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AN INVESTIGATION OF EMERGENT PERCEPTUAL PHENOMENA IN PRIMATES:
ILLUSIONS AND BIASES IN DECISION-MAKING

by

AUDREY E. PARRISH

Under the Direction of Michael J. Beran, PhD, and Sarah F. Brosnan, PhD

ABSTRACT

The perceptual system operates ideally to reveal rapidly processed, accurate and functional information to an organism. However, illusory phenomena emerge when there is discontinuity between sensory input and perception on the basis of misleading contexts. Because illusions emerge as a byproduct of an otherwise functional and efficient perceptual system, they provide a means to understand better mechanisms of perception within and across species. Beyond anatomical and functional similarities in the visual system across primates, nonhuman primate species reveal intriguing similarities in the perception of visual illusions with one another and humans.

This dissertation explored visual illusions across the Order Primates, including human adults and children, chimpanzees, rhesus monkeys, and capuchin monkeys, with a focus on

when, why and for whom geometric illusions emerge. Geometric illusions occur when a target's perceived properties (e.g., size, shape, color) are impacted by an illusory context. Specifically, I focused on similarities and differences in perceptual mechanisms across primate species and on the role of attention in illusion emergence. I also assessed the translational impact of visual illusions on everyday decision-making (i.e., food-choice behavior).

Overall, this research demonstrated that illusions are complex, and they emerged differently across species as a function of processing mode (i.e., global versus local processing) and attentional control. Further, not all illusions were perceived equally. External factors including illusory array design (i.e., the relationship between target and inducer stimuli) and testing paradigm directly impacted illusion perception. Response competition emerged if the illusory array was too heavily weighted towards inducing stimuli, such that the inducers were the more salient element within the array relative to the target stimulus. These methodological challenges proved to be especially true for local processors (e.g., monkeys) that first perceived the individual elements within an array prior to perceiving the global figure. The manner in which illusions are presented to pre- and non-verbal species can constrain or perhaps create a scaffold for illusory perception. Comparative research as in this dissertation provides a deeper understanding of how context influences perception and choice and will shed light on how we see and subsequently interact with our world.

INDEX WORDS: Perception, Visual illusions, Decision making, Biases, Nonhuman primates, Comparative

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AUDREY E. PARRISH

A Dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

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Georgia State University

2015

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2015

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December 2015

DEDICATION

I dedicate this dissertation to those who have supported me during this journey, especially my family. To Gio, my loving husband and best friend, I treasure your constant encouragement and support – I could not have done this without you by my side. I also thank my parents, Ellen and Herb, who have always encouraged me to reach for the stars. Your unconditional love and support make it possible to chase my dreams. To my sisters and their families and my grandparents, I am forever grateful for your support, love, and laughter.

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1 INTRODUCTION

In search of solving one of life's greatest mysteries – the human mind – we must strive to understand cognition and behavior, and its attendant mechanisms, to the deepest and most complete degree. In our best efforts to complete this mission, it is not only beneficial, but also mandatory, to understand how human cognition differs from that of other species. The comparative approach provides the unique opportunity and challenge of delving into the minds of nonhumans to understand better not only their unique cognition and behaviors, but also to understand better our own. The current dissertation adopts the comparative approach to address questions of perception and its fallacies and how these impact subsequent decision-making in the primates, both human and nonhuman. By observing which species fall prey to perceptual illusions and biases, we can better understand the evolution of the perceptual system and when perception might fail in predictable ways.

The question of how an organism obtains and uses information from its environment has a long-standing history in cognitive psychology and comparative ethology. A more basic question of how animals see the world around them has fascinated naturalists and scientists for much longer. The eminent biologist and ethologist Jakob von Uexküll (1934/1957) coined the phrase "*Umwelt*" to describe an animal's distinct phenomenal or perceptual world, noting that "there can be no doubt that a fundamental contrast prevails everywhere between the environment which we see spread around animals, and the *Umwelten* that are built up by the animals themselves and filled with the objects of their own perception." (p. 64). Understanding a species' unique construction of its external world is not an easy feat, and while we may come to understand what an animal sees, we may never fully understand what it experiences (Wasserman, 2012). Despite the challenging nature of this endeavor, comparative psychologists

have long “peered” inside the minds of animals and have made significant strides in understanding the private sensory worlds, or *Umwelts*, of multiple species, often through the use of noninvasive behavioral and physiological procedures (see Lazareva, Shimizu, & Wasserman, 2012, for a review).

Beyond the study of sensory input, the integration and use of this perceptual information is of interest. For example, how does an organism extract salient features from the environment to inform judgment and decision-making? This intersection of incoming perceptual information and outflowing decisional processes and behaviors is at the crux of this research program. In the current series of studies, I will investigate nonhuman primate perceptual phenomena to understand better how animals gather information from and subsequently interact with the world around them. Beyond basic perceptual processes, I am interested in emergent perceptual phenomena, including illusions and biases that sometimes lead to sub-optimal judgment and decision-making within this domain. Here, I argue that perceptual biases and visual illusions emerge from the exact properties of the stimuli themselves (i.e., bottom-up processes based on the information extracted from the visual array itself; Gibson, 1979) and from internal heuristics that guide decision-making (i.e., top-down processes based on memory, expectations, past-experiences, etc.; Neisser, 1976, and see Washburn, 2007).

The objective for this set of studies is to investigate context effects on judgment and decision-making in the perceptual domain across primates. More specifically, I will investigate biases in the perception of size and quantity as produced by geometric illusions. Furthermore, I will address how these illusions might be impacted by the manipulation of attention towards different aspects within the visual array. Finally, I will investigate how these perceptual biases influence subsequent behavior in the action domain. I begin with an introduction to the

experimental study of perception and a literature review on visual illusions with a focus on comparative research. Next, I discuss the critical role of experimental design and visual processing modes in the emergence of these illusions across multiple species, and how they may interact to impact illusory percept formation. Finally, I introduce the future studies that will extend and contribute to this extant body of knowledge.

1.1 Literature Review

1.1.1 Perception

The study of cognition often begins with an in-depth investigation into perception, a process by which incoming sensory stimuli from the environment are analyzed by the visual system, or other sensory modalities appropriate for the species under investigation (i.e., a species-typical *Umwelt*). Perceptual processes are often rapid and may even occur outside of conscious awareness. Although a seemingly simplistic component of cognition, perception relies on a crucial interplay between incoming stimulation from the environment (bottom-up processes) and extant knowledge and cognitive mechanisms that aid recognition and identification of incoming data (top-down processes). The perceptual system typically operates to reveal rapidly processed, accurate and functional information to the organism; however, illusory phenomena may emerge when there is discontinuity in sensory input and perception on the basis of misleading or altered contexts.

1.1.2 Visual Illusions

The study of cognition often begins with an in-depth investigation into perception, a process by which incoming sensory stimuli from the environment are analyzed by the visual system, or other sensory modalities appropriate for the species under investigation (i.e., a species-typical *Umwelt*). Perceptual processes are often rapid and may even occur outside of

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1.1.2 Visual Illusions

As visual creatures, seeing is our window into the world, and vision provides us with much of the information we use to interact with our world, attend to its features, memorize its content, form associations about its events, learn from its contingencies, and problem solve when faced with its uncertainties. Through experience, we come to rely on the veridical nature of sensory input such that information is expected to arrive not only quickly, but also accurately. Coren and Girgus (1978) referenced the common phrase that “seeing is believing” to highlight the dependence that we have on accurate depictions of our real world environment. When our conscious percept does not align with physical reality, it is important to uncover the causes of such errors. The study of visual illusions began in the mid-19th century, shortly before the formal recognition of psychology as a separate discipline distinct from physiology and philosophy (Robinson, 1972). The Oppel-Kundt illusion was the first established visual illusion in the psychological sciences whereby a divided space appears longer than an undivided space; see Figure 1 (Oppel, 1854). From this work, Oppel coined the concept of *geometrisch-optische taushung*, which roughly translates to geometrical optical illusion, and thus began the systematic study of visual illusions.

A variety of geometric illusions quickly emerged thereafter, the majority of which are 2-dimensional patterns distorting perceived size or distance and typically named after their originator (e.g., Baldwin illusion: Baldwin, 1895; Delboeuf illusion: Delboeuf, 1892; Ebbinghaus-Titchener illusion: Ebbinghaus, 1902; Mueller-Lyer illusion: Mueller-Lyer, 1889; Ponzo illusion: Ponzo, 1928; Zöllner illusion: Zöllner, 1860); see Figure 1. These early illusions often were touted more as curiosities or entertaining by-products of perceptual fallibility rather than important scientific phenomena. However, visual illusions have become a major topic within the perceptual sciences and a subfield of its own among cognitive psychologists. To date, there are well over 1,000 papers on visual illusions documenting their existence and their underlying causal mechanisms within multiple species.

Visual illusions are not merely academic in nature, but they also have strong implications for interactions with the external world, interfering with the perception of one's natural environment. In the mid 1700's, the astronomer Robert Smith outlined naturally occurring illusory phenomena, citing size contrast effects by which animals or objects in a distant valley appear much smaller than their true size or whereby a large, distant city or landmark appears closer than its true distance (Smith, 1739). Similar depth phenomena are deliberately used in traffic control so that people overestimate their speed and subsequently decelerate on the basis of road marking design and misperception (Denton, 1971). Moreover, there are multiple examples of airplane accidents as a result of the misperception of height or distance by pilots (e.g., the fatal plane crash of a Boeing 707 and an Eastern Airlines Lockheed 1049C in 1965; Coren & Girgus, 1978). Some of the oldest uses of illusions in everyday settings involve architectural design (e.g., the Grecian Parthenon which made use of convex and bowed features to enhance its perceived size; Luckiesh, 1922). A more pertinent and perhaps costly byproduct of visual illusions is their

common use in advertising and marketing. The shape of bottles and food packages are often designed so that they appear larger or fuller, influencing market prices and spending trends (e.g., Wansink, 2006). Thus, illusions are not limited to laboratory line drawings but are quite commonplace in the world that we inhabit and even may lead to serious mistakes in perception and behavior, emphasizing the need to understand when, why, and for whom these errors are most likely to occur.

Documenting and describing the shortcomings of any system allows one to understand better the system itself. The study of visual illusions is akin to the study of errors and biases in a heuristics-based system (e.g., Gigerenzer & Goldstein, 1996; Gilovich, Griffin, & Kahneman, 2002). Like the errors that arise from the misapplication of heuristics, illusions can be considered systematic errors that arise from the inappropriate application of some perceptual mechanisms (Robinson, 1972). This same research has referenced visual illusions as test instruments used to uncover the accuracy of the perceptual system from which other cognitive processes are built. Hermann von Helmholtz, a key contributor to the field of perception and vision in the 1800s, argued that the study of visual illusions plays a pivotal role in understanding the cognitive mechanisms underlying perception (e.g., Helmholtz, 1856). The sentiment of investigating perceptual errors to understand better perceptual functioning and visual cognition has since been reflected among many psychologists.

1.1.2.1 Illusions Classified

In the endeavor to understand better visual illusions and their attendant mechanisms, it is useful to organize the countless illusory percepts into general categories. Here, I will focus on the classification system devised by Coren and Girgus (1978) that largely is in agreement with the earliest division of illusions based on the type of figure distortion (Boring, 1942). Four major

classes of visual illusions are identified, including [1] limitations in sensitivity of the receptive organ, [2] direct distortion of stimulus input, [3] systematic perceptual errors, and [4] visual illusions. The first two classes represent actual distortions of visual input via structural errors (e.g., malfunctions within the eye itself) or direct manipulations of physical stimuli (e.g., via magnifying lens). The third class of perceptual errors e.g., brightness contrasts) are widespread across humans and other species, whereas the fourth class of illusions represent an inexplicable discrepancy between perception and reality and may or may not be universal among all humans or across all species (e.g., illusory patterns).

The current work will focus on the fourth class of visual illusions, which are also known as geometric illusions that emerge when a target's perceived physical properties (e.g., size, shape, length, width, diameter, orientation, etc.) are distorted on the basis of the target's surrounding figural context. These are further subdivided according to the nature of the distortion (i.e., distortions of direction or size; see Figure 1). Direction illusions occur when the perceived shape or orientation of a given figure is misperceived (e.g., Zöllner illusion, Poggendorff illusion, Twisted Cord illusion, Kindergarten illusion, etc.). Size illusions occur when line length is distorted (e.g., Opperl-Kundt illusion, Horizontal-Vertical illusion, Mueller-Lyer illusion, Baldwin illusion, Ponzo illusion, etc.) or when area is distorted via the target's interaction with contextual elements (e.g., Ebbinghaus-Titchener illusion, Delboeuf illusion, Jastrow illusion, etc.). The current studies will focus on those illusory phenomena that result in the misperceptions of size (i.e., Ebbinghaus-Titchener illusion, Delboeuf illusion, Baldwin illusion).

1.1.3 Illusions in Animals

Mechanisms that facilitate fast and accurate visual perception would presumably have high ecological validity among visual organisms and would be under strong selective pressure in a range of species (Agrillo, Petrazzini, & Dadda, 2013). Thus, there is a long-standing history within comparative psychology regarding how nonhuman animals whose primary sensory modality is vision perceive and categorize features within their environment. Comparative research in the perceptual domain covers a wide range of topics from early to late visual processes, such as perceptual grouping and segmentation, visual motion and depth perception, and the role of visual attention in perception (see Lazareva et al., 2012, for a review). Importantly, it is not only understanding when the visual system provides an accurate depiction of the external world, but also understanding when perception ‘fails,’ or leads to errors and biases that can reveal critical information on the organization and functioning of vision between species. Thus, the comparative study of visual illusions among nonhuman animals has emerged as an important sub-field within comparative cognition.

Although human studies of visual illusions are vastly more numerous in the field of perception, comparative investigations of illusory phenomena recently have gained momentum and increased in number. Interestingly, my own evaluation of the limited number of book reviews on visual illusions revealed virtually no discussion of animal research, sometimes dismissing the comparative approach altogether on the basis of the difficulty in testing nonverbal subjects (Coren & Girgus, 1978; Gregory, 2009; Luckiesh, 1922; Robinson, 1972). In the earliest review, animal illusions were discussed as a byproduct of the animal itself (i.e., the evolution of camouflage in some species), rather than the actual perception of illusions by animals (Luckiesh, 1922). Subsequently, comparative studies on visual illusions began as a justification for using

animal models to study physiological and structural factors of the visual system, including those that may be critical to illusion formation (Coren & Girgus, 1978). Current research on visual illusions in animals has expanded and now includes a range of species in an attempt to understand better the perception of complex stimuli and illusory phenomena within the organism itself. Comparative evidence of repeated and analogous responses to visual illusions within and between species, including humans, may reveal similarities across visual systems (Wasserman, 2012).

Comparative research, regardless of the topic area, has the challenge of investigating psychological phenomena without the use of verbal reporting. Moreover, perception research tests the subjective experience of an animal's sensory system, which can vary greatly within and between species. One such procedure for understanding the perceptual world of a nonhuman animal (or human) is through the use of psychophysics, which allows comparative psychologists to quantify the sensory experiences of non-verbal animals as they compare to humans or to other nonhuman species (Blough & Blough, 1977). A variety of psychophysical methods are used to establish the perception of the relative sensory quality of stimuli (e.g., larger or smaller, brighter or dimmer, etc.) or absolute detection of stimuli (e.g., presence or absence). An absolute threshold is established by calculating the average point between which a stimulus is no longer detected (0%) and when it is perfectly detected (100%), or by calculating the point of subjective equality (PSE) at which two stimuli are no longer distinguishable in a relative judgment. These psychophysical methods allow for the construction of an animal's subjective experiences that are otherwise inaccessible, including illusory percepts, by generating reports from the animals of what they do (or do not) perceive.

To date, a large number of illusory patterns have been studied among a wide range of animals using psychophysical procedures. Many early studies focused on documentation of visual illusions among avian species, which continue to provide a major contribution to the literature today, including the Ebbinghaus-Titchener illusion (*Columbidae*: Nakamura, Watanabe, & Fujita, 2008; *Gallus gallus*: Ducker, 1966; Rosa Salva, Rugani, Cavazzana, Regolin, Vallortigara, 2013), the Jastrow illusion (*Gallus gallus*: Revesz, 1924), the Mueller-Lyer illusion (*Columbidae*: Malott & Malott, 1970; Malott, Malott, & Pokrzywinski, 1967; Nakamura, Fujita, Ushitani, & Miyata, 2006; Nakamura, Fujita, & Watanabe, 2009; *Psittacus erithacus*: Pepperberg, Vicinay, & Cavanagh, 2008; *Turtur risorius*: Warden & Baar, 1929), the Horizontal-Vertical illusion (*Gallus gallus*: Winslow, 1933), the Ponzo illusion (*Columbidae*: Fujita, Blough & Blough, 1991, 1993) and the Zöllner illusion (*Columbidae*: Watanabe, Nakamura, & Fujita, 2011, 2013; *Gallus gallus*: Ducker, 1966; Watanabe, Nakamura, & Fujita, 2013). Recently, the study of visual illusions also has been expanded to the study of fish to illustrate even further continuity between human perception and distantly related animal species (e.g., Darmaillacq, Dickel, Rahmani, & Shashar, 2011; Sovrano & Bisazza, 2008, 2009; Wyzisk & Neumeier, 2007; see Agrillo et al., 2013, for a review).

Additionally, mammalian species have been tested on a number of visual illusions, including the Horizontal-Vertical illusion (*Cercopithecinae* and *Cebus*: Dominguez, 1954), the Zöllner illusion (*Macaca mulatta*: Agrillo, Parrish, & Beran, 2014; *Papio papio*: Benhar & Samuel, 1982), the Ebbinghaus-Titchener illusion (*Papio papio*: Parron & Fagot, 2007; *Tursiops truncatus*: Murayama, Usui, Takeda, Kato, & Maejima, 2012), the Ponzo illusion (*Equus*: Timney & Keil, 1996; *Macaca mulatta*: Bayne & Davis, 1993; Fujita, 1996; *Pan troglodytes*: Fujita, 1997, 2001), the Mueller-Lyer illusion (*Cebus apella*: Suganuma, Pessoa, Monge-

Fuentes, Castro, & Tavares, 2007), the Duncker illusion (*Macaca mulatta*: Zivotofsky, Goldberg, & Powell, 2005), the Opper-Kundt illusion (*Rattus*: Ducharme, Delorme & Boulard, 1967), the Delboeuf illusion (*Pan troglodytes*: Parrish & Beran, 2014a), the rectangle illusion (*Cercopithecinae* and *Cebus*: Dominquez, 1954; Harris, 1968) and the corridor illusion (*Papio papio*: Barbet & Fagot, 2002; *Pan troglodytes*: Imura, Tomonaga, & Yagi, 2008). Overall, this comparative research reveals similarities of illusory perception across several nonhuman animal species and humans, and also reveals interesting differences that appear to be the byproduct of the species' unique visual systems and important experimental effects.

1.1.3.1 Primate Perception

The vast majority of comparative visual illusion research has been conducted with nonhuman primates, which are the focus of the current work. Nonhuman primates provide a unique and invaluable resource for understanding perceptual processing and visual cognition in humans as they share similar functional and anatomical visual pathways. The reduced reliance on olfactory sensory information with the increased dependence on perceptual processing of visual information represents one of the defining characteristics of the Order Primates, and a critical shift in how monkeys and apes perceived their worlds compared to some other mammals. This shift to predominantly visual sensory input led to a reduction in snout size and stereoscopic vision denoted by large, forward-facing eyes that allowed for accurate depth perception via the overlap of vision from each eye (Strier, 2007). An astute visual system marked by accurate depth perception would have obvious advantages in the evolution of primates as they navigated an arboreal world and fed on small, fast-moving insects (Sussman, 1999).

Anatomically and functionally, the visual systems of human and nonhuman primates are highly congruent, with few major differences in the primary and secondary visual pathways

(Ungerleider & Mishkin, 1982; see Matsuno & Fujita, 2009 for a review). The visual systems of monkeys and humans are similar in the range of their visual field, detection of fine details via visual angle, and retinal sensitivity to fast stimulus changes (e.g., De Valois & De Valois, 1988; Fagot & Deruelle, 1997; Fobes & King, 1982; Weinstein & Grether, 1940; Wilson, Lavallee, Joessee, Hendrickson, Boothe, & Harwerth, 1989). Chimpanzees' visual acuity in response to color and form perception matches with that of Old World monkeys and humans, suggesting strong phylogenetic continuity of the primate visual system (e.g., Essock, 1977; Fobes & King, 1982; Grether, 1941; Matsuno, Kawai, & Matsuzawa, 2004; Matsuzawa, 1990). Thus, nonhuman primate perception provides an exceptional model of human visual cognition, and unsurprisingly, has a longstanding history in comparative psychology (for reviews, see Lazareva, et al., 2012; Roitblat, 1987; Wasserman, 1993).

1.1.3.2 Geometric Illusions in Primates

Nonhuman primates perceive a range of geometric illusions, many in the same direction and to the same extent as humans. Several illusions have received extensive attention in the comparative literature, with efforts to understand better their attendant mechanisms and how they manifest across multiple primate species. One example is the Ponzo illusion, in which identical horizontal lines situated between two converging lines appear unequal in length such that the line closer to the converging apex is perceived as longer than the line further from the apex (see Figure 1H). Fujita and colleagues studied this illusion extensively in pigeons and several primate species, including humans, chimpanzees, and rhesus monkeys, and demonstrated strong continuity in illusion perception across these species (Fujita, 1996, 1997; Fujita, Blough, & Blough, 1991, 1993). Other geometric illusions, including the Zöllner, Horizontal-Vertical, Mueller-Lyer, and corridor illusions are perceived similarly among monkeys and humans,

providing further support for homologous visual pathways among primates (Agrillo et al., 2014; Barbet & Fagot, 2002; Benhar & Samuel, 1982; Dominguez, 1954; Suganuma et al., 2007).

Although these studies provide evidence indicative of continuity in the perception of illusory phenomena across primates, evidence to the contrary also exists. An interesting case includes the comparative study of the well-known Ebbinghaus-Titchener illusion, which is one of the most extensively studied and robust size illusions among human subjects (e.g., Coren & Enns, 1993; Girgus, Coren, & Agdern, 1972; Massaro & Anderson, 1971; Weintraub, 1979). In this illusion and the related Delboeuf illusion, a target circle is embedded within one (Delboeuf) or multiple (Ebbinghaus-Titchener) inducing circles of variable size, which in turn directly impacts the perception of target circle diameter (see Figure 1A and Figure 1D).

Although the Ebbinghaus-Titchener and Delboeuf illusions and their underlying mechanisms are well studied among humans, there is rather limited comparative research regarding the perception of either of these illusory patterns in other primates. In fact, there is only one study of each of these illusions in nonhuman primates, with each study leading to a different pattern of results. The first study on the Ebbinghaus-Titchener illusion indicated that baboons did not perceive the illusion in a human-like fashion (Parron & Fagot, 2007), whereas the second study on the Delboeuf illusion indicated that chimpanzees did perceive the illusion as humans do (Parrish & Beran, 2014a). To muddle the story further, there are three additional comparative studies on the Ebbinghaus-Titchener illusion, including two among avian species that also lead to conflicting results, with domestic chicks perceiving the illusion as humans do (Rosa Salva et al., 2013), but pigeons perceiving an opposite pattern from humans (Nakamura et al., 2008). The third study found positive evidence for the illusion in a human-like fashion in a single bottlenose dolphin (Murayama et al., 2012). The limited number of comparative studies,

and the variability among the results, is striking given the extensive attention to these illusions in the human literature and the similarities between human and animals in other geometric size illusions.

In the current set of studies, I will explore the perception (or lack of perception) of the Ebbinghaus-Titchener and Delboeuf illusions across primates, with a focus on the factors that may lead to differences in illusion emergence. Uncovering similarities in the perception of illusory phenomena among primates has clear advantages and can suggest potential homologies between species. Beyond documentation of similarities in illusion perception, it is also necessary to investigate when and why key differences emerge. In the following sections, I will expand the discussion of the Ebbinghaus-Titchener and Delboeuf illusions, including coverage of their underlying mechanisms. Subsequently, I will consider the potential role of species' unique visual systems and key experimental differences that may lead to differences in reported illusion perception or non-perception. Finally, I will offer a series of experimental studies that will test these specific predictions among a range of primate species.

1.1.4 Ebbinghaus-Titchener Illusion and Delboeuf Illusion

The Delboeuf illusion occurs when the size of two identical target circles are misperceived on the basis of one concentric circle surrounding the target (Delboeuf, 1865). A target circle enclosed in a smaller concentric circle is perceived to be larger than the same-sized target circle enclosed in a larger concentric circle (see Figure 1A). Similarly, the Ebbinghaus-Titchener illusion occurs when the diameter of two identical target circles are misperceived on the basis of multiple inducing circles (Ebbinghaus, 1902; Titchener, 1901). Similar to the Delboeuf illusion, in the Ebbinghaus-Titchener illusion, target circle diameter is overestimated

when embedded within multiple smaller inducing circles and, inversely, target diameter is underestimated when embedded within multiple larger inducing circles (see Figure 1D).

The Ebbinghaus-Titchener and Delboeuf illusions are two of most robust geometric size illusions and have been the focus of an extensive experimental history within the field of human cognition (e.g., Delboeuf illusion: Coren & Girgus, 1978; Delboeuf, 1865; Nicolas, 1995; Oyama, 1960; Van Ittersum & Wansink, 2012; Ward & Lockhead, 1970, 1971; Ebbinghaus-Titchener illusion: Aglioti, De Souza, & Goodale, 1995; Coren & Enns, 1993; Choplin & Medin, 1999; Ebbinghaus, 1902; Girgus et al., 1972; Massaro & Anderson, 1971; Titchener, 1901; Weintraub, 1979). In addition to the extensive literature on adult subjects, both illusions spontaneously emerge in young children and infants (e.g., Kaldy & Kovacs, 2003; Piaget, Lamercier, Boesch, & von Albertini, 1942; Weintraub, 1979; Weintraub & Cooper, 1972; Yamazaki, Otsuka, Kanazawa, & Yamaguchi, 2010; Zanuttini, 1996). Beyond just demonstrating the existence of these illusions, much work has been done to document and describe the mechanisms that produce these illusions (e.g., Girgus et al., 1972; Morinaga & Noguchi, 1966; Weintraub, 1979).

1.1.4.1 Pool-and-Store Theory: Contrast and Assimilation

The Ebbinghaus-Titchener and Delboeuf illusions are often explained in light of the Pool-and-Store Model that incorporates the cognitive mechanisms of contrast and assimilation (Coren & Girgus, 1978; Goto, Uchiyama, Imai, Takahashi, Hanari, Nakamura, & Kobari, 2007; Jaeger & Lorden, 1980; Nicolas, 1995; Oyama, 1960; Roberts, Harris, & Yates, 2005; Ward & Lockhead, 1970, 1971). For these size illusions, there is a direct relationship between illusion magnitude and the ability to group or simultaneously process elements within the array (Parron & Fagot, 2007; Roberts et al., 2005). The distance between target and inducing circle(s) directly

impacts processing such that closer elements (i.e., higher density, lower inter-elemental distance between target and inducers) leads to a stronger illusion (Martin, 1979; Roberts, et al., 2005).

Contrast and assimilation can account for the relationship between illusion magnitude and array density. When the target and inducing circle(s) are similar in size and/or are proximally positioned, they are pooled in the visual system as one entity (Morinaga, 1956). The gap between the inner and outer circles is relatively small, leading the perceiver holistically to pool these individual elements (Girgus & Coren, 1982). This phenomenon, also known as *assimilation*, results in the overestimation of inner target size relative to an identical target. Contrary to this, when the gap between the inner and outer circles is relatively large and thus the circles are dissimilar in size and/or distally positioned, the actual difference between the two elements is exaggerated and they are perceived as distinct entities (Weintraub, Wilson, Greene, & Palmquist, 1969). This phenomenon is known as *contrast*, which creates the illusion that the inner target is smaller than it actually is, resulting in the underestimation of size relative to an identical target (Pollack, 1964). Although there is some variation in the effects of contrast and assimilation (Nicolas, 1995), there is an optimal ratio at which each effect can be predicted to occur (also known as Morinaga's Optimum Ratio; Morinaga, 1956; Oyama, 1960). Contrast, or underestimation of the target circle, is most likely to occur when the ratio between circles equals 0.33 (Ogasawara, 1952). Assimilation, or the overestimation of target diameter, is most likely to occur at a ratio of 0.67 (Piaget et al., 1942).

Furthermore, the extent to which the stimuli in a given set (both target and inducers) can be seen together in one glance or fixation (i.e., visual extent) predicts whether assimilation or contrast will occur (Coren & Girgus, 1978). If multiple visual glances are required to perceive all elements in an array (as is predicted by their proximity or the overall size of the array), contrast

is likely to occur as each entity is held as a separate percept and their differences are accentuated. Conversely, if the entire array (both target and inducers) is seen in one glance as is facilitated by close proximity, assimilation occurs in which the differences between elements is reduced and they are perceived as one entity.

Interestingly, the emergence and magnitude of the Ebbinghaus-Titchener and Delboeuf illusions are sensitive to experimental manipulations of stimuli properties. Specifically, the effects of contrast and assimilation are reduced when target and inducer features are altered so that one increases in salience over the other (e.g., Oyama, 1960; Rabin & Adams, 1993; Weintraub & Schneck, 1986). For example, in the Ebbinghaus-Titchener illusion, reducing the brightness, and subsequent salience, of the inducing circles decreases the illusion magnitude (Oyama, 1962; Weintraub & Cooper, 1972). A similar diminished effect is seen in the Delboeuf illusion by decreasing the brightness of the inducing circle (Weintraub et al., 1969). Moreover, increasing the number, and subsequent salience, of inducing circles increases the magnitude of the Ebbinghaus-Titchener illusion (Massaro & Anderson, 1970; Oyama, 1960). Along with increasing the salience of either the target or inducer, increasing their differences also impacts illusion emergence. For example, using incongruent shapes for the target and inducing stimuli decreased the strength of the Ebbinghaus-Titchener illusion, whereas using congruent shapes increased the illusion (e.g., Coren & Enns, 1993; Coren & Miller, 1974). These results taken together imply that highlighting the differences between target and inducer reduces the likelihood that the elements will be grouped together, thus reducing the likelihood for illusion emergence.

These results in combination with studies on the underlying mechanisms for the Ebbinghaus-Titchener and Delboeuf illusions suggest a critical interplay between individual

elements within an array. If target and inducer(s) are close enough in space to one another, they are pooled together leading to the overestimation of target size. Conversely, if target and inducer(s) are distant enough from one another, contrast occurs leading to the underestimation of target size. If either element (target or inducers) is emphasized, the typical illusory pattern is disrupted. Specifically, highlighting the target under judgment decreases illusion magnitude and increases accuracy, whereas highlighting the illusory inducing elements increases illusion magnitude.

1.1.4.2 Comparative Evidence for the Delboeuf Illusion

Despite the extensive research on the Ebbinghaus-Titchener and Delboeuf illusions among humans, there has been relatively limited comparative research on these patterns among nonhuman animals. To date, there is only one nonhuman animal study on the Delboeuf illusion, in chimpanzees (Parrish & Beran, 2014a). This work was motivated by the human consumption literature, in which food portion estimation and intake is directly related to the misperception of quantity as a function of dish size. Van Ittersum and Wansink (2012) reported an experimental analysis of the Delboeuf illusion in humans as it manifested in a food quantity judgment and serving task. People judged identical food portions to be larger when plated on a small dish and smaller when plated on a large dish. Moreover, subjects over-served onto (and over-consumed from) large plates but under-served onto (and under-consumed from) small plates. These findings were replicated with chimpanzees; although the apes were highly accurate in relative quantity judgments when different food portions were displayed on identically sized plates, the chimpanzees judged identical or even smaller food portions to be larger if they were plated on a small dish than an identical or larger portion of food on a large dish (Parrish & Beran, 2014a).

These results are explained in light of the Delboeuf illusion such that the size of the target circle (food portion) was misperceived on the basis of the surrounding context (plate). In these cases, assimilation can be explained by the fact that the gap between the plate edge and the food was relatively small, and thus the difference between the two was minimized, and potentially perceived as one entity. Contrary to this, large plates led to the underestimation and overconsumption of food because the gap between the plate edge and food was larger, leading to a contrast effect in which the difference between the two entities was exaggerated. These results suggest continuity in the perception of the Delboeuf illusion between chimpanzees and humans.

1.1.4.3 Comparative Evidence for the Ebbinghaus-Titchener Illusion

Similar to the Delboeuf illusion, there is rather limited comparative research on the Ebbinghaus-Titchener illusion. Thus far, four nonhuman animal species have been tested on the Ebbinghaus-Titchener illusion: baboons, dolphins, pigeons, and chicks. Interestingly, the only positive evidence of a human-like illusory pattern is from a dolphin and four-day-old domestic chicks (Murayama et al., 2012; Rosa Salva et al., 2013). Baboons apparently do not perceive the illusion, accurately judging target circle size without being influenced by surrounding inducers (Parron & Fagot, 2007), and a reversed illusion from the typical human pattern was found among pigeons in which small (or large) inducers resulted in the underestimation (or overestimation) of target size (Nakamura et al., 2008).

The null and negative effects among baboons and pigeons led the authors to suggest that perhaps the neural substrate necessary for perceiving the illusion was lacking among avian species and Old World monkeys, evolving late in the primate lineage (see Parron & Fagot, 2007). However, the recent evidence in domestic chicks and the dolphin challenges this hypothesis. The chick and dolphin data may suggest analogous visual pathways in which the

necessary neural substrate for perceiving this illusion would have evolved independently in these phylogenetically distant species (see Rosa Salva et al., 2013). Instead, perhaps these contradictory findings illustrate a more complicated picture in which variable results are a byproduct of differences among the experimental paradigms (e.g., in training procedures or stimuli used). The null results found in baboons for the Ebbinghaus-Titchener illusion are also interesting given our recent positive evidence for the Delboeuf illusion among chimpanzees (Parrish & Beran, 2014a). The perception of the very similar Delboeuf illusion, but not the Ebbinghaus-Titchener illusion, within closely related primate species warrants additional research.

1.1.5 Comparative Variance Explored

The evident variability in the perception of these two closely related illusions is suggestive of differences among species' visual cognition. This variance also may be a byproduct of experimental design, or perhaps an important combination of the two. Here, I argue that the mixed results are motivated by the interplay of the species' biology (e.g., their unique visual systems) and, importantly, the experimental paradigm used (e.g., training procedure and stimuli design). Human research has demonstrated that differential attention (via instructional or design cues) to target and inducing elements within an array can lead to critical differences in illusion direction and magnitude (e.g., Massaro & Anderson, 1970; Oyama, 1960, 1962; Weintraub & Cooper, 1972; Weintraub & Schneck, 1986). Moreover, visual processing mode plays a key role in grouping mechanisms and the temporal focus of perception between the entire array and the individual elements within the array, further impacting illusion emergence. I will introduce each of these components separately and then discuss how they may converge to

explain the variability within the comparative literature regarding the Ebbinghaus-Titchener and Delboeuf illusions.

1.1.5.1 Variance Explained via Experimental Paradigm

Geometric illusions emerge as a result of the interaction between figural elements within an array, including the target stimulus and the inducing context. The target's parameter of interest (e.g., size, direction, distance, etc.) may be misperceived on the basis of other components within the array, giving rise to the illusory percept. A large amount of evidence suggests that differential attention to these various elements (target or context) leads to differences in the perception and magnitude of many geometric illusions. Furthermore, differential attention may lead to the complete elimination or even reversal of some illusory phenomena.

A number of early studies on human perception of visual illusions demonstrated that verbal instructions to ignore the illusory inducing context and focus on the parameter of interest or target stimulus led to a decrease in illusion perception. Bates (1923) demonstrated an elimination and even reversal of the Mueller-Lyer illusion after he instructed subjects to focus on the target (horizontal line) and ignore the illusory-inducing stimuli (fins). A similar effect was found with the Delboeuf circles; the illusion was greatly reduced and even eliminated for some subjects after they were instructed to ignore the concentric circle and focus on the target circle (Restle, 1971). Similar results were noted in the absence of direct instruction; Gardner and Long (1961) found a decrease in the magnitude of the Mueller-Lyer illusion if subjects simply concentrated on the target stimulus.

Beyond verbal instruction, the magnitude and direction of several illusions are impacted via simple element manipulation. Manipulating stimuli brightness (via contrast), color, and

distance effectively influences illusion perception. Several investigators have documented that focused attention on the target via contrast or color manipulation led to a decrease in illusion magnitude and direction, whereas increased attention to the context led to an increase in illusion magnitude (e.g., Kindergarten illusion: Lipps, 1897; Muensterberg, 1897; Mueller-Lyer: Coren & Girgus, 1972; Dewar, 1967; Ebert & Pollack, 1972, 1973; Pollack & Chaplin, 1964; Delboeuf illusion: Oyama, 1962; Weintraub & Cooper, 1972; Weintraub et al., 1969). In several studies, the magnitude of the Ebbinghaus-Titchener illusion decreased if one isolated the target circle by increasing the distance between the target and inducers (Girgus et al., 1972; Martin, 1979; Morinaga & Noguchi, 1966; Weintraub, 1979). Alternatively, illusion magnitude increased if one focused on the inducing circles by increasing the number (and subsequent density) of inducers (Girgus et al., 1972; Massaro & Anderson, 1971; Morinaga, 1956; Yamazaki et al., 2010). Overall, then, illusion magnitude and direction decreases when the target stimulus is focused upon and, conversely, illusion magnitude increases when the surrounding context or illusory-inducing elements are the focus.

1.1.5.2 Variance Explained via Visual Processing Mode

In addition to experimental manipulation, the visual processing mode of multi-component figures (not limited to illusory figures) also influences the perception and grouping of separate components within a visual array. The perception of complex figures (i.e., those comprised of multiple elements) is hierarchically organized such that figures are processed at the overall group level and at the individual element level. Depending upon the temporal development or order of processing, a precedence effect emerges in which the group configuration (global precedence) or the individual elements (local precedence) are first processed. For humans, a robust global precedence emerges in which the overall configuration is first processed, followed by the

individual elements that comprise the object (e.g., Broadbent, 1977; Kimchi, 1992; Lamb & Robertson, 1988; Navon, 1977, 1981). This global-to-local perception of objects is facilitated by perceptual principles, such as the Gestalt laws by which certain properties of the figure (e.g., similarity, proximity, etc.) enhance the grouping of individual elements into a cohesive object (Koffka, 1935; Wertheimer, 1923). Conversely, a local precedence emerges if an organism first processes the individual elements prior to the overall configuration.

Despite evidence of a rather robust global precedence among humans, comparative evidence among nonhuman primates is much less consistent (see Matsuno & Fujita, 2009, and Fagot, Barbet, & Parron, 2012, for reviews). Fagot and colleagues' initial work on perceptual grouping by baboons (*Papio papio*) replicated the experimental studies from the classic Navon (1977) human research. These studies demonstrated multiple lines of evidence for a local precedence among baboons in which monkeys first attended to local elements prior to the overall group configuration (Deruelle & Fagot, 1997, 1998; Fagot & Deruelle, 1997; Fagot, Tomonaga, & Deruelle, 2001; Parron & Fagot, 2007). A local-to-global processing mode has since been documented among other primates including rhesus macaques (Hopkins & Washburn, 2002), capuchin monkeys (De Lillo, Spinozzi, Truppa, & Naylor, 2005; Spinozzi, De Lillo, & Salvi, 2006; Spinozzi, De Lillo, & Truppa, 2003), and some chimpanzees (Fagot & Tomonaga, 1999; Matsuno & Tomonaga, 2007). However, these results are not ubiquitous, as some primates demonstrate a human-like global precedence effect, including cotton-top tamarins (Neiworth, Gleichman, Olinick, & Lamp, 2006), macaques (Tanaka & Fujita, 2000; Tanaka, Onoe, Tsukada, & Fujita, 2001), and chimpanzees (Fagot & Tomonaga, 1999; Fujita & Matsuzawa, 1990; Hopkins, 1997; Hopkins & Washburn, 2002; Matsuno & Tomonaga, 2007; Matsuzawa, 1989; Tomonaga & Matsuzawa, 1992).

Precedence effects are subject to variability depending upon array presentation and design, and thus procedural differences may help explain the conflicting results. Considering first the evidence from human studies, processing mode is dependent upon the nature of the stimuli such that differential attention towards elements within an array can shift a global precedence to a local precedence (e.g., Grice, Canham, & Boroughs, 1983; Kinchla & Wolfe, 1979; Lamb & Robertson, 1988; Martin, 1979; Navon, 1981; Pomerantz & Sager, 1975; see Kimchi, 1992, for a review). Consistent with the literature from humans, several aspects of experimental design including stimulus properties and training procedures may explain the differences seen among nonhuman primate studies. Several comparative studies have specifically manipulated stimuli density by grouping individual elements closer in proximity or connecting these elements with small lines. Despite these experimental manipulations, a local precedence still emerged among baboons (Deruelle & Fagot, 1998; Fagot & Deruelle, 1997) and capuchin monkeys (Spinozzi et al., 2006). However, this hypothesis has been used to explain the positive evidence of a global precedence among nonhuman primates. For example, cotton-top tamarin monkeys are the only New World monkey species to thus far demonstrate a global precedence and this effect disappeared with the introduction of sparse stimuli (Neiworth et al., 2006). Moreover, Fagot and colleagues have argued that the global processing mode evident among several chimpanzee studies, including their own, is directly linked to higher stimuli density within the presented arrays (Fagot et al., 2012).

1.1.5.3 Precedence Effects and Visual Illusions

Pertinent to the current studies, processing mode may directly impact the emergence of visual illusions, and specifically of geometric illusions comprised of hierarchical, embedded stimuli. By definition, a global precedence favors the simultaneous evaluation of all elements as

a cohesive whole, or initial processing of the group configuration and secondary processing of elemental details. A local precedence favors the initial separate evaluation of the parts or elements of a hierarchical stimulus with a primary focus on the local details prior to overall group processing. The perception of visual illusions, which is dependent upon the interaction between elements within an array, is likely influenced by the mode of visual processing and the stage at which a given species perceptually groups multiple elements into a holistic configuration.

Experimental evidence from the human literature supports this link between visual processing mode and the emergence of visual illusions. Specifically, the global impression theory suggests that a global assessment of target and inducing stimuli leads to higher rates and magnitudes of geometric illusions (Coren & Girgus, 1978). Data from split-brain patients demonstrates that the right cerebral hemisphere is spatially oriented and more global in nature, whereas the left cerebral hemisphere is verbally oriented and more linear or local in nature (e.g., Bogen, 1969; Kimura, 1966, 1973; Levy-Agresti & Sperry, 1968; Ornstein, 1972). Based on this information, certain patterns of visual illusions should be more apparent when processed in the right hemisphere than the left hemisphere. Experimental data support this hypothesis. For example, the magnitude of the Mueller-Lyer illusion increased when stimuli were presented to the right hemisphere in comparison to when presented to the left hemisphere (Clem & Pollack, 1975; see Figure 1F).

