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REMEMBERING MORE THAN MET THE EYE: ASSESSING THE MECHANISMS
UNDERLYING VISUAL BOUNDARY EXTENSION IN HUMANS (*HOMO SAPIENS*),
RHESUS MONKEYS (*MACACA MULATTA*), AND CAPUCHIN MONKEYS (*CEBUS
APELLA*)

by

BRIELLE JAMES

Under the Direction of Michael Beran, PhD

ABSTRACT

Humans have been shown to falsely remember seeing the details just beyond the edges of a pictured scene. This constructive memory error is known as boundary extension. Either the traditional visual-cognitive model or the multisource model, which differ in their distinction between scene perception and representation, can explain boundary extension. Five experiments assessed boundary extension in humans (*Homo sapiens*), rhesus monkeys (*Macaca mulatta*), and capuchin monkeys (*Cebus apella*) using identical and equivalent delayed match-to-sample tasks. The present study replicated boundary extension in human adults. However, neither monkey species demonstrated boundary extension when viewing human-unique or monkey-relevant scenes. Unlike humans, monkeys may not have demonstrated boundary extension because they are local visual processors. This would have limited their view of the stimuli as scenes, allowing them to rely on direct visual input. This species discontinuity reflects the potentially human-unique qualities of boundary extension.

INDEX WORDS: Boundary extension, Scene perception, Multisource model, Rhesus monkeys, Capuchin monkeys

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by

BRIELLE JAMES

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

Master of Arts

in the College of Arts and Sciences

Georgia State University

2018

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Brielle Thomas James
2018

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December 2018

DEDICATION

This thesis is dedicated to my mother and father, who encouraged me, supported me, and believed in me before the journey even began. I could not have achieved any of this without you both, thank you. I also would like to thank all of my family and friends for the myriad of encouragement and unconditional love and support throughout this process that kept me going until the end.

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1 INTRODUCTION

Human vision is graded in nature, with visual acuity decreasing dramatically outside of the foveal region in the center of the visual field. As a result, accurate scene perception requires shifts in eye movement to reposition the fovea approximately three to four times per second (Rayner, 2009). In addition, whenever the eyes are moving (known as a saccade), vision is suppressed (known as saccadic suppression; Matin, 1974). However, despite these limitations, humans perceive a comprehensible and continuous world. The question of *how* this is achieved has long intrigued vision and cognition researchers (e.g., Davidoff, 1975; Gibson, 1950; Gordon, 2004; Hering, 1868/1977), including those who study perception across species and are interested in understanding the evolutionary foundations of human visual perception (Lazareva, Shimizu, & Wasserman, 2012).

Scene perception research has repeatedly demonstrated that humans are able to meaningfully perceive the surrounding world very quickly. In as little as one eye fixation, observers can identify complex views (e.g., drawings or photographs) by general categories (e.g., ‘ocean scene’) or words (e.g., Biederman, 1972; Biederman, Mezzanotte, & Rabinowitz, 1982; Potter, 1976), as well as describe them (Intraub, 1981). The specific time frame for scene classification has been identified to be within about 100 ms of picture onset (Davenport & Potter, 2004; Fei-Fei, Iyer, Koch, & Perona, 2007; Intraub, 1981; Potter, 1976; Vö & Henderson, 2010). Data from event-related potentials during a categorization task with rapid serial visual presentation (RSVP) of the photographs indicated identification of the scenes’ category occurred 150 ms after initial picture exposure (Thorpe, Fize, & Marlot, 1996), providing additional evidence of the rapidity of scene identification.

Nonhuman primates also quickly and accurately categorize objects (Vogels, 2012). Research with rhesus macaques has shown that they are able to distinguish stimuli from different categories and transfer their learning to categorization of new stimuli, which is evidence of concept formation for the categories (e.g., animals vs. non-animals and food vs. non-food, Fabre-Thorpe, Richard, & Thorpe, 1998; trees vs. non-trees and fish vs. non-fish, Vogels, 1999; monkeys vs. non-monkeys, Yoshikubo, 1985). For example, using a rapid visual categorization task, Fabre-Thorpe et al. (1998) trained two rhesus macaques to discriminate photographs based on visual concepts, classifying food vs. non-food or animal vs. non-animal. Once the task was learned, monkeys demonstrated categorization of 200 novel images with high accuracy (90.5% for foods and 84% for animals). Their performance was compared to performance of humans tested with the same new stimuli and similar errors were made across species, suggesting similar categorization strategies. As in human categorization, monkeys performed these categorizations within one eye fixation (the target image was flashed for only 80 ms) and very quickly, on average between 250 and 350 ms. Monkeys' ability to categorize stimuli that they had never seen suggests they developed a mental representation of the target category as a concept. Other species of monkeys and animals also can discriminate between stimuli of different categories and apply mental schemas for these concepts to new stimuli (e.g., capuchin monkeys, D'Amato & Van Sant, 1988; squirrel monkeys, Roberts & Mazmanian, 1988; stump-tailed monkeys, Schrier, Angarella, & Povas, 1984; see Zentall, Wasserman, Lazareva, Thompson, & Rattermann, 2008, for a review).

Abstract stimuli also can be categorized into explicit and implicit categories by capuchin monkeys (e.g., Smith et al., 2012b) and rhesus macaques (e.g., Smith, Beran, Crossley, Boomer, & Ashby, 2010). Rhesus macaques, along with humans, can generalize knowledge of these

abstract categories to novel stimuli (e.g., Smith et al., 2015; Zakrzewski, Church, & Smith, 2018). The results of these studies highlight the abstract mental representations that can be learned by nonhuman primates (Vogels, 1999). These mental concepts that developed to organize and interpret the presented stimuli into categories are evidence of schemas in nonhuman cognition.

Human recognition memory for rapidly identified pictures (presented in the absence of any masks) is generally poor (e.g., Intraub, 1981; Potter, 1976). However, if attention is shifted to some pictures of an RSVP sequence and not others (Intraub, 1984) or to a primary task (Lin, Pype, Murray, & Boynton, 2010) then memory improves for some of the briefly presented pictures in the sequence. Recognition memory for these pictures, however, does not last for long, with even a 1.4 second delay to an immediate recognition test having resulted in a decline in memory performance for a set of five pictures (Potter, Staub, Rado, & O'Connor, 2002). Thus, while visual perception and processing is complex and swift, the information that is perceived is quickly vulnerable to retrieval error.

