature*, *424*(6949), 674-677.

Krekelberg, B., Vatakis, A., & Kourtzi, Z. (2005). Implied motion from form in the human visual cortex. *Journal of Neurophysiology*, *94*(6), 4373-4386.

Lazareva, O. F., Shimizu, T., & Wasserman, E. A. (2012). *How animals see the world: comparative behavior, biology, and evolution of vision*. London: Oxford University Press.

Loidolt, M., Aust, U., Steurer, M., Troje, N. F., & Huber, L. (2006). Limits of dynamic object perception in pigeons: Dynamic stimulus presentation does not enhance perception and discrimination of complex shape. *Learning & behavior*, *34*(1), 71-85.

Lee, A. L., & Lu, H. (2010). A comparison of global motion perception using a multiple-aperture stimulus. *Journal of Vision*, *10*(4), 9.

Loffler, G. (2008). Perception of contours and shapes: Low and intermediate stage mechanisms. *Vision Research*, *48*(20), 2106–2127

Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*, *240*(4853), 740-749.

Martin, G. R., & Gordon, I. E. (1974). Visual acuity in the tawny owl (Strix aluco). *Vision Research*, *14*(12), 1393-1397.

Marr, D. (1982). *Vision: A computational investigation into the human representation and processing of visual information*. San Francisco: W. H. Freeman

Mather, G., Pavan, A., Marotti, R. B., Campana, G., & Casco, C. (2013). Interactions between motion and form processing in the human visual system. *Frontiers in computational neuroscience*, *7*.

McLeod, P. (1996). Preserved and Impaired Detection of Structure From Motion by a "Motion-blind" Patient. *Visual Cognition*, *3*(4), 363-392.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: two cortical pathways. *Trends in neurosciences*, *6*, 414-417.

Morrone, M. C., Burr, D. C., Di Pietro, S., & Stefanelli, M. A. (1999). Cardinal directions for visual optic flow. *Current Biology*, *9*(14), 763-766.

Morrone, M. C., Burr, D. C., & Vaina, L. M. (1995). 2 Stages of Visual Processing for Radial and Circular Motion. *Nature*, *376*(6540), 507-509.

Maldonado, P. E., Maturana, H., & Varela, F. J. (1988). Frontal and lateral visual system in birds. *Brain, Behavior and Evolution*, *32*(1), 57-62.

Martinoya, C., Rivaud, S., & Bloch, S. (1983). Comparing frontal and lateral viewing in the pigeon. II. Velocity thresholds for movement discrimination. *Behavioural brain research*, *8*(3), 375-385.

May, K. A., & Solomon, J. A. (2013). Four theorems on the psychometric function. *PloS one*, *8*(10), e74815.

Meese, T. S., & Anderson, S. J. (2001). Spiral mechanisms are required to account for summation of complex motion components. *Journal of Vision*, *1*(3), 160-160.

Meese, T. S., & Harris, M. G. (2001). Independent detectors for expansion and rotation, and for orthogonal components of deformation. *PERCEPTION-LONDON-*, *30*(10), 1189-1202.

Nankoo, J. F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2012). Perception of dynamic Glass patterns. *Vision research*, *72*, 55-62.

Nankoo, J. -F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2014). Perception of complex motion in humans and pigeons (Columba livia). *Experimental brain research*, *232*(6), 1843-1853.

Nankoo, J. -F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2015). Temporal summation of global form signals in dynamic Glass patterns. *Vision research*, *107*, 30-35.

Nakayama, K. (1999). Mid-level vision. In R. A. Wilson, F. C. Keil (Eds.), *The MIT encyclopedia of the cognitive science*s. Cambridge: MIT Press.

Nakayama, K. & He, Z. J. (1995). Attention to surfaces: beyond a Cartesian understanding of visual attention. In T. V. Papathomas, C. Chubb, A. Gorea, E. Kowler (Eds), *Early Vision and Beyond*, (pp. 181-188). Cambridge: M.I.T. Press, Cambridge.

Nelder, J. A., & Mead, R. (1965). A simplex method for function minimization. *The computer journal*, *7*(4), 308-313.

Newsome, W. T., & Pare, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual layer. *Journal of Neuroscience*, *8*(6), 2201–2211.

Nuboer, J. F. W., Coemans, M. A. J. M., & Vos, J. J. (1992). Artificial lighting in poultry houses: do hens perceive the modulation of fluorescent lamps as flicker?. *British poultry science*, *33*(1), 123-133.

Nakayama, K. (1985). Biological image motion processing: a review. *Vision research*, *25*(5), 625-660.

Nguyen, A. P., Spetch, M. L., Crowder, N. A., Winship, I. R., Hurd, P. L., & Wylie, D. R. (2004). A dissociation of motion and spatial-pattern vision in the avian telencephalon: implications for the evolution of "visual streams". *The Journal of neuroscience*, *24*(21), 4962-4970.