Moreover, earlier research demonstrated individual differences in ‘processing style’ such that some humans have a stronger global precedence than others. For these subjects, the magnitude of certain illusions was increased above and beyond the magnitude for those subjects with weaker global processing (e.g., Berry, 1966, 1968, 1971; Dawson, 1967; Witkin, 1967). A

similar effect of reduced illusory perception was found among children with autism who adopt a more locally-oriented processing mode than typically-developing children and adults (Dakin & Frith, 2005; Happé, 1996; Happé, Briskman, & Frith, 2001; but see Ropar & Mitchell, 1999). Additionally, a reduced bias towards the Ebbinghaus-Titchener illusion was documented in the Himba tribe, who also demonstrate a more pronounced locally-oriented precedence effect than typically-developing Westerners (de Fockert, Davidoff, Fagot, Parron, & Goldstein, 2007). One possible explanation is that the Himba people are seminomadic cattle herders from a remote area of Namibia who track the identity of individual cattle, placing a premium on attention to local details (de Fockert et al, 2007).

Clearly, processing mode directly impacts the perception of certain visual illusions among human subjects, and specifically the illusions that require the simultaneous processing of multiple elements within an array. However, the interaction between processing mode and visual illusions has received much less attention in comparative research. Next, I explore the interaction between species-unique processing mode and experimental design, and their joint influence on illusion perception. Specifically, I argue that species with a local precedence (or a less robust global precedence) may be less susceptible to perceiving geometric illusions. However, enhancing attention towards specific elements within an array (i.e., inducers) may increase likelihood of illusion emergence for all species. Thus, a species-unique perceptual style along with experimental manipulations that favor global or local processing of array elements should impact the emergence of illusory patterns.

1.1.5.4 Experimental Design and Processing Mode Jointly Impact Illusion Emergence

Visual illusions are dependent upon the simultaneous processing of multiple elements within an array, including target and inducing context stimuli (Roberts et al., 2005). Disruptions

to the simultaneous processing of or interaction between elements within an array would negatively impact the likelihood of illusion emergence. I have now discussed two separate components that influence the holistic processing of a visual array: experimental design and visual mode of processing. It is possible that these very factors led to the conflicting findings among nonhuman animal species for the Ebbinghaus-Titchener and Delboeuf illusions in the comparative literature.

Several key differences exist among the comparative studies for these two size illusions, including disparities among training procedures, reinforcement contingencies, and stimulus properties, all of which could impact the critical simultaneous processing of elements within an array (Murayama et al., 2012; Nakamura et al., 2008; Parrish & Beran, 2014a; Parron & Fagot, 2007; Rosa Salva et al., 2013). The training procedures utilized for both pigeons and baboons may have favored enhanced focusing of the target stimulus devoid of the illusory inducing context or stimuli. For example, Parron and Fagot (2007) presented different colored target and inducer circles, a manipulation which was aimed to promote attention to the bright yellow central target over the inducing circles. Furthermore, Nakamura and colleagues (2008) first trained pigeons to classify a series of target circles as large or small based on their diameters. Once they accurately and consistently classified targets into these two categories, six inducer circles were gradually faded in (from light to dark) to maintain accurate target discrimination. Thus, the pigeons were trained to effectively ignore inducing circles and selectively attend to target diameter. In addition, the pigeons were required continually to peck at the sample target circle in order to produce two choice keys representing the large and small classifications. Increasing the salience of, and subsequent attention towards, the target stimulus of the Ebbinghaus-Titchener and Delboeuf illusions has been known to reduce illusion magnitude and even the direction of

the illusion in human subjects (e.g., Coren & Girgus, 1972; Oyama, 1962; Weintraub & Cooper, 1972; Weintraub, et al., 1969). The enhanced attention towards the target stimulus in both Nakamura et al. (2008) and Parron and Fagot (2007) may have contributed to the lack of illusory percept formation.

Using a different approach, Rosa Salva et al. (2013) found positive evidence of the Ebbinghaus-Titchener illusion among four-day-old domestic chicks. There were several experimental differences between this design and the two previous animal studies. Most notably, the inducing circles were present throughout the training procedure, making them a relevant component of the array throughout the entire study. Similarly, Murayama et al. (2012) presented a relative size discrimination task to a dolphin subject who was trained to select the larger of two target dots surrounded by inducing circles. Critically, this study also featured the target and inducing stimuli during both training and testing. This key design feature of including the entire array throughout the entire study (including training and test trials) would support the necessary simultaneous processing of the full array, rather than presenting the inducers in a manner that reduces their salience or enhances attention towards the target. To further illustrate this point, the single study of the Delboeuf illusion with chimpanzees demonstrated a human-like perception of the illusion and, critically, presented both the target and inducing circle throughout the entire study rather than enhancing the salience of or attention towards one component of the array (Parrish & Beran, 2014a).

In conjunction with perceptual processing mode, precedence effects may further impact experimental procedures that favor the enhancement of local elements. Rosa Salva et al. (2013) argued that the procedures used with pigeons and baboons, both of which are known to display a robust local precedence (e.g., baboons: Deruelle & Fagot, 1998; Fagot & Deruelle, 1997; e.g.,

pigeons: Cavoto & Cook, 2001), may have worked in conjunction with their locally-oriented perception to jointly enhance attention toward the individual elements, rather than processing the overall global configuration. Training species with a local precedence further to isolate individual features within an array via experimental procedures and ignore the illusory-inducing context would effectively reduce (and perhaps reverse) the necessary holistic processing of individual elements, and potentially the illusory effect itself. Alternatively, dolphins, like humans, display a global precedence when perceiving objects through vision and echolocation, and also demonstrated perception of the illusion in a human-like fashion (Murayama et al., 2012; Pack, Herman, Hoffmann-Kuhnt, & Branstetter, 2002).

The key relationship between processing mode and illusion perception can be applied in nonhuman animal research where there is even greater variability within species-unique perceptual styles. Specifically, nonhuman primates provide a valuable resource to comparative research because of their close phylogenetic relatedness with humans and strong similarities in visual cognition (see Lazareva, et al., 2012; Roitblat, 1987; Wasserman, 1993 for reviews). Critically for my purposes, however, nonhuman primates also demonstrate key differences in processing mode, with some species demonstrating a more robust global precedence (like humans), and others demonstrating a rather robust local precedence. The selected species for the current work differ in their mode of perceptual processing: humans display a robust global precedence (e.g., Navon, 1977, 1981), chimpanzees display a global precedence, but this effect is subject to change depending upon experimental design (Fujita & Matsuzawa, 1990; Hopkins, 1997; Hopkins & Washburn, 2002; Matsuzawa, 1989; Tomonaga & Matsuzawa, 1992), and rhesus monkeys and capuchin monkeys display a local precedence (De Lillo et al., 2005; Hopkins & Washburn, 2002; Spinozzi, et al., 2003, 2006). Thus, these primates provide an

invaluable resource in the comparative study of visual illusions and a unique opportunity to explore the relationship between processing mode, experimental design, and the perception of visual illusions.

1.2 Current Aims

I propose a series of studies that will be used to investigate the emergence of illusory phenomena among four primate species, including humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), rhesus macaques (*Macaca mulatta*), and capuchin monkeys (*Cebus apella*). The ultimate goal is to compare and contrast the emergence of geometric size illusions among these primate species with the prediction that both experimental design and species' unique perceptual styles will influence perception and performance. To confirm that capuchin monkeys and rhesus monkeys are local processors, I will first assess their processing modes using a pre-established paradigm used to measure precedence effects within computer-trained nonhuman primates. Next, I will investigate the Delboeuf (Study 1) and Ebbinghaus-Titchener (Study 2) size illusions in these four primate species, using a psychophysical two-choice discrimination task. Despite species' differences in visual processing mode, I will employ an experimental procedure that emphasizes holistic processing of the entire array to provide the best possible chance for illusory percept formation across all species. Thus, the obtained results may differ from other comparative studies that intentionally directed attention towards local features within the illusory array (e.g., Nakamura et al., 2008; Parron & Fagot, 2007, but see Murayama et al., 2012 and Rosa Salva et al., 2013).

Furthermore, I will investigate how these and other geometric size illusions may be attenuated or eliminated via differential attention to separate elements with the perceptual array. Study 3 introduces a third geometric size illusion (the Baldwin illusion) within a concurrent-task

paradigm that allows for the modulation of attention across the visual array (exclusively towards the target or inducing elements). Finally, I will explore the relationship between visual illusions and decisional biases in a food-choice task with human children. Study 4 will extend the investigation of visual illusion perception into the domain of real-world, decisional biases.

1.3 Predictions

I had three over-arching hypotheses for this line of research. My first hypothesis was that illusion perception would be influenced by the species' unique perceptual styles. Because holistic processing of the entire visual array (i.e., simultaneous perception of both the target and inducing elements) is critical to the emergence of visual illusions, I predicted that the species with a more globally-oriented processing style (i.e., humans and apes) would be more likely to perceive these geometric illusions, whereas the species with a more locally-oriented processing style (i.e., monkeys) would be less likely to perceive the illusions.

My second hypothesis was that attention would influence performance and illusion perception throughout these studies. Differential attention towards individual elements within a visual array may disrupt the necessary holistic processing of the entire array that is key for illusion perception. Aside from being of theoretical importance in helping us understand how these biases emerge, this is of practical importance because previous studies have varied in how training and experimental procedures drew attention to various features within the illusory array. Apparent species differences may be due to these procedural variations. Thus, I predicted that paradigms that minimize enhanced attention towards separate features within the task would promote perception of the illusions (e.g., Studies 1 and 2), whereas paradigms that disrupted holistic processing of the visual array would reduce illusion perception (e.g., Study 3), irrespective of the species being tested. My final hypothesis was that illusory biases would

translate from perception of 2-dimensional visual illusions to 3-dimensional decisional biases, such as food choice behavior (e.g., Study 4). I predicted that decisional biases would manifest in accordance with perception of visual illusions using psychophysical measures.

1.4 References

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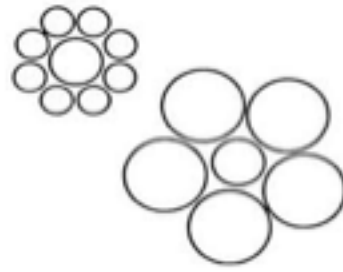
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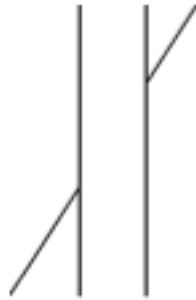
1.5 Figures



A. Delboeuf illusion



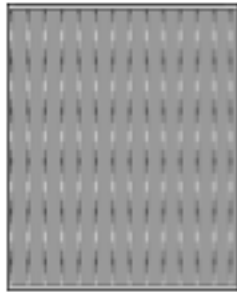
D. Ebbinghaus-Titchener illusion



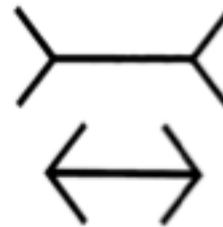
B. Poggendorff illusion



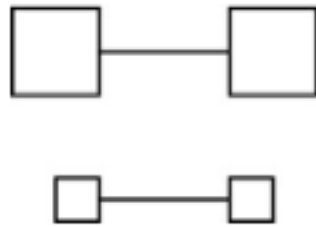
E. Horizontal-Vertical illusion



C. Twisted Cord illusion



F. Mueller-Lyer illusion



G. Baldwin illusion



J. Zöllner illusion



H. Ponzo illusion



K. Jastrow illusion



I. Oppel-Kundt illusion

Figure 1. Geometric illusions, including the (A) Delboeuf illusion, (B) Poggendorff illusion, (C) Twisted Cord illusion, (D) Ebbinghaus-Titchener illusion, (E) Horizontal-Vertical illusion, (F) Mueller-Lyer illusion, (G) Baldwin illusion, (H) Ponzo illusion, (I) Oppel-Kundt illusion, (J) Zöllner illusion, and (K) Jastrow illusion.

PERCEIVING COMPLEXITY:
PERCEPTUAL PROCESSING MODE IN MONKEYS

By

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ABSTRACT

Perceptual processing mode is the order in which hierarchical, complex visual stimuli are perceived. Human adults typically display a global precedence in which they perceive the larger, global configuration prior to the individual elements that comprise the figure. Interestingly, a variety of nonhuman species perceive complex visual arrays in the opposite manner from that described here. A local precedence emerges when individual elements are perceived prior to the larger configuration. Here, we tested the processing mode of rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*) using a delayed match-to-sample task that presented hierarchical compound stimuli in which the larger, global configuration was comprised of smaller elements. The global configuration (e.g., large letter 'E') either matched (e.g., small

letter 'E's) or differed (e.g., small letter 'F's) from the local elements from which it was comprised. The matching-to-sample task's response set contained an identical match to the sample or a foil that differed in its global pattern, its local elements, or both its global and local features. Both species of monkeys displayed a local precedence, showing significantly higher performance rates when stimuli matched on their local elements in comparison to when only their global features matched. These results are consistent with previous findings documenting a local processing style among monkeys.

INDEX WORDS: Perceptual Processing Mode; Precedence Effects; Local Processing; Capuchin monkeys; Rhesus monkeys; Perception

2 PERCEIVING COMPLEXITY: PERCEPTUAL PROCESSING MODE IN MONKEYS

Prior to the formal studies of this dissertation, I first assessed the perceptual mode of processing within capuchin monkeys and rhesus monkeys using a paradigm adapted from Hopkins and Washburn (2002). Hopkins and Washburn used a matching-to-sample procedure that presented a hierarchical compound stimulus in which the larger, global configuration was comprised of smaller elements. The global configuration either matched or differed from the local elements from which it was comprised. For example, a letter “F” could be comprised of multiple smaller “F”s or could be comprised of multiple smaller “E”s. The matching-to-sample task’s response set contained an identical match to the sample or a foil that differed in its global pattern, its local elements, or both its global and local features. Hopkins and Washburn reported that rhesus monkeys and chimpanzees discriminated stimuli using their global and local features, but chimpanzees demonstrated a global precedence (i.e., they showed higher performance rates and faster response times using global features in comparison to local elements), whereas rhesus monkeys demonstrated a local precedence.

In the current study, I presented the same matching-to-sample paradigm used by Hopkins and Washburn (2002) as it represents one traditional approach to assessing processing modes using computerized testing with primate species. My first objective was to confirm that rhesus monkeys and capuchin monkeys included in the current set of studies also demonstrated a local-to-global precedence as previously reported in the literature (*Cebus apella*: De Lillo, Spinozzi, Truppa, & Naylor, 2005; Spinozzi, De Lillo, & Salvi, 2006; Spinozzi, De Lillo, & Truppa, 2003; *Macaca mulatta*: Hopkins & Washburn, 2002). These results would be informative to

understanding potential species differences across primates in geometric illusion perception as investigated throughout this dissertation.

2.1 Methods

2.1.1 Subjects

The nonhuman primates included in the current study were housed and tested at the Language Research Center (LRC) of Georgia State University (GSU) in Atlanta, Georgia. LRC primates were never food or water deprived for testing purposes and had 24-hour access to water, including during testing. They received a daily diet of fruits, vegetables, and primate chow regardless of participation in testing, and daily caloric intake was kept consistent by taking into account the amount of food earned from testing. All testing protocols complied with guidelines for working with nonhuman primates as approved by the GSU Institutional Animal Care and Use Committee. GSU is fully approved by the Association for Assessment and Accreditation of Laboratory Animal Care.

Four male rhesus macaques (11 – 21 years of age) and eight capuchin monkeys (five females; 6 – 17 years of age) were included in the current study. Rhesus macaques were singly housed with 24-hour access to their computerized apparatus. Macaques had constant visual and auditory access to conspecifics and received weekly access to an indoor-outdoor enclosure with another monkey. Capuchin monkeys were socially housed and voluntarily separated into individual test boxes for computer testing. Monkeys worked on the current experiment for 4 hour (capuchin monkeys) or 8 hour (rhesus monkeys) test sessions during which time the monkeys worked or rested as they chose.

2.1.2 Apparatus

Monkeys were tested using the Language Research Center's Computerized Test System that includes a color monitor, personal computer, digital joystick, and food pellet dispenser (Evans, Beran, Chan, Klein, & Menzel, 2008; Richardson, Washburn, Hopkins, Savage-Rumbaugh, & Rumbaugh, 1990). Primates manipulated the joystick with their hands to isomorphically control a small round cursor on the computer screen. Correct responses led to banana-flavored pellet rewards (45-mg pellets for capuchin monkeys and 94-mg pellets for rhesus monkeys: Bio-Serv, Frenchtown, NJ) via a pellet dispenser interfaced to the computer through a digital I/O board (PDISO8A; Keithley Instruments, Cleveland, OH). Task programs were written in Visual Basic 6.0. All monkeys were computer trained and had participated in a number of perceptual experiments prior to the current study (e.g., Agrillo, Parrish, & Beran, 2014; Beran & Parrish, 2013).

2.1.3 Stimuli

Stimuli were hierarchically structured with multiple smaller (local) elements comprising the larger (global) pattern. Library 1 (EF) contained letters E and F, Library 2 (HL) contained letters H and L, and Library 3 (CS) contained circles and squares. For Library 1 and Library 2, large stimuli measured 5.5 cm x 9 cm and small stimuli measured 0.5 cm x 1 cm with an inter-elemental distance of 0.5 cm. For Library 3, large stimuli measured 4.5 cm x 6.5 cm and small stimuli measured 1 cm x 1 cm with an inter-elemental distance of 0.5 cm.

All stimuli were black on a white computer background. Figure 1 depicts the three libraries used in the current study. For each library, stimuli either differed based on their local elements, their global pattern, or both their local and global features. For all libraries, stimuli pairs [1 and 3] and [2 and 4] differed based on local elements. Stimuli pairs [1 and 2] and [3 and

4] differed based on global pattern. Stimuli 1 and 4 and 2 and 3 differed based on both their local and global features.

2.1.4 Procedure

Subjects completed a matching-to-sample task in which a sample stimulus was randomly drawn from one of the three libraries. Subjects first made contact with a “start” box and then touched the sample stimulus using their joystick-controlled cursor, following which two comparison stimuli were presented. One comparison stimulus matched the sample and the other comparison stimulus (the foil) was randomly drawn from the same library. The sample was centrally located in the top half of the computer screen. Comparison stimuli were presented equidistance to the right and left of the sample in the bottom half of the screen. Location (right or left) of the matching stimulus and the foil was randomized across trials.

Three conditions were presented: the foil could differ from the sample in its local elements (Local condition), its global pattern (Global condition), or in both its local *and* global features (Both condition). In training and testing, conditions were randomly presented in equal proportions. Contacting the identical matching stimulus on a trial led to feedback in the form of a positive auditory tone and one pellet reward. Contacting the foil led to a buzz tone and a 20 second timeout period during which the screen remained blank. The inter-trial interval was 1 second, following which the “start” box reappeared in the center of the screen.

2.1.4.1 Training

Monkeys were trained using a simultaneous matching-to-sample procedure in which the sample remained on the screen during selection of the match or the foil by the subject. This allowed the animals to learn the rules of the task. Half of the monkeys were trained on Library 1 (EF) and half of the monkeys were trained on Library 2 (HL). Criterion was set to 70% accuracy

on the most recent 50 trials for *each* condition: Local, Global, and Both. Once criterion was met, all subjects completed a generalization phase using the opposite library from the one that they used in training. For example, if a subject was trained on Library 1 (EF), they completed generalization using Library 2 (HL) and vice versa. In the generalization phase, subjects completed 50 trials of each condition (Local, Global, and Both) in random order with the given library.

2.1.4.2 Testing

In the test phase, all procedures were identical to those described above, except that the monkeys were tested using a sequential matching-to-sample procedure in which the sample was removed from the screen after subjects made contact with the stimulus. The sample was not present during selection of the match stimulus or foil stimulus.

All monkeys completed a minimum of 50 trials per library for each condition in the following order: Library 1 (EF), Library 2 (HL), and Library 3 (CS). Accuracy (selection of the matching comparison stimulus) and response latency (the time elapsed between comparison stimuli presentation and selection of a match on each test trial, measured in hundredths of a second) were recorded. Accuracy was measured for the first 50 trials per library for each condition. Latency was measured for the first 50 correct trials per library for each condition. To obtain an equal number of trials to measure latency, incorrect trials were re-presented until a minimum of 50 correct trials were obtained for each condition.

2.2 Results

2.2.1 Capuchin Monkeys

To examine performance in terms of accuracy in the test phase, a 3x3 repeated measures ANOVA was conducted with library (EF, HL, CS) and condition (Both, Global, Local) as

independent variables. Capuchin monkey performance (Figure 2) revealed a significant main effect of condition, $F(2, 14) = 14.59, p < .001, \eta^2 = .68$. There was not a main effect of library, $F(2, 14) = .11, p = .90, \eta^2 = .02$, nor a significant interaction between condition and library, $F(4, 28) = .28, p = .89, \eta^2 = .04$. To explore the condition variable further, we collapsed across libraries to compare each condition to one another using paired samples t-test. A Bonferroni adjusted alpha level of .016 was used per test given that three comparisons were made (.05/3). Performance in the Both condition was significantly higher than performance in the Global condition $t(7) = 3.92, p = .006$, and performance was significantly higher in the Local condition than in the Global condition, $t(7) = -6.09, p < .001$. Performance did not differ between the Local and Both conditions, $t(7) = .72, p = .49$. These results support the hypothesis of increased performance for Both and Local conditions relative to performance in the Global condition.

To examine performance in terms of latency for capuchin monkeys (Figure 3), a 3x3 repeated measures ANOVA was used to determine the effect of library and condition on response time. For capuchin monkeys, there was no main effect of library, $F(2, 14) = .53, p = .60, \eta^2 = .07$, nor of condition, $F(2, 14) = 1.48, p = .26, \eta^2 = .18$. There was no interaction between library and condition, $F(4, 28) = 1.04, p = .40, \eta^2 = .13$. Although performance data indicated higher accuracy for Both and Local conditions relative to the Global condition, there was not a facilitation of response times for capuchin monkeys in any one condition relative to the others.

2.2.2 Rhesus Monkeys

A 3x3 repeated measures ANOVA was conducted with library (EF, HL, CS) and condition (Both, Global, Local) as independent variables for test phase performance. Rhesus monkey performance (Figure 2) also revealed a significant main effect of condition, $F(2, 6) =$

14.91, $p = .005$, $\eta^2 = .83$, but no main effect of library, $F(2, 6) = 1.93$, $p = .23$, $\eta^2 = .39$. There was a significant interaction between condition and library, $F(4, 12) = 6.07$, $p = .007$, $\eta^2 = .67$. To explore the interaction further, I ran a separate one-way ANOVA comparing conditions for each library.

To subdivide data based on library, we separated each animal's test data based on the library that they initially trained on (EF or HL), the library that they completed generalization testing with (EF or HL, the opposite from training), and the library that they completed novel test trials with (CS for all monkeys). For test data using the training stimuli, there was not an effect of condition $F(2, 6) = 1.80$, $p = .24$, $\eta^2 = .38$, nor for the generalization library, $F(2, 6) = 4.03$, $p = .08$, $\eta^2 = .57$. There was a significant effect of condition for the CS library, $F(2, 6) = 93.27$, $p < .001$, $\eta^2 = .97$. To explore this effect of condition for the CS library further, we compared each condition to one another using paired samples t-test. A Bonferroni adjusted alpha level of .016 was used. Performance in the Both condition was significantly higher than performance in the Global condition ($t(3) = 16.01$, $p = .001$). Performance in the Local condition also was significantly higher than in the Global condition ($t(3) = -8.85$, $p = .003$). Performance did not differ between the Local and Both conditions ($t(3) = -1.26$, $p = .30$). As with capuchin monkeys, these results support the hypothesis of increased performance for Both and Local conditions relative to performance in the Global condition for rhesus monkeys.

To examine performance in terms of latency for rhesus monkeys (Figure 3), a 3x3 repeated measures ANOVA was used to determine the effect of library and condition on response time. For rhesus monkeys, there was a main effect of library, $F(2, 6) = 6.95$, $p = .03$, $\eta^2 = .70$, but not of condition, $F(2, 14) = 4.59$, $p = .06$, $\eta^2 = .61$. There was no interaction between library and condition, $F(4, 12) = .94$, $p = .47$, $\eta^2 = .24$. Although performance data

indicated higher accuracy for Both and Local conditions relative to the Global condition for the CS library, there was not a facilitation of performance in terms of response times for rhesus monkeys. The main effect of library was likely due to a learning effect; all monkeys were fastest with Library 3 (the last library presented) across all conditions. This pattern of results suggested that the rhesus monkeys came to respond faster to the general task demands with experience.

2.3 Discussion

For rhesus monkeys and capuchin monkeys, a local precedence was reported for the discrimination of hierarchical compound stimuli. Although both species performed best when they matched stimuli that were identical in terms of their global features and their local elements, the monkeys also were significantly better at matching stimuli when their local elements were identical in comparison to when only their global features matched. Thus, as previously reported, capuchin monkeys and rhesus monkeys demonstrated a local-to-global precedence in a perceptual task modeled off of the classic Navon (1977) paradigm in which human adults showed a clear global-to-local processing style when perceiving large letters comprised of smaller, individual letters. Further, these results match previous reports of a local processing style by capuchin and rhesus monkeys (*Cebus apella*: De Lillo et al., 2005; Spinozzi et al., 2003, 2006; *Macaca mulatta*: Hopkins & Washburn, 2002).

The differences in processing mode across primates and other nonhuman animal species is intriguing given overall commonalities in the primate visual system across monkeys, apes, and humans, including physical and functional similarities (see Matsuno & Fujita, 2009 for a review). First, the properties of the stimuli themselves can drive global or local processing within perceptual mode tasks, with stimuli size, density, visual angle, and spatial location impacting precedence effects in humans (e.g., Grice, Canham, & Boroughs, 1983; Kinchla & Wolfe, 1979;

Lamb & Robertson, 1990; Martin, 1979; Navon, 1981 Navon & Norman, 1983) and animals (e.g., Cavoto & Cook, 2001; De Lillo et al., 2005; Neiworth, Gleichman, Olinick, & Lamp, 2006). However, the results seen here among capuchin and rhesus monkeys are in line with previous local-precedence reports using a variety of tasks (e.g., visual search, matching-to-sample) and a variety of stimuli design within these two species (De Lillo et al., 2005; Hopkins & Washburn, 2002; Spinozzi et al., 2003, 2006).

Beyond influences of stimuli, adaptive hypotheses have been put forth to account for capuchin monkeys' local processing style, including the need to attend to local detail within their environments. For example, capuchin monkeys vigilantly search for very small, fast moving prey and forage for small seeds (Hladik, 1975). These foraging demands may place a premium on local detail focus within a capuchin monkey's natural environment (see De Lillo et al., 2005). Further, local processing in pigeons has been attributed to their myopic (nearsighted) foraging of small food on the ground, perceived by the frontal visual field (Bloch & Martinoya, 1982). Because of the nature of cognitive testing (nearby visual stimuli comprised of small detail), it is likely that pigeons process test stimuli with the frontal field, favoring attention to fine detail and a local precedence (Cavoto & Cook, 2001). Thus, the manner in which a species perceives its natural environment, with an emphasis either on global or local details, likely influence the evolution of either local or global precedence effects.

The role of executive function in precedence effects (specifically, the role of attention) also should be taken into account when considering the emergence of global processing. Research among children with autism spectrum disorder has revealed a strong local processing style, accompanied by decreased connectivity in the brain from areas that are key in global processing such as the right hemisphere and an overall reduction in white matter (Brock, Brown,

Boucher, & Rippon, 2002; Frith, 2004; Just, Cherkassky, Keller, & Minshew, 2004). Reduced connectivity also yields compromised top-down attention processes that are important in global processing of complex stimuli (Just et al., 2004). Attention control and, specifically, the ability to focus on global features appear to emerge secondary to local processing, perhaps as a byproduct of top-down attention modulation. Thus, there is unlikely any single factor in the emergence of global processing, but rather processing mode emerges as an interplay between a species ecology, its behavior, and the existing neural architecture supporting perception and attention. Future studies that seek to disentangle their complementary roles will shed light on the emergence of global processing in primates.

Relevant to this dissertation, perceptual processing mode has proven to be important in the emergence of some visual illusions, particularly those that integrate multiple elements into one overall figure (Coren & Girgus, 1978). These types of illusions rely upon the simultaneous processing of multiple elements within a visual array. Humans who demonstrated a strong global-to-local precedence also demonstrated increased perception of visual illusions (e.g., Berry, 1968, 1971; Dawson, 1967; Witkin, 1967), whereas those that were more locally-oriented often failed to perceive illusions in a similar manner or sometimes not at all (Dakin & Frith, 2005; de Fockert, Davidoff, Fagot, Parron, & Goldstein, 2007; Happé, 1996; Happé, Briskman, & Frith, 2001; but see Ropar & Mitchell, 1999). Similarly, several nonhuman species that are documented as being more local-processors failed to perceive illusions in a human-like manner, further supporting a link between processing mode and illusion perception (e.g., *Columba livia*: Nakamura, Watanabe, & Fujita, 2008; *Gallus gallus domesticus*: Nakamura, Watanabe, & Fujita, 2014; *Papio papio*: Parron & Fagot, 2007). Whether animals are constrained by perceptual

processing mode will be explored here in a series of geometric size illusions across primate species.

2.4 References

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2.5 Figures

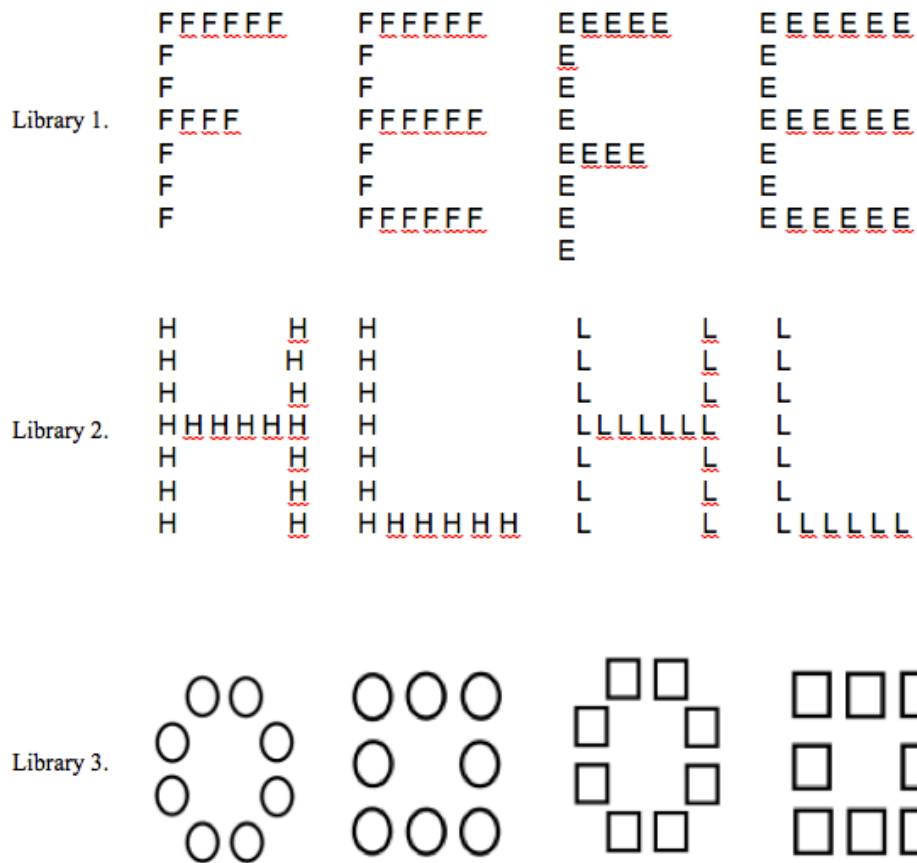


Figure 1. Stimulus Library 1 (EF), Library 2 (HL), and Library 3 (circle-square) for each condition (Both, Global, and Local).

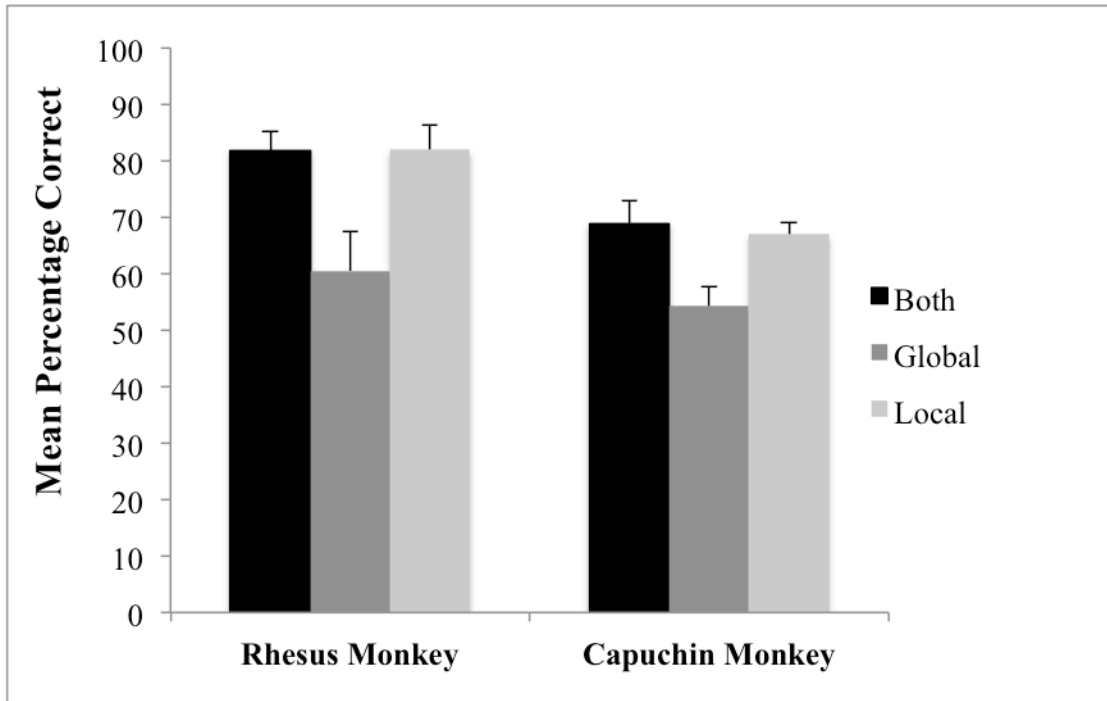


Figure 2. Mean percentage correct for rhesus monkeys and capuchin monkeys in each condition (Both, Global, and Local). Error bars depict corrected 95% confidence intervals for repeated measures tests (Cousineau, 2005).

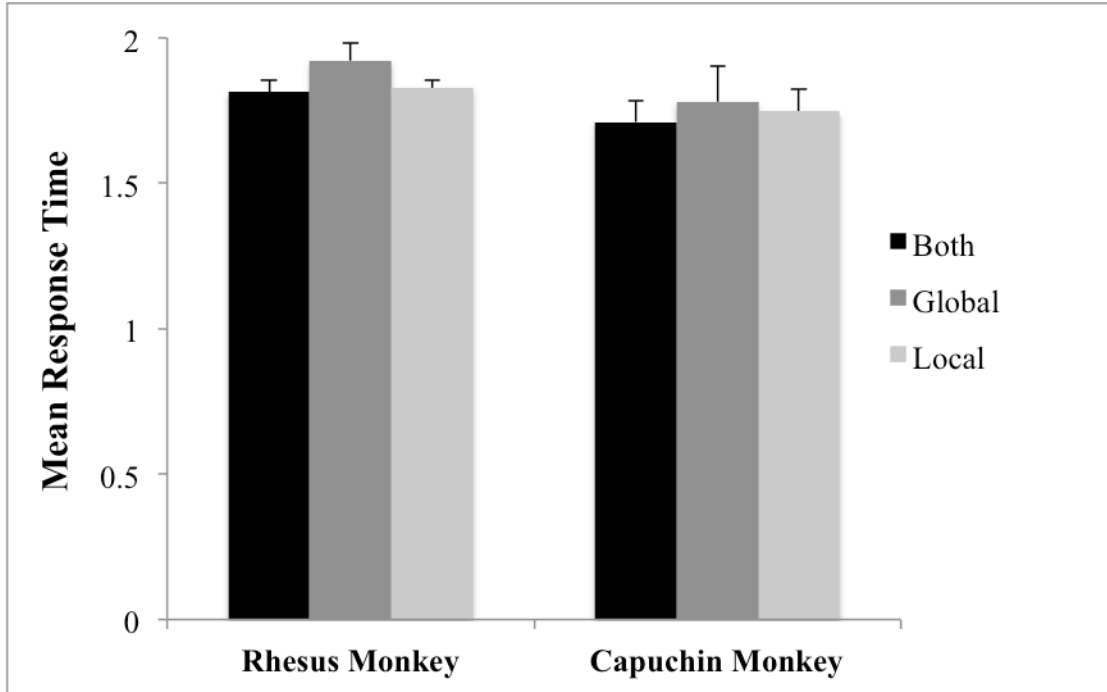


Figure 3. Mean response times (in seconds) for rhesus monkeys and capuchin monkeys in each condition (Both, Global, and Local). Error bars depict corrected 95% confidence intervals for repeated measures tests (Cousineau, 2005).

DO YOU SEE WHAT I SEE? A COMPARATIVE INVESTIGATION OF THE DELBOEUF
ILLUSION IN HUMANS (*HOMO SAPIENS*), RHESUS MONKEYS (*MACACA MULATTA*),
AND CAPUCHIN MONKEYS (*CEBUS APELLA*)

By

AUDREY E. PARRISH

ABSTRACT

Studying visual illusions is critical to understanding typical visual perception. We investigated whether rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*) perceived the Delboeuf illusion in a similar manner as human adults (*Homo sapiens*). To test this, in Experiment 1, we presented monkeys and humans with a relative discrimination task that required subjects to choose the larger of two central dots that were sometimes encircled by concentric rings. As predicted, humans demonstrated evidence of the Delboeuf illusion,

overestimating central dots when small rings surrounded them and underestimating the size of central dots when large rings surrounded them. However, monkeys did not show evidence of the illusion. To rule out an alternate explanation, in Experiment 2, we presented all species with an absolute classification task that required them to classify a central dot as 'small' or 'large.' We presented a range of ring sizes to determine whether the Delboeuf illusion would occur for any dot-to-ring ratios. Here, we found evidence of the Delboeuf illusion in all three species. Humans and monkeys underestimated central dot size to a progressively greater degree with progressively larger rings. The Delboeuf illusion now has been extended to include capuchin monkeys and rhesus monkeys, and through such comparative investigations we can better evaluate hypotheses regarding illusion perception among nonhuman animals.

INDEX WORDS: Visual illusions; Delboeuf illusion; Capuchin monkeys; Rhesus monkeys; Humans; Perception; Processing style

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3 DO YOU SEE WHAT I SEE? A COMPARATIVE INVESTIGATION OF THE DELBOEUF ILLUSION IN HUMANS (*HOMO SAPIENS*), RHESUS MONKEYS (*MACACA MULATTA*), AND CAPUCHIN MONKEYS (*CEBUS APELLA*)

Although understanding how perceptual mechanisms rapidly and accurately process sensory information is important, it is also informative to understand when and why perception ‘fails’. Such failures can reveal clues about how the perceptual system operates because those failures illustrate how perception interacts (correctly or incorrectly) with physical stimulation and sensory input. Studying misperception often involves studying susceptibility to illusions, and much of this work has been conducted from a comparative perspective, because in that way we can better understand the evolution of human perception. Comparative studies have revealed similarities and differences in ‘misperceptions’ or visual illusions across primates, including the Horizontal-Vertical illusion (Dominguez, 1954), the Zöllner illusion (Agrillo, Parrish, & Beran, 2014; Benhar & Samuel, 1982), the Ponzo illusion (Bayne & Davis, 1993; Fujita, 1996, 1997, 2001), the Mueller-Lyer illusion (Suganuma, Pessoa, Monge-Fuentes, Castro, & Tavares, 2007), the Duncker illusion (Zivotofsky, Goldberg, & Powell, 2005), the rectangle illusion (Dominguez, 1954; Harris, 1968), the corridor illusion (Barbet & Fagot, 2002; Imura, Tomonaga, & Yagi, 2008) and the Delboeuf illusion (Parrish & Beran, 2014)

Despite some continuity in perceptual illusions across species, differences in the perception of other visual illusions across primates have emerged as well. A notable example is the well-known Ebbinghaus-Titchener illusion (Figure 1), which is one of the most widely studied and robust size illusions among humans (e.g., Aglioti, DeSouza, & Goodale, 1995; Coren & Enns, 1993; Ebbinghaus, 1902; Massaro & Anderson, 1971; Weintraub, 1979). In this illusion, the sizes of two identical central dots are misperceived as a function of several

surrounding circles. If small circles surround the central dot, the dot is overestimated relative to the same-sized central dot surrounded by several large circles. Interestingly, baboons do not perceive this illusion as humans do (Parron & Fagot, 2007) despite positive evidence of other visual illusions in this species (e.g., Barbet & Fagot, 2002; Benhar & Samuel, 1982). When presented with the Ebbinghaus-Titchener illusion, baboons instead accurately discriminated central dot size even in the presence of the outer illusory circles, leading Parron and Fagot to argue that perhaps the neural substrate necessary for perceiving this illusion was lacking among Old World monkeys, instead evolving late in the primate lineage. This hypothesis was supported by a reversed Ebbinghaus-Titchener illusion documented in pigeons (*Columba livia*: Nakamura, Watanabe, & Fujita, 2008) and adult bantam chickens (*Gallus gallus domesticus*: Nakamura, Watanabe, & Fujita, 2014). However, complicating the question, various non-primate species have since shown evidence of perceiving the Ebbinghaus-Titchener illusion as humans do, including a dolphin (*Tursiops truncatus*: Murayama, Usui, Takeda, Kato, & Maejima, 2012), domestic chicks (*Gallus gallus domesticus*: Rosa Salva, Rugani, Cavazzana, Regolin, Vallortigara, 2013), and redbelt splitfin fish (*Xenotoca eiseni*: Sovrano, Albertazzi, & Rosa Salva, 2015).

Similar to the Ebbinghaus-Titchener illusion, the Delboeuf illusion presents two identically sized central dots that are surrounded by either a small outer ring or large outer ring (rather than multiple circles; Figure 1). Dots encircled by a large ring are underestimated in terms of their size, whereas dots encircled by a small ring are overestimated. This illusion has been studied extensively in human perception (e.g., Coren & Girgus, 1978; Delboeuf, 1865; Nicolas, 1995; Van Ittersum & Wansink, 2012; Ward & Lockhead, 1970). Despite the breadth of research with human participants on these highly similar size illusions and the comparative studies

investigating the Ebbinghaus-Titchener illusion in animal species, only one study has presented the Delboeuf illusion to an animal species (Parrish & Beran, 2014). In a food-choice task, chimpanzees were presented with two circular food items (to mimic central dots) from which they could choose one for consumption. Food sizes were misperceived on the basis of outer plate size (which mimicked outer rings), with chimpanzees choosing a smaller amount of food on a small plate relative to a larger amount of food on a large plate. Similar results in humans also have been reported in food choice and consumption contexts (e.g., Van Ittersum & Wansink, 2012).