1.1 Memory Errors

1.1.1 Errors of Omission

In addition to studies of picture recognition memory, memory researchers have also studied humans' ability to remember a picture's details. Errors in memory for picture details typically occur for long-term memory. However, change blindness (the failure to detect visual changes to an object or scene across brief interruptions; Simons & Levin, 1997; Simons & Rensink, 2005) highlights the fragility of detail retention even for extremely brief retention intervals. Using the flicker paradigm, Rensink, O'Regan, and Clark (1997) repeatedly presented alternating photographs of a real-world scene and a modified version of that scene to participants

for 240 ms each. Between the photographs, a blank screen was presented for 80 ms, creating a flickering appearance to mimic eye movements without requiring a change in fixation location (Simons & Levin, 1997). Under these conditions, observers struggled to identify the single change that had been made to the scene, even after repeated presentation. For some images, nearly a minute of alternations was required by observers for them to detect what had changed in the image. However, with the blank screen removed, changes were detected in less than one second on average. Similarly, a verbal cue of the change prior to stimuli presentation also produced significant improvement in observers' change detection.

This error of omission brought into question how much detail is retained between eye movements in visual memory representations. Rensink (2000; Rensink et al., 1997) proposed that without focused attention visual change was not perceived because observers do not maintain detailed visual scene representations in short-term memory that can be used to make comparisons across saccades and other similarly brief time intervals. However, visual memory theory (Hollingworth, 2006; Hollingworth & Henderson, 2002) provides an alternative explanation that identifies limits in attention, not representation detail, as the reason for change blindness. Other researchers (e.g., Hochberg, 1986, as cited in Intraub, Gottesman, Willey, & Zuk, 1996; O'Regan, 1992; Simons & Levin, 1997) have also argued that internal visual representations may lack much detail. In addition, research demonstrating the large capacity of human recognition memory (e.g., more than 2,000 photographs; Standing, Conezio, & Haber, 1970) also makes evident that this memory was not reliant on the precise visual details of the images. Stimuli were mirror-reversed at test without significant detriment to observers' recognition performance.

On the other hand, some studies (e.g., Intraub, 1980; Konkle, Brady, Alvarez, & Oliva, 2010) have provided evidence of accurate memory for specific visual details under difficult conditions, suggesting that details are normally retained in scene representations. For example, Intraub (1980) demonstrated that photographs presented briefly (110 ms) using an RSVP paradigm with varied inter-stimulus intervals (4,890 ms; 1,390 ms; 620 ms; 385 ms; 0 ms) could elicit recognition memory for photos' visuospatial orientation (assessed with reversal detection) at proportions better than chance when the inter-stimulus interval was at least 1,390 ms. More recently, observers have been shown to distinguish previously seen images and novel images from the same scene category in a recognition memory test, even after having studied categories with up to 64 other exemplar scenes and with approximately 3,000 images and 130 scene categories in memory at test – evidence that a sufficient amount of detail in addition to scene category is retained during scene perception (Konkle et al., 2010). This contradictory evidence makes it unclear just how much detail is held in visual scene representations during perception at different stages.

1.1.2 Errors of Commission

When thinking of failures in memory, errors of omission often first come to mind. However, errors of commission also are seen, in which details, words, or events that were never experienced are falsely remembered as having occurred. For example, false memories can be induced during list learning, resulting in participants “remembering” words that were never presented to them. Roediger and McDermott (1995) presented participants with lists of words to be studied, where each list had several words closely associated to a critical, non-presented word (e.g., “sleep” was a critical non-presented word for a list that included “bed,” “rest,” and “awake”). During the following free recall and recognition memory tests, this non-presented

word was frequently falsely included as having been on the list, and often was reported with high confidence. Similarly, short sentences can elicit false memories for the compound sentences that are created if they were to be combined, despite these longer sentences not having been presented (Bransford & Franks, 1971). Items not included in photographs of stereotypical scenes are also later falsely recognized (Miller & Gazzaniga, 1998) – evidence that false memories related to schematic knowledge can be created as well.

In addition to word and sentence associations, schemas can lead to commission errors in human memory. Schemas are a set of organized expectations, forming mental concepts of objects and events, that are involved in information processing, storage, and retrieval (Lewis & Durrant, 2011; Taylor & Crocker, 1981, as cited in Tuckey & Brewer, 2003; Tuckey & Brewer, 2003) and have implications for eyewitness memory of events, story recall, deductive inferences, and education (Greenberg, Westcott, & Bailey, 1998; Tse et al., 2007; Tuckey & Brewer, 2003). These “frameworks” for knowledge (Tse et al., 2007) develop from abstractions of newly encoded information (Kumaran, Summerfield, Hassabis, & Maguire, 2009; Lewis & Durrant, 2011) that explain the relations between similar objects or events (e.g. chihuahuas and Great Danes are both dogs, with “dogs” being the mental schema in this example; Kumaran et al., 2009). As new information is learned it is integrated into schemas (Dumay & Gaskell, 2007; Loftus, 1996; Tamminen, Payne, Stickgold, Wamsley, & Gaskell, 2010), especially when it is compatible with an already existing schema (Kumaran et al., 2009; Lewis & Durrant, 2011; Tse et al., 2007). Schemas can even be learned for abstract dot-patterns made from variations of prototypes (e.g., Posner & Keels, 1970). During integration, the details of a memory can sometimes be distorted to fit the existing schema (Lewis & Durrant, 2011), resulting in false memories. For example, Tuckey and Brewer (2003) presented witnesses with ambiguous

information. Witnesses interpreted this information using their schemas, resulting in schema-consistent false memories and reduced accuracy as a result of the underlying schema supporting the “true” events (Loftus, 1996). During a recognition task of ambiguous shapes with or without disambiguating labels, older adults (60 to 75 years old) especially showed more false recognition of related lures when semantic schemas were activated by the presence of labels (Koustaal et al., 2003). In addition, some of the categories studied had larger numbers of exemplars than others, resulting in higher rates of false recognition, presumably because of the more salient perceptual or conceptual schema for the items elicited during the study phase compared to categories for which only one item was presented. In the same study, older adults also showed higher false recognition of concrete objects (e.g., bed, candle) than abstract objects (e.g., pictures of abstract art), further demonstrating the role of schemas and conceptual representations in false memories. Schacter, Verfaellie, and Anes (1997) reported a distinction between conceptual false recognition and perceptual false recognition. Participants were presented with conceptually and perceptually related words (e.g., funnel and twister, related to the conceptual lure “tornado,” and hate and late, related to the perceptual lure “fate”). False recognition was seen more for conceptually related words than perceptually related words, and with higher levels of confidence. Similarly, older adults (63 to 75 years old) have shown a tendency to rely on conceptual and/or perceptual similarity when tested on a recognition memory test for colored pictures (Koustaal & Schacter, 1997). This reliance on the similarity of studied pictures impacted adults’ recognition of the unrelated items that they had previously studied. Like Koustaal et al. (2003), Koustaal and Schacter (1997) also reported an effect of category size on false recognition, where falsely recognized lures were more frequent for larger categories. Constructive memory errors in picture

memory, however, would not be expected under simple conditions, but research on boundary extension has demonstrated otherwise.