Nye, P. W. (1973). On the functional differences between frontal and lateral visual fields of the pigeon. *Vision Research*, *13*(3), 559-574.

Or, C. C. F., Khuu, S. K., & Hayes, A. (2007). The role of luminance contrast in the detection of global structure in static and dynamic, same-and opposite-polarity, Glass patterns. *Vision Research*, *47*(2), 253-259.

Ostwald, D., Lam, J. M., Li, S., & Kourtzi, Z. (2008). Neural coding of global form in the human visual cortex. *Journal of Neurophysiology*, *99*(5), 2456–69. doi:10.1152/jn.01307.2007

Porciatti, V., Fontanesi, G., & Bagnoli, P. (1989). The electroretinogram of the little owl (Athene noctua). *Vision Research*, *29*(12), 1693-1698.

Papini, M. R. (2002). Pattern and process in the evolution of learning. *Psychological Review*, *109*, 186–201. doi:10.1037/0033- 295X.109.1.186.

Parker, A. (2003). *In the blink of an eye: How vision sparked the big bang of evolution*. New York: Perseus Publishing.

Pei, F., Pettet, M. W., Vildavski, V. Y., & Norcia, A. M. (2005). Event-related potentials show configural specificity of global form processing. *Neuroreport*, *16*(13), 1427-1430.

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

Pelli, D. G., & Farell, B. (1999). Why use noise?. *JOSA A*, *16*(3), 647-653.

Pitzalis, S., Sereno, M. I., Committeri, G., Fattori, P., Galati, G., Patria, F., & Galletti, C. (2010). Human V6: the medial motion area. *Cerebral Cortex*, *20*(2), 411-424.

Pizlo, Z. (2001). Perception viewed as an inverse problem. *Vision Research*, *41*(24), 3145-3161.

Remy, M., & Güntürkün, O. (1991). Retinal afferents to the tectum opticum and the nucleus opticus principalis thalami in the pigeon. *Journal of Comparative Neurology*, *305*(1), 57-70.

Reymond, L. (1985). Spatial visual acuity of the eagle Aquila audax: a behavioural, optical and anatomical investigation. *Vision research*, *25*(10), 1477-1491.

Ross, J. (2004). The perceived direction and speed of global motion in Glass pattern sequences. *Vision Research*, *44*, 441–448.

Ross, J., Badcock, D. R., & Hayes, A. (2000). Coherent global motion in the absence of coherent velocity signals. Current Biology, 10, 679–682.

Riley, D. A., & Langley, C. M. (1993). The logic of species comparisons. *Psychological Science*, 4, 185–189

Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature neuroscience*, *2*(11), 1019-1025.

Rochon-Duvigneaud, A. (1943). *Les yeux et la vision des vertébrés*. Paris: Masson.

Rubene, D., Håstad, O., Tauson, R., Wall, H., & Ödeen, A. (2010). The presence of UV wavelengths improves the temporal resolution of the avian visual system. *The Journal of experimental biology*, *213*(19), 3357-3363.

Rubene, D., Håstad, O., Tauson, R., Wall, H., & Ödeen, A. (2010). The presence of UV wavelengths improves the temporal resolution of the avian visual system. *The Journal of experimental biology*, *213*(19), 3357-3363.

Scase, M. O., Braddick, O. J., & Raymond, J. E. (1996). What is noise for the motion system?. *Vision research*, *36*(16), 2579-2586.

Seu, L., & Ferrera, V. P. (2001). Detection thresholds for spiral Glass patterns. *Vision Research*, *41*(28), 3785-3790.

Siegel, R. M., & Andersen, R. A. (1988). Perception of three-dimensional structure from motion in monkey and man. *Nature*, *331*, 259-261.

Shlaer, R. (1972). An eagle's eye: quality of the retinal image. *Science*, *176*(4037), 920-922.

Shettleworth, S. J. (1993). Where is the comparison in comparative cognition? Alternative research programs. *Psychological Science*, *4*, 179–184.

Shettleworth, S. J. (2000). Modularity and the evolution of cognition. In C. M. Heyes & L. Huber (Eds.), the evolution of cognition (pp. 43–60). Cambridge, MA: MIT Press.

Shettleworth, S. J. (2010). *Cognition, evolution, and behavior*. New York: York: Oxford University Press.

Shimizu, T. & Karten, H. J. (1991). Central visual pathways in reptiles and birds: Evolution of the visual system. In J. Cronly-Dillon & R. Gregory (Eds.), *Vision and visual dysfunction, vol. 2: Evolution of the eye and visual system*. (pp. 421-441). London: Macmillan Press

Shimizu, T., Patton, T. B., & Husband, S. A. (2010). Avian visual behavior and the organization of the telencephalon. *Brain, behavior and evolution*, *75*(3), 204-217.