The perception of the very similar Delboeuf illusion, but not the Ebbinghaus-Titchener illusion, within closely related primate species warrants additional research. Beyond documenting the perception (or not) of an additional illusion among monkey species, understanding when this illusion is most likely to occur among different primate species is essential to establishing the mechanisms that underlie size illusions of this nature. Here, we assessed the Delboeuf illusion in two additional nonhuman primate species, the rhesus macaque and the capuchin monkey. We were interested in whether monkey species also might perceive this illusion in the way great apes and humans do, or if instead they might show patterns similar to Parron and Fagot's (2007) investigation of the highly similar Ebbinghaus-Titchener illusion with a monkey species (baboons).

In Experiment 1, we presented the monkeys with a relative discrimination task in which they were trained to choose the larger of two central dots that were sometimes surrounded by the illusory-inducing Delboeuf rings. This approach matched that of Parron and Fagot's (2007) study examining the Ebbinghaus-Titchener illusion, which used a 2-choice discrimination procedure. In order to more fully investigate why the illusion was absent in Experiment 1, we then

investigated the mechanisms underlying the Delboeuf illusion in Experiment 2. This was done by varying the ratio of the target dot diameter to concentric ring diameter to establish a range of diameter ratios at which the illusion was most likely to emerge. Here, we introduced an absolute classification task (instead of a relative discrimination) in which participants classified a central dot as ‘small’ or ‘large’ relative to a never presented central target size. We included the Delboeuf rings of variable size that may influence dot size perception. We presented both experiments to human participants to confirm our approach and to provide a comparison for the nonhuman primate species.

We predicted that size-judgment performance would be impacted by outer ring size for both experiments for all species. For Experiment 1, we predicted that all species would perceive the Delboeuf illusion, preferring the central dot encircled by the small ring relative to the same-sized central dot encircled by a large ring. For Experiment 2, we predicted that the larger concentric rings (target dot-to-ring ratios $< .50$) would lead participants to over-classify central dots as small as they should appear smaller in the large context. Alternatively, we predicted that the smaller concentric rings (target dot-to-ring ratios $> .50$) would lead participants to under-classify central dots as small as they should appear larger in the small context.

3.1 Experiment 1

3.1.1 Methods

3.1.1.1 Participants

Nonhuman Primates

The nonhuman primates included in all experiments were housed and tested at the Language Research Center (LRC) of Georgia State University (GSU) in Atlanta, Georgia. LRC primates are never food or water deprived for testing purposes and have 24-hour access to water,

including during test sessions. They receive a daily diet of fruits, vegetables, and primate chow regardless of participation in testing, and caloric intake is kept consistent by taking into account the amount of food earned from testing when determining the diet. All testing complied with guidelines for working with nonhuman primates as established by protocols approved by the GSU Institutional Animal Care and Use Committee. GSU is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care.

Seven adult rhesus macaques (all males) and thirteen adult capuchin monkeys (6 males and 7 females) were included in the following experiments. Rhesus monkeys are individually housed and have 24-hour access to a computerized testing apparatus within their home cage. Rhesus monkeys have constant visual and auditory access to conspecifics and receive weekly access to an indoor-outdoor enclosure with another monkey. Capuchin monkeys are group housed in indoor-outdoor enclosures, and they separate voluntarily into individual testing enclosures for computerized testing (with visual and auditory access to conspecifics). Monkeys have participated in several computerized perceptual discrimination tasks (e.g., Agrillo et al., 2014; Beran, 2006; Beran & Parrish, 2013; Beran, Smith, Coutinho, Couchman, & Boomer, 2009).

Humans

Twenty-two human participants were recruited from GSU's undergraduate student body (average age: 21 years old \pm 4, 12 females). Participants were required to give informed consent prior to participating in the experiment(s) and received course credit for their participation. Testing complied with the procedures and protocols that were approved by the Institutional Review Board.

3.1.1.2 Apparatus

Nonhuman Primates

Nonhuman primates included in this study were joystick trained for computerized testing using the Language Research Center's Computerized Test System, consisting of a color monitor, personal computer, digital joystick, and food pellet dispenser (Evans, Beran, Chan, Klein, & Menzel, 2008; Richardson, Washburn, Hopkins, Savage-Rumbaugh, & Rumbaugh, 1990). Primates manipulated the joystick with their hands to isomorphically control a small round cursor on the computer screen. Monkeys were not restrained during testing, thus the viewing distance from the monitor was approximately 30.5 cm to 40.5 cm. Correct responses led to banana-flavored pellet rewards (45-mg pellets for capuchins and 94-mg pellets for rhesus monkeys: Bio-Serv, Frenchtown, NJ) via a pellet dispenser interfaced to the computer through a digital I/O board (PDISO8A; Keithley Instruments, Cleveland, OH). Programs were written in Visual Basic 6.0.

Humans

Human participants were tested at individual computer carrels with a personal computer, a digital monitor, and mouse for testing. They were not given food rewards but were given written feedback on the computer screen regarding the accuracy of their responses.

3.1.1.3 Stimuli

On all trials, the stimuli, including dots and (when present) concentric rings, were black, presented on a white background, to minimize enhanced attention to one of these array elements over the other. For testing, one central target size was established and was present on every trial (standard target = 3 cm in diameter; designated as Level 7). Using a psychophysical step procedure, a range of 13 possible target dots to be compared to the Level 7 dot was established.

Levels 1-6 were all smaller than the Level 7 dot, and their size was generated by the following equation: $\text{Level} = 3 * 0.98^{(7 - \text{TrialLevel})}$. This made Level 1 dots the easiest to discriminate from Level 7 and Level 6 dots the hardest to discriminate. Levels 8-13 were all larger than the Level 7 dot, and their size was generated by the following equation: $\text{Level} = 3 * 1.02^{(\text{TrialLevel} - 7)}$. This made Level 13 dots the easiest to discriminate from Level 7 and Level 8 dots the hardest to discriminate. In this way, Levels 8-13 were progressively larger dots for which Level 8 dots were objectively hardest to discriminate from the Level 7 dot, and Level 13 dots were easiest to discriminate. When they were present, small or large concentric rings encircled the target dots. On those trials, both dots were encircled by an outer ring or both dots had no ring. There were never trials in which only one dot had a ring. A small ring was 4.5 cm in diameter for all target dots, and thus the Level 7 dot comprised 67% of the small ring, and a large ring diameter was 9 cm in diameter and thus the Level 7 dot comprised 33% of the large ring.

3.1.1.4 Design and Procedure

Nonhuman Primates

On each trial, participants made a relative size judgment between two target dots of variable diameter. Each trial presented the standard target dot (Level 7) versus a randomly selected dot from the range of Level 1 to Level 13. At the outset of each trial, participants moved a small round cursor that they controlled into contact with a grey button at the top center of the computer screen. Then, that button disappeared, the cursor re-centered, and two stimuli appeared as choice options. Each stimulus was comprised of a target dot. In some conditions, a ring surrounded the dot. These stimuli were simultaneously presented (left- and right-justified at center of the screen, with the larger dot size randomized for one of these two locations on each trial). Participants were required to contact one of the two stimuli within 3 s, or the trial was

scored as an error. After selection of a stimulus or after 3 s of inactivity, the screen was cleared completely. Selection of the stimulus that was the larger of the two dots led to a melodic chime and a pellet reward. Selection of the smaller of the two dots led to a buzz tone and a 20-s timeout period during which the screen remained blank. The inter-trial interval was 1 second. Monkeys worked on the task between 2- and 4-hours per day, completing as many trials as possible within a testing session given their motivation to engage the task.

There were six conditions. Trials in the Baseline condition presented two differently sized target dots on each trial with no concentric rings, and this established the baseline performance rate in discriminating dot sizes when concentric rings could not make any impact on the perception of the dot sizes. Trials in the Large Control condition also presented two differently sized target dots, but large rings surrounded each dot. Trials in the Small Control condition presented two differently sized target dots, but small rings surrounded each dot. These two conditions were considered control conditions because they presented an objectively larger dot to choose from in a non-illusory inducing context (i.e., identically-sized rings).

Trials in the Congruent Test condition presented the smaller of the two dots surrounded by a small ring and the larger dot surrounded by a large ring. If the Delboeuf illusion occurred, these Congruent Test trials should have led to a decrease in performance by leading participants to overestimate the small dot (because it appeared larger in the small ring) and to underestimate the large dot (because it appeared smaller in the large ring). Trials in the Incongruent Test condition presented the smaller of the two dots surrounded by a large ring and the larger dot surrounded by a small ring. If the illusion occurred, the Incongruent Test condition should have led to increased performance as the small dot appeared even smaller than it actually was in the large context, whereas the large dot in the small context appeared even larger than its true size.

Within the Congruent and Incongruent Test conditions, a special kind of test trial could occur that did not occur in the Baseline, Large Control, or Small Control conditions. In this trial type, called the Delboeuf Illusion trial (Figure 1), the dots were the same size (both Level 7). However, a large concentric ring surrounded one dot and a small concentric ring surrounded the other dot. This array created the context for the standard illusion in which the target surrounded by the large ring should appear to be smaller in size than the same sized target surrounded by the small ring. There was no objectively correct choice as both targets were identical. We subdivided the monkeys into two groups, one of which received no feedback at all for the Delboeuf illusion trials and immediately began the next trial upon completion of this trial type (Gambit, Gonzo, Han, Lily, Logan, Lou, Nala, Nkima, Obi, Wren). The other half were randomly given either positive feedback in the form of a food pellet or immediately sent to the inter-trial interval without any timeout on Delboeuf illusion trials (Chewie, Gabe, Gale, Hank, Gretel, Griffin, Liam, Mason, Murph, Widget).

3.1.1.4.1 Training

Monkeys completed a set of training trials to learn the rule of selecting the larger dot in the two-choice discrimination task. This was done using the three easiest absolute levels (Levels 1-3 and Levels 11-13), divided into 50% Baseline trials, 25% Large Control trials, and 25% Small Control trials. The criterion was set to 85% correct over the most recent 60 trials. After monkeys reached criterion, they immediately entered the test phase during that session.

3.1.1.4.2 Testing

In the testing phase, we introduced the full continuum of levels (Levels 1 – 13). Test sessions were divided into 30% Baseline trials, 20% Large Control trials, 20% Small Control trials, 15% Congruent Test trials, and 15% Incongruent Test trials. Delboeuf illusion probe trials

(Level 7) were presented only in the Congruent Test and Incongruent Test conditions, and they occurred with equal probability to the other 12 levels. Monkeys completed between 6,000 – 12,000 test trials depending upon their overall performance. We assessed overall accuracy after 6,000 test trials. If monkeys reached 75% accuracy across all conditions after 6,000 trials, they were finished with the experiment, and all of their data were included in the analyses. Otherwise, they continued in the experiment until they reached the 75% criterion, and we analyzed the last 6,000 test trials from those animals as we considered this mature performance on the task.

Humans

The general procedure was very similar to the monkeys' procedure described above, including the same stimuli and trial levels. Participants first were required to contact a trial-initiation stimulus and then used the computer mouse to select one of the two stimuli. Correct responses led to a flashing stimulus that said 'Correct!' in the middle of the screen, whereas incorrect responses led to a flashing stimulus that said 'Incorrect' in the middle of the screen. We shortened the timeout period for incorrect trials to 8 s. In accordance with the monkey procedure, Delboeuf Illusion trials were non-differentially reinforced. Failure to respond within 3 seconds of stimuli presentation led to an instruction to respond more quickly to the trials. The inter-trial interval was 1 s. A testing session was 60 minutes or until the participant completed 800 test trials. We only used data from those participants who completed at least 600 trials in the task because fewer trials than this would not have allowed for enough trials at each difficulty level for each condition. All participants met this requirement.

Minimal written instructions were provided instead of a training phase to maximize the number of test trials completed per session with each participant. Before starting the experiment, participants read the following text:

In this experiment, you will choose between two options on the screen, one on the left and one on the right. Please choose the larger of the two black dots. Click the Start button, and then click on one of the two options. You need to make these responses fairly quickly. Correct responses move you right to the next trial. Incorrect responses lead to a short period where the task is frozen. You need to complete 800 trials, so the better you do, the faster you will finish. When you are ready, click on the START button.

3.1.2 Results

For all analyses, difficulty level was the absolute value of the difference between the trial level (1-13) and Level 7. Thus, Level 6 and Level 8 stimuli, which were the objectively most difficult stimuli to discriminate from the Level 7 stimuli, were recoded as Difficulty 1 trials. Level 5 and Level 9 stimuli were recoded as Difficulty 2, and so on, so that we had a new range of levels - Difficulty 1 (hardest) to Difficulty 6 (easiest) for each condition.

Nonhuman Primates

Throughout the remaining analyses in the current and following experiments, we removed any trials on which the monkeys timed-out because they did not respond quickly enough. These were extremely infrequent throughout all testing (ranging from 0.57% to 5.62% of trials across all monkeys).

We conducted a mixed-design analysis of variance (ANOVA) to examine the effect of condition (Baseline, Small Control, Large Control, Congruent Test, and Incongruent Test) and absolute difficulty level (1-6) on the selection of the larger central dot with species (capuchin monkeys and rhesus monkeys) as the between-subjects variable. There was a significant main effect of condition, $F(4, 72) = 8.18, p < .001, \eta^2_p = .31$, and difficulty level, $F(5, 90) = 610.20, p < .001, \eta^2_p = .97$. There was not a significant main effect of species, $F(1, 18) = 1.46, p = .24, \eta^2_p$

= .08. There was a significant interaction between condition and difficulty level, $F(20, 360) = 2.89, p < .001, \eta^2_p = .14$. There was not a significant interaction between condition and species, $F(4, 72) = 0.71, p = .59, \eta^2_p = .04$, nor between difficulty level and species, $F(5, 90) = 1.05, p = .39, \eta^2_p = .06$, nor was there a three-way interaction, $F(20, 360) = .83, p = 0.68, \eta^2_p = .04$.

Figure 2 depicts group-level performance (i.e., selection of the larger central dot) as a function of condition and difficulty level for capuchin monkeys and rhesus monkeys.

Because there was no main effect of species and no interaction of species with either of the other variables, we combined the two species for subsequent analyses. We then used a t-test to compare performance in selected pairs of conditions with a focus on the test conditions, collapsing across difficulty level using the average mean percentage of correct choices. A Bonferroni adjusted alpha level of .016 was used per test given the three comparisons of interest (.05/3). Performance in the Baseline condition was significantly higher than the Incongruent Test condition ($t(19) = 4.22, p < .001$), but did not differ significantly from the Congruent Test condition ($t(19) = 1.85, p = .08$). Performance in the Congruent Test condition did not differ significantly from the Incongruent Test condition ($t(19) = 2.58, p = .018$).

For the Delboeuf Illusion probe trials, we conducted a one-sample t-test to compare selection of the illusory ‘larger’ dot (i.e., the Level 7 dot surrounded by the small ring) to chance level. Neither species’ selection of the illusory dot differed from chance (capuchins: $t(12) = -1.59, p = .14$; rhesus monkeys: $t(6) = 0.53, p = .62$). We ran individual binomial tests on these data for each monkey, which are provided in the online appendices.

Humans

We conducted a within-subjects repeated-measures analysis of variance (ANOVA) to examine the effect of condition (Baseline, Small Control, Large Control, Congruent Test, and

Incongruent Test) and difficulty level (1-6) on the selection of the larger central dot. There was a significant main effect of condition, $F(4, 84) = 45.11, p < .001, \eta^2_p = .68$, and difficulty level, $F(5, 105) = 231.54, p < .001, \eta^2_p = .92$. There also was a significant interaction between condition and difficulty level, $F(20, 420) = 12.98, p < .001, \eta^2_p = .38$. Figure 2 depicts group-level performance as a function of condition and difficulty level for human participants.

We then conducted a t-test to compare performance in selected pairs of conditions with a focus on the test conditions, collapsing across difficulty level using the average mean percentage of correct choices. A Bonferroni adjusted alpha level of 0.016 was used per test given that three comparisons were made ($.05/3$). Performance in the Baseline condition was significantly higher than performance in the Congruent Test condition ($t(21) = 9.21, p < .001$), but did not differ significantly from the Incongruent Test condition ($t(21) = .12, p = .91$). Performance in the Incongruent Test condition also was significantly higher than the Congruent Test condition ($t(21) = -6.07, p < .001$). Note that this was the expected pattern of results for illusion perception. These results differed from what was seen with monkeys, in which the Incongruent Test condition did not differ from the Congruent Test condition.

For the Delboeuf Illusion probe trials, we used a one-sample t-test to compare selection of the illusory ‘larger’ dot (i.e., the Level 7 dot surrounded by the small ring) to chance level. Human participants selected the illusory dot that was surrounded by the small ring significantly above chance levels ($t(21) = 4.71, p < .001$). We also ran individual binomial tests on these data for each participant, which are provided in the online appendices.

3.1.3 Discussion

Human participants perceived the Delboeuf illusion in the current task, underestimating the size of central dots when large rings surrounded them and overestimating central dots when

small rings surrounded them. Further, human performance was disrupted in the Congruent Test condition as expected. Participants overestimated smaller dot sizes (because they appeared larger when surrounded by the small ring) and underestimated larger dot sizes (because they appeared smaller when surrounded by the large ring). Perception of the Delboeuf illusion in the current task matches that of previous reports in the literature for human adults (e.g., Coren & Girgus, 1978; Delboeuf, 1865; Nicolas, 1995; Van Ittersum & Wansink, 2012).

Rhesus monkeys and capuchin monkeys successfully learned to choose the larger of two central dots in the relative discrimination task. In Delboeuf Illusion trials, some monkeys ($N = 2$) perceived the illusion in a human-like fashion, selecting the dot surrounded by a small ring as larger at significant rates. However, more monkeys ($N = 6$) appeared to perceive the illusion in a reversed manner whereas the remaining monkeys did not demonstrate a preference at all in this trial type. Further, the monkeys' performances were disrupted in the Incongruent Test trials, but in the opposite manner than was predicted and from that shown by humans (i.e., selected the small dot encircled by the large ring).

Although these results suggest that monkeys perceived the Delboeuf illusion in a reversed direction from humans, we were concerned that these results were instead driven by a bias towards selecting the dot that was encircled by a large ring. This bias would result in the same findings that we have reported here. Nothing in our training routine had necessarily instructed the monkeys that rings were not relevant to the discrimination (i.e., dots and rings were identical in color and presented equally in training and testing), thus, we were concerned that the monkeys may have approached the task as one in which the rings and dots were to be discriminated as one stimulus. Large rings would generally be more attractive than small rings, a bias that would work against any possible Delboeuf illusion. The design of Experiment 1 may have limited our ability

to interpret the resulting response patterns with regard to the Delboeuf illusion. To resolve this problem, and to better assess any possible illusion, we extended our investigation of the Delboeuf illusion to an absolute classification task with a range of ring sizes.

3.2 Experiment 2

Here, we introduced a task in which participants classified a target dot of variable size as either ‘small’ or ‘large’ in comparison to a never presented central target size (Level 7). This differed from Experiment 1 in which participants made a relative judgment, selecting the larger of two black dots sometimes encircled by a ring. Now there was only ever one dot present on a given trial, reducing the reliance on a rule such as ‘choose the larger of two dots and/or rings.’ As in the former experiment, we presented a condition with no ring. We also presented a condition with a .50 dot diameter to ring diameter ratio. Previous studies have shown that a .50 ratio does not induce an illusion (e.g., Van Ittersum & Wansink, 2012), and thus served as an additional baseline beyond the no ring condition in the current study. Other conditions involved rings that could serve to disrupt perceptual processing of the target dot. To avoid the concerns in Experiment 1 that the monkeys might not have understood that the rings were not part of the discrimination, we introduced a continuum of ring sizes. In Experiment 1, the standard dot (Level 7 – 3 cm in diameter) was presented in a .67 ratio with the small ring (4.5 cm in diameter) and a .33 ratio with the large ring (9 cm in diameter). Here, we introduced eight different dot-to-ring ratios 0 (no ring), .25, .33, .45, .50, .55, .67, and .75 that were proportional to each individual target dot. We predicted that if the Delboeuf illusion was perceived, then underestimation of dot size would be most likely to occur at lower ratios ($< .50$) as these produced larger rings relative to the target dots. Alternatively, overestimation of dot size would be most likely to occur at higher ratios ($> .50$) as these produced smaller rings relative to the

target dots. This manipulation was critical to establishing whether the Delboeuf illusion emerges using a wider range of ratios within nonhumans, and how these ratios compared to the optimal ratio for demonstrating the Delboeuf illusion using this task with humans.

3.2.1 Methods

3.2.1.1 Participants

Nonhuman Primates

The same seven rhesus monkeys were tested. Eleven of the thirteen capuchin monkeys from Experiment 1 (excluding Gabe and Widget, who were assigned to other unrelated experimental tasks) participated in the current study.

Humans

Twenty-four new human participants were recruited from GSU's undergraduate student body (average age: 19.41 years old \pm 2.24, 22 females). Participants were tested using the computerized system described in Experiment 1. Again, all participants were required to give informed consent prior to participating in the experiment(s) and received course credit for their participation. Testing complied with procedures and protocols approved by the GSU IRB.

3.2.1.2 Design and Procedure

Nonhuman Primates

Each trial proceeded as described in Experiment 1 (i.e., trial initiation, reinforcement, inter-trial interval) with one major difference. Now, a single target stimulus (a central dot that was sometimes surrounded by a concentric ring) was presented at the top middle of the screen, and participants were required to classify the central dot as 'small' (by moving the cursor to the bottom left of the screen to a blue rectangle) or 'large' (by moving the cursor to the bottom right of the screen to a green rectangle). Testing stimuli included the same 13 levels of dots that were

used in Experiment 1. A concentric ring sometimes surrounded the central dot at the top of the screen, and these rings could generate the following target dot to ring ratios: .25, .33, .45, .50, .55, .67, and .75. The baseline conditions were the 0 (no ring) ratio and the .50 ratio. These were used to establish classification performance without the effects of any inducing stimuli (0) or with a non-illusory ring size (.50). All other ring sizes were presented randomly with each of the target dot sizes (Levels 1-13, excluding Level 7). We oversampled the more difficult levels to increase the number of critical test trials presented (44% of test trials presented a randomly selected Level 4 to Level 10 trial whereas the remaining trials randomly sampled from the full range of levels).

3.2.1.2.1 Training

Monkeys completed a set of training trials to learn the rule of selecting the appropriate classification icon (small or large) using the three easiest difficulty levels. These were presented in half of the trials in the 0 (no ring) ratio condition and in half of the trials in the .50 ratio. The criterion for passing the training phase was set to 85% correct over the most recent 60 trials, at which point testing immediately began. One capuchin monkey (Gambit) failed to reach training criterion after 6,000 trials, and she was removed from the study.

3.2.1.2.2 Testing

Each monkey completed 12,000 testing trials including the following ratios presented in equal proportions: 0, .25, .33, .45, .50, .55, .67, and .75 ratios. Again, we analyzed the last 6,000 test trials as we considered this mature performance on the task.

Humans

Human participants were tested using the same apparatus as was used in Experiment 1. The same general procedures were presented to humans as were used with the monkeys,

including the same absolute judgment task, classifying a central dot as ‘small’ or ‘large.’

Participants were presented with as many as 800 trials, and we used data from those participants who completed at least 600 trials in the task. Seven participants failed to complete at least 600 trials, and the data from those participants were not included in the following analyses.

Minimal written instructions were provided instead of a training phase to maximize the number of test trials completed per session with each participant. Before starting the experiment, participants read the following text:

In this experiment, you will see a black dot at the top center of the screen. Then, you must assign that dot as being either ‘Small’ or ‘Large’ by clicking on one of those two words on the screen. Click the Start button, and then click on one of the two options. You need to make these responses fairly quickly. Correct responses move you right to the next trial. Incorrect responses lead to a short period where the task is frozen. You need to complete 800 trials, so the better you do, the faster you will finish. When you are ready, click on the START button.

3.2.2 Results

For all analyses, we reduced the number of levels from 13 levels to 6 levels. The new Levels 1 – 3 included all “small” dots (Level 1 combined former Levels 1 and 2, Level 2 combined former Levels 3 and 4, Level 3 combined Levels 5 and 6). The new Levels 4 – 6 included all “large” dots (Level 4 combined former Levels 8 and 9, Level 5 combined former Levels 10 and 11, Level 6 combined Levels 12 and 13). Thus, Levels 1 – 6 ranged from the smallest central dots to the largest central dots, with Level 1 (smallest) to Level 6 (largest).

Nonhuman Primates

Again, we removed any trials on which the monkeys timed-out of a trial because they did not respond quickly enough. These were extremely infrequent throughout all testing in the current experiment (ranging from 0.49% to 4.14% of trials across all monkeys).

We used a mixed-design analysis of variance (ANOVA) to examine the effect of ratio (0, .25, .33, .45, .50, .55, .67, and .75) and absolute difficulty level (1-6) on the proportion of trials where the participants made a dot classification of 'small' with species (capuchin monkeys and rhesus monkeys) as the between-subjects variable. There was a significant main effect of ratio, $F(7, 105) = 2.71, p = .01, \eta^2_p = .15$, difficulty level, $F(5, 75) = 106.63, p < .001, \eta^2_p = .88$, and of species, $F(1, 15) = 6.89, p = .02, \eta^2_p = .32$. There was a significant interaction between ratio and difficulty level, $F(35, 525) = 4.17, p < .001, \eta^2_p = .22$, and between difficulty level and species, $F(5, 75) = 5.62, p < .001, \eta^2_p = .27$. There was not a significant interaction between ratio and species $F(7, 105) = .54, p = .80, \eta^2_p = .04$. There was a three-way interaction between ratio, level, and species, $F(35, 525) = 1.94, p = .001, \eta^2_p = .11$. Figure 3 depicts group-level performance (i.e., selection of the larger central dot) as a function of target dot to ring ratio and difficulty level for capuchin monkeys and rhesus monkeys.

Given the three-way interaction, we conducted separate within-subjects repeated-measures ANOVAs for each species with ratio and difficulty level as within-subjects variables. For capuchin monkeys, there was a significant main effect of ratio, $F(7, 63) = 7.67, p < .001, \eta^2_p = .46$ and of difficulty level, $F(5, 45) = 291.93, p < .001, \eta^2_p = .97$, and a significant interaction between ratio and difficulty level, $F(35, 315) = 4.12, p < .001, \eta^2_p = .31$. For rhesus monkeys, the repeated-measures ANOVA revealed a significant main effect of difficulty level, $F(5, 30) =$

13.48, $p < .001$, $\eta^2_p = 0.69$, but not of ratio, $F(35, 210) = 2.13$, $p = .75$, $\eta^2_p = .09$. There was a significant interaction between ratio and difficulty level, $F(35, 210) = 2.13$, $p = .001$, $\eta^2_p = .26$.

Based on a visual inspection of Figure 3, the clearest examples of deviation from baseline were the .75 and .25 ring ratios. Here, and for the human participants, we used the .50 ratio as the baseline to compare against our critical test trials (.25 and .75 ratios) instead of the 0 (no ring) ratio as monkeys and human participants often over-classified the 0 (no ring) ratio as ‘small.’ Thus, the .50 ring ratio appeared to be a truer reflection of baseline performance given the full distribution of data across all ring ratios. A Bonferroni adjusted alpha level of .016 was used per test (.05/3). For capuchin monkeys, central dots were classified as ‘small’ significantly less often in the .75 ratio than in the .50 ratio ($t(9) = 7.18$, $p < .001$) or in the .25 ratio ($t(9) = 3.72$, $p = .005$), but there was not a significant difference between the .25 ratio and .50 ratio ($t(9) = 1.02$, $p = .33$). For rhesus monkeys, performance did not differ significantly for the .50 and .25 ratios ($t(6) = .86$, $p = .42$), for the .50 and .75 ratios ($t(6) = .72$, $p = .50$), nor for the .25 and .75 ratios ($t(6) = 1.06$, $p = .33$). Thus, capuchin monkeys over-classified dots as ‘small’ when surrounded by large rings as would be expected in a human-like perception of this illusion, but rhesus did not as a group. We also explored individual differences by comparing each animal’s performance (percentage correct) in the critical test trials (.25 versus .75 ratios). Individual data are provided in the online appendices.

Humans

We conducted a within-subjects ANOVA to examine the effect of target dot to ring ratio (0, .25, .33, .45, .50, .55, .67, and .75) and absolute difficulty level (1-6; as described in Experiment 1) on the proportion of trials where the participants made a dot classification of ‘small.’ There was a significant main effect of ring ratio, $F(7, 112) = 9.19$, $p < .001$, $\eta^2_p = .37$,

and difficulty level, $F(5, 80) = 351.07, p < .001, \eta^2_p = .97$. There was a significant interaction between ring ratio and difficulty level, $F(35, 560) = 2.26, p < .001, \eta^2_p = .12$. Figure 3 depicts group-level performance as a function of condition and difficulty level for human participants.

Collapsing across levels using the average mean percentage of small choices, we used a paired-samples t-test to compare the .50 ratio to the .25 ratio and .75 ratio. We also compared the .25 ratio to the .75 ratio. Finally, we compared the .75 and .67 ratios and the .25 and .33 ratios to establish whether there was an ‘optimal’ ratio at which under- or overestimation occurred as has been listed in the previous literature (e.g., Nicolas, 1995; Ogasawara, 1952; Piaget et al., 1942; Van Ittersum & Wansink, 2012). A Bonferroni adjusted alpha level of .01 was used per test (.05/5). Central dots were classified as ‘small’ significantly more in the .25 ratio than in the .33 ratio ($t(16) = 4.66, p < .001$), and in the .50 ratio ($t(16) = 5.35, p < .001$), and in the .75 ratio ($t(16) = 5.02, p < .001$). Performance did not differ significantly for the .50 and .75 ratios ($t(16) = -1.73, p = .10$), nor for the .67 and .75 ratios ($t(16) = -1.14, p = .27$). Data for individual participants are provided in the online appendices.

3.2.3 Discussion

As expected, the presence of smaller rings led to overestimation of dot size and larger rings led to underestimation of dot size for human participants. Ultimately, the .25 ratio led to the highest cases of underestimation in the present experiment, and did so significantly more often than the .33 ratio. Although previous studies reported that a ratio close to .33 led to maximal underestimation and a ratio close to .67 led to maximal overestimation of the central dot (e.g., Nicolas, 1995; Ogasawara, 1952; Piaget et al., 1942; Van Ittersum & Wansink, 2012), we did not find evidence of these as optimal ratios in the current experiment. Rather, the even more extreme ratios produced even greater evidence of the illusion.

Capuchin monkeys and some rhesus monkeys showed very similar performance patterns to the human participants, overestimating dots encircled by a small ring (.75 ratio) and underestimating dots encircled by a large ring (.25 ratio). The ratios of .25 and .75 appeared to be most effective for monkeys and humans, although there may be other ratios leading to a stronger illusion if the range were extended beyond the ratios presented here. Interestingly, an increased number of individual monkeys (14 of 17) perceived the illusion in Experiment 2 as compared to Experiment 1 (2 of 19; see Supplementary Materials). We did find evidence of a reversed illusion among three monkeys, but this was much less common than in Experiment 1 (where 6 monkeys showed evidence of the reversed illusion). This difference in results between Experiment 1 and Experiment 2 suggested that the classification task assisted in isolating the central dot, reducing the possible reliance that the monkeys had on using the outer ring to help guide choice behavior in the first experiment. The results from Experiment 2 suggest that two nonhuman primate species other than chimpanzees (Parrish & Beran, 2014) perceive the Delboeuf illusion in a human-like fashion when tested using an absolute classification task.

3.3 General Discussion

Humans and both species of monkeys were proficient in the current set of size-judgment experiments, successfully choosing the larger of two central dots in the relative discrimination task (Experiment 1) and the absolute classification task (Experiment 2). The introduction of Delboeuf rings impacted perception of central dot size to varying degrees. In Experiment 1, humans demonstrated evidence of the illusion, choosing the dot surrounded by the small ring as larger than the same-sized dot in the larger ring. The monkeys did not show the same evidence of this illusion in Experiment 1. Rather, several of the monkeys revealed a pattern indicative of a

potential reversed illusion (i.e., they preferred a dot in a *large* ring relative to an identical dot in a small ring).

Following Experiment 1, we were concerned that the monkeys may have had a bias to choose the larger of two stimuli when incorporating both dot size *and* ring size into the discrimination when differently sized rings were presented. This bias would conflict with the task demand to select only on the basis of target dot size. This large-ring bias could account for the current pattern of results, leading to a potential misidentification of a reversed Delboeuf illusion among monkey species. In Experiment 1, we presented stimuli (central dots and concentric rings) that were identical in their presentation (black on a white background). Further, we used a training procedure that presented dots and rings at equal rates to minimize enhanced attention towards either of these elements within the illusory array. This approach differed from similar illusion studies with animals using the Ebbinghaus-Titchener illusion that presented target and inducer features with different colors, or purposefully trained the animals to ignore the illusory-inducing stimuli (e.g., Nakamura et al., 2008, 2014; Parron & Fagot, 2007).

We chose our approach in Experiment 1 because there was sufficient evidence that differential attention to various elements within an array leads to differences in the perception and magnitude of many geometric illusions within humans, even leading to their complete elimination or reversal (e.g., Coren & Girgus, 1972; Ebert & Pollack, 1972, 1973; Girgus, et al., 1972; Martin, 1979; Massaro & Anderson, 1971; Weintraub & Cooper, 1972; Yamazaki, Otsuka, Kanazawa, & Yamaguchi, 2010). Further, positive comparative evidence for the Ebbinghaus-Titchener illusion has been cited in tasks that do not isolate the different features of the visual array during training or testing (e.g., Murayama et al., 2012; Rosa Salva et al., 2013; Sovrano et al., 2015). Thus, we deliberately did not enhance attention towards the central dot to avoid

inadvertently reducing the natural emergence of the Delboeuf illusion. However, our training paradigm and the results of Experiment 1 suggested that the monkeys may have inappropriately incorporated rings into their size judgments of central dots because we did not visually differentiate the feature of interest (dot or ring). This could have led to a reversed illusion.

In Experiment 2, we used an absolute classification task to eliminate this concern. In the classification task, the monkeys could no longer choose the stimulus with the larger ring, but instead had to learn to classify dot sizes surrounded by a continuum of outer ring sizes when only the target dot mattered to determining the correct classification. Human participants overestimated dot sizes surrounded by smaller rings and underestimated dot sizes surrounded by larger rings – this is the traditional illusion. We also found positive evidence of the illusion in capuchin monkeys at the group level and at the individual level for most capuchin and rhesus monkeys. These positive results matched evidence of the Delboeuf illusion in chimpanzees (Parrish & Beran, 2014) and of other geometric illusions among capuchin monkeys and rhesus monkeys (e.g., Agrillo et al., Bayne & Davis, 1993; Fujita, 1996; Suganuma et al., 2007; Zivotofsky et al., 2005).

Illusions rely on the simultaneous processing of multiple parts of a visual array. Humans with an increased global or holistic perceptual mode of processing demonstrate greater degrees of perceiving illusions (e.g., Berry, 1968, 1971; Dawson, 1967; Witkin, 1967), whereas humans who are more locally oriented failed to perceive illusions as readily (e.g., Dakin & Frith, 2005; de Fockert, Davidoff, Fagot, Parron, & Goldstein, 2007; Happé, 1996; Happé, Briskman, & Frith, 2001). Of interest to the current study, comparative evidence supports a more locally-oriented processing style for capuchin monkeys (De Lillo, Spinozzi, Truppa, & Naylor, 2005; Spinozzi, De Lillo, & Salvi, 2006; Spinozzi, De Lillo, & Truppa, 2003) and rhesus monkeys

(Hopkins & Washburn, 2002, but see Tanaka & Fujita, 2000; Tanaka, Onoe, Tsukada, & Fujita, 2001). Processing style plays a large role in the emergence of geometric illusions, but the methodology used to elicit these illusions can favor one style of processing over the other. Critically, using procedures that do not isolate or enhance attention to different elements may be an important feature for illusion emergence, especially among species that are more locally-oriented (see Rosa Salva et al., 2013, for more discussion). Of course, therein lies the challenge of instructing nonverbal species to attend to one specific element of interest in a complex multi-element array, especially if that one element is not visually differentiated from the other(s). This can inadvertently lead to a different, but equally challenging problem that we encountered in the first experiment, in which monkeys might have incorporated the inducer into their size judgment. The absolute classification task that we used in Experiment 2 allowed us to overcome these concerns, but this cannot eliminate these concerns completely.

Studies presenting the Delboeuf illusion (and other size illusions) to additional nonhuman species will be needed for establishing when, why, and for whom these illusions emerge and the mechanisms that lead to their emergence. Through the current and related investigations, we can begin to disentangle competing hypotheses of illusion perception among nonhuman animals, and the complementary roles that methodology and perceptual processing mode play.

3.4 References

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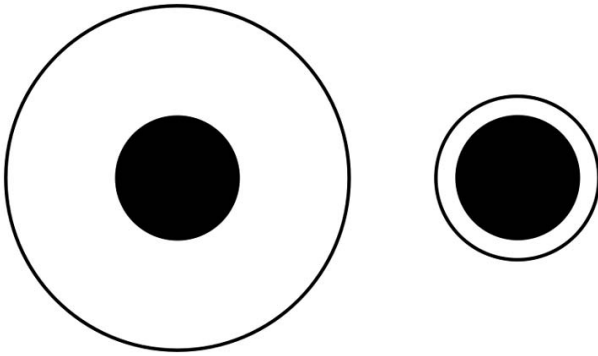
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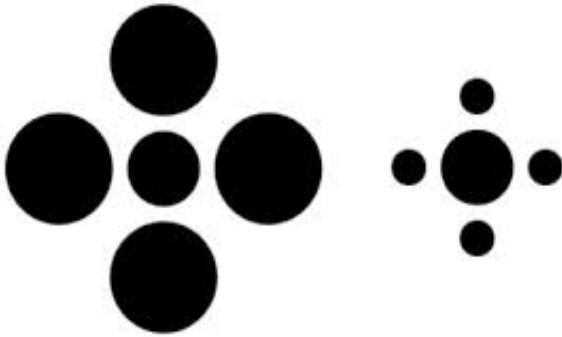
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3.5 Figures

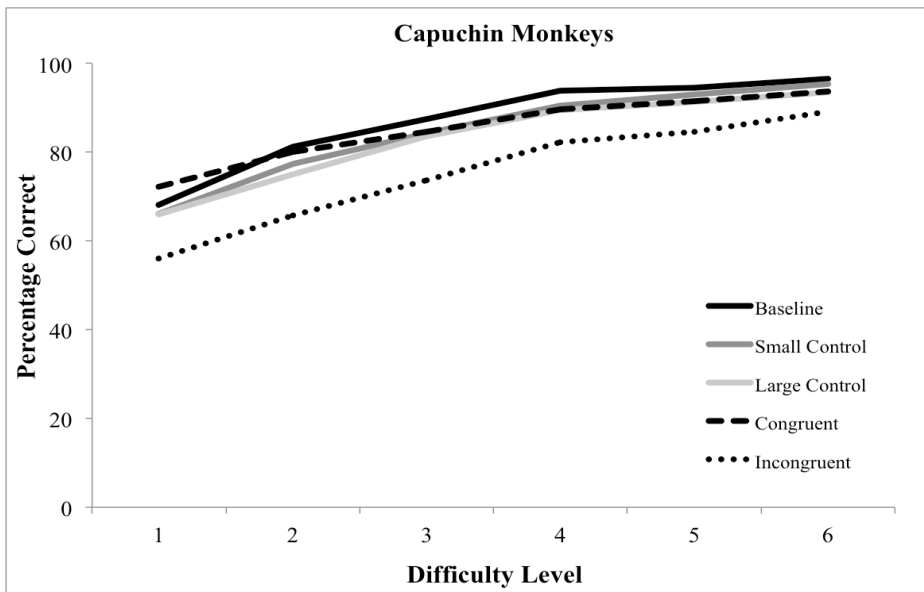


A. Delboeuf illusion

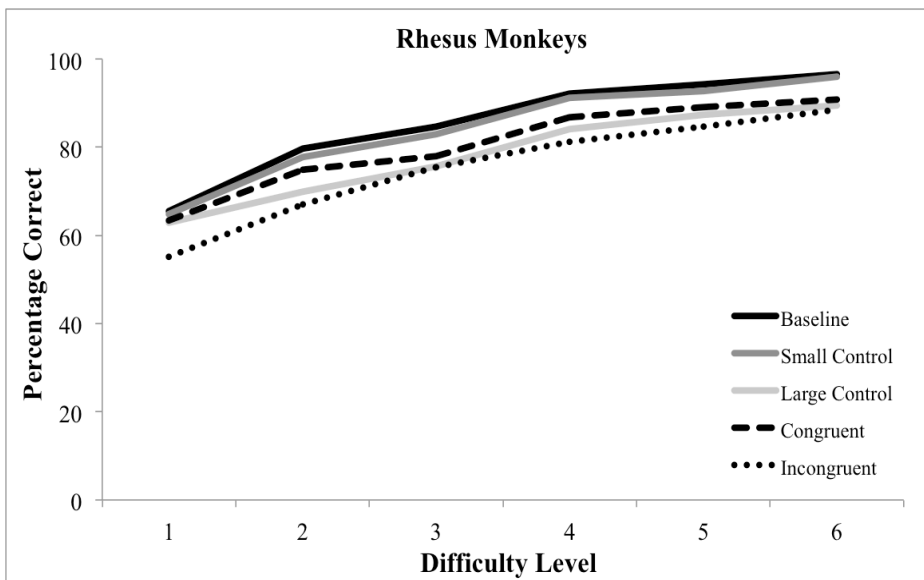


B. Ebbinghaus-Titchener illusion

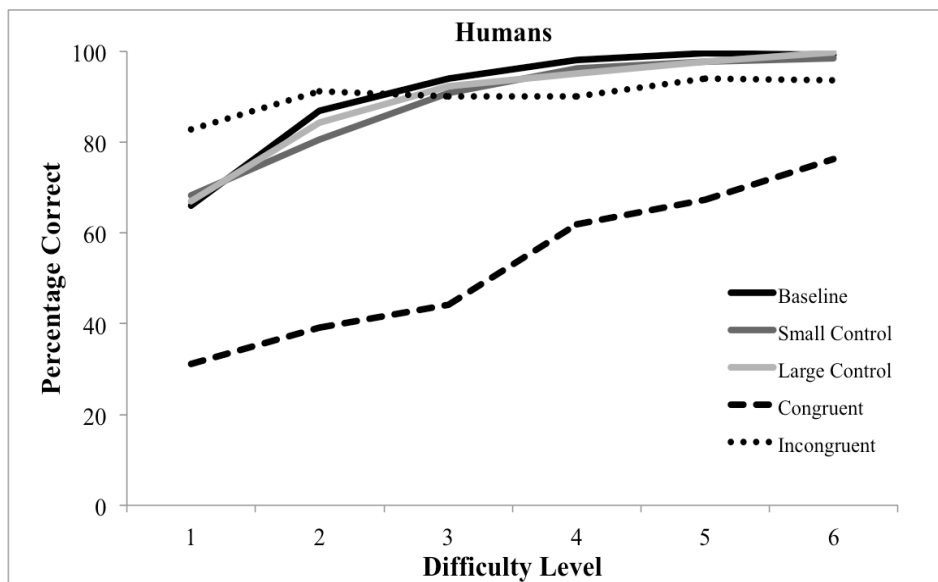
Figure 1. The Delboeuf (A) and Ebbinghaus-Titchener (B) illusions, both depicting identically sized central dots surrounded by differently sized inducers. The size of the central dot surrounded by a small inducer(s) (at left; ring: Delboeuf illusion or circles: Ebbinghaus-Titchener illusion) is typically overestimated relative to an identical dot surrounded by a large inducer (at right).