1.2 Boundary Extension

In studies of boundary extension (e.g., Intraub, Bender, & Mangels, 1992; Intraub & Richardson, 1989), participants are presented with a target image, typically a photograph or drawing of a scene (i.e., one or more objects placed within a larger, continuous spatial background), and they usually remember seeing parts of the image just beyond the edges of the pictured scene that were not originally visible. Participants' memory of the scenes is typically assessed by having them draw the target image from memory or rate whether a second photograph or drawing of the same scene (which is presented with either the same or a different viewpoint as the target image) has a closer viewpoint, the same viewpoint, or a more wide-angle viewpoint than the original image. When reporting on their memory for the viewed scenes, participants often draw the images with information that likely would have been present if the original boundaries of the scene had been extended outward slightly (e.g., more grass around an object on the lawn or the continuation of fencing in the background; see Figure 1.1). Similarly, when rating probe photographs or drawings, observers usually rate images with a more wide-angle view (i.e., a more "zoomed out" viewpoint) as being the same as the original image more often than they do for more close-up ("zoomed in") views. Together, these responses indicate that participants falsely remember seeing the target image with more information than was presented. The information just outside the boundaries of the actual view was incorporated into their memory for the scene, distorting the location of the view's boundaries.

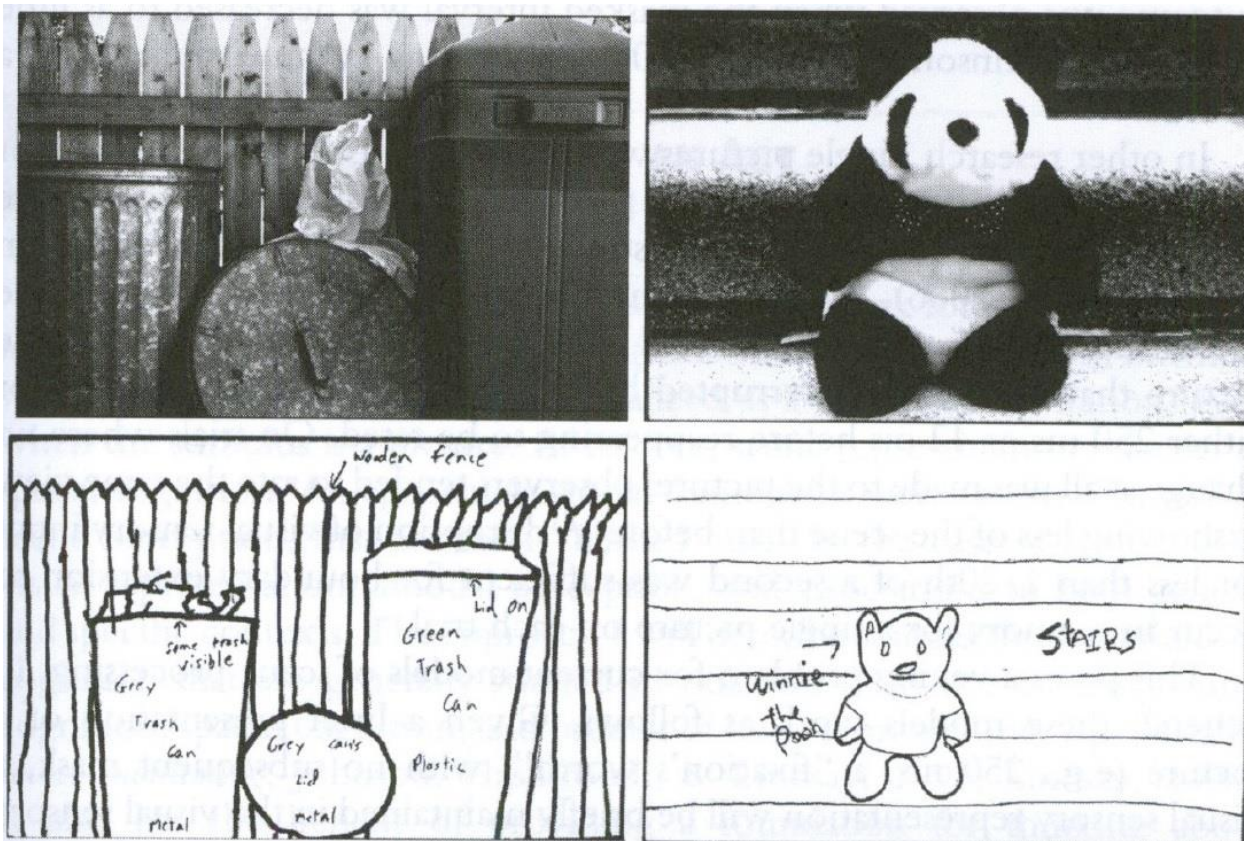


Figure 1.1 Examples of boundary extension.

The top row depicts close-up target images viewed by participants, with the participants' drawings from memory of those same scenes below. Boundary extension is seen in the drawings by the continuation of each scene at each edge compared to the close-up images. Images in the left column are from "Wide-Angle Memories of Close-Up Scenes," by H. Intraub and M. Richardson, 1989, *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 15, p. 182. Images in the right column are from "Boundary Extension for Briefly Glimpsed Photographs: Do Common Perceptual Processes Result in Unexpected Memory Distortions?" by H. Intraub, C. V. Gottesman, E. V. Willey, and I.J. Zuk, 1996, *Journal of Memory and Language*, 35, p. 124.

Since the first formal test of boundary extension (Intraub & Richardson, 1989), subsequent studies have revealed a specific diagnostic pattern indicative of the phenomenon (e.g., Hubbard, Hutchison, & Courtney, 2010; Intraub, 2010; Intraub & Dickinson, 2008). When no change is made between the target and probe images for an originally close-up view, participants usually rate the probe image as more close-up than the target image. The target image is remembered with extended boundaries, and as a result the close-up view is thought to

show less of the original image. However, when no change is made from a wide-angle view there is little or no directional error seen in participants' ratings. When the target and test pictures do not match in viewpoint (i.e., truly showing less or more of the scene in the test picture) a distractor image rating asymmetry is seen. When less of the scene is shown in the test picture (i.e., a wide-angle target is followed by a close-up probe), the difference between the images is easily detected as being more close-up in view. However, when more of the image is shown in the test picture (i.e., a close-up target is followed by a wide-angle probe), the images are more often thought to be the same or rated as more similar. As a result, a smaller range of differences in the rating of test images is seen for this trial type than when less of a scene is shown at test.