Smith, M. A., Bair, W., & Movshon, J. A. (2002). Signals in macaque striate cortical neurons that support the perception of glass patterns. *Journal of Neuroscience, 22*, 8334–8345.

Smith, M. A., Kohn, A., & Movshson, J. A. (2007). Glass pattern responses in macaque V2 neurons. *Journal of Vision*, *7*, 1–15.

Soto, F., & Wasserman, E. (2010). Comparative Vision Science: Seeing Eye to Eye. *Comparative Cognition & Behavior Reviews*, *5*, 148–154. doi:10.3819/ccbr.2010.50011

Tanaka, K., & Saito, H. A. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology*, *62*(3), 626-641.

Trestman, M. (2013). The Cambrian explosion and the origins of embodied cognition. *Biological Theory*, *8*(1), 80-92.

Tsao, D. Y., Freiwald, W. A., Tootell, R. B., & Livingstone, M. S. (2006). A cortical region consisting entirely of face-selective cells. *Science*, *311*(5761), 670-674.

Troje, N. F., Huber, L., Loidolt, M., Aust, U., & Fieder, M. (1999). Categorical learning in pigeons: the role of texture and shape in complex static stimuli. *Vision research*, *39*(2), 353-366.

Quick Jr, R. F. (1974). A vector-magnitude model of contrast detection. *Kybernetik*, *16*(2), 65-67.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge: MIT Press.

Vaina, L. M., Lemay, M., Bienfang, D. C., Choi, A. Y., & Nakayama, K. (1990). Intact "biological motion" and "structure from motion" perception in a patient with impaired motion mechanisms: A case study. *Visual neuroscience*, *5*(04), 353-369.

Van Essen, D. C., & Gallant, J. L. (1994). Neural mechanisms of form and motion processing in the primate visual system. *Neuron*, *13*, 1–10.

Vuong, Q. C., & Tarr, M. J. (2004). Rotation direction affects object recognition. *Vision Research*, *44*(14), 1717–1730.

Vuong, Q. C., Friedman, A., & Read, J. C. (2012). The relative weight of shape and non-rigid motion cues in object perception: A model of the parameters underlying dynamic object discrimination. *Journal of vision*, *12*(3), 16.

Walls, G. L. (1942). *The vertebrate eye and its adaptive radiation*. Oxford, England: Cranbrook Institute of Science.

Wallman, J. & Letelier, J. -C. (1993). Eye movements, head movements, and gaze stabilization in birds. In H. P. Zeigler, H. -J. Bischof (Eds), *Vision, brain, and behavior in birds* (pp. 245-263). Cambridge, MA, US: The MIT Press

Watanabe, S. (2001). Van Gogh, Chagall and pigeons: picture discrimination in pigeons and humans. *Animal Cognition*, *4*(3-4), 147-151.

Watanabe, S., Sakamoto, J., & Wakita, M. (1995). Pigeons' discrimination of paintings by Monet and Picasso. *Journal of the experimental analysis of behavior*, *63*(2), 165.

Watson, A. B., & Turano, K. (1995). The optimal motion stimulus. *Vision research*, *35*(3), 325-336.

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics*, *33*(2), 113–120.

Weibull, W. (1951). A Statistical Distribution Function of Wide Applicability. *Journal of Applied Mechanics*, *13*, 293-297.

Wertheimer, M. (1923). Untersuchungen zur Lehre von der Gestalt, II. *Psychologische Forschung* 4:301-350. Condensed translation published as Laws of organization in perceptual forms, in W. D. Ellis (1938), *A Sourcebook of Gestalt Psychology* (pp. 71 - 88). New York: Harcourt, Brace.

Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current opinion in neurobiology*, *8*(2), 227-233.

Wilkinson, F., James, T. W., Wilson, H. R., Gati, J. S., Menon,R. S., &Goodale,M.A. (2000). An fMRI study of the selective activation of human extrastriate form vision areas by radial and concentric gratings. *Current Biology*, *10*(22), 1455–1458.

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

Wilson, H. R., Loffler, G., Wilkinson, F., & Thistlethwaite, W. A. (2001). An inverse oblique effect in human vision. *Vision research*, *41*(14), 1749-1753.

Wilson, H. R., & Wilkinson, F. (1998). Detection of global structure in Glass patterns: implications for form vision. *Vision research*, *38*(19), 2933-2947.

Wylie, D. R. (2013). Processing of visual signals related to self-motion in the cerebellum of pigeons. *Frontiers in behavioral neuroscience*, *7*.

Zihl, J., Von Cramon, D., & Mai, N. (1983). Selective disturbance of movement vision after bilateral brain damage. *Brain*, *106*(2), 313-340.