A.

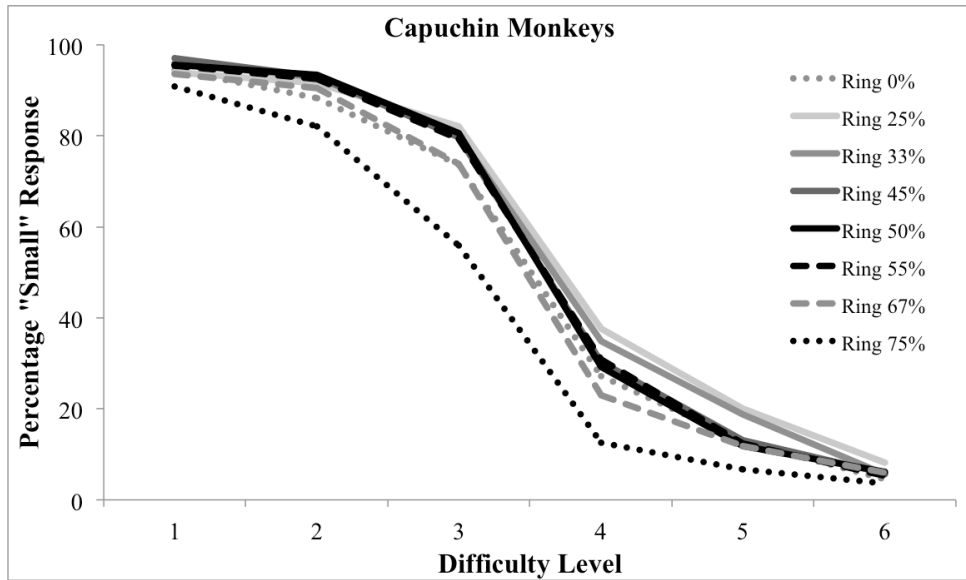


B.

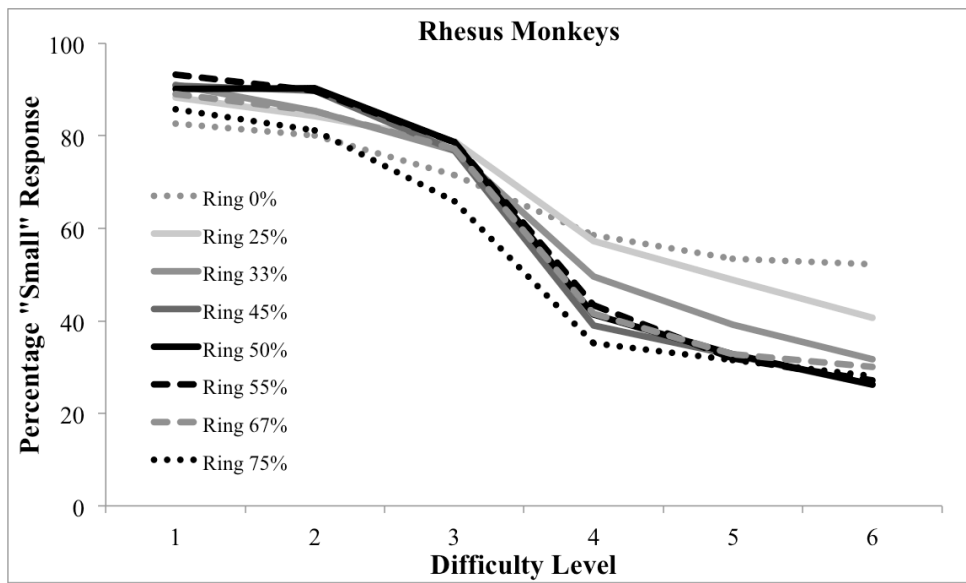


C.

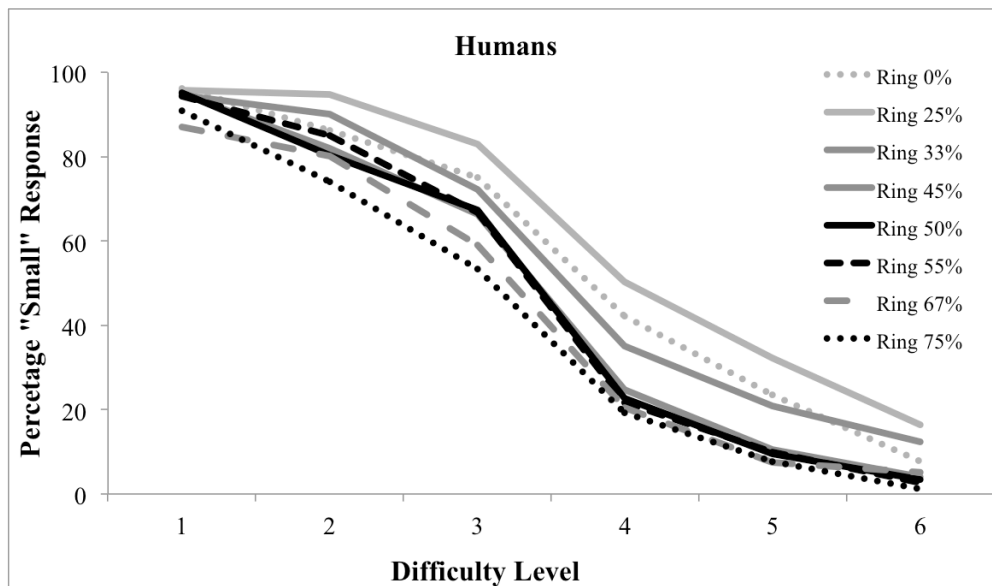
Figure 2. Mean percentage correct (i.e., selection of the larger central dot) for capuchin monkeys (A), rhesus monkeys (B), and human participants (C) in Experiment 1, including the following conditions: Baseline, Small Control, Large Control, Congruent Test, and Incongruent Test. Absolute difficulty levels progress from 1 (hardest) to 6 (easiest).



A.



B.



C.

Figure 3. Mean percentage of 'small' responses for capuchin monkeys (A), rhesus monkeys (B), and human participants (C) in Experiment 2, including the following ratios: 0, .25, .33, .45, .50, .55, .67, and .75. Difficulty levels progress from 1 (smallest dot) to 6 (largest dot).

INVESTIGATING THE EBBINGHAUS-TITCHENER ILLUSION:
LESSONS FROM NONHUMAN PRIMATES

By

AUDREY E. PARRISH

ABSTRACT

In the current set of studies, we investigated whether chimpanzees, rhesus monkeys, and capuchin monkeys perceived the Ebbinghaus-Titchener illusion in a similar manner as human adults. The Ebbinghaus illusion is a geometric size illusion that occurs because of contrast effects – large inducers lead to central dot size underestimation and small inducers lead to central dot size overestimation. In Experiment 1, we presented chimpanzees with a two-choice discrimination task where they selected the larger of two round food items on each trial. Round inedible inducers of different size surrounded the food items to create an illusory context. Chimpanzees did not experience the illusion, as they accurately selected the larger food portion

across control and test conditions. In Experiments 2 and 3, monkeys and humans were presented with a computerized task that required subjects to classify a central dot that was sometimes surrounded by small or large inducers as being either 'small' or 'large.' We found evidence of the Ebbinghaus-Titchener illusion as it typically manifests among human participants, but we did not find evidence of the illusion among monkeys. Rather, most monkeys demonstrated a response bias to incorporate outer inducers into their dot classification. The current results and previous comparative findings suggest that the Ebbinghaus-Titchener illusion presents a challenging test case for nonverbal species. Specifically, subjects tended to incorporate the inducers into target discrimination, which can lead to a non-illusion or a reversed illusion as a byproduct of misunderstanding the task rule.

INDEX WORDS: Visual illusions; Ebbinghaus-Titchener illusion; Chimpanzees; Capuchin monkeys; Rhesus monkeys; Perception; Response bias

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4 INVESTIGATING THE EBBINGHAUS-TITCHENER ILLUSION: LESSONS FROM NONHUMAN PRIMATES

Seeing is believing – we assess and react to the veridical nature of visual sensation, with our perceptual systems rarely misleading our subsequent thoughts and actions. Thus, visual illusions, when they occur, are an intriguing phenomenon in the world of perceptual science. Illusions emerge when we misperceive the most basic physical properties of our external world, such as object size, shape, and color, as a function of the context in which we perceive those objects. Intriguing as illusory phenomena are, they also function to provide information on the organization and processes by which we perceive physical stimuli. Further, studying illusions among nonhuman animals allows for the comparison of different species' perception. If an animal misperceives the world in a similar fashion to humans, perhaps those species share commonalities in their visual and perceptual systems (Agrillo, Petrazzini, & Dadda, 2013; Wasserman, 2012).

Geometric illusions comprise the largest category of perceptual illusions, and they emerge when a target's physical properties (e.g., size, shape, length, width, diameter, orientation, etc.) are distorted on the basis of the target's surrounding context. Because of their seemingly simple 2-dimensional format, geometric illusions have been presented to several species of nonhuman animals including a number of nonhuman primates (hereafter primates). Typically, primates perceive these geometric illusions in a similar fashion to humans, including the Delboeuf illusion (*Cebus apella* and *Macaca mulatta*: Parrish, Brosnan, & Beran, 2015; *Pan troglodytes*: Parrish & Beran, 2014a), the Horizontal-Vertical illusion (*Cercopithecinae* and *Cebus*: Dominguez, 1954), the Zöllner illusion (*Macaca mulatta*: Agrillo, Parrish, & Beran, 2014; *Papio papio*: Benhar & Samuel, 1982), the Ponzo illusion (*Macaca mulatta*: Bayne &

Davis, 1993; Fujita, 1996; *Pan troglodytes*: Fujita, 1997, 2001), the Mueller-Lyer illusion (*Cebus apella*: Suganuma, Pessoa, Monge-Fuentes, Castro, & Tavares, 2007), the Duncker illusion (*Macaca mulatta*: Zivotofsky, Goldberg, & Powell, 2005), the rectangle illusion (*Cercopithecinae* and *Cebus*: Dominquez, 1954; Harris, 1968) and the corridor illusion (*Papio papio*: Barbet & Fagot, 2002; *Pan troglodytes*: Imura, Tomonaga, & Yagi, 2008). Overall, comparative research reveals similarity of illusory perception across several primate species and humans, suggesting commonalities in the perceptual systems of these highly related species.

The Delboeuf illusion emerges when a central dot encircled by a small ring is perceived to be larger than the same-sized dot encircled by a large ring (Delboeuf, 1869). Chimpanzees demonstrated perception of this illusion in a food choice task, selecting the larger of two circular food portions (mimicking central dot) when plated on same-sized plates (creating the ring; Parrish & Beran, 2014a). However, small plates were preferred to large plates when identical portions were presented, much like the Delboeuf illusion demonstrates. Further, we tested capuchin and rhesus monkeys on a computerized two-choice task similar to the chimpanzee task, but with 2-dimensional dots and rings (Parrish et al., 2015). The monkeys developed a response bias, erroneously incorporating outer ring size into the dot discrimination, leading to what might be interpreted as a reversed illusion (a preference for the dot encircled by the *large* ring). We extended our work with monkeys to a computerized classification task in which monkeys classified a central dot as 'small' or 'large.' Monkeys' judgments of dot size varied as a function of ring size similarly to humans, such that larger rings led to dot underestimation and smaller rings led to dot overestimation. Transforming the question from a relative discrimination task to a classification task removed the possibility for monkeys to simply choose the dot with the

bigger ring. The classification task helped to isolate the target of interest (the dot), which then allowed for a fairer assessment of the Delboeuf illusion.

In the related Ebbinghaus-Titchener illusion (Ebbinghaus, 1902) a central dot surrounded by several small outer dots is perceived as larger than the same-sized central dot surrounded by several large outer dots (see Figure 1). The Delboeuf and Ebbinghaus illusions are highly similar geometric size illusions that occur due to contrast effects – large contexts lead to underestimation of target size and small contexts lead to overestimation of target size (e.g., Nicolas, 1995). Although the Ebbinghaus-Titchener illusion quite literally is the textbook example of visual illusions and has been widely studied among human adults (e.g., Coren & Enns, 1993; Girgus, Coren, & Agdern, 1972; Massaro & Anderson, 1971; Weintraub, 1979), there is relatively little research on this illusion in nonhuman animals.

The single primate study investigating the Ebbinghaus-Titchener illusion revealed a non-effect in which baboons accurately perceived target circle size in control trials and were indifferent to the illusion probe trials presenting the illusory-inducing circles (Parron & Fagot, 2007). That study presented the baboons with different colored target and inducer circles with the specific intent to promote attention to the bright yellow central target over the inducing circles. Additional negative evidence for the existence of the illusion among animals comes from a study that used a fading procedure to gradually introduce the inducer circles after pigeons (*Columbidae*) had been trained to discriminate a range of target diameters (Nakamura, Watanabe, & Fujita, 2008).

Arguably, these previous procedures may have enhanced attention towards the target and trained animals to ignore the inducers, leading to a decrease in the likelihood of illusion emergence. Positive evidence of a human-like Ebbinghaus-Titchener illusion among nonhumans

comes from a dolphin (*Tursiops truncatus*: Murayama, Usui, Takeda, Kato, & Maejima, 2012) and four-day-old chicks (*Gallus gallus*: Rosa Salva, Rugani, Cavazzana, Regolin, Vallortigara, 2013) using procedures that did not enhance attention to the target or inducing stimuli, but rather presented both features throughout the entire experiment. Because of our recent studies of the Delboeuf illusion (Parrish & Beran, 2014a, Parrish et al., 2015), and given the positive evidence among monkeys using a computerized classification task, we introduced the Ebbinghaus-Titchener illusion to chimpanzees, rhesus monkeys, and capuchin monkeys to test whether this illusion might emerge using different methodological approaches from those used previously with other nonhuman species.

In Experiment 1, chimpanzees were presented with a relative quantity judgment paradigm that required subjects to choose between two sets of food that differed based on their relative size. Also known as the natural choice paradigm, this procedure has many advantages, including the requirement of little to no training, high levels of motivation, establishment of subjective food preferences, and the demonstration of perceptual sensitivity to quantity, size, or amount of food arrays (see Beran, Ratliff, & Evans, 2009; Silberberg, Widholm, Bresler, Fujita, & Anderson, 1998). Menzel (1961) discussed the utility of this direct choice paradigm in that it facilitates reliable and rapid measures of food-size preferences that are stable across time and other variables (e.g., aging, etc.). This paradigm also was successful in testing the Delboeuf illusion among chimpanzees in our previous work (Parrish & Beran, 2014a).

In Experiment 2, we extended these questions to rhesus monkeys and capuchin monkeys using a computerized methodology to further establish whether other, more distantly related primate species perceived the Ebbinghaus-Titchener illusion. Here, we tested monkeys using a computerized classification task, in which subjects had to classify target size when surrounded

by inducing circles of variable size. A classification task was used because this methodology had proven to be successful in testing similar illusions among nonhuman primate species, such as the Delboeuf illusion (Parrish et al., 2015). In Experiment 3, human adults were presented with the same computerized task to establish how monkey illusion perception related to that of human adults.

4.1 Experiment 1

4.1.1 Methods – Phase 1

4.1.1.1 Participants

The primates included in all studies were housed and tested at the Language Research Center (LRC) of Georgia State University (GSU) in Atlanta, Georgia. LRC primates were never food deprived for testing purposes and had 24-hour access to water, including during test sessions. They received a daily diet of fruits, vegetables, and primate chow regardless of participation in testing, and caloric intake was kept consistent by taking into account the amount of food earned from testing when determining the diet. All testing protocols complied with guidelines for working with primates as established by protocols approved by the GSU Institutional Animal Care and Use Committee. GSU is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care.

Three chimpanzees participated in this study including one female (Lana – 44 years) and two males (Sherman – 41 years, Mercury – 28 years). All chimpanzees were housed together in the same building and spent time together in social groups daily, but they voluntarily separated for test sessions. All chimpanzees had extensive prior experience making choices between different quantities of foods (e.g., Beran 2001, 2004, 2012; Beran et al., 2009; Parrish & Beran, 2014a, 2014b; Parrish, Evans, & Beran, 2015; Rumbaugh, Savage-Rumbaugh, & Hegel, 1987).

4.1.1.2 Apparatus

Chimpanzees were presented with two food quantities via an 80 cm wide by 28 cm deep sliding tray mounted to a 45 cm high bench outside of their enclosure. The test bench also included an opaque blind that could be lowered completely to prevent the chimpanzee from viewing the food items before the beginning of the trials. During the choice phase, the blind was lowered partially so the chimpanzee could only view the choices and the experimenter could only view the chimpanzee's hands once a response had been made (to prevent the experimenter from providing inadvertent cues to the chimpanzee). To further prevent cuing, the experimenter closed her eyes during the choice phase and a second experimenter out of view of the chimpanzees announced the chimpanzee's choice. These response choices by the chimpanzees were unambiguous in terms of direct points to one of the two options.

4.1.1.3 General Procedure

The testing setup included two choice arrays from which the chimpanzees chose one of those arrays. Choice stimuli were comprised of an edible central target dot (lunchmeat slices) that in some conditions were surrounded by several inedible inducer circles of variable size. The lunchmeat was cut into a round shape using a circular cookie cutter. When present, the inducing circles were comprised of smaller circular pieces of felt material that were similar in color to the lunchmeat. In critical test trials, the inducing circles served to create a potential illusory inducing context in which the participants might misperceive the size of the central target.

Two different sizes of lunchmeat were used, including a larger portion (7.3 cm in diameter) and a smaller portion (6.35 cm in diameter). When present, several small and large inedible circles surrounded the target dots. The small inducing circles were 2.8 cm in diameter and the large inducing circles were 7.9 cm in diameter. Inducing circles were positioned so that

they were equidistant from the center of the lunchmeat. Large inducing circles were positioned approximately 5.1 cm away from the center point of the food portion. Small inducing circles were positioned approximately 3.8 cm away from the center point of the food portion.

After preparing the food choices, Experimenter 1 (E1) raised the blind approximately 10 cm and slid the shelf (and food choices) toward the chimpanzee after 3 s. The second experimenter (E2) observed and recorded the chimpanzee's selection of the left or right food choice. Following the chimpanzee's selection, E1 immediately delivered the contents of the chosen food option to the chimpanzee for consumption.

Table 1 outlines the seven trial types and predicted performance patterns for each trial type. Baseline trials presented two target dots with no inducer circles, and this established baseline performance regarding how well the chimpanzees could select the larger of two pieces of lunchmeat without any illusory inducing circles. The two dot sizes were always different, and thus there was always an objectively correct choice in these trials.

Small Control trials presented the two different target dots, each surrounded by the small inducer circles. Large Control trials presented the two different target dots, each surrounded by the large inducer circles. These arrays served as control trials as they presented two objectively different-sized food portions that should be easily differentiated, as the inducers were identical in size between the two arrays, and thus should not generate an illusory context.

Four test trial types were presented, including Small Mixed trials, Large Mixed trials, Inducer Control trials, and Ebbinghaus-Titchener Illusion trials. In the Small Mixed and Large Mixed trials, inducers surrounded one dot in the array whereas inducers did not surround the second dot. In both of these trial types, the two different lunchmeat portions were presented. The Small Mixed trials presented the smaller portion with no inducers versus the larger portion

surrounded by small inducers. If the illusion were to occur, these trials should increase accuracy in the task compared to baseline and control trials, as the large portion may be over-estimated because it would appear even larger when surrounded by small inducers. The Large Mixed trials presented the smaller food portion with no inducers versus the larger portion surrounded by larger inducers. This trial type should decrease accuracy in the task relative to baseline and control trials, as the large target may be under-estimated, as it would appear smaller than its true size when surrounded by large inducers. Subjects may perceive these two dots as being close to equal in size rather than perceiving their true difference.

The Inducer Control trials presented the small portion surrounded by large inducers and the large portion with no inducers. In this trial type, the chimpanzees should select the large portion at even greater levels than Baseline or Control trials as the small portion would appear even smaller inside of the large context. This trial type introduced a trial in which the large portion was *not* located inside of inducers, which was true for all other test trial types. We included this trial type to prevent the animals from learning a simple rule such as ‘select the portion surrounded by inducers.’

Finally, the Ebbinghaus-Titchener Illusion test trials presented two identical food portions surrounded by different-sized inducers. This array typically generates the Ebbinghaus-Titchener illusion in humans such that the target dot surrounded by small inducers appears larger than the equal-sized target surrounded by large inducers.

Chimpanzees completed a total of 66 testing trials, including 30 Baseline trials, 10 Control trials (5 Large Control and 5 Small Control), 10 Mixed trials (5 Small Mixed and 5 Large Mixed), 6 Inducer Control trials, and 10 Ebbinghaus-Titchener Illusion trials. Trial types were pseudo-randomly presented, with at least one inducer trial presented in every block of three

trials and at least one Inducer Control in a test session. Chimpanzees completed 10 to 20 trials per day, depending upon their motivation to continue working on the task.

4.1.2 Methods - Phase 2

Phase 2 was identical to Phase 1, except for the introduction of different food portion sizes. Because we documented a ceiling effect in Phase 1 in which the animals were highly proficient in selecting the larger portion of meat across all trial types, we introduced slightly more difficult discriminations in Phase 2. In Phase 1, the larger portion of lunchmeat measured 53.3 sq. cm and the smaller portion measured 40.4 sq. cm. Here, the larger portion of lunchmeat measured 64 sq. cm and the smaller portion measured 53.3 sq. cm.

Chimpanzees completed a total of 124 testing trials, including 24 Baseline trials, 32 Control trials (16 Large Control and 16 Small Control), 32 Mixed trials (16 Small Mixed and 16 Large Mixed), 12 Inducer Control trials, and 24 Ebbinghaus-Titchener Illusion trials. Trial types were randomly presented. Chimpanzees completed 10 to 20 trials per day, depending upon their motivation to continue working on the task.

4.1.3 Results - Phase 1

First, we examined performance in the non-illusion trial types, including Baseline and Control trials. Chimpanzees performed very well in Baseline trials, significantly preferring the larger portion of food to the smaller portion of food in Baseline trials: Binomial tests, all chimpanzees $p < .0001$ (see Figure 2). The same was true for Control trials for Mercury and Lana. Collapsing across control trial type (Small Control and Large Control), Mercury and Lana significantly preferred the larger food portion over the smaller portion in Control trials; Binomial tests, both chimpanzees: $p = .02$. Sherman chose the larger food portion in 70% of Control trials, but this did not exceed levels of statistical significance.

Chimpanzees continued to choose the largest portion of food in all test trials that presented a true difference in food amount despite the illusory contexts. Because of the high performance rates across Small Mixed, Large Mixed, and Inducer Control trials, we collapsed across trial types. All chimpanzees performed significantly better than chance; Binomial tests: Sherman $p < .001$, Mercury $p = .02$, and Lana $p = .04$.

In the test of the Ebbinghaus-Titchener illusion, we compared each chimpanzee's percentage of trials selecting the food portion surrounded by small inducers to chance levels. None of the chimpanzees chose the food surrounded by small inducers at levels exceeding chance; Binomial tests: all chimpanzees $p > .05$.

4.1.4 Results - Phase 2

Again, we first examined performance in the non-illusion trial types, including Baseline and Control trials for Phase 2. Chimpanzees performed very well in Baseline trials, significantly preferring the larger portion of food to the smaller portion of food: Binomial tests: Sherman $p = .02$, Mercury $p < .0001$, and Lana $p < .001$ (see Figure 3). Collapsing across control trial type, all three chimpanzees significantly preferred the larger food portion over the smaller portion; Binomial tests: Sherman $p = .002$, Mercury $p < .001$, and Lana $p < .001$.

To examine performance in the test trials that presented a true difference in food amount, we compared performance in the Small Mixed, Large Mixed, and Inducer Control trials to performance in the Baseline trials for each chimpanzee. Large Mixed trials should have decreased performance relative to Baseline as the large portion should be underestimated in the large inducers. However, chimpanzees were equally proficient in choosing the larger portion in Large Mixed and Baseline trials (Fisher's Exact test: Sherman $p = .73$, Mercury $p = .09$, Lana $p = .23$). Small Mixed trials should have increased performance relative to Baseline, as the large

portion should be overestimated in the small inducers. The opposite was true for Sherman; he selected the *smaller* portion of food significantly more often in the Small Mixed trials versus Baseline trials (Fisher's Exact test: Sherman $p = .02$). The other two chimpanzees again did not show a difference in performance for this comparison (Fisher's Exact test: Mercury $p = .20$ and Lana $p = 1.0$). Finally, Inducer Control trials should have increased performance relative to Baseline as the small portion should be judged as even smaller than it truly was in the large inducers. Chimpanzees again were equally proficient in selecting the larger food portion across trial type (Fisher's Exact test: Sherman $p = .69$, Mercury $p = .31$, Lana $p = 1.0$).

For Ebbinghaus-Titchener illusion trials, we compared each chimpanzee's selection of the food portion surrounded by small inducers to chance levels. As in *Phase 1*, none of the chimpanzees chose the food surrounded by small inducers at levels exceeding chance; Binomial tests: all chimpanzees $p > .05$.

4.1.5 Discussion

Chimpanzees were highly proficient in choosing the larger of two food portions across baseline, control, and test conditions in both Phase 1 and Phase 2. These high performance rates mirrored performance by these chimpanzees and others in various tests of quantity judgment (Beran, 2001, 2004, 2012; Beran & Beran, 2004; Boysen & Berntson, 1995; Dooley & Gill, 1977; Hanus & Call, 2007; Menzel, 1960, 1961; Menzel & Davenport, 1962; Menzel & Draper, 1965; Rumbaugh et al., 1987). Ultimately, the chimpanzees did not perceive the illusion in this food choice context despite recent successful efforts to induce the Delboeuf illusion in the same chimpanzees using a food choice task (Parrish & Beran, 2014a). In addition to misjudgments of quantity in the Delboeuf illusion, other misleading contexts have impacted chimpanzee quantity judgment, including container size, cohesiveness of food sets, and the presence and location of

the largest single item (Beran, Evans, & Harris, 2008; Boysen, Berntson, Mukobi, 2001; Parrish & Beran, 2014a).

That the Ebbinghaus-Titchener array does not lead to similar quantity biases and errors is intriguing. Qualitatively speaking, the Ebbinghaus-Titchener inducers were quite salient in comparison to previous contexts that have produced quantity misjudgments or biases. Although we presented inducers that were color-matched to the lunchmeat slices in the current task to increase similarity between target and inducers, the inducers were still visually distinctive, whereas the previous studies reported above incorporated subtle differences to the context or food arrangement (e.g., plate size and spatial arrangement of food items within sets). Further, the chimpanzees may have actively discounted the inducers as they were clearly inedible, whereas the contexts were less overt and perhaps more difficult to discount in previous illusory studies (Beran et al., 2008; Boysen et al., 2001; Parrish & Beran, 2014a). The Ebbinghaus-Titchener illusion is, by definition, a more complex array than the Delboeuf array, with multiple large stimuli from which it is difficult to visually isolate the target of interest (the central dot). This unique characteristic of the Ebbinghaus-Titchener array creates a particularly challenging methodological task to present to nonverbal species.

We thought that perhaps more difficult food size discriminations would evoke the Ebbinghaus-Titchener illusion in Phase 2 due to the ceiling effect documented in Phase 1. Chimpanzees remained proficient in selecting the larger portion of food across trial types and, again, did not fall prey to the illusion even with less discrepant portion sizes. These results suggest that chimpanzees do not perceive the Ebbinghaus-Titchener illusion in the current food-choice task. Future studies with chimpanzees and other great apes that extend the illusion to different contexts (e.g., computerized psychophysics task) are needed to establish whether the

illusion emerges under different methodological circumstances. We next extended this investigation to other primate species, including rhesus monkeys and capuchin monkeys, to establish whether monkey species also fail to perceive the illusion, or if perhaps, they perceive the illusion similarly to how humans perceive it.

4.2 Experiment 2

4.2.1 Methods

4.2.1.1 Participants

Six adult rhesus macaques (all males) and eight adult capuchin monkeys (4 females) were included in the following experiments. Rhesus monkeys were individually housed and had 24-hour access to a computerized testing apparatus within their home cage. Rhesus monkeys had constant visual and auditory access to conspecifics and received weekly access to an indoor-outdoor enclosure with another monkey. Capuchin monkeys were group housed in indoor-outdoor enclosures, and they separated voluntarily into individual testing enclosures for computerized testing (with visual and auditory access to conspecifics). These monkeys have participated in several computerized perceptual discrimination tasks (e.g., Agrillo et al., 2014; Beran & Parrish, 2013; Beran, Smith, Coutinho, Couchman, & Boomer, 2009; Parrish et al., 2015).

4.2.1.2 Apparatus

Nonhuman primates included in this study were joystick trained for computerized testing using the Language Research Center's Computerized Test System consisting of a color monitor, personal computer, digital joystick, and food pellet dispenser (Evans, Beran, Chan, Klein, & Menzel, 2008; Richardson, Washburn, Hopkins, Savage-Rumbaugh, & Rumbaugh, 1990). Primates manipulated the joystick with their hands to isomorphically control a small round

cursor on the computer screen. Monkeys were not restrained during testing, and thus the viewing distance from the monitor was approximately 30.5 cm to 40.5 cm. Correct responses led to banana-flavored pellet rewards (45-mg pellets for capuchins and 94-mg pellets for rhesus monkeys: Bio-Serv, Frenchtown, NJ) via a pellet dispenser interfaced to the computer through a digital I/O board (PDISO8A; Keithley Instruments, Cleveland, OH). Programs were written in Visual Basic 6.0.

4.2.1.3 Stimuli

On all trials, the stimulus, including a central dot and (when present) inducing circles, was black presented on a white background, to minimize enhanced attention to one of these array elements over the other. Using a psychophysical step procedure, a range of 13 possible target dots was established. Levels 1-6 were all smaller than the Level 7 dot, and their size was generated by the following equation: $\text{Level} = 3\text{cm} * 0.98^{(7 - \text{TrialLevel})}$. Levels 8-13 were all larger than the Level 7 dot, and their size was generated by the following equation: $\text{Level} = 3\text{cm} * 1.02^{(\text{TrialLevel} - 7)}$. This made Level 1 and Level 13 dots the easiest to discriminate from Level 7 and Level 6 and Level 8 dots the hardest to discriminate from Level 7. When they were present, small or large inducing circles surrounded the target dot. Small inducing circles were 1 cm in diameter. Large inducing circles were 4 cm in diameter.

4.2.1.4 Design and Procedure

At the outset of each trial, participants moved a small round cursor that they controlled into contact with a grey button at the top center of the computer screen. Then, that button disappeared, the cursor re-centered, and the test stimulus and two classification icons appeared as choice options. Each trial presented a single target stimulus (a central dot that was sometimes surrounded by inducing dots) at the top middle of the screen. Participants were required to

classify the central dot as ‘small’ (by moving the cursor to the bottom left of the screen to a blue rectangle) or ‘large’ (by moving the cursor to the bottom right of the screen to a green rectangle). Participants were required to select one of the classification icons within 3 s, or the trial was scored as an error. After selection of a stimulus or after 3 s of inactivity, the screen was cleared completely. Selection of the correct classification icon led to a melodic chime and a pellet reward. Selection of the incorrect classification icon led to a buzz tone and a 20-s timeout period during which the screen remained blank. The inter-trial interval was 1 second. Monkeys worked on the task between 4- and 6-hours per day, completing as many trials as possible within a testing session given their motivation to engage the task.

There were three conditions. Trials in the Baseline condition presented a central target dot on each trial with no inducing circles, and this established the baseline performance rate in classifying dot sizes when inducing circles could not make any impact on the perception of the dot sizes. Trials in the Large Inducer condition presented a target dot on each trial surrounded by six large inducing circles. Trials in the Small Inducer condition presented a target dot on each trial surrounded by eight small inducing circles.

4.2.1.4.1 Training

Monkeys completed a set of training trials to learn the rule of classifying the central target dot as ‘large’ or ‘small.’ This was done using the three easiest absolute levels for each classification (Levels 1-3 and Levels 11-13), divided into 50% Baseline trials, 25% Large Control trials, and 25% Small Control trials. The criterion was set to 85% correct over the most recent 60 trials. After monkeys reached criterion, they immediately entered the test phase during that session.

4.2.1.4.2 Pilot Test Data

Four capuchin monkeys completed a pre-study test in which they were randomly presented with all conditions within a test session (50% Baseline trials, 25% Small Inducer trials, and 25% Large Inducer trials). Pilot data suggested that the monkeys were classifying central dot size according to the inducing circle size in test trials, with Large Inducer trials posing a particular problem for animals. Overall, monkeys performed well in classifying central dot size in the Baseline and Small Inducer conditions, with an average accuracy of 86.5% for Baseline trials and 70.43% for Small Inducer trials (with a slight tendency to over-classify Small Inducer trials as ‘small’). On average, monkeys classified nearly all of Large Inducer trials as large (79.84% ‘large’ responses). Because of this early evidence of a response bias towards classification based on inducer size (especially for Large Inducer trials), we presented conditions in the formal testing phase sequentially rather than intermixed. Thus, the monkeys now completed 3,000 Baseline trials followed by 3,000 Small Inducer or 3,000 Large Inducer trials rather than trial-by-trial randomization of condition type. This blocked-presentation style was introduced in an attempt to reduce the reliance on inducer size during classification because, now, each trial presented the same inducer type for a larger number of trials. Three out of four of these monkeys who completed the pilot testing advanced to the formal testing phase. One monkey (Liam) was discontinued from the study for reasons unrelated to this experiment.

4.2.1.4.3 Testing

In the formal testing phase, we introduced the full continuum of levels (Levels 1 – 13, excluding Level 7 which never was presented). We oversampled the more difficult levels to increase the number of critical test trials presented (44% of test trials presented a randomly selected Level 4 to Level 10 trial whereas the remaining trials randomly sampled from the full

range of levels). Monkeys iterated between the three conditions, completing approximately 3,000 trials per block. Monkeys were required to meet criterion (85% correct over the most recent 60 trials) prior to the start of each new block using that condition type only and the three easiest small and large levels (Levels 1-3 and Levels 11-13).

We analyzed the first block of each condition (Baseline, Small Inducer, and Large Inducer) for the monkeys who completed all conditions (seven animals). Half of the animals did not pass training for the Large Inducer condition, displaying a response bias to classify all Large Inducer training trials as ‘large’, and thus they were not included in any of the following analyses.

4.2.2 Results

For all subsequent analyses in Experiment 2 and Experiment 3, we reduced the number of dot size levels from 13 levels to 6 levels, binning Levels 1 and 2 as the new Level 1, Levels 3 and 4 as the new Level 2, Levels 5 and 6 as the new Level 3, Levels 8 and 9 as the new Level 4, Levels 10 and 11 as the new Level 5, and Levels 12 and 13 as the new Level 6. Thus, Levels 1-6 progressed from smallest to largest.

We removed any trials in which the monkeys timed-out because they did not respond quickly enough. These were infrequent throughout all testing in the current experiment (1.7% of all trials).

Figure 4 depicts group-level performance (i.e., selection of the larger central dot) as a function of condition and dot size for the seven monkeys who completed all three conditions (Baseline, Large Inducer, Small Inducer). We used a mixed-design repeated-measures analysis of variance (ANOVA) to examine the effect of level (1-6) and condition (Baseline, Large Inducer, and Small Inducer) on the proportion of trials where the participants made a dot classification of

‘small’ with species (capuchin monkey and rhesus monkey) as the between-subjects variable. There was a significant main effect of level, $F(5, 25) = 407.27, p < .001, \eta^2_p = .99$, but not of condition, $F(2, 10) = 1.42, p = .29, \eta^2_p = .22$, nor of species, $F(1, 5) = .06, p = .82, \eta^2_p = .01$. There was a significant interaction between level and condition, $F(10, 50) = 37.49, p < .001, \eta^2_p = .88$. There was not a significant interaction between level and species, $F(5, 25) = .19, p = .96, \eta^2_p = .04$, nor between condition and species, $F(2, 10) = 40.73, p = .33, \eta^2_p = .20$. There was not a three-way interaction between level, condition, and species, $F(10, 50) = .48, p = .90, \eta^2_p = .09$.

Based on a visual inspection of Figure 4, we collapsed across species, small dot size levels (Levels 1-3) and large dot size levels (Levels 4-6) and compared all conditions to one another to explore the interaction of condition by level. A Bonferroni adjusted alpha level of .016 was used per test for the small and large levels (.05/3). For small levels, central dots were classified as ‘small’ significantly less often in the Large Inducer condition than in the Baseline condition ($t(6) = 8.04, p < .001$) and in the Small Inducer condition ($t(6) = 6.34, p = .001$), but there was not a significant difference between the Baseline and Small Inducer conditions ($t(6) = -1.02, p = .35$). For large levels, central dots were classified as ‘small’ significantly more often in the Large Inducer condition than in the Baseline condition ($t(6) = -4.14, p = .006$) and in the Small Inducer conditions ($t(6) = -10.67, p < .001$), but there was not a significant difference between the Baseline and Small Inducer conditions ($t(6) = 3.05, p = .02$).

4.2.3 Discussion

Rhesus monkeys and capuchin monkeys performed well in the basic classification task, accurately classifying central dot size in the Baseline condition when a dot was presented without outer inducers. Pilot data revealed that inducer size presented a unique challenge to the monkeys when conditions were intermixed randomly within a test session. Monkeys classified

central dots according to outer inducer size, with a tendency to classify Small Inducer trials as ‘small’ and Large Inducer trials as ‘large.’ Using these pilot data to guide modifications to the task, we introduced a testing phase that presented only one condition type per 3,000 trial block.

Using this blocked procedure, monkey performance improved somewhat; half of the monkeys successfully completed the training for all conditions and engaged the testing phase for all trial types, including Baseline trials, Small Inducer trials, and Large Inducer trials. However, these animals did not show evidence of the illusion. An effect of level was observed for all conditions, but the function appeared shallower for the Large Inducer condition. This performance pattern can be accounted for if one considers the amount of pixilation on screen for each condition.

The proportion increase in pixel amount between central dot size levels (Level 1 to Level 2 to Level 3 and so on until Level 13) in the Baseline condition is larger than the proportion increase in pixel amount between levels in the Small Inducer condition, which again is larger than the proportion increase in pixel amount between levels in the Large Inducer condition. Thus, as predicted by Weber’s law, it would be most difficult to discriminate pixel number in the Large Inducer condition because discriminations become more difficult as the difference between sets is reduced (see Brannon & Roitman, 2003; Gallistel & Gelman, 2000). Using the number of pixels onscreen to guide discrimination behavior would reproduce the findings reported here by the animals that learned to discriminate dot size in all three trial types. Animals using a rule such as ‘classify stimuli based on total pixel amount’ would be immune to an illusion that instead requires one to discriminate pixel amount in the central dot size alone, while ignoring the contribution of pixel amount by the outer inducing circles. We explore potential

explanations for a non-illusion among monkeys for the Ebbinghaus-Titchener array in the General Discussion.

4.3 Experiment 3

In Experiment 3, we extended the computerized classification task to human participants to compare performance with monkeys in the current experiment and to specifically assess whether human adults reproduced the response biases observed among monkeys using the current procedure.

4.3.1 Methods

4.3.1.1 Participants

Twenty-four human participants were recruited from GSU's undergraduate population (average age: 21 years old \pm 4, 12 females). Participants were required to give informed consent prior to participating in the experiment(s) and received course credit for their participation. Testing complied with the procedures and protocols that were approved by GSU's Institutional Review Board.

4.3.1.2 Apparatus

Human participants were tested at individual computer carrels with a personal computer, a digital monitor, and a mouse for responding. They were not given food reward but were given written feedback on the computer screen regarding the accuracy of their responses.

4.3.1.3 Stimuli and General Procedure

The same stimuli and general procedures were presented to humans as were used with the monkeys. Participants were presented with 50% Baseline trials, 25% Small Inducer trials, and 25% Large Inducer trials, randomly presented within the test session. Participants first were required to contact a trial-initiation stimulus and then used the computer mouse to select one of

the two stimuli. Correct responses led to a flashing stimulus that said ‘Correct!’ in the middle of the screen, whereas incorrect responses led to a flashing stimulus that said ‘Incorrect’ in the middle of the screen. We shortened the timeout period for incorrect trials to 8 s. Failure to respond within 3 seconds of stimuli presentation led to an instruction to respond more quickly to the trials. The inter-trial interval was 1 s. Participants were presented with as many as 800 trials, and we used data from those participants who completed at least 500 trials in the task. One participant failed to complete at least 500 trials, and the data from that participant was not included in the following analyses.

Minimal written instructions were provided instead of a training phase to maximize the number of test trials completed per session with each participant. Before starting the experiment, participants read the following text:

In this experiment, you will see a black dot at the top center of the screen.

Sometimes, the dot will be surrounded by other dots of a different size. You must assign that central dot as being either ‘Small’ or ‘Large’ by clicking on one of those two words on the screen. Click the Start button, and then click on one of the two options. You need to make these responses fairly quickly. Correct responses move you right to the next trial. Incorrect responses lead to a short period where the task is frozen. You need to complete 800 trials, so the better you do, the faster you will finish. When you are ready, click on the START button.

4.3.2 Results

Figure 5 depicts group-level performance as a function of condition and difficulty level for human participants. We conducted a within-subjects ANOVA to examine the effect of condition (Baseline, Small Inducer, and Large Inducer) and absolute difficulty level (1-6) on the

proportion of trials where the participants made a dot classification of ‘small.’ There was a significant main effect of condition, $F(2, 44) = 39.26, p < .001, \eta^2_p = .64$, and difficulty level, $F(5, 110) = 221.05, p < .001, \eta^2_p = .91$. There was a significant interaction between condition and difficulty level, $F(10, 220) = 20.47, p < .001, \eta^2_p = .48$.

Collapsing across levels using the average mean percentage of small choices, a paired-samples t-test was used to compare the Baseline condition to the Small Inducer. A Bonferroni adjusted alpha level of .0167 was used per test (.05/3). Central dots were classified as ‘small’ significantly less often in the Small Inducer condition than in the Baseline condition ($t(22) = 6.54, p < .001$), and in the Large Inducer condition ($t(22) = -7.70, p < .001$). Central dots were classified as ‘small’ significantly more in the Large Inducer condition than in the Baseline condition ($t(22) = -3.37, p = .003$).