The typical response pattern (that boundary extension is larger for close-up views than wide-angle views) is also seen when a medium-angle view is included in the stimulus set, with boundary extension for the medium-angle view dependent on whether it is the more close-up or wide-angle view relative to the other picture(s) (Intraub et al., 1992). When presented with a more close-up view, boundary extension was not seen for the medium-angle view, but when the medium-angle view was presented with a more wide-angle view, the medium-angle view led to boundary extension, while the wide-angle view did not. When all three views were presented together, after a 48-hour retention interval, only the close-up and medium-angle views resulted in boundary extension, with accurate memory reported for wide-angle views. In the original test of boundary extension, Intraub and Richardson (1989) used a large number of pictures, ample stimulus presentation time, and rather long retention intervals. However, boundary extension has since been demonstrated under a variety of conditions not expected to generate false memories.

1.2.1 Previous Research of Boundary Extension

Even in the absence of large stimulus sets, boundary extension has been demonstrated. Several studies have shown evidence of boundary extension despite low memory loads of only one to three pictures presented per trial (e.g., Bertamini, Jones, Spooner, & Hecht, 2005; Dickinson & Intraub, 2008; Intraub et al., 1996; Intraub, Daniels, Horowitz, & Wolfe, 2008; Intraub & Dickinson, 2008; Intraub, Hoffman, Wetherhold, & Stoebs, 2006; Kreindel & Intraub, 2017; Seamon, Schlegel, Hiester, Landau, & Blumenthal, 2002). Most interesting in relation to the present study is the occurrence of boundary extension even when only one target image was presented at a time, and participants commented on their memory for the item immediately after its presentation and before the next target image (e.g., Beighley & Intraub, 2016; Intraub et al., 2006, 2008; Intraub & Dickinson, 2008; Kreindel & Intraub, 2017; Seamon et al., 2002).

Explicit instructions to pay close attention to the test images' background and main objects or its boundaries also do not eliminate the presence of boundary extension from memory (e.g., Gagnier, Dickinson, & Intraub, 2013; Intraub & Bodamer, 1993; Intraub & Richardson, 1989). Intraub and Bodamer (1993), for example, informed some participants of the nature of the drawing and rating tasks prior to viewing the target images (test-informed condition), as well as demonstrated the boundary extension effect to other participants and instructed them to avoid the memory error during study and later memory reports (demo condition). However, when compared to the control condition (standard task instructions), boundary extension was observed across all conditions for both tasks. Although participants in the test-informed and demo conditions displayed reduced boundary extension during the drawing task, as well as reduction during the rating task only for the test-informed condition, levels of boundary extension in both groups across tasks were still significantly different from control conditions. Gagnier et al.

(2013) also found a reduction, but not elimination, of boundary extension during boundary rating and border adjustment tasks for test-informed participants.

Boundary extension also has been demonstrated in humans across the lifespan. Recently, Kreindel and Intraub (2017) have reported observations of boundary extension in preschool children (4 to 5 years old) and adults (18 to 21 years old) using a drawing and forced-choice immediate recognition memory task. Seamon et al. (2002) observed boundary extension in young children (5 to 7 years old), adolescents (10 to 12 years old), young adults (18 to 21 years old), and older adults (58 to 84 years old) using a drawing task and single picture stimulus presentations. Similarly, Chapman, Ropar, Mitchell, and Ackroyd (2005) reported boundary extension during a magnification adjustment task (in which probe images were zoomed in or out by the participant to match their remembered view of the target image) in adolescent males 9 to 16 years old with Asperger's syndrome, an age- and intelligence-matched control group, and a control group of adult male and female participants (18 to 53 years old). Candel, Merckelbach, Houben, and Vandyck (2004) also have provided evidence of boundary extension in children (10-12 years old) during the standard drawing task. Spanò, Intraub, and Edgin (2017) reported boundary extension in preschoolers (4 to 7 years old), adolescents (13 to 17 years old), and participants with Down's Syndrome (11 to 25 years old) across three different tasks (drawing, recognition, and 3D scene reconstruction tasks), demonstrating this memory error across stages of development and impairment in memory. Claims of boundary extension in infants (3 to 4 months old and 6 to 7 months old) have even been made (Quinn & Intraub, 2007), using preferential looking procedures. After familiarization to a target picture, infants were simultaneously presented with wide-angle and close-up views of the same scene and were found

to look at the close-up views during test trials at rates significantly above chance (taken to indicate that the wide-angle view was considered more familiar).

Additionally, a wide range of retention intervals, from days to milliseconds, have been found to elicit boundary extension. In a recognition test after 6 to 13 days of retention, Safer, Christianson, Autry, and Österlund (1998) found strong evidence for boundary extension of a neutral image. Intraub et al. (1992), Intraub and Berkowits (1996), and Intraub and Richardson (1989) all found boundary extension in participants' memory after a 48-hr retention interval. Intraub et al. (1992, 1996) reported boundary extension within minutes of participants viewing multiple pictures. Boundary extension also has been reported after 1 s (e.g., Bertamini et al., 2005; Dickinson & Intraub, 2008; Intraub et al., 1996) and 2.5 s (e.g., Dickinson & Intraub, 2009) retention intervals. Shortening retention intervals even further, Dickinson and Intraub (2008; Intraub & Dickinson, 2008) also obtained boundary extension with 42-, 100-, 250-, and 625-ms retention intervals. These shorter retention intervals clearly indicate that boundary extension is independent of long-term memory processes. In one of the fastest examples of boundary extension to date, photographs were interrupted by a mask for only 42 ms before reappearing to be rated (Intraub & Dickinson, 2008). For identical close-up views, for example, this extremely brief break in visual input was enough for observers to falsely remember the target view with more of the scene than was presented and rate the identical probe image as having a more close-up view than before. Intraub and Dickinson's (2008) finding that boundary extension occurs across such a brief retention interval is significant because 42 ms is also the duration of a saccade. A retention interval quicker than an eye blink suggests that observers may be extending their scene representations as their eyes rapidly move between fixation points. This

would mean that during saccadic suppression, when vision is suppressed as the eyes are moving, may be when boundary extension occurs.

Boundary extension also has been observed with a wide range of target durations. Presentation times ranging from less than one second per picture (133 ms – Beighley & Intraub, 2016; 250-750 ms – e.g., Beighley & Intraub, 2016; Bertamini et al., 2005; Dickinson & Intraub, 2008, 2009; Intraub et al., 1996, 2006, 2008; Intraub & Dickinson, 2008; Munger, Owens, & Conway, 2005) to three to five seconds per picture (e.g., Chapman et al., 2005; DeLucia & Maldia, 2006; Intraub et al., 1996, 2006) have all resulted in boundary extension effects in memory. Even longer presentation times that allow for ample studying of the test pictures and should protect against memory errors (e.g. 15 seconds: Gottesman & Intraub, 2002; Intraub et al., 1992; Intraub, Gottesman, & Bills, 1998; Kreindel & Intraub, 2017) still result in boundary extension.

Additionally, boundary extension has been observed for scenes within scenes (i.e., a smaller picture within a larger one; Gottesman & Intraub, 2003) and regardless of whether the scenes were viewed inverted or upright (Beighley & Intraub, 2016; Intraub & Berkowits, 1996). This memory error also has been repeatedly demonstrated across different response measures and modalities (e.g., haptic studying of a 3D scene and 3D scene reconstruction), and to be unrelated to whether the objects within the original scene were cropped by the view's boundaries (e.g., Chapman et al., 2005; Gagnier et al., 2013; Gottesman & Intraub, 2003; Intraub et al., 1992; Intraub, 2004; Intraub & Bodamer, 1993; Intraub & Richardson, 1989; Spanó et al., 2017). However, the presented stimuli must be of a continuous view that in the real-world would extend beyond the presented picture's edges (including simple textured backgrounds, such as concrete pavement; although see Blazhenkova, 2017, for evidence of boundary extension in recognition

memory of faces). Non-scenes or single objects not a part of any larger surrounding context (e.g., on a blank background) do not produce boundary extension (Hubbard et al., 2010), evidence that this error is not simply one of misrepresenting the size of a focal object. Intraub et al. (1998) presented participants with line drawings of scenes and line drawings of the same scenes' central objects on a blank background. Both a rating task and drawing task produced boundary extension for the line drawings of the scenes, but not the line drawings of the objects. When participants were instructed to envision a described scene around the line drawings of the objects, however, boundary extension for the images was observed (Gottesman & Intraub, 2002; Intraub et al., 1998). Similar results of boundary extension for photographs but not "background-less drawings," were also found by Legault and Standing (1992). However, Munger and Multhaup (2016) found no additive effects of imagining additional details about a scene (e.g., smells, sounds, scene surroundings) for boundary extension.

Mamus and Boduroglu (2018) compared boundary extension of scenes presented with semantically consistent objects, semantically inconsistent objects, and objects without a background. They found that semantically consistent scenes produced the most boundary extension. Whereas objects presented without a background also produced boundary extension, they argued that this was because the real objects elicit a pretense of a background scene (similar to the results of envisioned scenes by Gottesman & Intraub, 2002). In a second experiment, pictures of abstract shapes, for which scene schemas were completely removed, resulted in no boundary extension, which Mamus and Boduroglu claimed further suggests the necessity of schemas in boundary extension. While Mamus and Boduroglu found that contextual consistency is not necessary for boundary extension to occur, it should be noted that Bertamini et al. (2005)

did not observe boundary extension when scenes were presented with less clear details by removing the context of the scene.

1.2.2 Role of Boundary Extension

Boundary extension may have an adaptive role in visual scene perception. Hypothesized to facilitate the integration of successive views (e.g., Intraub, 1997, 2002), boundary extension reflects anticipation of the upcoming scene during visual scanning to generate the coherent and continuous view of the world that we perceive (Intraub, 2012; Intraub & Dickinson, 2008). Scene perception may involve representations that prime future spatial processing of a scene as they are integrated (e.g., Sanocki, 2003). Boundary extension may be evidence of this priming for expected, “soon-to-be-visible” aspects of a scene in the next fixation (Intraub & Dickinson, 2008). Consistent with this idea are the findings of Ménétrier, Didierjean, and Barbe (2018) that showed reduced boundary extension when participants had knowledge of a picture’s larger spatial context. Participants studied a very wide view of test images before completing a rating recognition task with closer views of the same scenes. This study period induced contextual knowledge for the images, reducing the need for boundary extension. Under some conditions (high-confidence ratings), boundary extension was eliminated completely. Scene perception processes are in less need of predictions from boundary extension when contextual spatial knowledge of a scene is already known, highlighting the role of these predictions. While Intraub and Dickinson (2008; Intraub, 2010) have proposed an alternative model of scene representation to explain the mechanisms leading to boundary extension, the traditional visual-cognitive model of scene perception must first be reviewed.

1.3 The Traditional Visual-Cognitive Model

Human memory for scenes is not ‘picture perfect,’ and how imperfect scene representations are created in human memory is unclear. This question has driven research by many cognitive psychologists over the years, and several short-term memory buffers have been identified that facilitate the integration of visual information into visual memories, presumably also contributing to “mis-memories.”

During scene perception, information is first held in visual sensory memory, also called iconic memory (Sperling, 1960). Visual sensory representations, however, quickly fade, and are maintained for only approximately 300 ms in this short-term buffer. Loftus, Johnson, and Shimamura (1985) found that representations for briefly presented, unmasked pictures are maintained for approximately 100 ms after the visual stimulus is removed. If the presented visual stimulus is masked (disrupting sensory memory), visual information can be stored in one of several other short-term memory buffers: transsaccadic memory for the duration of an eye movement (Irwin, 1991, 1993), visual short-term memory for a few seconds (Phillips, 1974), conceptual short-term memory for the time between picture identification (approximately 100 ms after stimulus presentation) and consolidation (Potter, 1976), or visual working memory across ongoing tasks (the visuospatial sketchpad; Baddeley & Hitch, 1974). Information in these stores can then either be consolidated in long-term memory or lost.

These different short-term memory systems should not necessarily be thought of as discrete entities, but instead as different stages of visual information processing (Intraub, 2012). For example, due to saccadic suppression as the eyes are moving, the visual-cognitive system relies on transsaccadic memory across fixations. This means humans alternate between visual sensory input and memory during initial formation of visual representations. In this model,

conceptual knowledge is prompted by visual sensory information, but remains a separate type of representation (Intraub, 2012). In other words, bottom-up processing of visual sensory input results in the initial mental representations during scene perception. Top-down processing, as a result of conceptual knowledge, then interacts with and alters these representations. Support for this distinction can be found in Potter's (1976) explanation for why recognition memory for pictures presented with RSVP was poor. Potter (1976) identified conceptual masking within conceptual short-term memory as the cause of poor recognition memory during RSVP tasks; an effect distinct from visual masking experienced within iconic memory. Conceptual masking is brought on by the conceptual processing of a subsequent picture that interrupts the conceptual representation of a scene currently being maintained in conceptual short-term memory (resulting in the forgetting of this previous representation). However, if processing and consolidation of the initial conceptual representation into long-term memory occurs prior to this interruption, it is protected from conceptual masking and remembered, even in the face of a visual mask. This distinction between conceptual and visual masking, supported by other studies of memory for briefly presented pictures as well (e.g., Intraub, 1980, 1984; Loftus & Ginn, 1984), suggests a distinction between processes of perception and representation that is central to the traditional visual-cognitive model.