4.3.3 Discussion

Human participants perceived the Ebbinghaus-Titchener illusion in the current classification task, underestimating central dot size when surrounded by large inducers and overestimating central dot sized when surrounded by small inducers. These results matched previous reports of the Ebbinghaus-Titchener illusion among human adults (e.g., Coren & Enns, 1993; Girgus et al., 1972; Massaro & Anderson, 1971; Weintraub, 1979). Humans did not reveal the same response bias to classify central dot size based on inducer size, likely due to the verbal instructions provided prior to testing. Future research might address whether human adults also struggle to isolate the target of interest without explicit verbal instructions on the task’s rule.

4.4 General Discussion

Like other size illusions (e.g., Delboeuf illusion, Badlwin illusion), the Ebbinghaus-Titchener illusion emerges due to contrast effects – objects surrounded by large inducers are

underestimated in size relative to objects surrounded by small inducers (e.g., Ebbinghaus, 1902; Nicolas, 1995). Despite this similarity, the Ebbinghaus-Titchener illusion is unique among its peers in that the target (central black dot) is identical in form to the surrounding inducers (outer black dots). This similarity between target and inducer form presents a unique challenge in instructing nonverbal species to the task rule – discriminate the stimuli based on the central black dot alone. In the current study, chimpanzees, rhesus monkeys, and capuchin monkeys were presented with a range of experimental procedures in attempts evoke the classic Ebbinghaus-Titchener effect.

Primates were proficient in discriminating the central target in the absence of outer inducers in Experiment 1 and Experiment 2. Chimpanzees persisted in selecting the larger of two edible targets regardless of the ‘illusory’ context in which they were presented in Experiment 1. The monkeys that passed the training phase for all conditions in Experiment 2 (Baseline, Small Inducer, and Large Inducer) revealed an interesting pattern of results in which the function for classifying stimuli correctly was shallower for the Large Inducer condition relative to the Baseline and Small Inducer conditions. This phenomenon could be explained using a simple rule such as ‘classify stimuli according to total pixel amount.’ Monkeys would be very successful using such a rule; however, this would not result in illusion emergence or address whether this illusion emerges within these species of monkey.

When given almost identical procedures to those presented to the monkeys, human participants demonstrated the predicted performance patterns in Experiment 3, overestimating central dot size when surrounded by small inducers and underestimating central dot size when surrounded by large inducers. Thus, using such a rule (i.e., classify based on total pixel amount) is not inherent in this task, but only emerged within nonverbal species that could not be

instructed explicitly as to the task objective. Future studies that isolate the target of interest from the inducers without using explicit instructions will be key in understanding these null results. We think that the current absence of evidence of the Ebbinghaus-Titchener illusion among nonhuman primates does not translate into evidence of absence, at least not without more testing and new methodological approaches.

Moreover, the process by which animals perceive complex visual arrays likely contributes to the emergence (or non-emergence) of geometric size illusions, like the Ebbinghaus-Titchener illusion. Illusions are comprised of multiple elements (e.g., outer inducing circles and target central dot) that must be perceived simultaneously in order for the illusion to emerge. For example, perceiving the central dot of the Ebbinghaus-Titchener array in the absence of the illusory inducers would lead to a non-illusion. The tendency to perceive complex arrays as one cohesive figure (i.e., all elements first are perceived simultaneously) versus individual elements (i.e., all elements first are perceived as separate units) can be determined via perceptual processing mode tasks. Our own work (Chapter 2) and previous studies demonstrate a robust local-precedence (i.e., individual elements perceived prior to cohesive figure) among rhesus and capuchin monkeys (De Lillo, Spinozzi, Truppa, & Naylor, 2005; Hopkins & Washburn, 2002; Spinozzi, De Lillo, & Salvi, 2006; Spinozzi, De Lillo, & Truppa, 2003). These results stand in contrast to widespread evidence of a global precedence among human participants (e.g., Broadbent, 1977; Kimchi, 1992; Lamb & Robertson, 1988; Navon, 1977, 1981).

Despite a local-precedence, monkeys have shown susceptibility to illusory stimuli in tasks designed to minimize (but not completely ignore) the illusory array (e.g., Parrish et al., 2015). In the current set of experiments, we were cautious not to train the animals to disregard

the inducers as this has produced null results for the Ebbinghaus-Titchener illusion in previous comparative studies (Nakamura et al., 2008; Parron & Fagot, 2007), whereas human-like patterns of illusion perception were documented among various species using experimental procedures that did not specifically train animals to ignore inducing stimuli (Murayama et al., 2012; Rosa Salva et al., 2013). Illusions such as the Ebbinghaus-Titchener illusion appear highly sensitive to task design and stimuli presentation, likely due to the large overlap in target and inducer features (i.e., both large black dots). Thus, future studies that balance rule training, stimuli presentation and design, and species' perceptual processing mode are necessary to uncover the elusive Ebbinghaus-Titchener illusion.

4.5 References

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4.6 Tables

Table 1. Experiment 1 trial types outlined with predicted performance patterns.

Trial Type	Description	Prediction
Baseline	Large portion (no inducers)	Choose large portion. No illusion.
	vs. Small portion (no inducers)	
Small Control	Large portion (small inducers)	Choose large portion. No illusion.
	vs. Small portion (small inducers)	
Large Control	Large portion (large inducers)	Choose large portion. No Illusion
	vs. Small portion (large inducers)	
Small Mixed	Large portion (with small inducers)	Choose large portion at levels exceeding Baseline.
	vs. Small portion (no inducers)	
Large Mixed	Large portion (with large inducers)	Erroneously choose small portion at levels exceeding Baseline.
	vs. Small portion (no inducers)	
Inducer Control	Large portion (no inducers)	Choose large portion at levels exceeding Baseline.
	vs. Small portion (large inducers)	
Ebbinghaus Illusion	Large portion (small inducers)	Bias to choose large portion with small inducers.
	vs. Large portion (large inducers)	

4.7 Figures

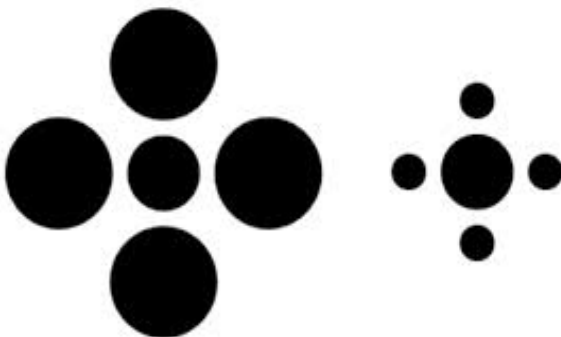


Figure 1. The Ebbinghaus-Titchener illusion. Humans typically perceive the central dot surrounded by small inducers (to the right) to be larger than the same-sized central dot surrounded by large inducers (to the left).

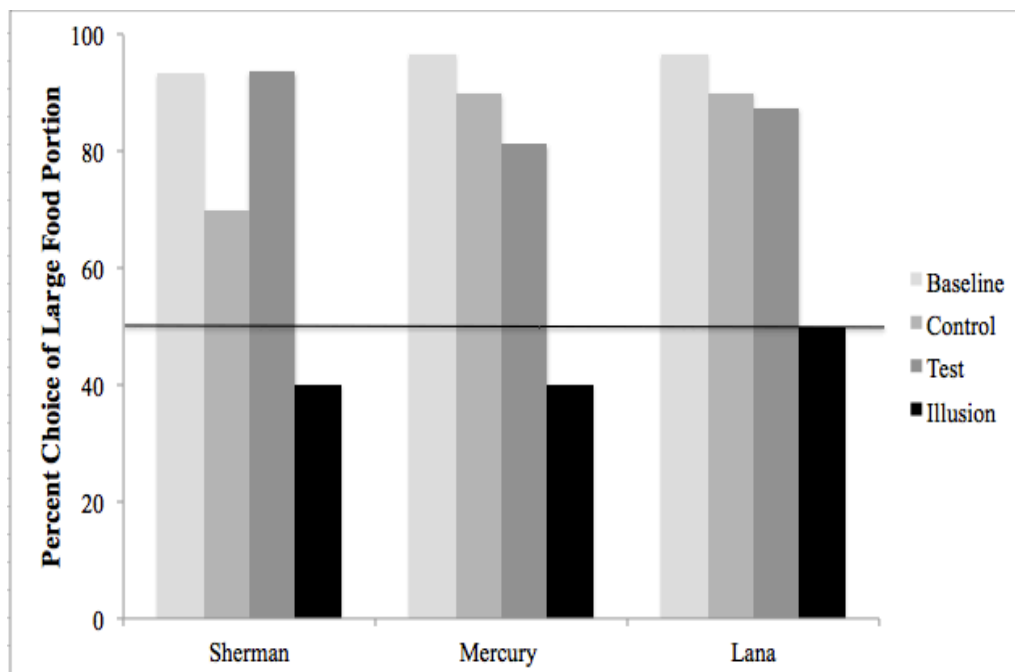


Figure 2. The percentage of large food choices for the four trial types in Experiment 1. The three bars at left in grey shading are statistically different from chance levels of responding, but the black bar (Illusion trials) is not.

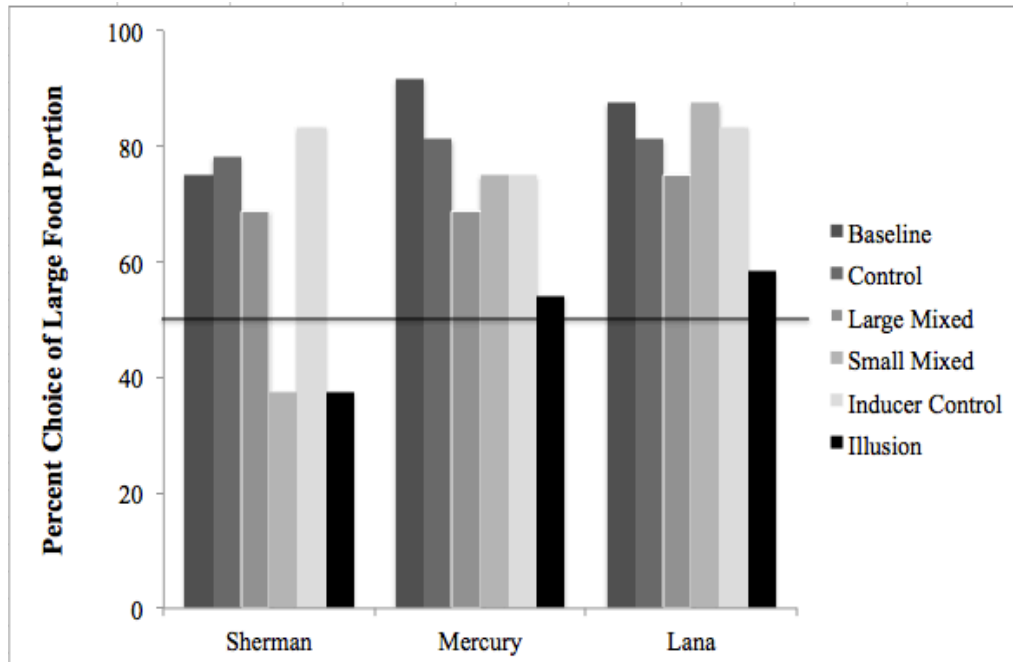


Figure 3. The percentage of large food choices for the seven trial types in Experiment 2.

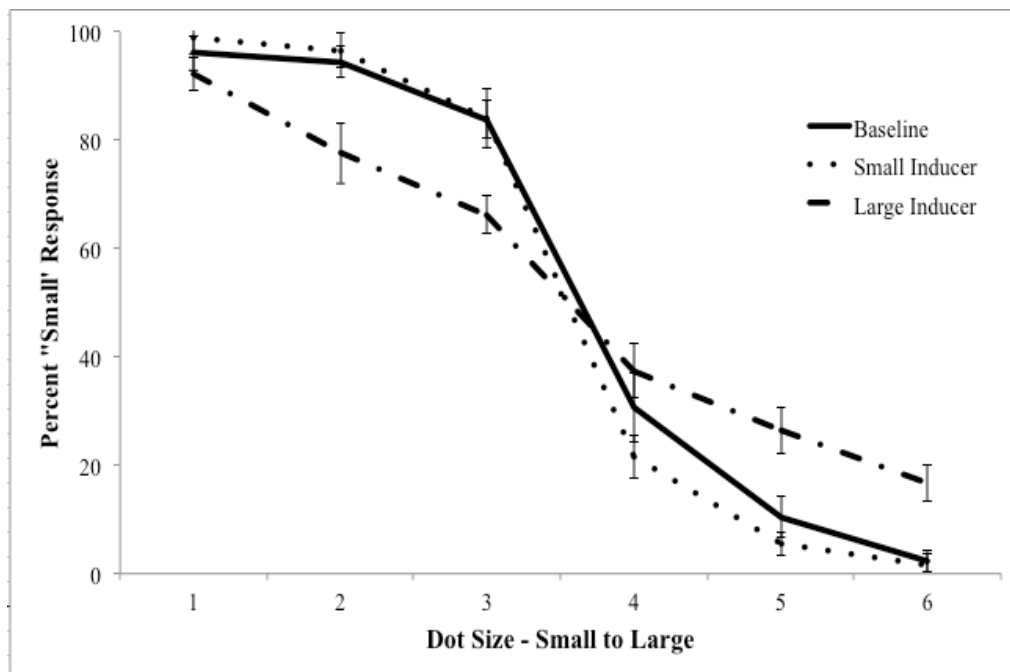


Figure 4. Mean percentage of ‘small’ responses for dot size for the Baseline, Small Inducer, and Large Inducer conditions for monkey participants in Experiment 2. Dot size levels progress from 1 (smallest) to 6 (largest). Error bars depict corrected 95% confidence intervals for repeated measures tests (Cousineau, 2005).

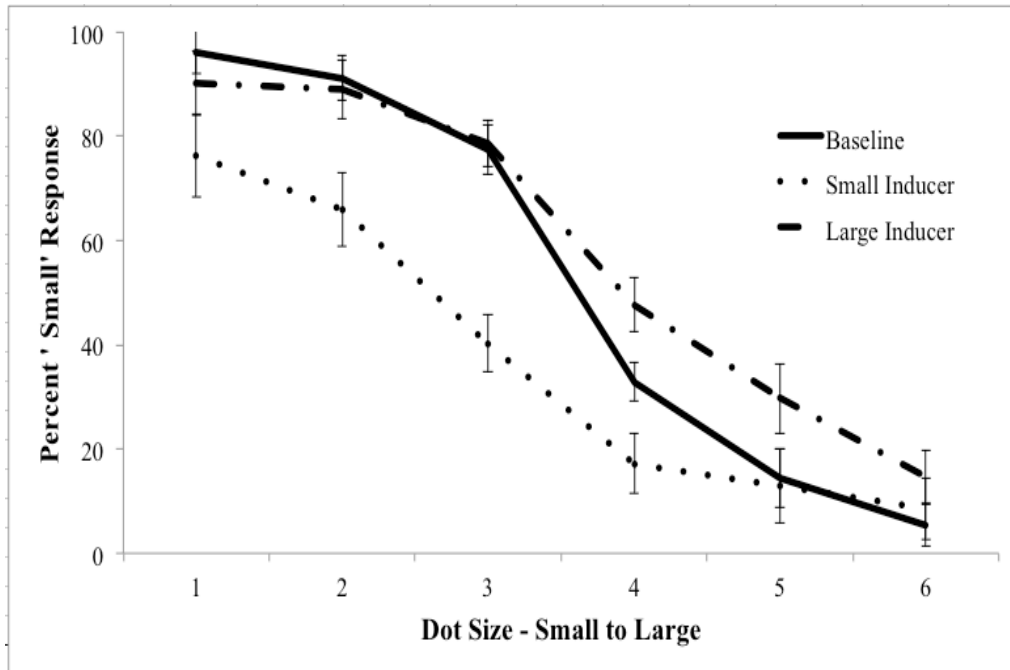


Figure 5. Mean percentage of ‘small’ responses for dot size for the Baseline, Small Inducer, and Large Inducer conditions for human participants in Experiment 3. Dot size levels progress from 1 (smallest) to 6 (largest). Error bars depict corrected 95% confidence intervals for repeated measures tests (Cousineau, 2005).

RESPONSE BIASES IN THE BALDWIN ILLUSION IN RHESUS MONKEYS (*MACACA
MULATTA*) AND CAPUCHIN MONKEYS (*CEBUS APELLA*)

By

AUDREY E. PARRISH

ABSTRACT

In the current set of studies, we investigated whether rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*) perceived the Baldwin illusion in a similar manner as human adults (*Homo sapiens*). The Baldwin illusion emerges when line length is misperceived as a function of flanking square size. Large squares lead to line length underestimation and small squares lead to line length overestimation. In Experiment 1, we presented monkeys with an absolute classification task that required monkeys to classify a horizontal line that was sometimes flanked by small or large squares as being either 'short' or 'long.' We did not find evidence of the Baldwin illusion. Rather, most monkeys demonstrated a response bias in which

they incorporated square size into their line classification, classifying lines flanked by large squares as 'long' and lines flanked by small squares as 'short.' To isolate the horizontal line, we presented an extended training procedure in Experiment 2. Squares were presented first at a distance from the line and then moved progressively closer to the horizontal line in attempts to isolate the target of interest. We found more promising evidence of the Baldwin illusion in Experiment 2, with some monkeys showing less response bias and performance patterns indicative of a human-like illusion.

INDEX WORDS: Visual illusions; Baldwin illusion; Capuchin monkeys; Rhesus monkeys; Perception; Response bias

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5 RESPONSE BIASES IN THE BALDWIN ILLUSION IN RHESUS MONKEYS (*MACACA MULATTA*) AND CAPUCHIN MONKEYS (*CEBUS APELLA*)

Whether, and to what extent, we share commonalities in our perceptual systems across species has captured the attention of comparative scientists for many decades (see Lazareva, Shimizu, & Wasserman, 2012, for a review). Specifically, the extent to which we misperceive our external worlds was a topic of intense study even prior to the establishment of psychology as a formal discipline (Boring, 1942; Luckiesh, 1922). A natural question in comparative perception is whether animals fall prey to visual illusions in a similar fashion as humans. Similarities across visual processing would suggest commonalities in the visual and perceptual systems of closely-related, or perhaps even distantly-related, species (Agrillo, Petrazzini, & Dadda, 2013; Wasserman, 2012).

Nonhuman primates (hereafter primates) have been at the forefront of comparative visual illusion research as they are our closest-related living relatives, and they share many features of the visual system with humans, including anatomical structure of the eye and how information is processed in the brain (e.g., De Valois & De Valois, 1988; Essock, 1977; Fobes & King, 1982; Matsuzawa, 1990; see Matsuno & Fujita, 2009 for a review). Not surprisingly, given these similarities, several species of primates also have demonstrated visual illusion perception similar to humans, including but not limited to the Delboeuf illusion (Parrish, Brosnan, & Beran, 2015), the Ebbinghaus-Titchener illusion (Parron & Fagot, 2007), the Ponzo illusion (Bayne & Davis, 1993; Fujita, 1996, 1997), the Zollner illusion (Benhar & Samuel, 1982), and the corridor illusion (Barbet & Fagot, 2007).

It is interesting that some studies have revealed differences in visual illusion emergence across different primate species. For example, baboons do not perceive the Ebbinghaus-

Titchener illusion in a human-like manner, but instead perceive the anti-illusion (Parron & Fagot, 2007). Our own work on the similar Delboeuf illusion suggests that monkeys perceive the illusion in a human-like manner, but only under certain methodological circumstances (Parrish et al., 2015). When given a relative-discrimination task, many animals erroneously incorporated the outer ring inducers into the dot judgment, leading to a performance pattern indicative of an anti-illusion as reported by Parron and Fagot. However, we established a task in which reliance on outer ring size would not be beneficial – we introduced a classification task in which animals were required to assign dots a value of ‘small’ or ‘large.’ In that context, monkeys readily perceived the illusion as do humans, overestimating dot size encircled by small rings and underestimating dot size encircled by large rings. These different results among the same individuals were interesting and informative regarding the nature of visual illusion testing among nonverbal species. Isolating the target of interest (and reducing the chances for a response bias towards inclusion of inducing stimuli) is key for a species-fair test of visual illusion perception.

In the current study, we extended our research of geometric size illusions and investigated the emergence of the Baldwin illusion in rhesus monkeys and capuchin monkeys. This illusion is relatively understudied in the human literature (e.g., Baldwin, 1895; Pressey & Smith, 1986; Pressey & Wilson, 1980) in comparison to other size illusions, and it has never been presented to a nonhuman animal species. Similar to the Delboeuf and Ebbinghaus-Titchener size illusions, a contrast effect occurs in the Baldwin illusion in which target stimulus size (line length) is misperceived as a function of inducer stimuli size (flanking squares). In the Baldwin array, two equal-length horizontal lines appear to be unequal such that the line flanked by large squares is underestimated in comparison to an equal-length line flanked by small squares (see Figure 1).

We noted an interesting response bias in Experiment 1 of the current work, in which several animals incorporated the flanker squares into their line classification. For example, lines with large squares on either end were classified as ‘long’ and lines with small squares on either end were classified as ‘short.’ This response pattern is indicative of a reversed human-like illusion. Reversed patterns have been reported within nonhuman primates for similar, size illusions, including the Ebbinghaus-Titchener illusion (Parron & Fagot, 2007) and the Delboeuf illusion (Parrish et al., 2015). Although these reversed patterns could suggest a different perceptual experience across primates, an alternative hypothesis is that the animals confused the rule, erroneously incorporating inducing squares into the total line length. To explore this secondary hypothesis, we introduced an extended training procedure to the monkeys in Experiment 2. The animals were trained to isolate target line length as squares were moved progressively closer to the line. This method of progressively introducing the inducers so that the target might be isolated as the stimulus of interest has been used in several nonhuman animal studies investigating visual illusions (e.g., Salva, Rugani, Cavazzana, Regolin, & Vallortigara, 2013). We predicted that this extended training procedure would reduce the response bias of square inclusion observed in Experiment 1.

5.1 Experiment 1

5.1.1 Methods

5.1.1.1 Participants

The nonhuman primates included in all experiments were housed and tested at the Language Research Center (LRC) of Georgia State University (GSU) in Atlanta, Georgia. LRC primates were never food or water deprived for testing purposes and had 24-hour access to water, including during test sessions. They received a daily diet of fruits, vegetables, and primate chow

regardless of participation in testing, and caloric intake was kept consistent by taking into account the amount of food earned from testing when determining the daily diet. All testing protocols complied with guidelines for working with nonhuman primates as established by protocols approved by the GSU Institutional Animal Care and Use Committee. GSU is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care.

We tested five adult male rhesus macaques and nine adult capuchin monkeys (4 males) in the following experiments. Capuchin monkeys were group housed in indoor-outdoor enclosures, and they separated voluntarily into individual testing enclosures for computerized testing (with constant visual and auditory access to conspecifics). Rhesus monkeys were individually housed and had 24-hour access to a computerized testing apparatus within their home cage. Rhesus monkeys had constant visual and auditory access to conspecifics and received one-a-week access to an indoor-outdoor enclosure with another monkey during which both monkeys spent approximately 12 hours together and not engaged in computerized testing. These monkeys have participated in several computerized perceptual discrimination tasks (e.g., Agrillo et al., 2014; Beran, 2006; Beran & Parrish, 2013; Beran, Smith, Coutinho, Couchman, & Boomer, 2009; Parrish et al., 2015).

5.1.1.2 Apparatus

Nonhuman primates included in this study were joystick trained for computerized testing using the LRC's Computerized Test System consisting of a color monitor, personal computer, digital joystick, and food pellet dispenser (Evans, Beran, Chan, Klein, & Menzel, 2008; Richardson, Washburn, Hopkins, Savage-Rumbaugh, & Rumbaugh, 1990). Primates manipulated the joystick with their hands to isomorphically control a small round cursor on the computer screen. Monkeys were not restrained during testing. The viewing distance from the

monitor was approximately 30.5 cm to 40.5 cm. Correct responses led to banana-flavored pellet rewards (45-mg pellets for capuchins and 94-mg pellets for rhesus monkeys: Bio-Serv, Frenchtown, NJ) via a pellet dispenser interfaced to the computer through a digital I/O board (PDISO8A; Keithley Instruments, Cleveland, OH). Programs were written in Visual Basic 6.0.

5.1.1.3 Stimuli

The Baldwin stimuli consisted of a horizontal line (target) flanked on both sides by square inducers (see Figure 1). On all trials, a stimulus was presented in the middle of the screen, and subjects were required to classify the central line as ‘short’ (by moving the cursor to the bottom left of the screen to a orange rectangle) or ‘long’ (by moving the cursor to the bottom right of the screen to a green rectangle). The line and the inducing squares were black, presented on a white background. The squares that flanked either side of the horizontal line were both small (1 x 1 cm) or were both large (3 x 3 cm). In some phases these squares were positioned flush against the end of either side of the horizontal line (no gap between line and square). In Experiment 2, the squares were near to the line but not in contact with it in some phases.

Using a psychophysical step procedure, a range of 11 possible target line lengths was established. A Level 6 (midpoint) line was established with a length of 4 cm. Level 6 stimuli were never presented as they were neither long nor short lines. Levels 1 to 5 were all shorter than the Level 6 line, and their length was generated by the following equation: $\text{Level} = 3 * 0.98^{(6 - \text{TrialLevel})}$. Levels 7 to 11 were all longer than the Level 6 line, and their length was generated by the following equation: $\text{Level} = 3 * 1.02^{(\text{TrialLevel} - 6)}$. Thus, Levels 1 to 11 were progressively longer lines for which the Level 5 and Level 7 lines were the objectively hardest to discriminate from the midpoint (Level 6). Level 1 (shortest) and Level 11 (longest) were the objectively easiest to discriminate.

5.1.1.4 General Procedure

At the outset of each trial, subjects directed the cursor into a trial initiation stimulus at the center of the computer screen ('Start' button). That button disappeared and the test stimulus and the two classification icons appeared as choice options. Test stimuli were presented in the center of the screen with the classification icons left-justified ('short') and right-justified ('long') at the bottom of the screen. Subjects used the joystick to direct the cursor into contact with one of the two classification icons, thereby classifying horizontal line length on each trial. Monkeys were required to make their response within 3 seconds of the test stimuli appearing onscreen. After selection of a stimulus or after 3 seconds of inactivity, the screen then cleared completely. Correct responses led to a pellet reward and a melodic tone, whereas incorrect responses led to a buzz tone and a timeout period of 20 s. Failure to respond within 3 seconds of stimuli presentation led to a timeout period of 20 s. The inter-trial interval was 1 s.

Three conditions were included. The Baseline condition presented a horizontal line with no flanking squares. This condition was used to establish classification performance without the effects of any inducing stimuli. The Small Square condition presented two small squares flanking either side of the horizontal line. The Large Square condition presented two large squares flanking either side of the horizontal line. We never presented a line with flanking squares of different sizes on opposite ends of the line.

5.1.1.4.1 Training

Monkeys completed a set of training trials to learn the rule of selecting the appropriate classification icon using the three easiest short levels (Levels 1 to 3) and the three easiest long levels (Levels 9 to 11) in the Baseline condition. The criterion for passing the training phase was set to 85% correct over the most recent 60 trials, at which point testing immediately began. One

rhesus monkey and four capuchin monkeys failed to reach training criterion after 6,000 trials and were removed from the study.

5.1.1.4.2 Testing

In the testing phase, we introduced the full continuum of levels (Levels 1 to 11). We randomly intermixed all conditions, presenting the Baseline condition in 33.3% of trials, the Small Square condition in 33.3% of trials, and the Large Square condition in 33.3% of trials. We oversampled the more difficult levels to increase the number of critical test trials presented (50% of test trials presented a randomly selected Level 3 to Level 9 trial whereas the remaining trials randomly sampled from the full range of levels). The true midpoint line (Level 6) was never presented. Monkeys completed approximately 6,000 trials, except for rhesus monkey Murph, who completed approximately 2,500 trials.

5.1.2 Results

Because we oversampled the more critical test levels (Levels 3 to 9), for all subsequent analyses, we reduced the number of line length levels from 10 levels to 8 levels, binning the easiest ‘short’ levels (Level 1 and Level 2) and the easiest ‘long’ levels (Level 10 and Level 11).

Figure 2 depicts group-level performance (i.e., classification of the line as short) as a function of condition (Baseline, Small Square, and Large Square) and line length (1 to 8). We conducted a mixed-design analysis of variance (ANOVA) to examine the effect of condition and line length (8 levels) on the proportion of trials in which the participants made a line classification of ‘short’ with species (capuchin monkeys and rhesus monkeys) as the between-subjects variable. There was a significant main effect of line length, $F(7, 84) = 14.38, p < .001, \eta^2_p = .55$. There was not a significant effect of condition, $F(2, 24) = 2.27, p = .13, \eta^2_p = .16$, nor of species, $F(1, 12) = .13, p = .72, \eta^2_p = .01$. There was a significant interaction of line length

and condition, $F(14, 168) = 24.57, p < .001, \eta^2_p = .67$. There was not a significant interaction of species and condition, $F(2, 24) = 1.07, p = .36, \eta^2_p = .08$, nor an interaction of species and line length, $F(7, 84) = .12, p = 1.0, \eta^2_p = .01$. There was not a three-way interaction, $F(14, 168) = .72, p = .75, \eta^2_p = .06$.

Given that the factor of interest was condition, we collapsed across line lengths (and species) using the mean percentage of short choices across line lengths. We conducted a paired-samples t-test to compare the Baseline condition to the Small Square and Large Square conditions. We also compared the Small Square and Large Square conditions to one another. A Bonferroni adjusted alpha level of .016 was used given the three comparisons of interest (.05/3). Lines were classified as ‘short’ significantly more in the Small Square condition ($M = 65.52, SD = 24.26$) than in the Large Square condition ($M = 55.84, SD = 27.60$), $t(13) = 3.27, p = .006$. Performance did not differ significantly for the Baseline ($M = 51.85, SD = 12.50$) and Small Square conditions, $t(13) = -1.89, p = .08$, nor for the Baseline and Large Square conditions, $t(13) = -.49, p = .63$.

We plotted several monkeys’ performance to highlight the representative individual differences in this experiment (see Figure 3). Two patterns that emerged among several monkeys (e.g., capuchin monkeys Gonzo and Widget), despite good Baseline performance, were 1) a tendency to over-classify *any* trial presenting a square as ‘long’ (Gonzo) and 2) to over-classify Small Square trials as ‘short’ and Large Square trials as ‘long’ (Widget). Similar response biases to over-incorporate inducers into target classification were seen among the six other capuchin monkeys, including Bailey, Liam, Mason, Nala, Nkima and Wren, and the four other rhesus monkeys, including Obi, Chewie, Han, and Murph. Despite widespread response biases,

capuchin monkey Logan and rhesus monkey Lou showed the best performance patterns across all three conditions, without an overt response bias to classify trials based on inducer square size.

5.1.3 Discussion

As expected, monkeys performed well in the basic line classification task in the Baseline condition, which did not present inducing squares. The addition of inducing squares in the test conditions (Small Square and Large Square) disrupted classification performance for both species, but not in the predicted direction. Markedly, most monkeys over-classified lines in the Small Square condition as ‘short’ and the Large Square condition as ‘long.’ This performance pattern is indicative of an inversed Baldwin illusion. Human participants typically perceive lines surrounded by Small Squares as *longer* than their true length and lines surrounded by Large Squares as *shorter* than their true length (e.g., Brigell, Uhlarik, Goldhorn, 1977; Clavadetscher & Anderson, 1977; Wilson & Pressey, 1988).

Because of the biases displayed by several monkeys in Experiment 1, we were concerned that they may have included the inducing squares in their classifications in the test conditions or classified each trial based on inducer size alone. A response bias towards using inducer size or incorporating the illusory inducers into target classification has been documented in other illusion tasks in monkeys (Parrish et al., 2015) and young children (Hanley & Zerbolio, 1965; Pressey & Wilson, 1978). These response biases might reflect a misunderstanding of the rule to isolate the target of interest (Hanley & Zerbolio, 1965; Pressey & Wilson, 1978). To address this concern, we extended our training procedure in Experiment 2 to highlight the line as the stimulus for classification. We did this through a series of training steps that positioned the outer inducing squares progressively closer to the horizontal line. At each training stage, the monkeys had to pass criterion in the line classification task.

5.2 Experiment 2

5.2.1 Methods

5.2.1.1 Participants

Half of the original subjects (five capuchin monkeys and two rhesus monkeys; those that were first to complete Experiment 1) continued to Experiment 2. All methods and materials were identical to Study 1 (i.e., Apparatus, Stimuli, and General Procedure) with one exception – training.

We introduced four training conditions. As before, all training phases used the three easiest short levels (Levels 1 to 3) and the three easiest long levels (Levels 9 to 11). Criterion for passing to the next training phase or to testing following the final training phase was set to 80% correct over the most recent 40 trials, at which point the next phase immediately began. A lower criterion was used here so that the monkeys potentially could advance through all four training phases in one session as these procedures were designed to aid in response biases during testing. Training Phase 1 was identical to Experiment 1 Training – only the Baseline condition was presented (no inducing squares). Training Phases 2 to 4 introduced the inducing squares, such that half of training trials in each of these phases included Small Squares and half of trials included Large Squares. In Training Phase 2, the inducing squares were presented 4 cm away from either end of the horizontal line. This distance positioned the squares near the outer edges of the computer screen while the horizontal line remained in the middle. In Training Phase 3, the inducing squares were moved 2 cm away from either end of the line. In Training Phase 4, the inducing squares were 1 cm away from the either end of the horizontal line. Following training, monkeys completed approximately 6,000 test trials with the inducing squares touching the ends of the horizontal line as in Experiment 1.

5.2.2 Results

Figure 4 depicts group-level performance (i.e., classification of the line as short) as a function of condition (Baseline, Small Square, and Large Square) and line length (1 to 8). We conducted a mixed-design analysis of variance (ANOVA) to examine the effect of condition and line length (8 levels) on the proportion of trials where the participants made a line classification of 'short' with species (capuchin monkeys and rhesus monkeys) as the between-subjects variable. There was a significant main effect of line length, $F(7, 35) = 6.74, p < .001, \eta^2_p = .57$. There was not a significant effect of condition, $F(2, 10) = .91, p = .43, \eta^2_p = .15$, nor of species, $F(1, 5) = 1.75, p = .24, \eta^2_p = .26$. There was a significant interaction of line length and condition, $F(14, 70) = 12.44, p < .001, \eta^2_p = .71$. There was not a significant interaction between species and condition, $F(2, 10) = 1.48, p = .28, \eta^2_p = .23$, nor between species and line length, $F(7, 35) = .01, p = 1.0, \eta^2_p = .002$. There was not a three-way interaction, $F(14, 70) = .28, p = 1.0, \eta^2_p = .05$.

Given that the factor of interest was condition, we collapsed across line lengths (and species) using the mean percentage of short choices for all line lengths. We conducted a paired-samples t-test to compare the Baseline condition to the Small Square and Large Square conditions. We also compared the Small Square and Large Square conditions to one another. A Bonferroni adjusted alpha level of .016 was used per test given the three comparisons of interest (.05/3). Performance did not differ significantly for the Baseline ($M = 50.00, SD = 12.89$) and Large Square ($M = 56.77, SD = 23.12$) conditions, $t(6) = -.51, p = .63$, nor for the Baseline and Small Square ($M = 54.68, SD = 21.78$) conditions, $t(6) = -.39, p = .71$, nor for the Small Square and Large Square conditions, $t(6) = -.53, p = .62$.

Again, we plotted several monkeys' performance to highlight individual differences in this experiment (see Figure 5). Some monkeys (e.g., capuchin monkey Mason) persisted with the tendency to over-classify any trial presenting a square as "long." Similar response biases persisted for a number of monkeys not pictured, including rhesus monkey Chewie and capuchin monkeys Liam and Nkima as was the case in Experiment 1. Capuchin monkeys Wren and Logan and rhesus monkey Lou showed the best performance patterns across all three conditions (see Figure 5), with some indication of a human-like illusion pattern (over-classifying lines with Large Squares as small relative to Baseline and Small Square trials).

5.2.3 Discussion

Consistent with the results from Experiment 1, monkeys performed well in the basic classification task when only a line was present, appropriately classifying lines as 'short' or 'long' based upon their true line lengths in the Baseline condition. We did see some overall improvements in the degree to which monkeys were biased to classify lines in the test conditions according to the square size. Whereas in Experiment 1 monkeys over-classified lines in the Small Square condition as 'short', we now documented no differences in line classification across conditions. Thus, the training procedure appeared to eliminate the bias for some animals to include the inducing squares as part of the line classification. Despite this improvement, we did not document evidence of the Baldwin illusion at the group level. Although some individual monkeys persisted in their response biases seen in Experiment 1, we documented promising individual results from capuchin monkeys Wren and Logan and rhesus monkey Lou with trends toward a human-like Baldwin illusion.

5.3 General Discussion

Although inducer stimuli create context within an illusory array, they should not be included as part of the to-be-judged target, but without verbal instruction, it can be difficult to instantiate these task demands. Critically, response biases to include inducers into target judgment often lead to a reversed illusion, in which targets surrounded by large stimuli are classified as ‘large’ or judged to be greater in size in a relative task (Hanley & Zerbolio, 1965; Parrish et al., 2015; Pressey & Wilson, 1978). In contrast, targets surrounded by small stimuli are classified as ‘small’ or judged to be smaller in size in a relative task. These response biases fundamentally oppose geometric illusion emergence, especially size illusions, in which large contexts cause underestimation and small contexts create overestimation (Baldwin illusion: Baldwin, 1895; Delboeuf illusion: Delboeuf, 1892; Ebbinghaus-Titchener illusion: Ebbinghaus, 1902; Mueller-Lyer illusion: Mueller-Lyer, 1889; Ponzo illusion: Ponzo, 1928). Interestingly, responses biases of this nature emerge within young children (e.g., Hanley & Zerbolio, 1965; Pressey & Wilson, 1978) and nonhuman animals (e.g., Nakamura, Watanabe, & Fujita, 2014; Parrish et al., 2015, Experiment 1; Parron & Fagot, 2007). The inability effectively to communicate the rule or isolate the stimulus of interest clearly is a greater risk in pre- or non-verbal populations. Here, we report similar response biases in rhesus monkey and capuchin monkeys presented with the Baldwin illusion.

Our extended training procedures in Experiment 2 mediated the inclusion of squares into line judgment to a degree for some monkeys. Interestingly, for the monkeys that no longer displayed a bias towards classifying stimuli according to square size (or simply classifying all squares with one response) in Experiment 2, we documented evidence of a human-like illusion in

which lines flanked by large squares were judged to be shorter in length than lines flanked by small squares.

The training procedures introduced a variety of conditions in which the squares were moved progressively closer to the central line. When the squares were non-contiguous with the line, the animals progressed through training, meeting criterion for line classification. For the animals that persisted in the response bias, they passed training criterion, but their bias reemerged once the squares were contiguous with the line in testing trials. These results suggested that the animals perceived the Baldwin stimuli as one unit to be classified together (line with squares) rather than the target alone (just line flanked by squares). Follow-up studies could address whether the illusion emerges with distally placed squares, and this methodology offers a potentially advantageous route for future inquiry.

5.4 References

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5.5 Figures

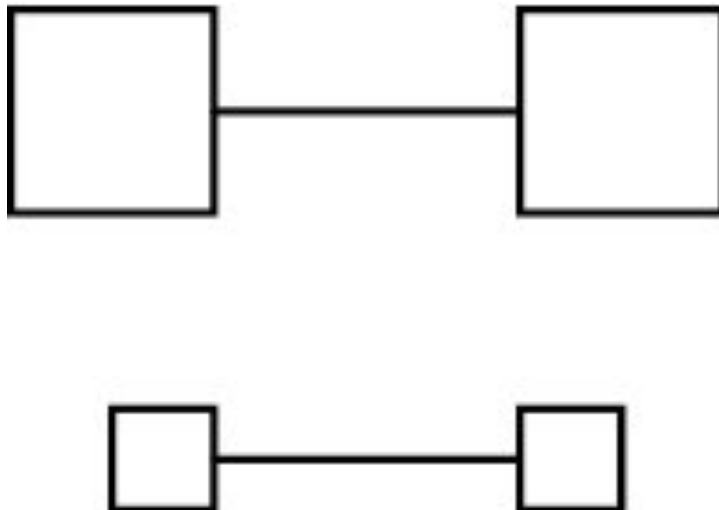
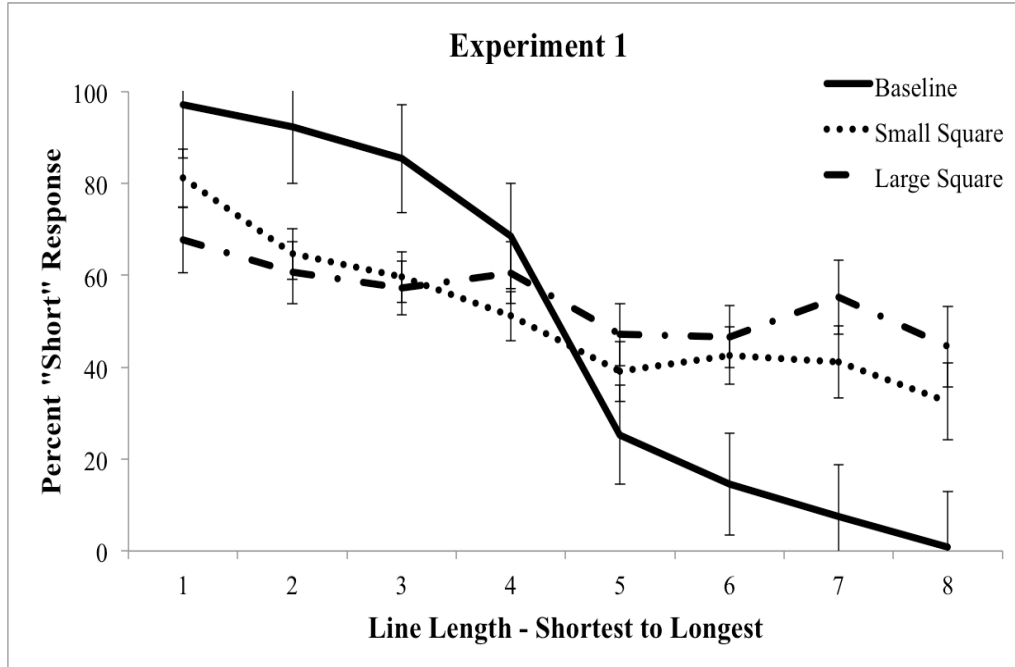


Figure 1. The Baldwin illusion: humans typically perceive the horizontal line flanked by small squares (bottom) as longer than an identical horizontal line flanked by large squares (top).



a.

Figure 2. Mean percentage of ‘Short’ responses for the Baseline, Small Square, and Large Square conditions. Line Length levels progress from 1 (shortest) to 8 (longest) in Experiment 1. Error bars depict corrected 95% confidence intervals for repeated measures tests (Cousineau, 2005).