While the visual stimuli are still present, an observer would readily discern the location of a picture's boundaries. Given this fact, it should be assumed that the extended representations reported during tests of boundary extension are not constructed within the visual-cognitive model until the viewed scene has been removed. Taking into consideration the rapidity of boundary extension (e.g., Dickinson & Intraub, 2008; Intraub & Dickinson, 2008), the extrapolation of the scene representation must be constructed not only after the view is gone but also completed

before the observer's next fixation. In other words, between saccades (Intraub & Dickinson, 2008). However, Intraub and Dickinson (2008; Intraub, 2010, 2012) have found this hard to explain with the traditional visual-cognitive model. They have argued that a "scene extrapolation buffer" (Intraub, 2010) would need to be added alongside the other short-term memory buffers in the model or extrapolation capabilities added to transsaccadic or visual short-term memory. Assuming these additions unlikely, they have proposed an alternative model of visual scene processing to explain boundary extension – the multisource model (Intraub, 2010; Intraub & Dickinson, 2008).

1.4 The Multisource Model of Scene Perception

Unlike the traditional visual-cognitive model, for which visual sensory input is the sole basis of visual perception and the representation, in the multisource model scene perception begins with an underlying spatial framework that is simultaneously filled in by information from multiple sources (both internal and external; Intraub, 2010; Intraub & Dickinson, 2008). According to this model, viewing a picture elicits several sources of input that are then organized within an egocentric frame of reference and provide the observer with a mental representation of the scene centered around their viewpoint (e.g., viewpoint of the camera when looking at a photograph; Bryant, Tversky, & Franklin, 1992; Franklin & Tversky, 1990). This scene representation is created from visual sensory input of the stimulus, amodal perception of objects and surfaces (Kanizsa, 1979, as cited in Intraub, 2010; Yin, Kellman, & Shipley, 1997), and conceptual knowledge associated with the view (scene categorization; e.g., Greene & Oliva, 2009; Tversky & Hemenway, 1983, and contextual associations made from objects within the scene; e.g., Bar, 2004). In other words, information from sensory input and top-down processing critical for view comprehension are combined together to form one's conceptualization of the

likely overall surrounding spatial context of the view. This compiled scene representation is considered, in this model, to be scene perception. Intraub (2012) likens this multisource representation to a “simulation” described by Barsalou (1999) in his theory of grounded cognition (see Barsalou, 2010, for a review). In the multisource model, bottom-up and top-down processing interact simultaneously to form even the initial mental representations of scene perception, in contrast to the step-wise nature of the traditional visual-cognitive model.

The fundamental spatial structure of this model does not have to be egocentric in nature (Intraub, 2010), and can take on different frames of reference depending on the viewpoint taken by the observer (e.g., allocentric or geographic; see Allen, 2004, for a review of this topic). Amodal perception is prompted by visual obstructions of the physical world and allows an observer to infer the likely surroundings of a scene by completing cropped objects (Kanizsa, 1979) and surfaces (Yin et al., 1997). It is named as such because it does not employ any specific sensory modalities (Kellman, Yin, & Shipley, 1998). In the multisource model of scene perception, extrapolation of the visual input just beyond the edges of the view by amodal perception is constrained by the visual details at the picture’s boundaries (Gottesman & Intraub, 2003) and the general categorization and associations of the scene from conceptual knowledge. Because amodal perception and the observer’s associated conceptual knowledge of the view contribute to scene perception even initially, boundary-extended regions are not constructed after stimulus offset but instead are already present in the scene representation while the scene is being viewed. This is a distinction from the traditional model (see Figure 1.2 for a pictorial depiction of this difference). The error is, therefore, believed to occur from the observer misreporting the source of this extended region as being externally generated (i.e., from visual

input) instead of internally generated (i.e., amodal perception and conceptual knowledge) – a source monitoring error (Johnson, Hashtroudi, & Lindsay, 1993).

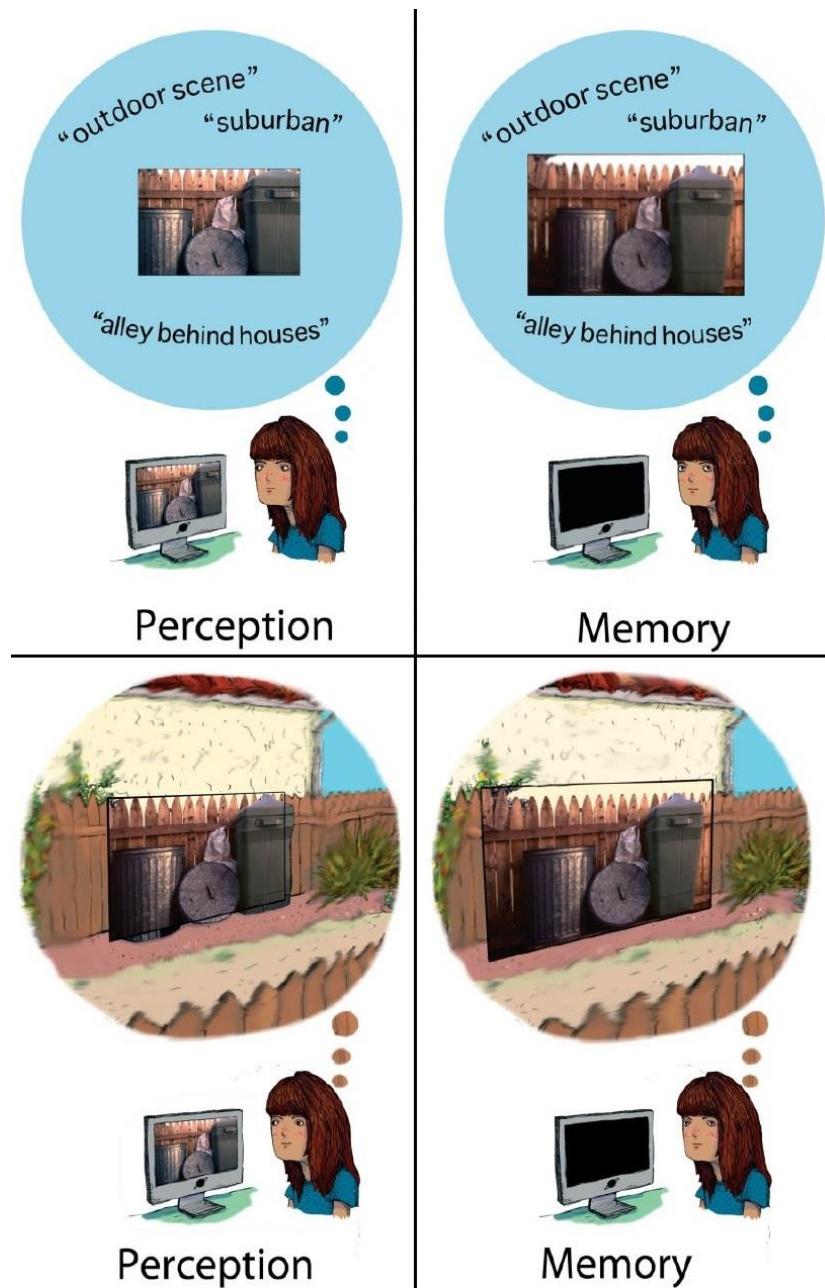


Figure 1.2 Boundary extension in the context of the traditional visual-cognitive model (top) and the multisource model (bottom).

In both cases, the perception panels represent what occurs while the picture is available, compared to when the stimulus is removed (memory panels). Relevant abstract concepts associated with the scene representation are shown in verbal form for the visual-cognitive model. Illustrations are from "Rethinking visual scene perception," by H. Intraub, 2012, WIREs Cognitive Science, 3, p. 123.

1.4.1 Boundary Extension as a Source Monitoring Error

When reflecting on memory for the target view during tests of boundary extension, according to the multisource model, observers must discern from the different sources of their scene representation (visually perceived information, amodal perception, and elicited conceptual knowledge) to determine which aspects of the representation originated from visual sensory input and were seen in the target image (Intraub, 2010, 2012; Intraub & Dickinson, 2008). Source monitoring errors occur, typically in long-term memory, when the source of a memory is incorrectly determined based on the memory's number and quality of perceptual, contextual, semantic, and emotional details (Johnson et al., 1993). The high level of similarity between an observer's memory from visual input for the details at the edge of a picture and their memory from amodal perception for the continuation of those details leads to source misattribution (Intraub, 2010, 2012; Intraub & Dickinson, 2008). As a result, information generated from amodal perception is thought to have come from visual sensory input. Observers, therefore, believe that they originally saw this information and boundary extension is seen in memory. This source monitoring error is specifically an error in reality monitoring (Johnson & Raye, 1981), as the observer has failed to determine where externally-generated visual input ended and internally-generated amodal perception began within their mental representation of the scene (Intraub, 2010; Intraub & Dickinson, 2008).

Experimental support for this source monitoring hypothesis has come from studies of the effects that divided attention and varied stimulus duration have on boundary extension. Intraub et al. (2008) found that divided visual attention (using a visual search task) increased boundary extension in participants' boundary ratings, compared to those from participants only engaged in the memory task. Random error during the search task, however, did not increase for the dual-

task participants compared to those in the search-only condition, indicating that this increase in boundary extension was not due to an overall increase in errors as a result of divided attention. These results have been considered supportive of the multisource model and source monitoring hypothesis (e.g., Intraub, 2010, 2012) because they suggest that divided attention lowered the threshold for information generated by amodal perception to be attributed to visual sensory input, resulting in source attribution error.

Similarly, reduced stimulus duration also increased boundary extension (Intraub et al., 1996). As previously discussed, stimulus presentation durations of 250 ms and 4 s both resulted in boundary extension across recall (drawing) and recognition (rating) tasks (Intraub et al., 1996). Interestingly, however, across both tasks a significant main effect for stimulus duration was also found, with the shorter duration resulting in an increased degree of boundary extension compared to the 4 s stimulus duration. Intraub (2010, 2012) has also described this study as support for the hypothesis that boundary extension is a source monitoring error, because the reduction in stimulus duration reduces the observer's memory strength for visual details originating from visual input. As a result, memory for visual input becomes more similar to details originating from amodal perception and more vulnerable to source misattribution, as predicted by source monitoring theory.

2 PRESENT STUDY

While the source monitoring hypothesis seems like a probable explanation of why boundary extension occurs in human memory for scenes, it is unclear why the shift in the distinction between perception and memory that is suggested by the multisource model is needed to explain boundary extension. In the multisource model (Intraub, 2010; Intraub & Dickinson, 2008), representation is *equal* to perception. Upon seeing a scene, the observer's internal spatial

framework (a representation of their understanding of the scene and its likely surrounding spatial layout) is filled in by visual sensory information, amodal perception, and general conceptual associations, forming the basis of scene perception. Amodal perception within the representation results in boundary extension. The traditional visual-cognitive model retains the distinction between perception and representation that was suggested by Potter (1976), and supported by others (e.g., Intraub, 1980; Loftus & Ginn, 1984), with representation occurring after perception. In this model, an observer's memory for the details of a scene results in a representation based solely on visual input and separate from the subsequent top-down processing needed for scene comprehension (amodal perception, conceptual knowledge from categorization and contextual object associations, etc.) that would be responsible for boundary extension. The difference between these models lies in the timing of when boundary extension occurs (after the stimulus is gone according to the traditional model or during perception, as a part of the multisource representation), as well as by what mechanism boundary extension happens (general top-down processing in the traditional model or amodal perception, specifically, in the multisource model).

It is possible that either amodal perception or context-based scene interpretations could result in a continuation of the view beyond its original boundaries, as the result of an error in source monitoring. Despite Intraub and Dickinson's attribution of boundary extension to only amodal perception, they have also repeatedly suggested that scene categorization and the observer's contextual knowledge of the scene have similar constraints to amodal perception on scene representation (e.g., Intraub, 2010, 2012). Unlike Intraub and Dickinson (2008), I do not find the rapidity of boundary extension as a limitation to the traditional model's potential to explain this memory phenomenon. As previously discussed, pictured scenes can be rapidly categorized within 100 to 150 ms of picture onset (e.g., Davenport & Potter, 2004; Fei-Fei et al.,

2007; Intraub, 1981; Potter, 1976; Thorpe et al., 1996; Vö & Henderson, 2010). Even the studies of boundary extension designed to push the limits of stimuli presentation (e.g., 133 ms: Beighley & Intraub, 2016; 250 ms: Intraub et al., 1996, 2006; Intraub & Dickinson, 2008; Munger et al., 2005) have used presentation lengths long enough for scene categorization and similar in length to a single eye fixation during scene perception (260 to 330 ms; Rayner, 2009; although see Hale, Brown, & McDunn, 2016, for a demonstration of boundary extension with 46 ms scene presentation). Conceptual information and contextual associations would, therefore, be available during a saccade and able to influence an observer's next view fixation.