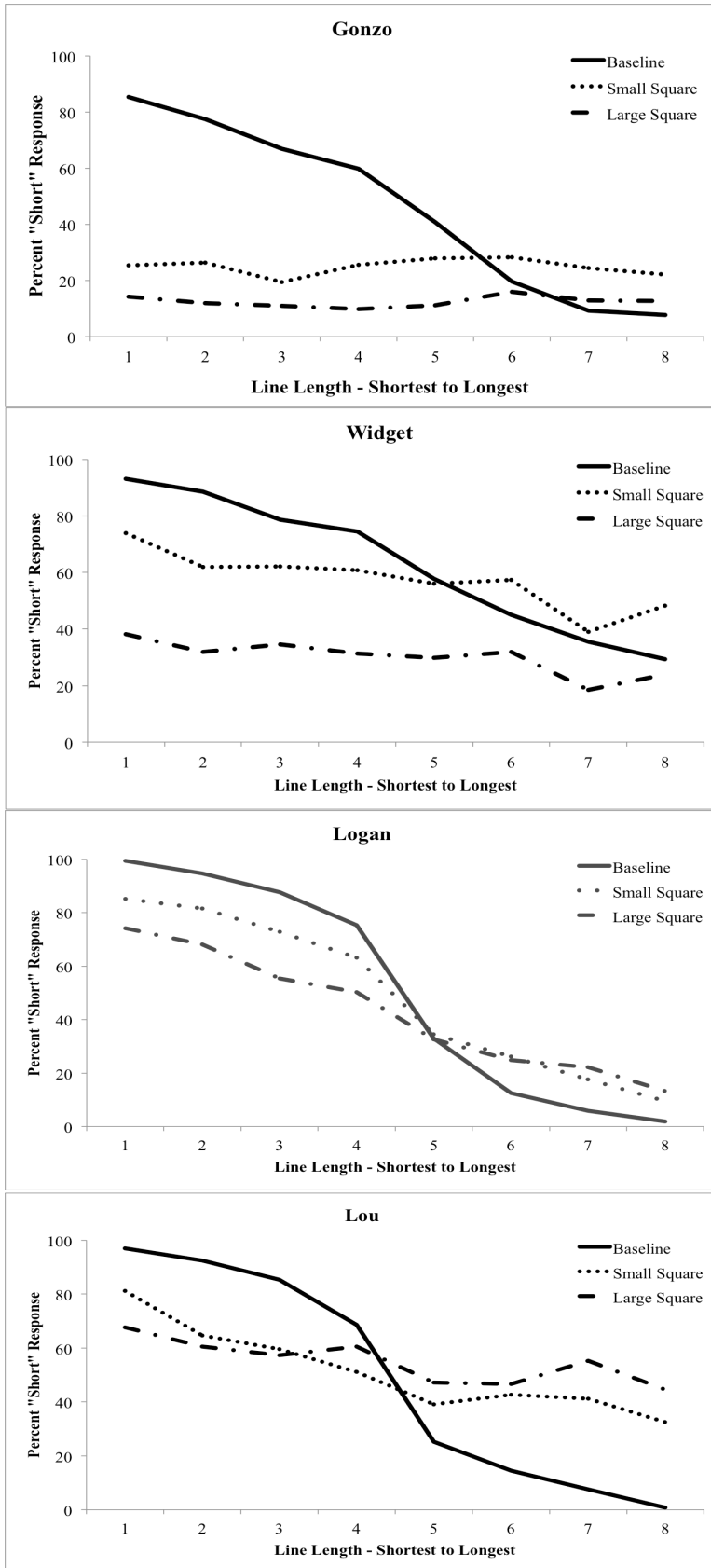
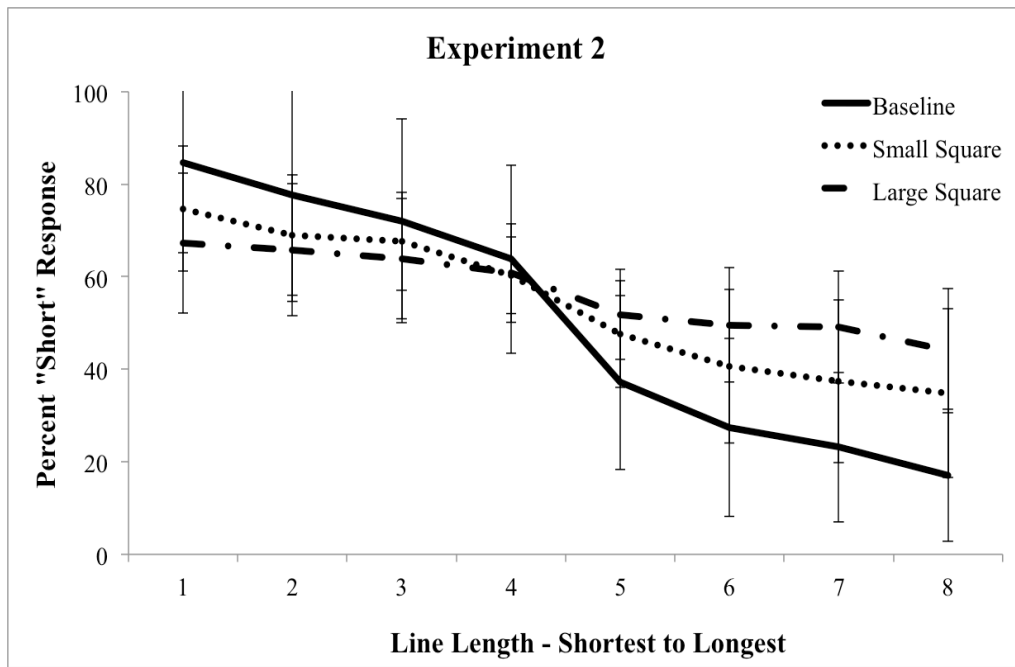


Figure 3. Example individual monkey performance in Experiment 1. Gonzo and Widget displayed a response bias to classify test conditions according to one or both inducer square sizes. Lou and Logan showed the best performance across individuals, with no overt response biases.



a.

Figure 4. Mean percentage of ‘Short’ responses for the Baseline, Small Square, and Large Square conditions. Line Length levels progress from 1 (shortest) to 8 (longest) in Experiment 2. Error bars depict corrected 95% confidence intervals for repeated measures tests (Cousineau, 2005).

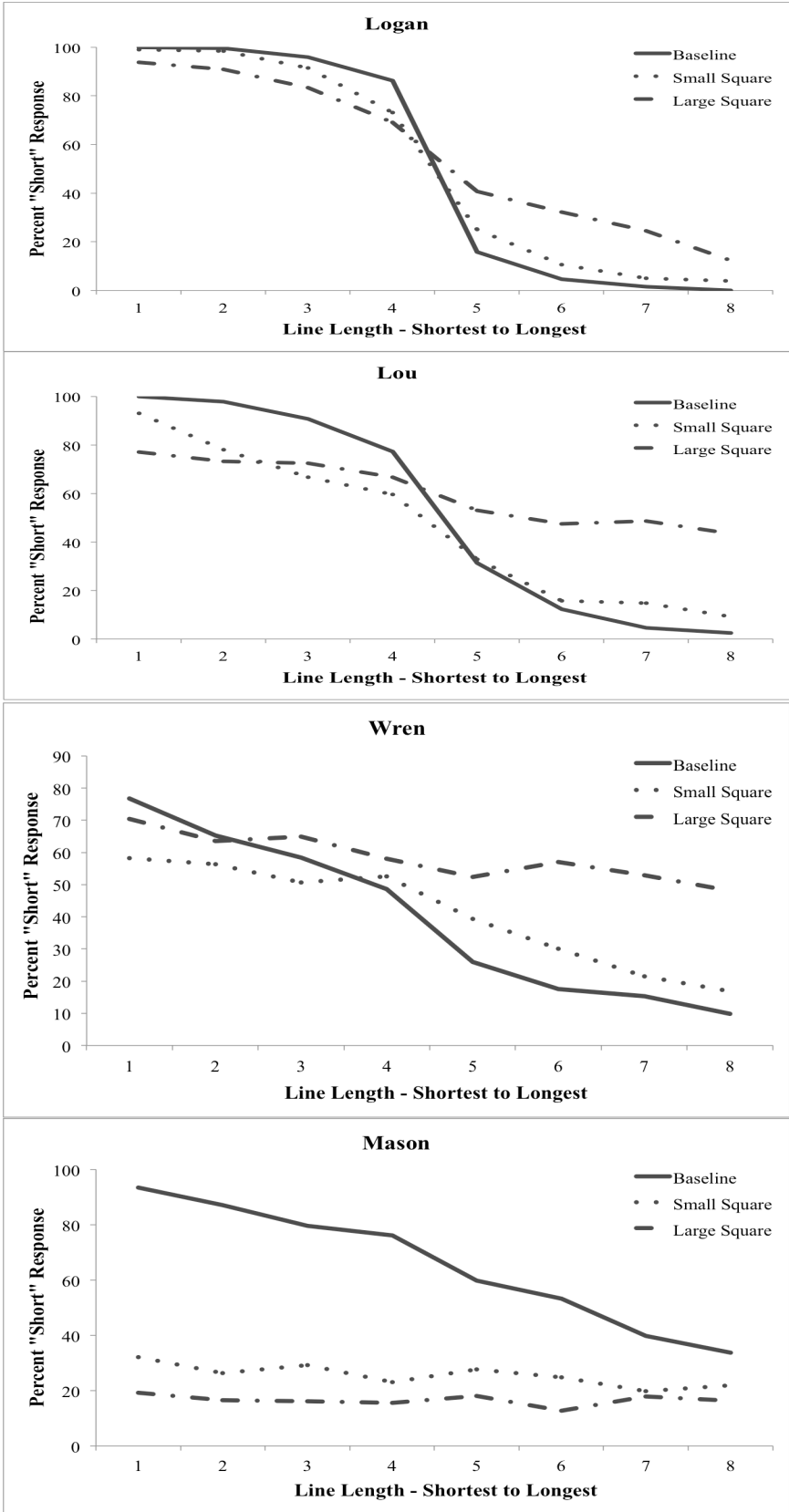


Figure 5. Example individual monkey performance in Experiment 2. Monkeys Lou, Logan, and Wren did not display a strong response bias to incorporate inducer squares into target classification as did monkey Mason.

LOOK THERE!

MODULATING ATTENTION WITHIN THE BALDWIN ILLUSION

By

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ABSTRACT

Attention plays a vital role in the emergence of geometric size illusions. Attending to the illusion target increases illusion magnitude, whereas attention to the illusory-inducing stimuli typically decreases illusion magnitude or even reverses the direction of the illusion. Previous studies have successfully manipulated attention, altering illusion perception, through verbal instructions or featural changes (e.g., color, density, luminance) to the visual array. Here, we extended these questions to investigate the extent to which attention can be manipulated prior to viewing the Baldwin illusion. Using an interleaved task, participants completed a primary task with either squares (Baldwin inducers) or lines (Baldwin target). Participants then completed a secondary task with the Baldwin array, classifying lines flanked by squares of different size as

‘short’ or ‘long.’ Participants readily perceived the Baldwin illusion, underestimating line length when flanked by large squares and overestimating line length when flanked by small squares. Illusion magnitude was not impacted by the primary task designed to manipulate attention towards either the Baldwin squares or lines. Thus, although attention plays an important role in illusion emergence, manipulating attention prior to perceiving the illusory array was ineffective in mediating or increasing the magnitude of the Baldwin illusion.

INDEX WORDS: Visual illusions; Baldwin illusion; Attention; Interleaved task; Dual task; Visual search

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6 LOOK THERE!

MODULATING ATTENTION WITHIN THE BALDWIN ILLUSION

How we see the world and, ultimately, how we interact with our physical environments largely is driven by the context in which we perceive objects or events. Visual illusions provide a unique opportunity to understand better how context shapes our perception and, crucially, our (mis)perception of the world. Illusions have a long history in the perceptual and cognitive sciences and date back prior to the establishment of psychology as its own discipline (for reviews, see Coren & Girgus, 1978; Gregory, 2009; Luckiesh, 1922; Robinson, 1972). The study of visual illusions and how they impact high-risk real-world scenarios is one early translation of basic psychological research (e.g., explaining the fatal plane crash of a Boeing 707 and an Eastern Airlines Lockheed 1049C in 1965; Coren & Girgus, 1978). More recently, psychologists have focused on when and why visual illusions occur and which populations are most susceptible to misperceptions (e.g., Dakin & Frith, 2005; de Fockert, Davidoff, Fagot, Parron, & Goldstein, 2007; Happé, 1996; Witkin, 1967).

For example, some people more readily perceive geometric illusions than others based on their perceptual style of processing. Geometric illusions emerge when a target's physical properties (e.g., size, shape, length, width, diameter, orientation, etc.) are distorted on the basis of the target's surrounding figural context or its inducing elements. The perception of multi-element figures (e.g., an illusory array) is hierarchically organized such that stimuli are processed at the overall group level and at the individual element level. Depending upon the order of processing, a precedence effect emerges in which the whole configuration (global precedence) or the individual elements (local precedence) are first processed. Specifically, geometric illusions require global processing of the illusory array such that all individual elements are processed

simultaneously. Although humans primarily are classified as global-processors (e.g., Broadbent, 1977; Navon, 1977, 1981), individual differences emerge. Those individuals with a stronger global precedence perceive visual illusions more readily than those with a stronger local precedence (e.g., Berry, 1966, 1968, 1971; Dawson, 1967; Witkin, 1967). In contrast, certain populations that are defined as local processors show evidence of reduced illusory perception relative to others (e.g., Himba tribesman of Namibia: de Fockert, Davidoff, Fagot, Parron, & Goldstein, 2007; children with autism spectrum disorder: Dakin & Frith, 2005; Happé, 1996; Happé, Briskman, & Frith, 2001).

Beyond processing style, differential attention towards elements within an illusory array has a robust effect on the emergence and magnitude of visual illusions (e.g., Daini & Wenderoth, 2008; Gardner & Long, 1961; Goryo, Robinson, & Wilson, 1984; Jordan & English, 1989; Lester & Dasonville, 2011; Predebon, 2004, Shulman, 1992; Tsal, 1984). Researchers have manipulated attentional focus via instructions to ignore certain elements within the visual array while focusing on others. Selective attention to only some features within an array interrupts the global processing that is necessary to perceive illusions. Illusion magnitude decreases when participants focus on the to-be-discriminated target element, but illusion magnitude tends to increase when participants focus on the contextual features (e.g., Bates, 1923; Gardner & Long, 1961; Predebon, 2004; Restle, 1971).

For example, Predebon (2004) demonstrated that the magnitude of the Muller-Lyer illusion decreases over the course of an experiment when participants are directly instructed to ignore the inducers (wings) and instead focus on the target stimulus (the horizontal line). Further, simple manipulations of stimulus properties (e.g., color, contrast, density) can direct attention towards or away from the target stimulus, effectively decreasing or increasing the illusion

magnitude (e.g., Coren & Girgus, 1972; Dewar, 1967; Ebert & Pollack, 1972, 1973; Weintraub & Cooper, 1972). Attention also is modulated via contextual cues; altering the color of surrounding features so that they match an illusory array can lead to increased instances of some visual illusions (e.g., Roelofs effect; Lester & Dassonville, 2011).

Taken together, these findings demonstrate that modulating attention within a visual array serves to impact illusion perception by placing the focus on the target (reducing the illusion) or by placing the focus on the illusory inducing context (increasing the illusion). A question remains regarding the extent to which attentional cues impact illusion emergence. Specifically, is it possible to manipulate attention even before the illusory array is presented? Here, we tested this idea using an interleaved task paradigm to create a carryover effect between two tasks featuring similar stimuli.

Dual tasks are used in psychological research to create a scenario in which performance or demands from one task may interfere or carryover to performance in a secondary task (e.g., Bourke & Duncan, 2005; He & McCarly, 2010; Olivers, Meijer, & Theeuwes, 2006; Pannebakker, Band, & Ridderinkhof, 2009; Soto, Hodsoll, & Rotshtein, 2008; Woodman & Luck, 2004). Primary tasks within an interleaved paradigm vary in their ability to create demands on cognitive resources (e.g., working memory), which subsequently impact which resources are available (or depleted) for a subsequent task. In the current study, we used a set of interleaved perceptual tasks in an attempt to manipulate attention and subsequently alter perception of the Baldwin illusion.

The Baldwin illusion features two horizontal lines of equal length that are misperceived in terms of length on the basis of flanking squares (Baldwin, 1895; Pressey & Smith, 1986; Pressey & Wilson, 1980; see Figure 1). A line flanked by large squares on either end is perceived

to be shorter in length than an identical line flanked by small squares on either end. The primary task in the interleaved set was designed to direct attention towards either the target element (horizontal line) or the inducing elements (squares) within the Baldwin array, which was presented in the second task in the interleaved set. We predicted that participants would be less likely to perceive the Baldwin illusion when the primary task featured the target stimulus (horizontal line) as focusing on the to-be-discriminated stimulus reduces illusory perception. In contrast, we predicted that participants would be more likely to perceive the illusion when the concurrent task featured the inducing squares (squares) as attention to the illusory-inducing context increases illusory perception.

6.1 Experiment 1

6.1.1 Methods

6.1.1.1 Participants

Thirty-eight undergraduate participants were recruited from Georgia State University's (GSU) Psychology Department participant pool (average age: 20.71 years old \pm 5.05, 29 females). Participants were required to give informed consent prior to participating in the experiment(s) and received course credit for their participation. Testing complied with the procedures and protocols that were approved by the Institutional Review Board of GSU.

6.1.1.2 Apparatus

Participants were tested at individual computer carrels with a personal computer, a digital monitor, and a mouse for responding. They were given written feedback on the computer screen regarding the accuracy of their responses.

6.1.1.3 Illusion Task

6.1.1.3.1 Stimuli

The Baldwin stimuli consisted of a horizontal line (target) flanked on both sides by square inducers (see Figure 1). On all trials, a stimulus was presented in the middle of the screen, and participants were required to classify the central line as ‘short’ (by moving the cursor to the bottom left of the screen to a green rectangle including the word ‘short’) or ‘long’ (by moving the cursor to the bottom right of the screen to a green rectangle including the word ‘long’). The line and the inducing squares were black, presented on a white background. The squares that flanked either side of the horizontal line were both small (2.5 cm x 2.5 cm) or were both large (5 x 5 cm). Squares were positioned flush against the end of either side of the horizontal line (no gap between line and square).

Using a psychophysical step procedure, a range of 11 possible target line lengths was established. A Level 6 (midpoint) line was established at 4 cm. Level 6 stimuli were never presented as they were neither long nor short lines. Levels 1-5 were all shorter than the Level 6 line, and their length was generated by the following equation: $\text{Level} = 3 * 0.98^{(6 - \text{TrialLevel})}$. Levels 7-11 were all longer than the Level 6 line, and their length was generated by the following equation: $\text{Level} = 3 * 1.02^{(\text{TrialLevel} - 6)}$. Thus, Levels 1 – 11 were progressively longer lines for which the Level 5 and Level 7 lines were the objectively hardest to discriminate from the midpoint (Level 6). Level 1 (shortest) and Level 11 (longest) were the objectively easiest to discriminate.

6.1.1.3.2 General Procedure

Prior to beginning the study, participants were instructed that they would be working on two tasks. In the first task, they would see a horizontal line that could be presented in isolation or

surrounded by squares. They were told that they were to assign the line as being ‘short’ or ‘long’ using two buttons on the screen. In the second task, they were instructed that they would be presented with two lines or two squares. On those trials, participants were instructed to choose the line or square that was rotated to a greater degree relative to the other. Figure 2 presents the layout of trials.

At the outset of each Illusion Task trial, participants clicked a trial initiation stimulus at the center of the computer screen (‘Start’ button). Then that button disappeared and the test stimulus and the two green classification icons appeared as choice options. Stimuli were presented in the center of the screen with the classification icons left-justified (‘short’) and right-justified (‘long’) at the bottom of the screen. Participants used the mouse to contact one of the two classification icons, thereby classifying horizontal line length on each trial. Participants were required to make their response within 3 seconds of the stimuli appearing onscreen. After selection of a stimulus or after 3 seconds of inactivity, the screen then cleared completely. Correct responses led to a flashing stimulus that said ‘Correct!’ in the middle of the screen, whereas incorrect responses led to a flashing stimulus that said ‘Incorrect’ in the middle of the screen followed by a timeout period of 5 s. Failure to respond within 3 seconds of stimuli presentation led to an instruction to respond more quickly to the trials. The inter-trial interval was 1 s.

Three Illusion Task conditions were included. The Baseline condition presented a horizontal line with no flanking squares. This condition was used to establish classification performance without the effects of any inducing stimuli. The Small Square condition presented two small squares flanking either side of the horizontal line. The Large Square condition

presented two large squares flanking either side of the horizontal line. We never presented a line with flanking squares of different sizes on either end of the line.

We presented the Baseline condition in 33.3% of trials, the Small Square condition in 33.3% of trials, and the Large Square condition in 33.3% of trials. We oversampled the more difficult levels to increase the number of critical test trials presented (50% of test trials presented a randomly selected Level 3 to Level 10 trial whereas the remaining trials randomly sampled from the full range of levels). The true midpoint line (Level 6) was never presented.

6.1.1.4 Interleaved Task

6.1.1.4.1 Stimuli

Interleaved Task stimuli were comprised of either target elements (lines) or inducer elements (squares; see Figure 2). Line stimuli were identical in length and color to the standard target line described above at Level 6 (4 cm long; black), but were presented in one of nine different orientations with respect to the horizontal axis of the computer screen (0° or vertical, $\pm 10^\circ$, $\pm 20^\circ$, $\pm 30^\circ$, $\pm 40^\circ$). Square stimuli were presented in a range of nine different orientations with respect to the horizontal axis of the computer screen (0° or parallel, 10° , 20° , 30° , 40° , 50° , 60° , 70° , 80°). Squares were 4 x 4 cm in size and were black presented on a white background.

6.1.1.4.2 General Procedure

At the outset of each Interleaved Task trial, participants clicked a trial initiation stimulus at the center of the computer screen ('Start' button). Then that button disappeared and two stimuli (two squares or two lines) appeared as choice options. Stimuli were presented top-left and top-right justified on the screen. Participants were required to select the line or square that had a greater degree of rotation than the other line or square on screen. One stimulus always was

presented with 0° of rotation and the second stimulus was presented with a randomly selected greater degree of rotation (see Stimuli section above for rotation options). Participants were not required to make a speeded response. Selecting the choice stimulus that had a greater degree of rotation led to a flashing stimulus that said ‘Correct!’ in the middle of the screen, whereas incorrect responses led to a flashing stimulus that said ‘Incorrect’ in the middle of the screen followed by a timeout period of 5 s. The inter-trial interval was 1 s.

Two interleaved task conditions were established – Interleaved Square that presented two squares and Interleaved Line that presented two lines. The Interleaved Task and Illusion Task iterated back and forth trial by trial throughout the session, so that participants completed one Interleaved Task trial and then one Illusion Task trial. Each participant completed a total of 800 trials – 400 Interleaved Task trials and 400 Illusion Task trials. Half of the participants began with 200 Interleaved Square trials iterated with 200 Illusion Task trials and then completed 200 Interleaved Line trials iterated with 200 Illusion Task trials. The other half of participants began with 200 Interleaved Line trials iterated with 200 Illusion Task trials and then completed 200 Interleaved Square trials iterated with 200 Illusion Task trials.

All participants completed the 800 test trials in the experiment, and all data were included in the analyses. Test sessions lasted as long as one hour.

6.1.2 Results

We first examined performance in the Interleaved Task. As predicted, participants performed very well, rarely making mistakes in choosing the stimulus with a greater degree of rotation (99.4% accuracy for the Interleaved Square condition and 99.1% accuracy for the Interleaved Line condition).

For all subsequent analyses for the Illusion Task, we reduced the number of line length levels from 10 levels to 8 levels, binning the easiest ‘short’ levels (Level 1 and Level 2) and the easiest ‘long’ levels (Level 10 and Level 11). We excluded all trials in which participants timed-out (response times exceeding 3 seconds). These trials were very infrequent, occurring in only 0.36% of the trials.

Figure 3 depicts group-level performance in the Illusion Task (i.e., classification of the line as short) as a function of Illusion Task condition and Line Length for the (a) Interleaved Line condition and (b) Interleaved Square condition. We conducted a repeated-measures ANOVA with Interleaved Task condition (Line and Square), Illusion Task condition (Baseline, Small Square, Large Square), and Line Length (8 levels) as independent variables with proportion of trials where the participants made a line classification of ‘short’ as the dependent variable. There was a significant main effect of Line Length, $F(7, 259) = 141.06, p < .001, \eta^2_p = .79$, and Illusion Task condition, $F(2, 74) = 104.52, p < .001, \eta^2_p = .74$. Crucially, there was not a significant main effect of Interleaved Task condition, $F(1, 37) = 2.04, p = .16, \eta^2_p = .05$. There was a significant interaction of Line Length and Illusion Task condition, $F(14, 518) = 16.33, p < .001, \eta^2_p = .31$. There was not a significant interaction of Line Length and Interleaved Task condition, $F(7, 259) = 1.02, p = .42, \eta^2_p = .03$, nor of Interleaved Task condition and Illusion task condition, $F(2, 74) = .29, p = .75, \eta^2_p = .08$. There also was not a significant three-way interaction, $F(14, 518) = .96, p = .49, \eta^2_p = .03$.

To explore the interaction between Line Length and Illusion Task, and based upon a visual inspection of Figure 3, we divided Line Length into short line levels (Levels 1-4) and long line levels (Levels 5-8). Because there was no effect of Interleaved Task, we collapsed performance across Interleaved Task condition (Line and Square). We used a paired-samples t-

test to compare the Baseline condition to the Small Square and Large Square conditions for short and long lines levels. We also compared the Small Square and Large Square conditions to one another. A Bonferroni adjusted alpha level of .016 was used per test given the three comparisons of interest (.05/3) for short lines and long lines. For the short line lengths (Levels 1-4), lines were classified as ‘short’ significantly less in the Small Square condition ($M = 38.35$, $SD = 16.65$) than in the Baseline condition ($M = 82.62$, $SD = 14.11$), $t(37) = -12.12$, $p < .001$, and in the Large Square condition ($M = 77.91$, $SD = 17.26$), $t(37) = -11.93$, $p < .001$. Performance did not differ significantly for the Baseline and Large Square conditions, $t(37) = 2.23$, $p = .03$.

For the long line lengths (Levels 5-8), lines again were classified as ‘short’ significantly less often in the Small Square condition ($M = 11.91$, $SD = 13.09$) than in the Baseline condition ($M = 34.01$, $SD = 20.28$), $t(37) = -6.91$, $p < .001$, and in the Large Square condition ($M = 34.67$, $SD = 15.07$), $t(37) = -9.75$, $p < .001$. Performance did not differ significantly for the Baseline and Large Square conditions $t(37) = -.23$, $p = .82$. Thus, for both short and long line lengths, small squares flanking the horizontal line led to overestimations of line length relative to no squares or large squares flanking the line.

6.1.3 Discussion

Our findings from Experiment 1 matched previous reports of the Baldwin illusion among human adults in which participants overestimated line length when lines were flanked by small squares (e.g., Brigell, Uhlarik, Goldhorn, 1977; Clavadetscher & Anderson, 1977; Wilson & Pressey, 1988). Despite evidence that attentional focus impacts illusion perception (e.g., Coren & Girgus, 1972; Ebert & Pollack, 1972, 1973; Weintraub & Cooper, 1972), we did not document an effect of interleaved task performance in the present study. A crucial difference in our study from previous studies reporting attentional effects on illusion magnitude is that we manipulated

attention via a secondary task rather than directly within the illusory array itself. Perhaps we would have seen greater carryover between the interleaved tasks with more salient featural cues. However, our interest was in whether modulation of illusory perception could occur through sequential visual experiences in different contexts.

To explore further whether an interleaved task modulates attention in a subsequent illusion task, we altered the features of both tasks via changes in stimuli color. Altering stimuli color within an illusory array has proven effective in changing the magnitude of several visual illusions (e.g., Coren & Girgus, 1972; Dewar, 1967; Ebert & Pollack, 1972, 1973; Weintraub & Cooper, 1972). In Experiment 2, we presented the same set of interleaved tasks, but we changed the color of the stimuli across tasks so that the interleaved tasks shared more in common in terms of visual features. For example, in the Interleaved Line condition, we presented red lines. We also presented a red center line in the Illusion Task, but the inducing squares remained black. In the Interleaved Square condition, we presented red squares, and in the Illusion Task, we also presented red inducing squares but a black center line. We predicted that further increasing the salience of the to-be-oriented stimuli across interleaved tasks may enhance our efforts to direct attention within the illusory array.

6.2 Experiment 2

6.2.1 Methods

6.2.1.1 Participants

Sixteen different undergraduate participants were recruited from GSU's Psychology Department participant pool (demographic information is not available for this experiment because of an error in collecting those data; however, anecdotally these participants were highly similar to those tested in Experiment 1). Participants were required to give informed consent

prior to participating in the experiment(s) and received course credit for their participation.

Testing complied with the procedures and protocols that were approved by the IRB of GSU.

All methods and materials were identical to Study 1 (i.e., Apparatus, Stimuli, and General Procedure) except for one difference – stimuli color. In Study 1, all stimuli were black presented on a white background. In Study 2, stimuli could either be black or red presented on a white background depending upon the condition. In the Interleaved Square condition, the squares were red and, in the Illusion Task, the squares also were red but the line was black. In the Interleaved Line condition, the lines were red, and in the Illusion Task, the center line also was red but the inducing squares were black. Essentially, the Interleaved Task and Illusion Task contained corresponding color stimuli.

A testing session was 60 minutes or until the participant completed the 800 test trials. We only used data from those participants who completed at least 600 trials in the task because fewer trials than this would not have allowed for enough trials at each difficulty level for each condition. All but one participant met this trial requirement.

6.2.2 Results

Participant performance was excellent in the Interleaved Task (99.13% accuracy for the Interleaved Square condition and 98.97% accuracy for the Interleaved Line condition).

In this experiment, no trials timed out due to participants not responding within three seconds. Figure 4 depicts group-level performance (i.e., classification of the line as ‘short’) as a function of Illusion Task condition and Line Length for the (a) Interleaved Line condition and (b) Interleaved Square condition. Again, we conducted a repeated-measures ANOVA with Interleaved Task condition (Line and Square), Illusion Task condition (Baseline, Small Square, Large Square), and Line Length (8 levels) as variables on the proportion of trials where the

participants made a line classification of ‘short.’ There was a significant main effect of Line Length, $F(7, 98) = 126.86, p < .001, \eta^2_p = .90$, and Illusion Task condition, $F(2, 28) = 48.85, p < .001, \eta^2_p = .78$. As in Experiment 1, there was not a significant main effect of Interleaved Task condition, $F(1, 14) = .01, p = .91, \eta^2_p = .001$. There was a significant interaction between Line Length and Illusion Task condition, $F(14, 196) = 7.88, p < .001, \eta^2_p = .36$. There was not a significant interaction of Line Length and Interleaved Task condition, $F(7, 98) = .68, p = .69, \eta^2_p = .05$, nor of Interleaved Task condition and Illusion Task condition, $F(2, 28) = .90, p = .42, \eta^2_p = .06$. There was not a significant three-way interaction, $F(14, 196) = 1.43, p = .14, \eta^2_p = .09$.

To explore the interaction between Line Length and Illusion Task, and based upon a visual inspection of Figure 4, we divided Line Length into short line levels (Levels 1-4) and long line levels (Levels 5-8). Because there was no effect of Interleaved Task, we collapsed performance across Interleaved Task condition (Line and Square). We used a paired-samples *t*-test to compare the Baseline condition to the Small Square and Large Square conditions for short and long line levels. We also compared the Small Square and Large Square conditions to one another. A Bonferroni adjusted alpha level of .016 was used per test given the three comparisons of interest (.05/3) for short lines and long lines. For the short line lengths (Levels 1-4), lines were classified as ‘short’ significantly less often in the Small Square condition ($M = 40.99, SD = 12.96$) than in the Baseline condition ($M = 82.76, SD = 7.65$), $t(14) = -9.83, p < .001$ and in the Large Square condition ($M = 79.74, SD = 10.58$), $t(14) = -11.70, p < .001$. Performance did not differ significantly for the Baseline and Large Square conditions, $t(14) = .98, p = .35$. For the long line lengths (Levels 5-8), lines again were classified as ‘short’ significantly less often in the Small Square condition ($M = 12.73, SD = 9.84$) than in the Baseline condition ($M = 33.06, SD = 14.35$), $t(14) = -4.12, p = .001$, and in the Large Square condition ($M = 29.69, SD = 14.98$), $t(14)$

= -3.82, $p = .002$. Performance did not differ significantly for the Baseline and Large Square conditions $t(14) = .86, p = .40$. For short and long line lengths, small squares flanking the horizontal line led to overestimations of line length relative to no squares or large squares flanking the target line.

6.2.3 Discussion

We replicated our findings from Experiment 1 for Baldwin illusion perception among human adults. Despite further featural changes (i.e., stimuli color) to the interleaved task paradigm, viewing squares or lines prior to the illusion task did not differentially impact participant performance. The illusion emerged readily, but not differentially, for both Interleaved Task conditions. To further investigate the role, if any, that an interleaved task might play in the magnitude of subsequent illusion perception, we extended our attempts to modulate attention via a more active attentional task in our primary task in the interleaved set – a visual search task.

6.3 Experiment 3

6.3.1 Methods

6.3.1.1 Participants

Forty-nine different undergraduate participants were recruited from GSU's Psychology Department participant pool (average age: 20.69 years old \pm 8.53, 40 females). Participants were required to give informed consent prior to participating in the experiment(s) and received course credit for their participation. Testing complied with the procedures and protocols that were approved by the IRB of GSU. The apparatus and testing location were identical to Study 1 and Study 2.

6.3.1.2 Illusion Task

Illusion task stimuli and General Procedures were identical to those from Study 1 and Study 2, except that we no longer included Large Square trials in which large squares flanked the horizontal line. Instead, we presented the Baseline condition in 50% of trials and the Small Square condition in 50% of trials. Again, we oversampled the more difficult levels to increase the number of critical test trials presented (50% of test trials presented a randomly selected Level 3 to Level 10 trial whereas the remaining trials randomly sampled from the full range of levels). The true midpoint line (Level 6) was never presented. We did not include Large Square trials in Experiment 3 because this condition did not lead to a difference in performance patterns relative to the Baseline condition in Experiment 1 or Experiment 2. Eliminating this condition from Experiment 3 allowed us to increase the critical trial types as this study required more time to complete than the previous experiments.

6.3.1.3 Visual Search Task

6.3.1.3.1 Stimuli

Visual Search Task stimuli were comprised of either target elements (lines) or inducer elements (squares; see Figure 2). Lines in the Visual Search task were identical in length and color to the standard target line described above at Level 6 (4 cm long; black). Squares were identical in size and color to the small squares in the Small Square condition from the Illusion task (2.5 cm x 2.5 cm).

6.3.1.3.2 General Procedure

At the outset of each Visual Search Task trial, participants clicked a trial initiation stimulus at the center of the computer screen ('Start' button). Then that button disappeared and stimuli (squares or lines) appeared onscreen. On each trial, participants were required to identify

whether a target that differed from all other stimuli onscreen was present among a set of distractors (which all were identical to each other). Participants were presented with either squares (Visual Search Square task) or lines (Visual Search Line task). Two conditions were established for Visual Search trials, including Target-Present trials (target present among a set of distractors) and Target-Absent trials (target absent among distractors). Participants were instructed to select the “Z” key if they did not locate a target (i.e., if all stimuli were identical to one another) or the “M” key on the computer keyboard if they located the target (i.e., the stimulus set contained one stimulus that differed in its visual properties from all others). The Visual Search trials presented 8, 16, 32, or 64 stimuli. All distractor stimuli (squares and lines) had a border width of 3 mm but, if a target was present, one of the stimuli had a slightly larger border width of 5 mm. Stimuli were presented in one of 64 randomly selected locations on screen, equidistant from one another.

Participants were not required to make a speeded response. If a participant correctly identified target-present trials as containing a visually distinct stimulus (via the “M” key) or if a participant correctly identified target-absent trials (via the “Z” key), a flashing stimulus that said ‘Correct!’ in the middle of the screen appeared. Incorrect responses led to a flashing stimulus that said ‘Incorrect’ in the middle of the screen followed by a timeout period of 5 s. The inter-trial interval was 1 s.

As in Experiment 1 and Experiment 2, the Visual Search Task and the Illusion Task iterated back and forth trial by trial throughout the session, so that participants completed one Visual Search Task trial and then one Illusion Task trial. Each participant completed a total of 800 trials – 400 Visual Search Task and 400 Illusion Task. Half of the participants began with the 200 Visual Search Square trials iterated with 200 Illusion Task trials and then completed 200

Visual Search Line trials iterated with 200 Illusion Task trials. The other half of participants began with 200 Visual Search Line trials iterated with 200 Illusion Task trials and then completed 200 Visual Search Square trials iterated with 200 Illusion Task trials. A testing session was 60 minutes or until the participant completed the 800 test trials. Data from participants completing fewer than half of the classify trials were not included in the following analyses. All but one participant met this requirement.

6.3.2 Results

Table 1 depicts group level performance in the Visual Search Line and Visual Search Square tasks as a function of correctly identifying target presence among the distractors and the response times for each trial type. Participants performed above chance in each task, but did not reach accuracy levels documented in Experiments 1 and 2 for the primary task (>98% accuracy). Average group performance for the Visual Search Line task was 65.92%. Average group performance for the Visual Search Square task was 66.86%. As predicted, there was a negative correlation of performance and set size for Visual Search Line Target-Present trials, $r(2) = -.99, p = .005$. There was a similar trend in performance as a function of set size for Line Target-Absent trials, $r(2) = -.64, p = .18$, Square Target-Present trials, $r(2) = -.72, p = .14$, and Square Target-Absent trials, $r(2) = -.48, p = .26$, but none of these conditions were statistically significant.

For the Illusion Task, we excluded all trials in which participants timed-out (response times exceeding 3 seconds). These trials were very infrequent, occurring in only 2.10% of the trials.

Figure 5 depicts group-level performance (i.e., classification of the line as ‘short’) as a function of Illusion Task condition and Line Length for the (a) Visual Search Line task and (b) Visual Search Square task. We conducted a repeated-measures ANOVA with Visual Search

Task condition (Line and Square), Illusion Task condition (Baseline and Small Square), and Line Length (8 levels) as variables on the proportion of trials where the participants made a line classification of ‘short.’ There was a significant main effect of Line Length, $F(7, 322) = 82.02, p < .001, \eta^2_p = .64$, and Illusion Task condition, $F(1, 46) = 54.54, p < .001, \eta^2_p = .54$. As in Experiment 1 and Experiment 2, there was not a significant main effect of Visual Search Task condition, $F(1, 46) = 1.99, p = .17, \eta^2_p = .04$. There was a significant interaction between Line Length and Illusion Task condition, $F(7, 322) = 9.86, p < .001, \eta^2_p = .18$. There was not a significant interaction of Line Length and Interleaved Task condition, $F(7, 322) = 1.48, p = .17, \eta^2_p = .03$, nor of Interleaved Task condition and Illusion Task condition, $F(1, 46) = 1.36, p = .25, \eta^2_p = .03$. There was not a significant three-way interaction, $F(7, 322) = 1.38, p = .21, \eta^2_p = .03$.

Based on a visual inspection of Figure 5, the effect of condition appeared to be driven by the more difficult levels, and less so at the easier short levels (Levels 1-2) and the easier long levels (Levels 7-8), likely due to ceiling effects. Because there was no effect of Visual Search Task, we collapsed performance across conditions (Line and Square). We used a paired-samples t-test to compare the Baseline condition to the Small Square condition at the more difficult test levels (Levels 3-6). Lines were classified as ‘short’ significantly less in the Small Square condition ($M = 37.61, SD = 12.99$) than in the Baseline condition ($M = 63.15, SD = 15.63$), $t(47) = 9.34, p < .001$.

6.3.3 Discussion

The Baldwin illusion, again, readily emerged in a classification task among human adults despite the completion of an interleaved visual search task that featured illusion targets (lines) or inducers (squares). Taken together with the results from Experiment 1 and Experiment 2, the emergence of the Baldwin illusion is robust and not impacted via an interleaved task presenting

perceptually similar stimuli. These results indicate that effective attempts to manipulate attention within a visual illusion array may only occur when the array is physically present. Efforts to manipulate attention in this manner have been effective in past studies using verbal instructions to attend to different features within the array and through simple manipulations of illusory elements (e.g., Daini & Wenderoth, 2008; Gardner & Long, 1961; Goryo, Robinson, & Wilson, 1984; Jordan & English, 1989; Lester & Dassonville, 2011; Predebon, 2004, Shulman, 1992; Tsal, 1984).

6.4 General Discussion

Attention plays a critical role in the emergence of perceptual illusions. Increased attention towards an illusory-inducing context, unsurprisingly, increases illusion magnitude and inattention towards this context reduces or even reverses illusion magnitude or direction (e.g., Bates, 1923; Coren & Girgus, 1972; Dewar, 1967; Ebert & Pollack, 1972, 1973; Gardner & Long, 1961; Predebon, 2004; Restle, 1971; Weintraub & Cooper, 1972). In the current study, we introduced an interleaved task paradigm that included a primary task presenting either targets (lines) or inducers (squares) followed by a secondary task to classify horizontal lines as ‘short’ or ‘long’ when presented as part of the illusory array. Illusion perception was robust among participants, with human adults overestimating line length when presented with small flanker squares. The magnitude of the illusion did not differ as a function of primary task in the current experiments – the illusion was perceived to the same extent whether squares or lines were presented prior to the classification task.

We utilized an interleaved task in which participants completed a two-choice discrimination or a visual search task and then completed the illusion classification task. A dual task paradigm is used to assess whether performance or demands from one task interfere or

carryover to performance in a second, perhaps related task (e.g., Bourke & Duncan, 2005; He & McCarly, 2010; Pannebakker et al., 2009; Woodman & Luck, 2004). Often, a concurrent task design is used when implementing a dual task paradigm versus the interleaved task adopted here. Concurrent tasks introduce the secondary task *during* the completion of the primary task, rather than the iterated procedure used here. Thus, the concurrent task creates a demand on cognitive resources as the tasks are completed simultaneously. This higher demand of a concurrent task may have increased the likelihood of interference from the primary task with the illusion task. For example, requiring participants to store an image of a horizontal line (target) or square (inducer) in working memory while completing the illusion classification task may create differences in illusion perception if the stimulus differs from that of the classification task.

Future studies also might consider the role of perceptual processing mode when studying attentional effects in illusions. Specifically, geometric illusions require the simultaneous processing of the entire figure rather than perceiving each element individually (Coren & Girgus, 1978). Previous research has demonstrated that human adults with a stronger global precedence perceive geometric illusions more readily than those participants with a more locally-oriented processing mode, presumably because they have a stronger tendency to perceive multi-element arrays as one larger configuration rather than individual parts (e.g., Berry, 1966, 1968, 1971; Dawson, 1967; Witkin, 1967). An interesting question concerns whether these individual differences in processing mode influence the likelihood for attentional biases within an illusory array. Perhaps those with a stronger global precedence are immune to attentional manipulation as investigated in the current work. In contrast, a local processor might be subject to greater manipulations of a secondary task that directs attention to the individual elements.

Further, certain species (e.g., monkeys or pigeons) or populations such as children with Autism Spectrum Disorder display a more locally-oriented processing style and subsequently fail to perceive some geometric illusions (e.g., Dakin & Frith, 2005; Happé, 1996; Happé, Briskman, & Frith, 2001). Thus, their perceptions of visual illusions may be more pliable via a secondary task than typically-developing children and adults. Attentional manipulations as tested here in an interleaved paradigm would likely result in slight differences in illusion perception that interact with base perceptual processing styles.

6.5 References

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6.6 Tables

Table 1. Group performance for the Visual Search task in Experiment 3, including average performance (accuracy in identifying target presence) and average response times for each trial type (in seconds).

Set Size	Line – Target Present		Line – Target Absent		Square – Target Present		Square – Target Absent	
	Accuracy	RT (s)	Accuracy	RT (s)	Accuracy	RT (s)	Accuracy	RT (s)
8	70.65	1.43	72.12	1.72	64.03	1.55	76.46	1.69
16	64.66	1.64	69.26	1.81	61.70	1.66	72.09	1.86
32	58.78	1.67	67.67	1.93	55.19	1.78	74.63	2.11
64	47.70	1.68	76.78	1.87	57.18	1.7	72.64	2.82

6.7 Figures

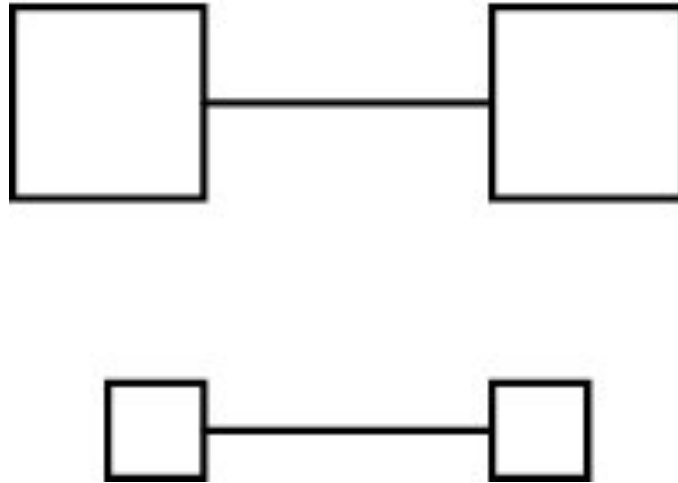


Figure 1. The Baldwin illusion: humans typically perceive the horizontal line flanked by small squares (bottom) as longer than an identical horizontal line flanked by large squares (top).

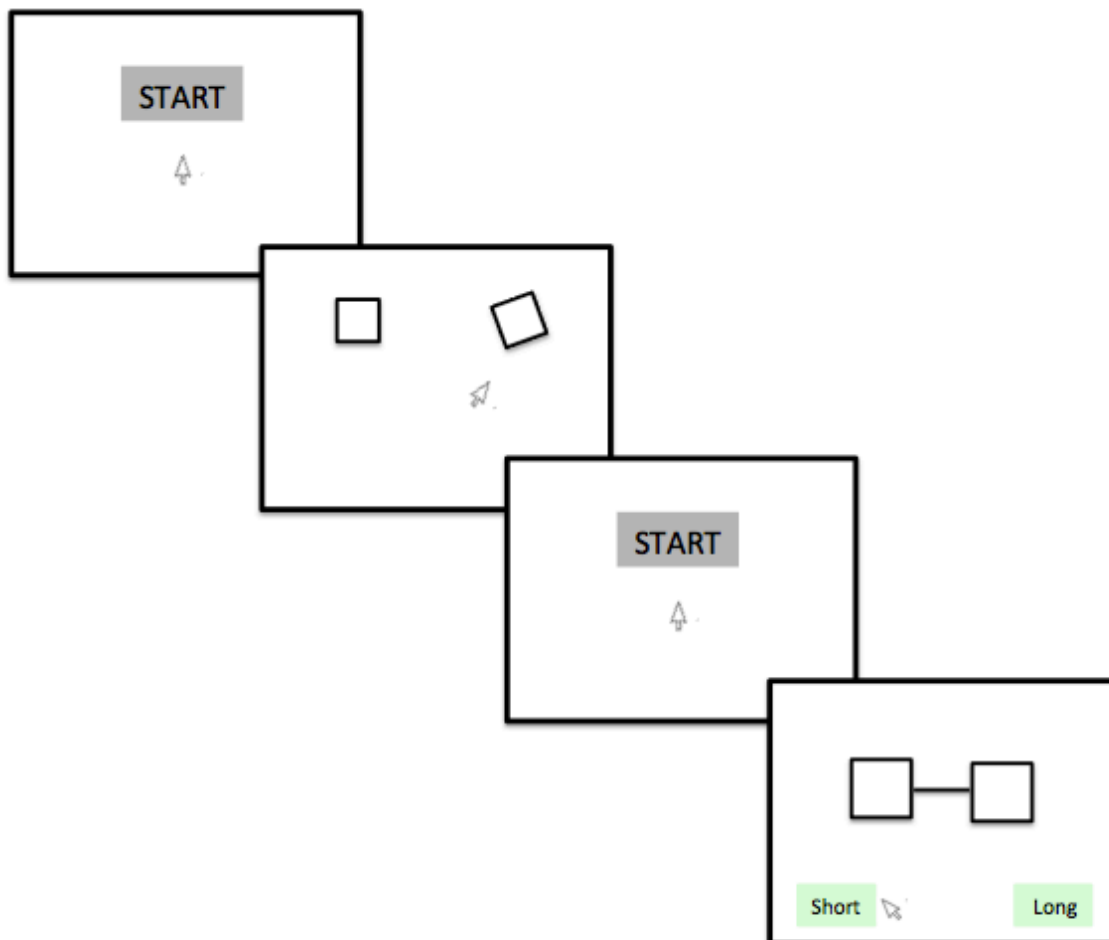
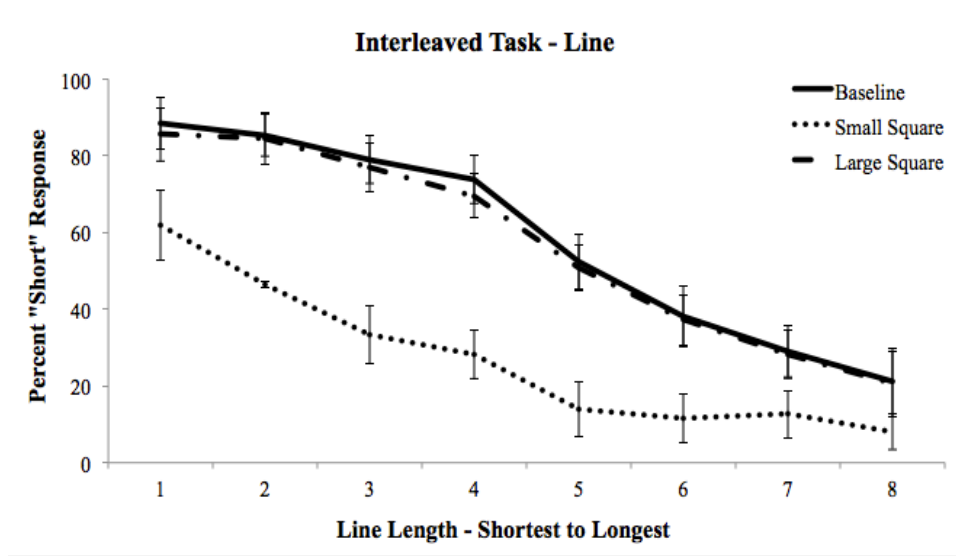
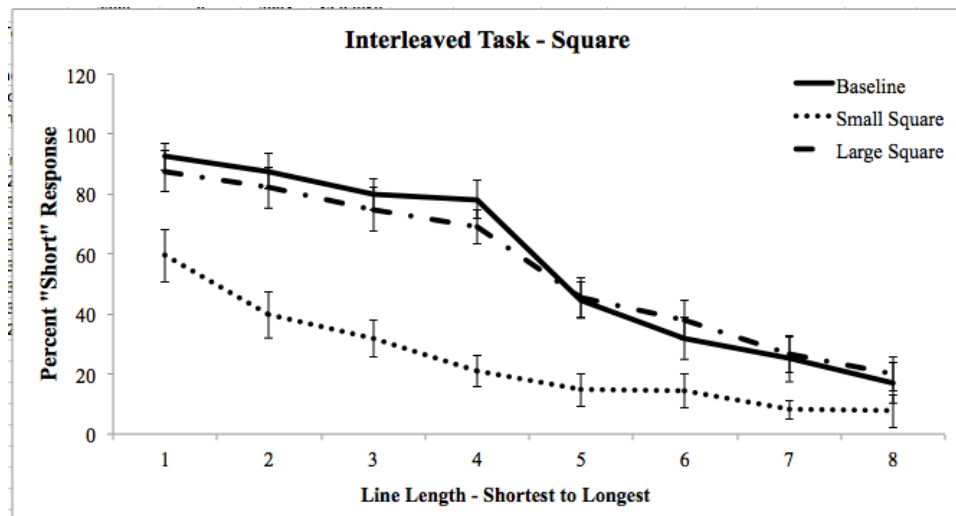


Figure 2. Example of trial progression between the Interleaved Task-Squares (select the square with the greater degree of rotation) and the Illusion Task (classify the central line as ‘Short’ or ‘Long’). The cursor arrow present in each frame is used to illustrate selection by the participant; arrows were not present during testing. Participants alternated between one Interleaved Task followed by one Illusion Task throughout testing.

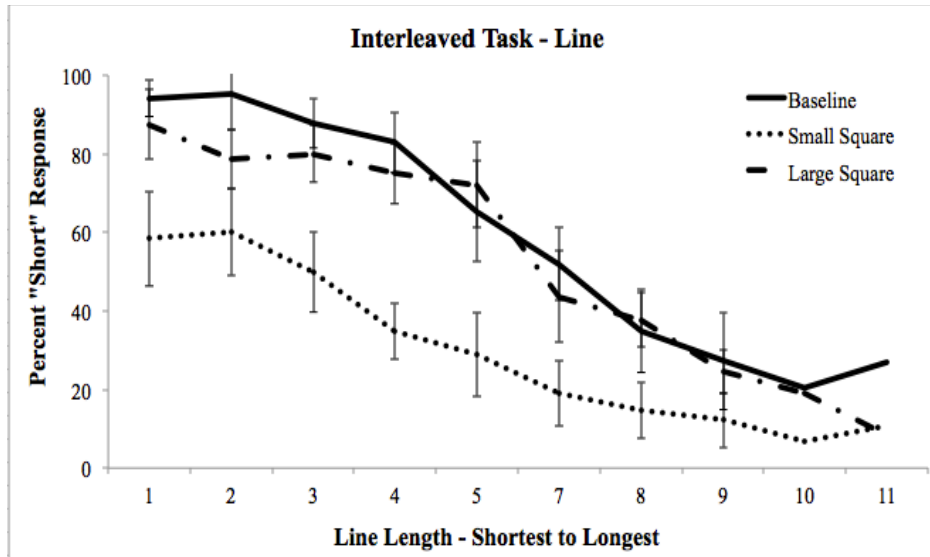


a.

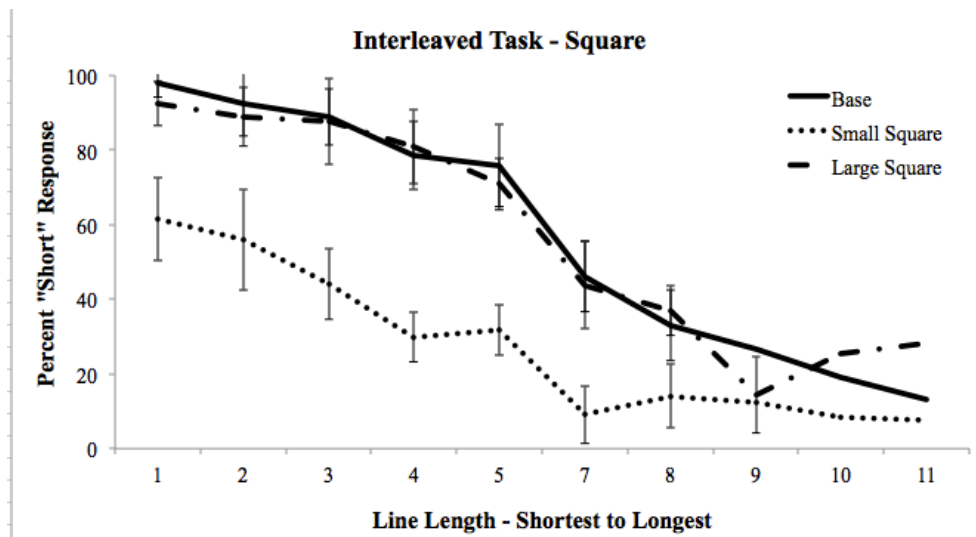


b.

Figure 3. Mean percentage of ‘Short’ responses for the Baseline, Small Square, and Large Square conditions for the (a) Interleaved Line task and the (b) Interleaved Square task. Line Length levels progress from 1 (shortest) to 8 (longest) in Experiment 1. Error bars depict corrected 95% confidence intervals for repeated measures tests (Cousineau, 2005).

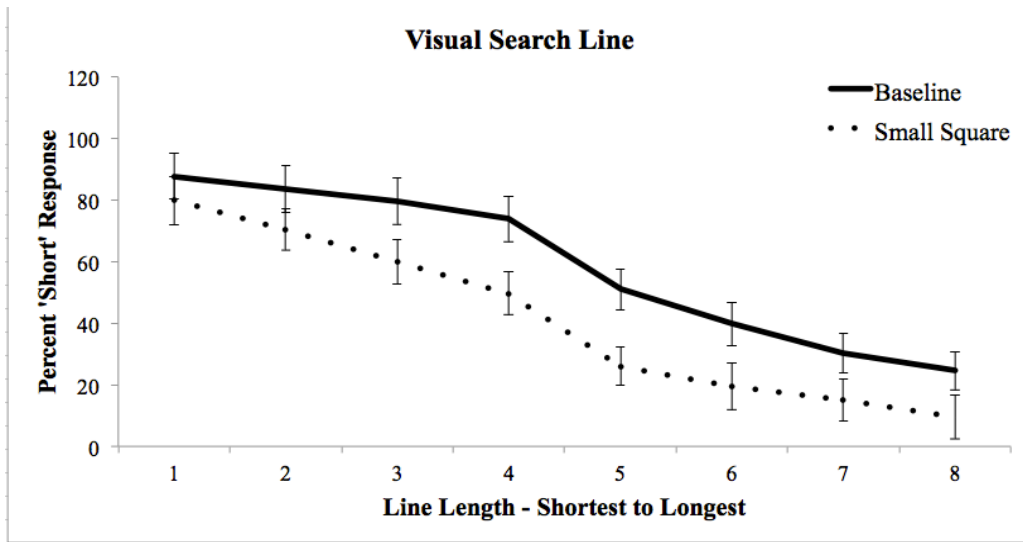


a.

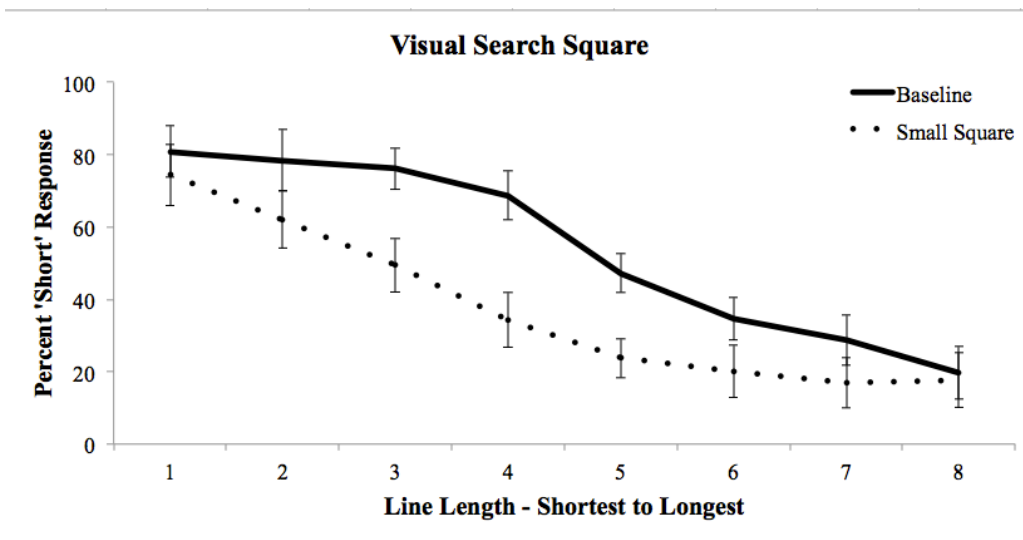


b.

Figure 4. Mean percentage of ‘Short’ responses for the Baseline, Small Square, and Large Square conditions for the (a) Interleaved Line task and the (b) Interleaved Square task. Line Length levels progress from 1 (shortest) to 8 (longest) in Experiment 2. Error bars depict corrected 95% confidence intervals for repeated measures tests (Cousineau, 2005).



a.



b.

Figure 5. Mean percentage of ‘Short’ responses for the Baseline, Small Square, and Large Square conditions for the (a) Visual Search Line task and the (b) Visual Search Square task. Line Length levels progress from 1 (shortest) to 8 (longest) in Experiment 3. Error bars depict corrected 95% confidence intervals for repeated measures tests (Cousineau, 2005).

DOES PERCEPTION OF THE TWO-DIMENSIONAL DELBOEUF ILLUSION PREDICT
FOOD CHOICE BIASES IN PRESCHOOLERS?

By

AUDREY E. PARRISH

ABSTRACT

The Delboeuf illusion is a 2-dimensional geometric illusion in which people typically perceive a central black dot as being larger when encircled by a small outer ring than the same sized dot encircled by a large outer ring. Interestingly, food on round plates mimics this visual illusion in a 3-dimensional setting. Food portions on small plates are overestimated in size relative to same-sized food portions on large plates. Although a number of studies have investigated the Delboeuf illusion in 2-dimensional format, less research has investigated the application of this illusion in food-choice scenarios. Moreover, there is no research explicitly linking illusory experiences in these two contexts within the same individuals. To explore this potential link, preschool children first completed a psychophysical method-of-adjustment

computer task in Experiment 1 and then a food-choice task in Experiment 2. Children showed evidence of the Delboeuf illusion in the computerized task, but did not show evidence of the illusion in the food-choice task. Thus, the degree to which these children perceived the 2-dimensional Delboeuf illusion using psychophysical procedures in Experiment 1 did not predict whether they also were more or less likely to see food items on small plates as constituting more food than the same amounts on large plates. Future research is needed to determine the mechanisms that underlie illusory emergence as it manifests in real-world, decision-making settings and the potential role of motivation and other factors impacting illusory biases.

INDEX WORDS: Delboeuf illusion; Perception; Children; Visual illusion; Food choice; Consumption; Method of Adjustment

7 DOES PERCEPTION OF THE TWO-DIMENSIONAL DELBOEUF ILLUSION PREDICT FOOD CHOICE BIASES IN PRESCHOOLERS?

Consumer research is heavily influenced by basic psychological science (see Ariely, 2008, 2010). One excellent example lies within the human consumption domain. What we eat, how much we eat, what we serve ourselves, whether we clean our plates, and how much money we spend on food is directly influenced by how we perceive food quantities (e.g., Wansink 2004, 2006). Food quantity perception is directly influenced by the context in which food items or portions are presented. For example, tall thin glassware often is perceived to hold more liquid than short, squat glassware holding the exact same amount of liquid (e.g., Chandon & Ordabayeva, 2009; Piaget, Inhelder, & Szeminska, 1960; Raghubir & Krishna, 1999; Wansink & Van Ittersum, 2003, 2005). People also are willing to pay more for less food based on the appearance of that food. For example, overflowing ice cream cups are valued more highly than a larger amount of ice cream that does not overflow a larger container (Hsee, 1998).

These mistakes are ubiquitous – children (e.g., DiSantis, Birch, Davey, Serrano, Zhang, Bruton, & Fisher, 2013; Wansink, Payne, & Werle, 2008; Wansink, Van Ittersum, & Payne 2014) and adults alike fall prey to these food-choice biases (e.g., Van Ittesum & Wansink, 2012; Wansink & Van Ittersum, 2013). Even nutritional and food service experts are not immune to quantity perception errors despite their extensive experience in measuring and serving food portions (Wansink & Van Ittersum, 2003; Wansink, Van Ittersum, & Painter, 2006). Finally, animals such as chimpanzees (*Pan troglodytes*) make errors in food maximization based on presentation style in ways that are similar to the choices of humans (Beran, Evans, & Harris, 2008; Boysen, Berntson, & Mukobi, 2001; Parrish & Beran, 2014a, 2014b).

Ultimately, overconsumption has detrimental effects on our waistlines and wallets, leading to overeating and overspending, further contributing to chronic illnesses such as obesity, diabetes, and heart disease (e.g., Allison, Fontaine, Manson, Stevens, & VanItallie, 1999; Calle, Rodriguez, Walker-Thurmond, & Thun, 2003; Rolls, 2003). Because of the universality of errors in food quantity judgment and the detrimental consequences of overconsumption, researchers have begun to explore the mechanisms that underlie these biases. Recently, one illusion has received much attention in terms of how we perceive food on plates and, subsequently, how much food we consume. The Delboeuf illusion is a 2-dimensional geometric visual illusion that causes most people to perceive a central black dot as larger when encircled by a small outer ring than the same sized dot encircled by a large outer ring (Delboeuf, 1865; see Figure 1). Interestingly, food on round plates mimics this visual illusion in a 3-dimensional, decision-making setting, and the choice of people when faced with such plates suggests that a similar perceptual bias may be at work. Food portions on small plates are overestimated in size relative to food portions on large plates, much like dot size misperception (see Figure 1).

Although a number of studies with adult humans (e.g., Coren & Girgus, 1978; Nicolas, 1995; Ward & Lockhead, 1970) and children (e.g., Hanley & Zerbolio, 1965; Piaget, Lambercier, Boesch, & van Albertini, 1942; Pressey & Wilson, 1978; Weintraub & Cooper, 1972) have investigated the Delboeuf illusion in the 2-dimensional format via pen-and-paper or computerized testing, less research has investigated the application of this illusion in food-choice scenarios. Van Ittersum and Wansink (2012) first appealed to the Delboeuf illusion when reporting food choice biases in their work investigating serving behavior among human adults. They reported that bowl size influenced serving behavior in a manner in line with the visual illusion. People over-served food into large bowls (underestimating portion size in the large

context) and under-served food into small bowls (overestimating portion size in the small context). Recent studies have reported similar findings among human adults and children in a variety of scenarios, including serving tasks and food-choice scenarios (e.g., DiSantis et al., 2013; Murphy, Lusby, Bartges, & Kirk, 2012; Robinson & Matheson, 2014; Van Ittersum & Wansink, 2007, 2011; Wansink & Cheney, 2005; Wansink et al. 2008, 2014).

We have tested this phenomenon in chimpanzees using a two-choice discrimination food task (Parrish & Beran, 2014b). Chimpanzees were presented with two different food portions on the same sized plates (control conditions) or different sized plates (test conditions). They were excellent in choosing the larger amount of food in control conditions; however, like human adults, chimpanzees overestimated foods presented on small plates (even if it sometimes meant choosing a *smaller* amount of food) relative to the same-sized or larger portion on a large plate. Furthermore, we have documented the 2-dimensional Delboeuf illusion using a computerized dot-discrimination task in rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*), and those monkeys performed much as human adults do when shown these stimuli (Parrish, Brosnan, & Beran, 2015). These comparative results suggested that the phenomena underlying the food choice biases and the 2-dimensional Delboeuf illusion are perhaps linked to basic perceptual mechanisms that we share with closely related species, such as nonhuman primates.

Despite the seemingly clear link between the Delboeuf illusion and errors in food quantity judgment, there is no research explicitly linking these two perceptual experiences within the same individuals. We do not know whether individuals would perceive the Delboeuf illusion to the same degree in the traditional, 2-dimensional task as they do in a 3-dimensional, food-choice task. If this were true, then perhaps one could predict which individuals will fall prey to

food biases based on their 2-dimensional perceptions or misperceptions of the illusion. The current study served to assess the link between perception of the 2-dimensional Delboeuf illusion and the biases that emerge within food-choice tasks. Further, because food-choice studies have revealed interesting results among children who also demonstrate biases to over-serve, misjudge, and over-eat based on dish size (e.g., DiSantis et al., 2013; Robinson & Matheson, 2014; Wansink et al., 2008 2014), the current research was conducted with preschool children who might be subject to early interventions that mediate these biases.

To explore the link between 2-dimensional and 3-dimensional illusion perception, a within-subjects, repeated testing design was used, in which the same children were tested on the black-and-white Delboeuf illusion presented on computer screen followed by a food-choice task that presented real food items on plates, mimicking the dots and rings of the 2-dimensional illusion. The within-subjects design allowed for testing a predictive relationship between the two tasks.

To test the Delboeuf illusion in 2-dimensional format, children 3 to 5.5 years old were tested on a computerized task in which they had to judge and manipulate dots surrounded by outer rings of variable size. The psychophysical method of adjustment procedure was introduced in which participants were presented with a standard dot of one size and a second dot that had to be adjusted in size so that it matched the standard dot. Control trials were presented with the same sized rings (both were small rings or both were large rings) encircling each dot. Control performance was contrasted against test trials with variable sized rings (one large ring and one small ring) around each dot. The method of adjustment has proven to be successful with children as it offers an intuitive task in which the child controls the size of the target (Hanley & Zerbolio, 1965; Pressey & Wilson, 1978). Because of this, the method of adjustment isolates the target of

interest (in this case, the central dot) and reduces a bias to include the inducers (the outer ring) into the size judgment (Hanley & Zerbolio, 1965; Pressey & Wilson, 1978). It has been demonstrated that the method of adjustment is a particularly robust measure for the Delboeuf illusion as it yields highly stable results over time within the same individuals and requires a smaller number of trials than other psychophysical measures (Pressey, 1977).

In Experiment 2, the same children participated in a food-choice task in which food portions mimicked inner dots and plates mimicked the outer rings that created the context in which those portions were assessed. Participants were presented with two types of food choices on different plates and were instructed to select the larger of the two food portions. Control trials presented identical plates (both large plates or both small plates), whereas test trials presented different-sized plates (one large plate and one small plate). Children's performance was compared across both experiments to test for a predictive link between perceiving the illusion in the computerized task and perceiving the illusion in the food choice task. Establishing whether such a link exists for illusion perception across domains is crucial to understanding better the mechanisms that drive erroneous, and potentially costly, errors in judgment and decision-making.

7.1 Experiment 1

Preschool children between 3 and 5.5 years of age were presented with a computerized method of adjustment task. Two dots were presented on a computer screen, one of which was established at a standard size of 3 cm in diameter and one of which could be adjusted to increase or decrease in size through key presses. The objective was to adjust this dot until it was determined to be equal in size to the standard-sized 3 cm dot.

7.1.1 Methods

7.1.1.1 Participants

Twenty-seven typically-developing preschool children (11 females) between the ages of 40 and 68 months (average = 53 months) were included in the current study. The age of one participant was unknown as this information was not provided in the parental demographic report. These children attended a daycare and preschool center near Atlanta, Georgia. Participants were recruited via monthly newsletters from the preschool. Parental permission forms were distributed, and signed consent forms from parents were required prior to children participating in the experiment. Testing complied with the procedures and protocols that were approved by the Institutional Review Board of Georgia State University.

7.1.1.2 Materials and Procedure

Testing occurred on a voluntary basis and the children were allowed to stop testing and return to their classroom at any point during a test session. Children received a small toy following test sessions as a prize regardless of performance. Testing took place in the preschool's lunchroom, and test sessions lasted approximately 10 minutes with children typically working one time per week. Children were tested in pairs, seated across from one another at a lunchroom table with their own experimenter. Children could not see each other's computer monitor during testing.

Children were tested using a 13.5 in HP Pavilion laptop touch-screen computer. They viewed the monitor from a distance of approximately 40 cm to 50 cm. Children were familiarized with the laptop and touch-screen monitor prior to testing to ensure they understood the contingency between key presses and the responses of the computer program (see below).

Children were presented with two dots on screen – a standard dot (3 cm in diameter) presented on the right side of the screen and an adjustable dot presented on the left side of the screen that varied in its starting size. To provide equal experience increasing and decreasing the adjustable dot size, the adjustable dot was presented as larger than the standard dot (5.02 cm in diameter) in half of the trials and smaller than the standard dot (1.77 cm in diameter) in half of the trials. Children were given verbal instructions to first indicate whether the adjustable dot was smaller or larger than the standard dot. Next, they were instructed that they could make this dot bigger or smaller and that the rule was to indicate when the dots were equal in size or exactly the same in size. The experimenter then demonstrated the key presses that controlled the dot size by pressing the “M” key which made the dot bigger (a .05 cm increase in the diameter with each key press) and the “Z” key, which made the dot smaller (a .05 cm decrease in diameter with each key press). When a child indicated that he or she believed the dots were equal in size, pressing the space bar advanced the program to the next test trial.

To keep the response method consistent across children, the experimenter controlled the key presses for all participants because pilot testing had indicated that children varied widely in their capacity to make key presses while simultaneously attending to the screen and making a judgment about dot size. Children verbally instructed the experimenter to make the dot bigger or smaller and indicated when the dots were equal in size. To prevent inadvertent bias or expectation on the part of the experimenter, he or she did not look at the screen during the trials but rather pressed the keys according to the child’s verbal instruction. There was no onscreen feedback at trial’s end other than the experimenter consistently praising the child’s efforts. Children were not required to complete a trial in any pre-set amount of time. Because the adjustable dot began at different sizes relative to the standard dot and because children differed

in the pace at which they gave instructions to grow or shrink the dot, response time data were not collected in this experiment.

Four test conditions were established - Small Control, Large Control, Small Mixed, and Large Mixed trials. Control trials established baseline performance in this task and presented both dots encircled by the same-sized rings. Small Control trials presented the standard dot and the adjustable dot encircled by small rings (4.5 cm in diameter). Large Control trials presented the standard dot and the adjustable dot encircled by large rings (9 cm in diameter). Mixed trials presented a large ring encircling one dot and a small ring encircling the other dot. Small Mixed trials presented the standard dot encircled by a large ring and the adjustable dot encircled by a small ring. If the Delboeuf illusion were to occur, participants would not make the adjustable dot large enough relative to the standard dot on these trials because the adjustable dot presented in the small context (i.e., small ring) would be over-estimated. Conversely, Large Mixed trials presented the standard dot encircled by a small ring and the adjustable dot encircled by a large ring. If the Delboeuf illusion were to occur, participants would make the adjustable dot too large relative to the standard dot on these trials because the adjustable dot presented in the large context (i.e., large ring) would be under-estimated.

Participants completed a total of 20 trials (5 trials per condition). Children worked on the task until they completed the test session (20 test trials) or until they asked to return to the classroom. All children completed the test trials within one or two test sessions (conducted on separate days). Two children completed only 19 out of 20 trials due to computer malfunction.

7.1.2 Results

Each child's average difference score was established for each condition. To do this, on each trial the difference between the standard dot and the adjusted dot was recorded, and then the

average of this difference was calculated across all trials in a given condition. Figure 2 depicts group-level performance (i.e., mean difference score) as a function of condition (Small Control, Large Control, Small Mixed, Large Mixed). A repeated-measures ANOVA was conducted to examine the effect of condition on adjusted dot size. There was a significant main effect of condition, $F(3, 78) = 43.45, p < .001, \eta^2_p = .63$.

Based on a visual inspection of Figure 2, paired-samples t-tests were used to compare the size of the adjusted dot in the test conditions (Small Mixed and Large Mixed) to one another and to the two control conditions (Small Control and Large Control). A Bonferroni adjusted alpha level of .01 was used per test given the five comparisons of interest (.05/5). As predicted, adjusted dot size was significantly smaller in the Small Mixed condition relative to the Large Mixed condition: $t(26) = -11.77, p < .001$, Small Control condition: $t(26) = -5.39, p < .001$, and Large Control condition: $t(26) = -4.89, p < .001$. As predicted, adjusted dot size was significantly larger in the Large Mixed condition relative to the Small Control condition: $t(26) = 7.58, p < .001$, and Large Control condition: $t(26) = 6.16, p < .001$.

7.1.3 Discussion

Overall, children performed very well in the control conditions, adjusting dot size within 1 mm of the standard dot size. In contrast, the rings that surrounded the dots in the test conditions led to greater degrees of over- or under-estimation of dot size, depending on outer ring size. As predicted, a small ring encircling the adjustable dot led children to overestimate dot size and subsequently undersize the adjustable dot. In contrast, a large ring encircling the adjustable dot led children to underestimate how large the dot was and this led children to make the dot too large. These results match previous reports of the 2-dimensional Delboeuf illusion among children (e.g., Hanley & Zerbolio, 1965; Piaget et al., 1942; Pressey & Wilson, 1978; Weintraub

& Cooper, 1972), adults (e.g., Coren & Girgus, 1978; Nicolas, 1995; Ward & Lockhead, 1970), and nonhuman primates (Parrish et al., 2015). Next, the children were presented with the Delboeuf illusion in a different domain (i.e., a food choice task) to determine whether these same children perceived the illusion in a 3-dimensional, real-world choice setting.

7.2 Experiment 2

Children were shown two food portions presented on same-sized or different-sized plates. These plates created the context in which the food portions were judged, potentially leading to over- or under-estimation of food size depending on the size of the plate. Several studies have referenced the Delboeuf illusion as potentially underlying decisional biases that often are observed during food judgments or food serving scenarios (e.g., McClain, van den Bos, Matheson, McClue, & Robinson, 2014; Van Ittersum & Wansink, 2012).

7.2.1 Method

7.2.1.1 Participants

The same participants from Experiment 1 were tested in Experiment 2. One participant from Experiment 1 was not included in Experiment 2 as this child moved to a different school before Experiment 2 began. Testing again took place in the preschool's lunchroom.

Materials and Procedure Children were presented with a two-choice discrimination task in which they chose between two plates of food on a bench, each containing a separate portion of food. Plates were baited and covered prior to the children entering the lunchroom so that they could not see the plates or food until the test trial began. Children did not consume the food items in this experiment. Instead, a stuffed animal was shown to the participants during the instructions, and they were allowed to hold the stuffed animal at this time. A stuffed kitten was used for half of the trials (cereal trials – see below) and a stuffed puppy was used for the other

half of the trials (lunchmeat trials – see below). Experimenter 1 then provided children with the following scenario and instructions prior to testing: “We are going to play a game with Kitty and Puppy today. Kitty and Puppy forgot their breakfast and they are very hungry! I am going to show you two different plates of food. Your job is simple – point to the plate that has the bigger amount of food. Make sure you look at both plates before you choose. It is very important to find the biggest amount of food for Kitty and Puppy!” Within this script, children were told that the kitty ate cereal and the puppy ate lunch meat. Following these instructions, children were shown 8 pairs of plates in succession. For each pair, both lids were lifted off those plates, revealing the food on those plates simultaneously. Participants indicated which plate contained the estimated larger amount of food through pointing and/or verbal reports.

To prevent cuing, the experimenter removed the plate covers for the two plates under comparison at the start of each trial and then stood behind the child during this choice phase (out of view of the child). Experimenter 2 sat at a table behind the testing area and recorded the selected food item and recorded the response latency for each trial. Experimenter 2 also was out of view during the choice phase. Children were not required to complete the trial in any pre-set amount of time, but rather completed each trial at their own pace, working through each of the 8 pairs of plates. Trial-by-trial feedback was not given other than the experimenter consistently praising the child’s efforts.

Testing involved two types of foods, a discrete type (cereal pieces) and a continuous type (round pieces of lunch meat). These food types were used as previous studies have included a range of foods and we were interested in the generality of any emerging illusion across different food types. Only one food type was ever used in a given trial, thus lunch meat and cereal were never directly compared within a trial.

Two different portion sizes were used. For the discrete food type (cereal), round cookie cutters were used to mold the cereal pieces into a round presentation form. For the large cereal amount, the cutter had an area of 64 sq cm (holding 30 cereal pieces) and for the smaller cereal amount the area of the cutter was 53.3 sq cm (holding 25 cereal pieces). For the continuous food type (lunchmeat slices), cookie cutters were used to cut the lunchmeat into a round presentation form. The large lunchmeat portion was cut to an area of 64 sq. cm and the small lunchmeat portion was cut to an area of 53.3 sq. cm. Figure 1 provides examples of the food and plate combinations for some test trials. Two different sizes of identical white dinner plates were used for both food types. The larger plates measured 26 cm in diameter and the smaller plates measured 18 cm in diameter.

Four trial types were introduced: Small Plate Control trials, Large Plate Control trials, Standard Illusion trials, and Non-Standard Illusion trials. All trial types were presented for both types of food, continuous and discrete. Control trials involved presenting two different food portions on the same sized plates (both small plates or both large plates) to determine whether the children could discriminate between the two portion sizes when presented in an identical context. Standard Illusion trials used a mixed-plate design in which equal food portions were presented. These trials matched the standard Delboeuf illusion in which different-sized rings (i.e., plates) encircled the same-sized dot (i.e., food portions) so that the food should appear larger when placed on the smaller plate if the illusion was in effect. The Non-Standard Illusion trials used a mixed-plate, mixed-portion design in which a smaller portion of food was placed on a smaller plate in comparison to a larger food portion on the larger plate. In this case, the illusion would occur when the different-sized foods appeared to be equal in size.

Each participant completed a total of 16 test trials, eight trials with each food type. Participants completed two sessions (one per day), with four trials (Small Plate Control, Large Plate Control, Standard Illusion, and Non-Standard Illusion) of each food type (continuous and discrete) per session. In Session 1, participants completed the four continuous trials (lunchmeat) prior to the four discrete trials. In Session 2, participants completed the four discrete trials (cereal) prior to the four continuous trials. Within each four-trial block, both control trials were presented first followed by the Standard Illusion and then the Non-Standard Illusion trials. Plate position and food portion location were randomized in each trial (i.e., right versus left placement on the bench and small versus large portion on the plates).

7.2.2 Results and Discussion

Figure 3 presents group-level performance in Experiment 2. The first question was whether participants performed differently depending on the type of food that was presented (continuous versus discrete). There was not a significant difference across food types in the number of large-food selections in Small Control trials, $X^2(1) = .38, p = .54$, Large Control trials, $X^2(1) = 2.23, p = .14$, and Non-Standard Illusion trials $X^2(1) = 3.04, p = .08$. Standard Illusion trials were not included here because the food sizes were identical and thus, there was not a larger food portion to select. Because choice behavior was consistent across the two food types, all remaining analyses combined the two food types.

The second question concerned whether performance differed across the control conditions – Large Control versus Small Control. Overall performance was good; children chose the large food portion in 88.5% of trials in the Small Control condition and in 80.8% of trials in the Large Control condition. There was not a significant difference between control trials, $X^2(1) = 2.36, p = .12$.

The third question was whether the children showed a bias towards a particular plate size when identical food portions were presented on large and small plates in the Standard Illusion condition. Preferring the small plate would be an indication of the Delboeuf illusion. At the group level, participants did not select the portion that was on the small plate at levels that were significantly above chance, one-sample *t* test: $t(25) = -1.43, p = .16$. Despite perception of the illusion in Experiment 1, the illusion did not emerge in Experiment 2 with food choices.

Finally, children performed very well in the Non-Standard illusion trials, selecting the larger portion of food on the large plate on 91.3% of these trials. If any illusion were occurring, children should have performed below how they performed on control trials in this trial type. However, the children performed at their highest level of any trial type for this arrangement, despite the expected illusory context of different-sized plates.

Finally, I investigated whether a link existed between performance in Experiment 1 and Experiment 2. For Experiment 1, an average difference score was calculated for the Small Mixed and Large Mixed test conditions by dividing the difference score (standard dot size minus adjusted dot size) by the standard dot size (3 cm). This score ranged from 0% to 100%, with a higher score reflecting a stronger illusion bias in which a participant over- or under-adjusted dot size to a greater degree. Similarly, for Experiment 2, a food-bias score was calculated for the Standard Illusion trials in which identical food portions were presented on a small plate and a large plate. This score ranged from 0% to 100%, with a higher score reflecting a stronger food bias. For example, a child with a food-bias score of 0% never selected the small plate in the Standard Illusion trials, whereas a child with a food-bias score of 100% selected the small plate in 4 of 4 Standard Illusion trials. Illusion perception did not correlate for Experiment 1 and Experiment 2 (Exp. 1 – Small Mixed condition and Exp. 2 – Standard Illusion condition: $r(24) =$

.02, $p = .91$; Exp. 1 – Large Mixed condition and Exp. 2 – Standard Illusion condition: $r(24) = -.16$, $p = .45$). Thus, the degree to which these children perceived the 2-dimensional Delboeuf illusion using psychophysical procedures in Experiment 1 did not predict whether they were more or less likely to see food items on small plates as constituting more food than the same amounts on large plates.

7.3 General Discussion

Food choice behavior is impacted directly by the context in which food is judged, served, and eaten (e.g., Chandon & Ordabayeva, 2009; DiSantis et al., 2013; Raghubir & Krishna, 1999; Wansink 2004, 2006; Wansink & Van Ittersum, 2003, 2005, 2012). Similarly, visual illusions emerge when stimuli are misperceived due to the context in which they are judged, created, or measured (for reviews, see Coren & Girgus, 1978; Robinson, 1972). The link between the Delboeuf illusion as a 2-dimensional dot illusion and food choice errors in a 3-dimensional choice setting seem clear – foods on plates mimic dots inside of rings, both of which create the context for misperceptions and erroneous choices. However, whether actual performance by participants on the 2-dimensional Delboeuf illusion correlates with food choice behavior in a 3-dimensional setting had yet to be tested. The current study assessed this potential link among preschool children.

Children perceived the 2-dimensional Delboeuf illusion using the method of adjustment procedure in Experiment 1. The current results of the Delboeuf illusion match previous findings among children (Hanley & Zerbolio, 1965; Piaget et al., 1942; Pressey & Wilson, 1978; Weintraub & Cooper, 1972). Performance patterns also match those of human adults when presented with the 2-dimensional Delboeuf (e.g., Coren & Girgus, 1978; Nicolas, 1995; Ward & Lockhead, 1970). The method of adjustment used in the current study offered an intuitive

approach to testing perceptual size illusions among young children as it focused attention on the target (i.e., dot) as participants directly manipulated the size of the target itself. Isolating the target in this way may reduce biases to include the inducers (i.e., outer rings) into target discrimination (Hanley & Zerbolio, 1965; Pressey & Wilson, 1978). Reducing response bias of this nature is essential in pre- and non-verbal populations such as young children and nonhuman species because the bias to include the outer inducers into target judgment may erroneously lead to a reversed illusion as a byproduct of not understanding the task's rule (see Parrish et al., 2015, for further discussion).

Despite evidence of the 2-dimensional Delboeuf illusion using the computerized task in Experiment 1, children did not show the illusion in Experiment 2, with no preference for either the small or large plate when identical food portions were presented. Further, performance by children in Experiment 1 on the computerized illusion task was not predictive of their behavior in response to food choices in Experiment 2. These results are interesting in light of previous food choice studies among adults and children, demonstrating biases as a function of dishware size (DiSantis et al., 2013; Van Ittersum & Wansink, 2007; Wansink et al., 2008, 2014).

A few key differences exist between the current two-choice food discrimination task and previous serving studies. In the current study, children made their food selections in 3 seconds or less in the vast majority of trials (75%). This approach served the children well in control trials with same-sized plates, but did not lead to illusion emergence in test trials. In contrast, serving studies require that participants spend more time manipulating the stimuli themselves. Perhaps an extended choice phase would have led to a different pattern of results in the current study. Specifically, illusory perception may have emerged with longer viewing times in which children could isolate the food to discriminate rather than potentially using external cues such as plate

size to guide choice behavior. Future studies should vary the presentation time during food choice tasks with young children (and older adults and other species) to explore whether there is a crucial viewing duration that is required for these decisional biases to emerge most robustly.

A more likely factor in the emergence of food choice biases is motivational state. Previous studies have presented food-choice tasks using edible items that the participants consume during or immediately following the study. Research on the Delboeuf food illusion with chimpanzees presented food rewards that were highly salient and motivating, presumably leading the chimpanzees to point to the larger amount because of a prepotent response to do so (Parrish & Beran, 2014b). Relatedly, a recent study with children reported that a greater degree of food choice error (i.e., over-serving as a function of plate size) emerged as a function of household food-insecurity. Children from households where food was scarcer at times were more likely to fall prey to dishware illusions (DiSantis et al., 2013).

It also has been suggested that positive findings of food biases are typically reflected in larger, more social settings with higher-preference, sugary foods like ice cream (see Rolls, Roe, Halverson, and Meengs, 2007). The current study presented a vignette regarding a toy animal that wanted to be fed the larger amount of food, rather than using edible foods that the child would consume. Future work comparing food choice behavior using different food types and under different motivational states regarding one's own hunger state versus the imagined hunger state of others should be considered. Beyond presentation time and motivation, food biases are more widely documented in field settings (e.g., Wansink et al., 2006) versus laboratory settings (e.g., Rolls et al., 2007; Yip, Wiessing, Budgett, & Poppitt, 2013) where participants are more distracted and pay less attention to food that is served. An over-reliance on context (e.g.,

dishware size) may increase in settings in which one is less focused on appropriate measures of food choice, serving, and consumption.

Thus, like visual illusions, food choice biases that emerge as a function of contextual features such as dishware size are tenuous in nature. Internal factors (i.e., motivation, attention, rule maintenance/understanding) and external factors (i.e., social setting, food type, context properties) influence the degree to which these biases manifest (see Robinson et al., 2014). The current study opens up avenues of research into the link between perception and decision-making, especially in situations where our perceptions mislead our judgments in real-world scenarios. Within-subjects approaches that allow one to track misperceptions across domains within the same individuals offer ways to study the mechanisms that underlie illusory emergence as it manifests in real-world, decision-making settings. Such research has clear translational impact for potential at-risk populations who fall prey to over-consumption and over-serving biases as a function of plate size and shape.

7.4 References

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7.5 Figures

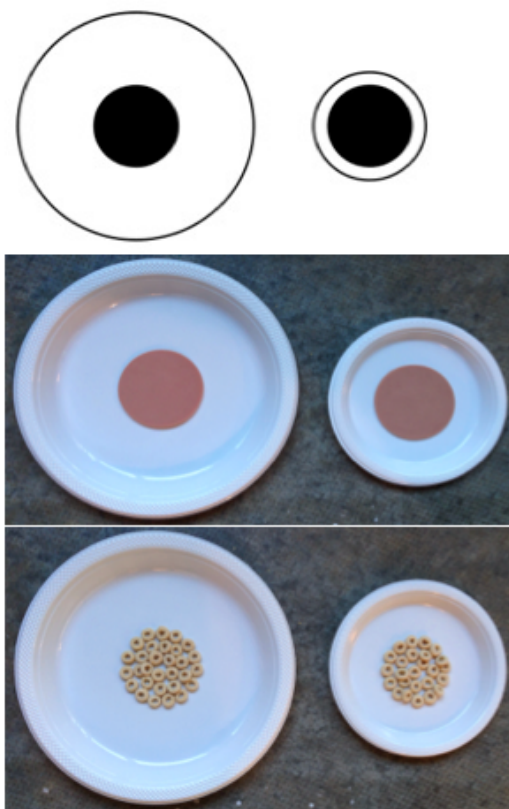


Figure 1. (A) The Delboeuf illusion occurs when a central black dot is perceived as smaller when encircled by a large outer ring (at left) than the same sized dot encircled by a small outer ring (at right). (B) Test stimuli for the Standard Illusion trials are shown where equal-sized continuous food portions are presented on a large and small plate so that the food on the large plate (left) appears to be smaller than the food on the small plate (right). (C) Test stimuli for the Non-Standard Illusion trials are shown where a larger discrete food portion on a large plate appears to be equal to the smaller portion on the small plate.

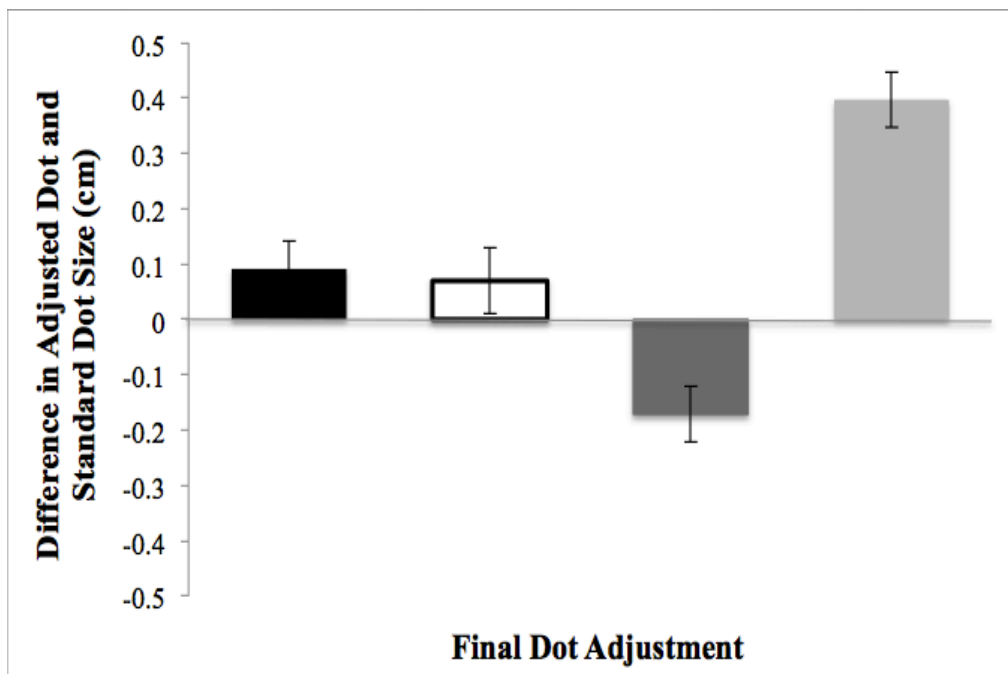


Figure 2. Group-level performance depicting final adjusted dot size (in cm) relative to standard dot size (3 cm) for each condition - Small Control (in black), Large Control (in white), Small Mixed (in dark gray), and Large Mixed (in light gray). Error bars depict corrected 95% confidence intervals for repeated measures tests (Cousineau, 2005).

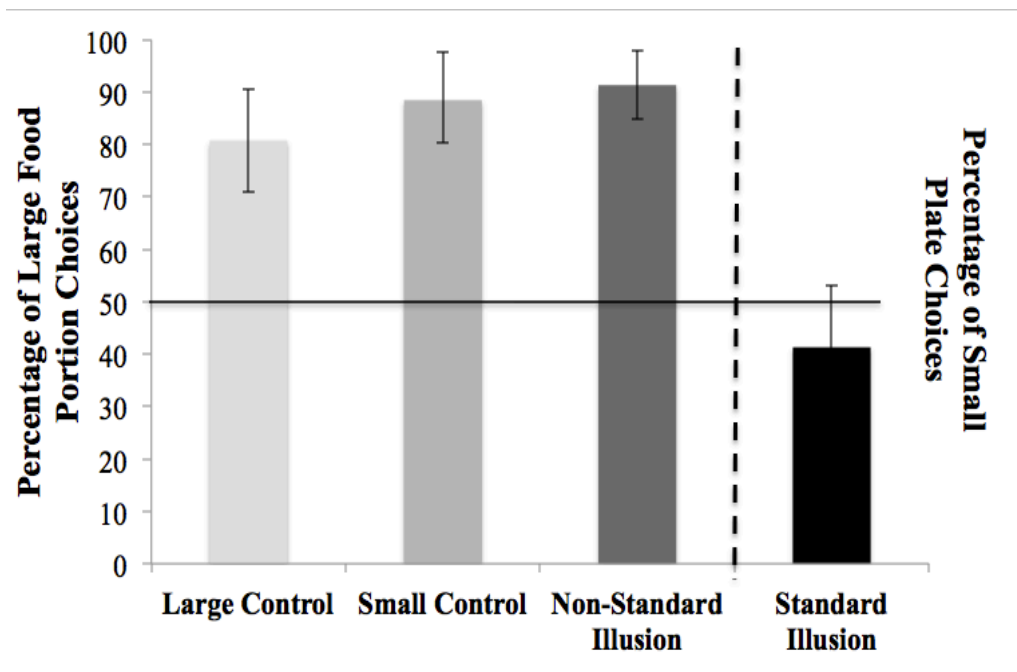


Figure 3. The percentage of large food choices for the Large Control condition, Small Control condition, and Non-Standard illusion condition, in which two different-sized food portions were presented. The black bar shows the percentage of small plate choices in the Standard Illusion condition in which the same-sized food portion were presented on different-sized plates. The three bars at left are statistically different from chance levels of responding, but the black bar is not. Error bars depict corrected 95% confidence intervals.

MORE THAN MEETS THE EYE:
COMPARATIVE CONTRIBUTIONS TO THE STUDY OF
VISUAL ILLUSIONS AND THEIR IMPLICATIONS

By

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8 MORE THAN MEETS THE EYE: COMPARATIVE CONTRIBUTIONS TO THE STUDY OF VISUAL ILLUSIONS AND THEIR IMPLICATIONS

A perceptual system's primary function is to feed sensory information upstream to be interpreted, manipulated, and utilized. A perceptual system that is fast (in terms of processing time), frugal (in terms of resource use), and efficient (in terms of precision) ultimately will be selected for above a system that does not balance these features. In fact, we rely on these very properties of our perceptual system when interacting with the physical world. The oft-used phrase 'seeing is believing' captures our dependence on the rapid veridicality of our perceptions when interpreting physical stimuli (Coren & Girgus, 1978). Such a system that prioritizes a balance between speed, frugality, and accuracy likely exists despite occasional costs for such efficiency. These tradeoffs manifest in the form of illusory phenomena when there is a disparity in sensory input and perception on the basis of misleading contexts. Crucially, illusions should be rare and universal, but not random. Because illusions emerge as a byproduct of an otherwise functional and efficient perceptual system, we should be able to predict the circumstances under which errors and biases might emerge.

More broadly, visual illusions provide a window into the perceptual world of animals including humans. Mechanisms that facilitate fast and accurate visual perception would presumably have high ecological validity among visual organisms and would be under strong selective pressure in a range of species (Agrillo, Petrazzini, & Dadda, 2013). We would predict this to be true especially among closely related species that process their worlds similarly to humans, such as nonhuman primates. One of the defining characteristics of the Order Primates is an increased dependence on perceptual processing of visual information as primate species

evolved to navigate in a visually complex arboreal world (Strier, 2007; Sussman, 1999).

Anatomically and functionally, the visual systems of human and nonhuman primates are highly congruent (e.g., De Valois & De Valois, 1988; Fagot & Deruelle, 1997; Fobes & King, 1982; Ungerleider & Mishkin, 1982; Weinstein & Grether, 1940; Wilson, Lavalley, Joessee, Hendrickson, Boothe, & Harwerth, 1989; see Matsuno & Fujita, 2009, for a review).

Further, the study of visual illusions among primates has proven to be a fruitful field of inquiry, with a growing number of monkeys and apes demonstrating illusion perception similarly to one another and to humans, including the Zöllner illusion (*Macaca mulatta*: Agrillo, Parrish, & Beran, 2014; *Papio papio*: Benhar & Samuel, 1982), the Ebbinghaus-Titchener illusion (*Papio papio*: Parron & Fagot, 2007), the Ponzo illusion (*Macaca mulatta*: Bayne & Davis, 1993; Fujita, 1996; *Pan troglodytes*: Fujita, 1997, 2001), the Mueller-Lyer illusion (*Cebus apella*: Suganuma, Pessoa, Monge-Fuentes, Castro, & Tavares, 2007), the Duncker illusion (*Macaca mulatta*: Zivotofsky, Goldberg, & Powell, 2005), the Delboeuf illusion (*Cebus apella* and *Macaca mulatta*: Parrish, Brosnan, & Beran, 2015; *Pan troglodytes*: Parrish & Beran, 2014a), the rectangle illusion (*Cercopithecinae* and *Cebus*: Dominguez, 1954; Harris, 1968) and the corridor illusion (*Papio papio*: Barbet & Fagot, 2002; *Pan troglodytes*: Imura, Tomonaga, & Yagi, 2008). Taken together, these findings suggest continuity in visual processing across primates, including the perception of illusory phenomena.

My dissertation has expanded on and added to this line of research, with a focus on when, why and for whom visual illusions emerge. I have investigated these questions with specific attention to similarities and differences in basic perceptual mechanisms across primate species. I also focused on the significant, but often underestimated role of methodology, and the question of the translational impact of basic research into visual illusions on everyday decision-making.

Geometric illusions were the primary focus of the current work. These emerge when a target's perceived properties (e.g., size, shape, color, orientation) are impacted by an illusory context. This context is comprised of one or more inducer stimuli that surround the target that is being evaluated. Because geometric illusions are multi-element, complex visual stimuli, they require the simultaneous processing of target and inducer elements (Coren & Girgus, 1978). Thus, these illusions do not emerge if target and inducers are processed sequentially or non-holistically. This defining characteristic of geometric illusions is critical to the development of this dissertation.

8.1 Perceptual Processing Mode

Processing mode is the manner in which complex visual arrays are perceived, such that global processing occurs if the array stimuli first are perceived as one cohesive unit, whereas local processing occurs if the stimuli first are perceived as individual elements. Humans typically display a global precedence, first perceiving the entire array as one holistic figure prior to processing individual details (e.g., Broadbent, 1977; Kimchi, 1992; Lamb & Robertson, 1988; Navon, 1977, 1981). Crucially, nonhuman primates vary in the degree to which they process stimuli at the global level. In fact, most monkey species that have been tested display a local processing style in which they perceive the individual elements in the array prior to the global figure (*Cebus apella*: De Lillo, Spinozzi, Truppa, & Naylor, 2005; Spinozzi, De Lillo, & Salvi, 2006; Spinozzi, De Lillo, & Truppa, 2003; *Macaca mulatta*: Hopkins & Washburn, 2002; *Papio papio*: Deruelle & Fagot, 1997, 1998; Fagot & Deruelle, 1997; Fagot, Tomonaga, & Deruelle, 2001; Parron & Fagot, 2007). However, chimpanzees appear more human-like in their processing style, often displaying a global-to-local precedence (Fagot & Tomonaga, 1999; Fujita & Matsuzawa, 1990; Hopkins, 1997; Hopkins & Washburn, 2002; Matsuno & Tomonaga, 2007; Matsuzawa, 1989; Tomonaga & Matsuzawa, 1992). Differences in perceptual processing mode

may impact illusion emergence, as explored across primate species in the current work. These predictions are supported by research with human adults demonstrating that individuals with a stronger global precedence also perceive certain illusions to a greater degree than individuals with weaker global processing (e.g., Berry, 1968, 1971; Dawson, 1967; Witkin, 1967).

I first established perceptual processing mode in the primate subjects in Chapter 2. Rhesus monkeys and capuchin monkeys were given a delayed matching-to-sample task that presented hierarchical compound stimuli in which the larger, global configuration was comprised of smaller elements. The global configuration (e.g., large letter ‘E’) either matched (e.g., small letter ‘E’s) or differed (e.g., small letter ‘F’s) from the local elements from which it was comprised. The matching-to-sample task’s response set contained an identical match to the sample or a foil that differed in its global pattern, its local elements, or its global and local features. Both species of monkeys displayed a local precedence, showing significantly higher performance rates when stimuli matched on their local elements in comparison to when only their global features matched. These results were consistent with previous research (see above), and established the perceptual processing style of monkeys, a processing style that might impact how they perceive complex visual arrays, such as geometric visual illusions.

8.2 The Delboeuf Illusion

An important illusion to this program of research was the Delboeuf illusion, in which a central dot is overestimated when encircled by a small ring relative to the same sized dot encircled by a large ring (Delboeuf, 1865). I was interested in this illusion for several reasons. First, we previously documented evidence of the Delboeuf illusion in a food-choice task in chimpanzees (Parrish & Beran, 2014a). When discriminating round foods on round plates (mimicking central dots encircled by rings), chimpanzees were proficient in selecting the larger

of two foods if plate size was identical. However, if plate size differed, chimpanzees preferred an equal portion (or sometimes even a smaller portion) placed on a small plate relative to one placed on a large plate. These results were reflective of the context in which the Delboeuf illusion occurs, as had been documented among humans using a similar food choice paradigm (Van Ittersum & Wansink, 2012).

Previous comparative work revealed negative evidence for the highly similar Ebbinghaus-Titchener illusion among baboons (Parron & Fagot, 2007), which occurs when a central dot is overestimated in size when surrounded by small circles relative to an identical dot surrounded by large circles (Ebbinghaus, 1902). When presented with the Ebbinghaus-Titchener illusion, baboons accurately discriminated central dot size even in the presence of the outer illusory circles, leading the authors to argue that perhaps the neural substrate necessary for perceiving this illusion was lacking among Old World monkeys, instead evolving late in the primate lineage. This hypothesis was supported by a reversed Ebbinghaus-Titchener illusion documented in pigeons (*Columba livia*: Nakamura, Watanabe, & Fujita, 2008) and adult chickens (*Gallus gallus domesticus*: Nakamura, Watanabe, & Fujita, 2014). Complicating the question, however, is the finding that various non-primate species have shown evidence of perceiving the illusion as humans do, including a dolphin (*Tursiops truncatus*: Murayama, Usui, Takeda, Kato, & Maejima, 2012), chicks (*Gallus gallus domesticus*: Rosa Salva, Rugani, Cavazzana, Regolin, Vallortigara, 2013), and redbill splitfin fish (*Xenotoca eiseni*: Sovrano, Albertazzi, & Rosa Salva, 2015).

These discrepant findings for the Ebbinghaus-Titchener illusion among nonhuman animals and the positive evidence for the Delboeuf illusion among chimpanzees warranted additional comparative investigations among different species. Thus, in Chapter 3, I assessed the

Delboeuf illusion in rhesus macaques and capuchin monkeys. I was interested in whether these monkey species also might perceive this illusion in the way great apes and humans do, or if instead they might show patterns similar to Parron and Fagot's (2007) investigation of the highly similar Ebbinghaus-Titchener illusion with a monkey species (baboons). In a computerized relative discrimination task, monkeys were proficient in selecting the larger of two dots in control trials (identical ring size). But, monkeys displayed a *reversed* illusion in critical test trials (different-sized rings) relative to human participants presented with an identical task. Both monkey species chose the dot surrounded by a large ring as larger than a dot surrounded by a small ring.

Although these results suggested that monkeys perceived the Delboeuf illusion in an opposite manner from humans, I was concerned that these results were instead driven by a bias towards selecting the dot that was encircled by a large ring. This bias would result in the same pattern of results, disguising itself as a difference in illusion perception. To eliminate the concern that monkeys relied on outer ring size during the relative discrimination, I presented a classification task in which monkeys had to assign dot size as 'small' or 'large' on each trial. Because only one dot was ever presented at a time, monkeys no longer could select the larger of two rings in a given trial. Here, there was evidence of the Delboeuf illusion in both species of monkeys as it manifested in human adults, with dot classification varying as a function of outer ring size (large rings led to dot underestimation and small rings led to dot overestimation).

Despite monkeys' local precedence, the Delboeuf illusion emerged when monkeys were given a paradigm that reduced the likelihood of response bias to include inducer elements into target discrimination. A response bias of this nature may be increased in non-verbal species, in which one must rely on training procedures to instruct the subject to the target of interest in a

multi-element visual array. Biases of this type might further be enhanced in species that process stimuli at the local level prior to the global level. Thus, local processors likely first attend to the most salient feature of a complex array, which, in the case of the Delboeuf illusion, was the outer ring. Methods that reduce the possibility of a reliance on inducer elements during target discrimination, such as the classification task in Chapter 3, will be important in assessing geometric illusions in nonverbal species. Given the positive evidence of the Delboeuf illusion in monkeys in Chapter 3, I turned my attention to the Ebbinghaus-Titchener illusion, now equipped with a methodology that reduced a response bias to include outer inducers into target discrimination.

8.3 The Elusive Ebbinghaus-Titchener Illusion

In Chapter 4, I introduced the Ebbinghaus-Titchener illusion to human participants, rhesus monkeys, and capuchin monkeys using a computerized classification task as described above for Chapter 3. As predicted, humans misperceived central dot size as a function of inducer size, overestimating dots surrounded by small circles and underestimating dots surrounded by large circles. However, rhesus and capuchin monkeys did not show evidence of the illusion. The monkeys displayed a response bias to classify central dot size according to inducing circle size in pilot work. In an attempt to eliminate this bias, I introduced a blocked-presentation style that presented only one trial type at a time for a set of 3,000 trials (Baseline – no inducers, Small Inducer – small inducing circles, or Large Inducer – large inducing circles). This approach eliminated the ability to discriminate each trial exclusively by inducer size, as all trials within a testing session (or across several testing sessions) presented the same trial type. The blocked presentation was successful in eliminating the response bias to a degree.

When some monkeys no longer classified central dot size according to inducer size, I documented an interesting pattern of results. Although an effect of level was observed for all trial types (i.e., subjects classified central dots as a function of true dot size), the function was shallower for the Large Inducer trials. This performance pattern can be accounted for if one simply considers the total amount of pixilation on screen for each trial type. The proportion increase in pixel number between levels of central dot size was smallest between levels in the Large Inducer trials relative to Small Inducer and Baseline trials. Thus, it would have been most difficult to discriminate pixel number in the Large Inducer condition if one was taking into account both targets *and* inducers into the size discrimination. Discriminating set size becomes more difficult as the difference between sets is reduced, which was truest for the Large Inducer condition (see Brannon & Roitman, 2003; Gallistel & Gelman, 2000). Crucially, an animal using such a rule would not perceive the illusion because it would be assessing the total size of the array, rather than simply the size of the target. I also introduced the Ebbinghaus-Titchener illusion to chimpanzees in a two-choice food discrimination task in which round foods were encircled by inedible inducers of variable size (either large or small circles). Regardless of inducer size, chimpanzees accurately selected the larger of the two food portions across control and test trial types.

Despite positive evidence of the Delboeuf illusion in Chapter 3 (see Parrish & Beran, 2014a; Parrish et al., 2015), the Ebbinghaus-Titchener illusion did not emerge among these same species in Chapter 4. Rather, it appeared that the Ebbinghaus-Titchener illusion introduced a unique challenge in instructing nonverbal animals to the target of interest (central dot) when displayed amongst nearly identical inducer circles (also black dots). Although the blocked-presentation style corrected some monkeys' bias towards classifying dot size according to outer

inducer size, it did not completely eliminate the bias. Instead, the animals shifted towards using *entire* array size into dot classification (target and inducers combined). This approach resulted in high performance levels across all conditions (albeit slightly lower performance patterns for Large Inducer trials), but did not circumvent the issue of inducer-inclusion into target discrimination.

It is interesting to note the difference between strategies that mediated the bias to include inducers into target discrimination for the highly similar Delboeuf and Ebbinghaus-Titchener illusions. Simply eliminating the ability to select the larger of two inducers (i.e., rings) by transforming the problem set from a relative discrimination to an absolute classification was successful for reducing the bias in the Delboeuf illusion. Further, a rule of using total pixel amount cannot account for the Delboeuf results among monkeys, as monkeys underestimated central dot size to a progressively greater degree with progressively *larger* rings. Thus, such a rule (classify based on total pixel amount) would have resulted in an opposite pattern of results than was documented. My prediction that a similar approach to the Ebbinghaus-Titchener illusion would be successful in eliciting the illusion among monkeys did not hold. Instead, the monkeys persisted in a response bias to incorporate inducers into the target classification despite additional attempts to eliminate this bias (i.e., blocked presentation of trial type). There appears to be fundamental differences in the Delboeuf and Ebbinghaus-Titchener illusions, at least in so far as the interaction between target and inducers. Specifically, the relative size of target to inducers is more discrepant for the Ebbinghaus-Titchener illusion (i.e., inducers comprise an overall larger amount of the array) than the Delboeuf illusion in which the central dot is the larger and more salient stimulus. In the next chapter, I introduced the Baldwin illusion, which

was a third geometric size illusion to explore further the interaction between target and inducer stimuli.

8.4 The Baldwin Array: Not All Illusions are Equally Perceived

In Chapter 5, I investigated the Baldwin array, in which horizontal line length is underestimated when flanked by large squares and overestimated when flanked by small squares (Baldwin, 1895). Using a classification task, monkeys were trained to assign a horizontal line as ‘short’ or ‘long;’ sometimes this line was flanked by small or large squares. Similar to the response bias shown in the Ebbinghaus-Titchener illusion, most monkeys demonstrated a bias to incorporate inducer squares into line length classification, classifying lines flanked by large squares as ‘long’ and lines flanked by small squares as ‘short.’ Using an extended training procedure, I isolated the target of interest in a follow-up experiment to decrease this response bias. Squares were presented first at the edges of the computer screen and were moved progressively closer to the line to isolate the target while maintaining exposure to the inducing squares. Following this extended training procedure, I found more promising evidence of the Baldwin illusion, with monkeys showing less response bias and a trend towards human-like illusion perception among some animals.

Taken together, these findings revealed that not all illusions are equally experienced. The Delboeuf, Ebbinghaus-Titchener, and Baldwin illusions are geometric size illusions that emerge due to contrast and assimilation. *Contrast* results in the underestimation of target stimuli when the differences between target and inducers are exaggerated and they are perceived as distinct entities (Weintraub, Wilson, & Greene, & Palmquist, 1969). When the target and inducers are similar in size and/or are proximally positioned, stimuli are pooled in the visual system as one

entity (Morinaga, 1956). This phenomenon, also known as *assimilation*, results in the overestimation of inner target size relative to a proximal or smaller target.

Despite the similarity in mechanism and kind, these illusions are qualitatively different in the makeup of target and inducer elements. As mentioned, the target is the most salient feature within the Delboeuf array, whereas the inducers are the most salient feature within the Ebbinghaus-Titchener and Baldwin arrays. This difference in inducer quality appears to be key in whether nonhuman animals first orient to the target or inducer stimuli, which ultimately can lead to illusion emergence or a response bias. Furthermore, local processors perceive individual elements within the array prior to the cohesive unit, which likely enhances response bias towards particularly salient inducing stimuli. Thus, it is apparent that the focus within an array differentially impacts whether illusions are perceived. This focus is determined by processing style, but also may be directed through manipulations of attention as explored in the next section.

8.5 Modulation of Attention

Previous human work has demonstrated that attentional focus within a visual array has a direct impact on the emergence and magnitude of visual illusions (e.g., Daini & Wenderoth, 2008; Gardner & Long, 1961; Jordan & English, 1989; Lester & Dassonville, 2011; Predebon, 2004). A focus on the target stimulus decreases illusion magnitude, whereas a focus on the illusory-inducing context increases the magnitude of an illusion (e.g., Coren & Girgus, 1972; Ebert & Pollack, 1972, 1973; Gardner & Long, 1961; Predebon, 2004; Restle, 1971; Weintraub & Cooper, 1972). In the previous chapters, I designed methodologies to reduce enhanced attention towards either the target or inducer stimuli as this has led to a non- or reversed-illusion among nonverbal species, as one runs the risk of training participants to ignore the illusory context (e.g., Nakamura et al., 2008, 2014; Parron & Fagot, 2007). Further, a key difference in

the design of Chapter 6 concerned how attention was manipulated relative to other studies investigating attentional influences on illusion emergence. Past research exclusively directed attention when the figure of interest was visually present. For example, researchers instructed participants to focus on certain aspects of a figure *as* they were viewing the figure, or featural changes (e.g., color, density, etc.) were manipulated within the array itself.

I tested the bounds of attentional control in Chapter 6 by investigating whether attention could be manipulated *prior* to viewing the illusory array via an interleaved task paradigm. Here, I examined whether one could create carryover effect between two tasks with highly similar stimuli, one of which presented a visual illusion and the other that presented inducer or target stimuli from the illusory array in a separate task. Whether a carryover effect of attention was possible in this scenario would increase our understanding of how illusions emerge, including how robust they are in the face of competing (and perhaps complementary) information. Participants were presented with the Baldwin array using a perceptual classification task, assigning horizontal lines as ‘short’ or ‘long’ that were presented alone or flanked by either small or large squares. A series of primary tasks were introduced prior to the classification task that contained either the Baldwin target (lines) or Baldwin squares (inducers). Illusion magnitude was robust, but not differentially impacted by the interleaved tasks presenting either the target or inducers of the Baldwin array. Although attention plays an important role in illusion emergence, manipulating attention prior to perceiving the illusory array was ineffective in mediating or increasing the magnitude of the Baldwin illusion. Of course, there may be influences of attentional carryover within geometric illusions that are less readily perceived than the Baldwin illusion or within populations that less-readily perceive geometric illusions. For example, locally processing monkeys may perceive illusions to a greater degree via an interleaved task paradigm

that presents target stimuli in a secondary task that is completed in conjunction with the illusion task.

8.6 Deconstructing Illusion Perception

The current research has demonstrated that perceptual processing mode and top-down modulation of attention shape and even constrain the perception of complex visual arrays, such as geometric illusions. Thus, it seems that illusory phenomena are the consequence of bottom-up processes that provide basic sensory stimuli to the perceptual system from the external world (see Gibson, 1979) and top-down contributions from our existing cognitions and experiences (see Neisser, 1976). I have demonstrated that certain methodological approaches can transcend these constraints within monkeys (local processors), providing a scaffold for the cohesive processing of complex stimuli. But, there are likely limits in the modulation of attention, as demonstrated in the interleaved task paradigm in Chapter 6. To understand why processing mode and attention play supporting roles in illusion perception, one must consider the role of executive functioning and neural organization.

Research with Autism Spectrum Disorder (ASD) populations highlights this delicate interplay. Three hallmark perceptual features characterize ASD, including enhanced local processing of details, reduced global processing and an inability to ignore contextual information, and reduced motion perception (for a review, see Dakin & Frith, 2005). Subsequently, children with ASD reveal compromised illusion perception relative to typically developing children and adults (e.g., Happé, 1996; Happé, Briskman, & Frith, 2001) and an increased performance in tasks favoring local processing (i.e., visual search, O’Riordan, 2004; O’Riordan, Plaisted, Driver, & Baron-Cohen, 2001; featural detection, Jolliffe & Baron-Cohen, 1997; Shah & Frith, 1983).

Several hypotheses have been put forth to account for global versus local processing among various human populations and different species. First, the right hemisphere has been deemed key in global processing whereas the left hemisphere is responsible for local processing. Neural research with split brain and lesion patients reveals an increased ability to perceive and recreate the global configuration of visual images by the right hemisphere and an increase in local processing by the left hemisphere (Bogen, 1969; Delis, Robertson, & Effron, 1986; Kimura, 1966, 1973). Further, evidence for abnormalities in the right hemisphere in ASD populations has been reported as partially responsible for enhanced local processing (McKelvey, Lambert, Mottron, & Shevell, 1995; Waiter, Williams, Murray, Gilchrist, Perrett, & Whiten, 2005). Additional works suggests that an increase in the development of low-level perceptual operations leads to local processing whereas higher visual areas control global processing (e.g., Mottron & Burack, 2001). Comparative research complements these neural signatures in processing style. Hopkins (1997) reported evidence for a left hemisphere-advantage for processing local elements of hierarchical, compound stimuli in chimpanzees. These results were consistent with human research (e.g., Martin, 1979; Sergent, 1982; Van Kleeck, 1989), suggesting homologous cerebral lateralization with chimpanzees and humans.

Neural research also suggests that top-down attentional processes play an important role in global cohesion of complex visual stimuli. For example, reduced brain connectivity among ASD populations leads to a lack of synchrony of neural activity that is necessary for global processing (Brock, Brown, Boucher, & Rippon, 2002; Frith, 2004; Just, Cherkassky, Keller, & Minshew, 2004). Crucially, reduced connectivity and a reduction in white matter yield compromised top-down attentional processes that are key in perceiving complex stimuli (Just et al., 2004). Relatedly, research on executive functioning reveals general discrimination capacities

(e.g., distinguishing line length, circle size, etc.) are higher among participants with high working memory capacity in typically developing adults. These results are attributed to an increase in attentional control and rule maintenance within these individuals (R. Engle, personal communication). The ability to attend to the appropriate features within a complex visual array, the inhibition of responses to the illusory context, and the maintenance of task rules are necessary components within illusion perception.

Thus, establishing when, why and who perceives visual illusions ultimately requires a broad approach that accounts for basic perceptual mechanisms, the role of executive function, and methodological design. Doing so is best served through a comparative approach that extends beyond WEIRD populations (Western, educated, industrialized, rich, and democratic; Henrich, Heine, & Norenzayan, 2010) and considers performance by different species, populations, age groups, and cultures. Comparative approaches that incorporate nonhuman primates are especially valuable in that one can sample different processing styles among closely related-species. Further, primates experienced a massive radiation in brain size relative to (most) other mammals, accompanied by complementary increases in executive functioning and global processing across the Order Primates. The great apes have larger brains than Old World monkeys, many of whom have larger brains than most New World monkeys, a pattern that is complementary to the extent of higher executive functions across these species (e.g., Rilling & Insel, 1999; Rumbaugh & Pate, 1984). Comparing different primate species offers appropriate models to test the role of these critical players in illusion emergence.

8.7 Translational Illusions: Decision Errors in Food Choice

Beyond the basic cognitive science underlying visual illusions, there remains the question of translational impact in studying and understanding these phenomena. Because illusions are

rare by nature, how might they impact everyday judgments and decision-making? Should we expect them to pervade our everyday experiences, or instead be constrained to the psychological laboratory and textbook? Recently, geometric size illusions have garnered the interest of decision-making scientists, nutritionists, and economists. For example, the Delboeuf illusion has contributed to our understanding of decisional biases in the food choice and consumption domain, leading to the recently popularized ‘small plate movement’ (e.g., DiSantis, Birch, Davey, Serrano, Zhang, Bruton, & Fisher, 2013; Parrish & Beran, 2014a; Van Ittesum & Wansink, 2012).

Akin to central dots encircled by an outer ring, round food portions on circular dinnerware impact food quantity judgments such that people underestimate portions on large plates and overestimate portions on small plates. Misjudgments of food quantity have direct impacts on serving and consumption behavior, which subsequently impacts our dietary health. Obesity, diabetes, and heart disease play a critical role in the health disparities within the United States and throughout much of the industrialized world (e.g., Allison, Fontaine, Manson, Stevens, & VanItallie, 1999; Calle, Rodriguez, Walker-Thurmond, & Thun, 2003; Rolls, 2003). Thus, understanding the cognitive mechanisms that contribute to quantity misjudgment and subsequent overconsumption is critical to long-term health and wellbeing. However, much work remains in directly connecting perceptual illusions and decisional biases, and the connections between these areas may be tenuous and fragile in some cases. Other researchers have suggested that food choice biases may not be so easily related to simple perceptual phenomena (e.g., Robinson et al., 2015), and so there is great need to continue to examine choice behavior, perceptual experiences, and their interplay across contexts.

My research interests have centered on understanding the contextual contributions that impact perceived quantity and size of stimuli such as food sets. In an earlier study, we explored whether dishware size might influence chimpanzee food choice behavior to determine the role of cultural effects on overconsumption (e.g., ‘clear your plate’) versus perceptual mechanisms that lead to an over-contribution of context (e.g., plate size) on quantity judgments. It was observed that chimpanzee quantity judgments were directly influenced by plate size, leading to a bias for a small plate over a large plate when presented with equal portions and some errors in food judgments, selecting a small food portion when it was plated on a small plate relative to a larger portion on a large plate (Parrish & Beran, 2014a). Despite a growing body of evidence for food perception biases as a function of the context in which portions are presented among humans (e.g., DiSantis et al., 2013; Van Ittesum & Wansink, 2012; Wansink, Payne, & Werle, 2008; Wansink & Van Ittersum, 2013; Wansink, Van Ittersum, & Payne 2014) and animals (Beran, Evans, & Harris, 2008; Boysen, Berntson, & Mukobi, 2001; Parrish & Beran, 2014a, 2014b), there has been virtually no work investigating whether actual perception of the 2-dimensional Delboeuf illusion correlates with food choice behavior in a 3-dimensional setting within the same participants.

In Chapter 7, I examined this relationship by testing preschool children on the 2-dimensional Delboeuf illusion via a computerized method of adjustment task and a food judgment task. Children were presented with two dots of different sizes and were instructed to adjust one dot in size (increasing or decreasing its diameter) until it matched the second dot on screen. Children’s performance reflected the standard illusion, with children underestimating (and thus over-adjusting) dot size when encircled by a large ring and overestimating (and thus under-adjusting) dot size when encircled by a small ring. Interestingly, children did not

demonstrate the Delboeuf illusion in the 3-dimensional food choice task in which they were presented with round foods on different sized plates. Several factors may have influenced the null results in the food-choice task, including speeded response times and motivational factors.

Ultimately, the degree to which these children perceived the 2-dimensional Delboeuf illusion using psychophysical procedures did not predict whether they also were more or less likely to fall prey to the same biases in a food-choice task. Whether this relationship (or lack thereof) holds as executive function and attentional skill develop across the lifespan remains to be explored. Finding such an effect, if it exists, might be more likely in older age groups or under different circumstances. Secondly, the role of culture and the increase in experiences choosing among food options among different contexts likely solidify these decisional biases. In a recent comparative study, we documented an age effect in which older children (> 53 months) perceived the Solitaire illusion more consistently than younger children and monkeys (Parrish, Agrillo, Perdue, & Beran, 2016). This age effect suggested that human-unique perceptual experiences with the world (i.e., experiences making quantity judgments, development of executive functions, maturation of Gestalt principles) play an important role in the emergence of the Solitaire illusion (and possibly others) in human adults. Future research exploring the relationship between 2-dimensional illusion perception and 3-dimensional decisional biases across development will address these questions, as will a broader assessment of other contexts in which illusory features may or may not affect choice behavior.

8.8 Concluding Thoughts and Future Directions

Visual illusions emerge as a byproduct of an otherwise functional and efficient system, providing a window into the inner workings of perception within and across species, populations, and across the lifespan. Crucially, our perceptions are relative – relative to the context in which

we are viewing a stimulus or event, what we have just experienced, and what we might experience next. As demonstrated throughout this dissertation, illusions emerge as a byproduct of perceptual mechanisms (such as grouping principles). Figure 1 presents an overview of factors influencing the emergence of illusory phenomena. Specifically, illusions manifest differently across species and human development as a function of processing mode (global versus local) and attentional control, and may be impacted by working memory capacity. Decisional biases appear to be contingent upon experience and motivation, including food type and prepotency of rewards.

Further, external factors such as illusory array design and testing paradigm directly impact illusion perception. Array design, as defined by the relationship between inducer and target elements within an illusory array, directly impacts illusion perception. Response competition may emerge if the size of the illusory array is too heavily weighted towards inducing stimuli, such that the inducers are the more salient element within the array relative to the target stimulus. Relationships of this nature between inducer and target stimuli create a unique challenge within comparative and developmental work in that the task rule (i.e., “discriminate target amongst inducers”) must be supported by stimuli design and presentation, task style, and training protocols. For example, task designs that increase focus on target features (i.e., method of adjustment, absolute classification, etc.) may assist in decreasing response biases to incorporate inducers into target discrimination. Thus, the manner in which illusions are presented to pre- and non-verbal species and populations can constrain or perhaps create a scaffold for illusory perception. In my work, these methodological challenges proved to be especially true for local processors (e.g., monkeys) that first perceive the individual elements within an array prior to the global figure.

Future work that extends illusion perception to other classes of stimuli (e.g., numerosity illusions) will shed light on the circumstances under which perception ‘goes awry’ across species and the processes that lead to such misperceptions. Further, between-subjects designs that investigate the role of individual differences (i.e., differences in working memory, attention span, processing style) are vital in determining the role of top-down versus bottom-up processes in illusion perception. Understanding these individual differences will provide predictive power to the study of perceptual illusions. Within-subjects designs that investigate the emergence of different types of illusions within the same individuals (and across the lifespan within the same participant) will be key in determining when and why seemingly similar illusions (such as the Delboeuf and Ebbinghaus-Titchener illusions) are perceived differently. More broadly, I am interested in the extent to which context impacts choice behavior beyond geometric illusions, including the extension of context across time and space (e.g., as manipulated via the interleaved task paradigm). Ultimately, deepening our understanding of how context influences perception and choice, and disentangling what is unique in human perception versus the perceptual experiences of other species and across the lifespan, will shed light on how we see and subsequently interact with our world.

8.9 References

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8.10 Figures

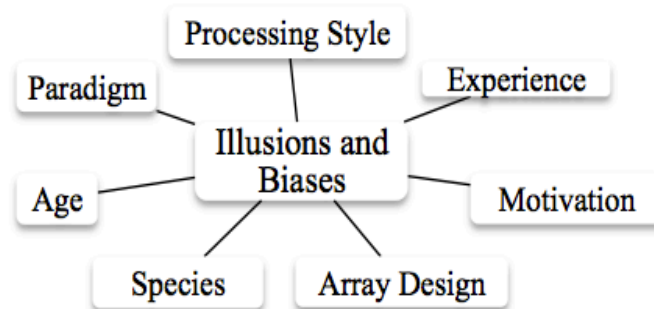


Figure 1. An overview of the factors impacting visual illusion emergence and decisional biases, including species, age, task design (i.e., paradigm and array design) and internal factors (i.e., processing style, attention, executive functions such as working memory, experience, and motivation). Each of these factors may also interact with each other, and future research could illustrate those interconnections and provide a clearer model of the degree to which each factor causes illusions and biases.