While boundary extension has been proven to occur across a variety of testing conditions and serve an adaptive role in visual scene perception, previous research has not clearly identified the underlying mechanisms of this phenomenon nor which model offers the best explanation of this memory error. A comparative approach to studying boundary extension would help identify the necessary mechanisms and appropriate model of this constructive error in human scene memory. To test the multisource model, assessments of an observer's picture memory in the absence of predictive conceptual knowledge (scene categorization and contextual associations of objects) of the view are needed to determine the mechanistic role of top-down processing in scene representation and boundary extension. Assessing scene memory in nonhuman primates would demonstrate amodal perception and visual sensory input's effects on boundary extension in the absence of effects from human conceptual scene knowledge. This dissociation of processes would be much more difficult to achieve with humans without using purely abstract stimuli or extremely brief stimuli presentation durations. A comparative approach would allow for the presentation of pictured scenes in ways similar to that of previous research, affording more direct comparisons of findings. Studying boundary extension through a comparative lens would

disentangle the mechanistic roles of these processes in boundary extension, as well as perhaps point to the model that most accurately explains this memory error.

In addition to minimizing the potential effects of associated conceptual knowledge on boundary extension, use of the comparative method to study animal visual perception and cognition provides an informative reference point for human perception. Studying whether humans and nonhuman animals' perceptual organization is the same allows for a better understanding of the evolutionary origins and phylogeny of perception and gives insight into the fundamental aspects of human perception and mental representation. Comparative psychology informs theory and evolution (Call, 2017) and plays a crucial role in psychology by connecting the natural and social sciences within and between disciplines (e.g., psychology and biology; Call, Burghardt, Pepperberg, Snowdon, & Zentall, 2017). Laboratory studies with nonhuman animals have better control over a study's design and stimuli, as well as subjects' past and future experience, than do many studies with humans (Call et al., 2017). General life experience and the specific testing environment can be more easily manipulated as needed to serve research aims in comparative research. Past comparative analyses have shown that the basic principles of visual perception are similar across multiple species, including humans (see Lazareva, 2017, for a review). As discussed earlier, nonhuman primates can also categorize stimuli and form schematic equivalence classes, recognizing abstract perceptual and functional relations between stimuli (see Aust, 2017, for a review). These similarities in perception and cognition make nonhuman primates an ideal model to compare and generalize results to humans.

Through five experiments assessing boundary extension in humans and nonhuman primates (rhesus monkeys and capuchin monkeys) I investigated whether boundary extension is best explained by the traditional visual-cognitive model or the multisource model, while

revealing what specific psychological processes (e.g., conceptual knowledge, contextual associations, and amodal perception) lead to boundary extension. In the first comparative study of boundary extension, identical tasks (for humans and rhesus macaques) and equivalent tasks (for capuchin monkeys) were given to three species to compare the possibility of boundary extension occurring. Human adults (*Homo sapiens*), adult male rhesus macaques (*Macaca mulatta*), and adult male and female capuchin monkeys (*Cebus apella*) completed a computerized, delayed matching-to-sample (DMTS) task with various picture stimuli of common scenes encountered by humans (Pilot study, Replication study, and Experiment 1) or monkeys (Experiment 2A and Experiment 2B). Building off of previous forced-choice recognition tasks (Kreindel & Intraub, 2017; Mathews & Mackintosh, 2004; Safer et al., 1998; Spanó et al., 2017), the objective was to choose which of two simultaneously presented images exactly matched a previously shown sample image. The target scene was shown alongside either a closer or wider view of the same image. In the absence of boundary extension, matching responses would not differ across these conditions. However, if boundary extension had occurred participants would be more likely to select the wider angle image compared to the closer angle image. This would result in a decrement in performance when the sample image was the closer view (*close* trials) and an aid in performance when the sample image was the wider view (*wide* trials), an asymmetrical error pattern indicative of boundary extension.

Consistent with previous research, human participants were expected to demonstrate boundary extension in a DMTS task with pictures of human-unique scenes. Given the necessity of schematic and contextual knowledge for boundary extension (e.g., Bertamini et al., 2005; Mamus & Boduroglu, 2018), it was predicted that monkeys would not show boundary extension with human-unique scenes but would with monkey-relevant scenes. These results, demonstrating

that amodal perception alone is not sufficient to produce boundary extension with human-unique stimuli, would point towards a traditional visual-cognitive model explanation of boundary extension. This finding would add to the literature that suggests specific conceptual knowledge of a scene is a necessary mechanism of boundary extension. However, if boundary extension was not observed at all in the monkeys, such a result would demonstrate the potentially human-unique qualities of boundary extension and a species discontinuity in perceptual experiences.

3 PILOT STUDY WITH ADULT HUMANS

Visual inspection of initial testing ($N = 8$) with the below procedure, except with a 250 ms sample duration, suggested that this presentation time was too fast for participants to make meaningful responses (participants answered only 62% of total trials correctly). As a result, performance with two presentation times (500 and 750 ms) was compared to determine the appropriate testing parameters for the following experiments.

3.1 Participants

Undergraduate students ($N = 23$, 22 females, M age = 18.65 years, $SD = 1.19$) recruited from the Georgia State University (GSU) psychology research pool participated for course credit. All participants provided informed consent and all research procedures were approved by the GSU Institutional Review Board. A total of nine participants were excluded, due to changes to the testing protocol (stopped using the above described 250 ms sample duration) and because one participant was not attentive during the task, resulting in a total of 14 participants for analysis.

3.2 Apparatus

All participants worked on individual 19-inch desktop computers, including individual headphones. Participants used a standard mouse to respond to stimuli. A total of 90 stimuli

images were used, including 30 different common human scenes (e.g., backyard, beach, park) and a closer and wider view of each scene (see Figure 3.1). The different stimuli images were created using a program written in Visual Basic 6.0, which created a close-up image (showing 13% less of the scene) and a wide-angle image (showing 13% more of the scene) of each of the 30 scenes. The pilot study computer task was also written in Visual Basic 6.0.

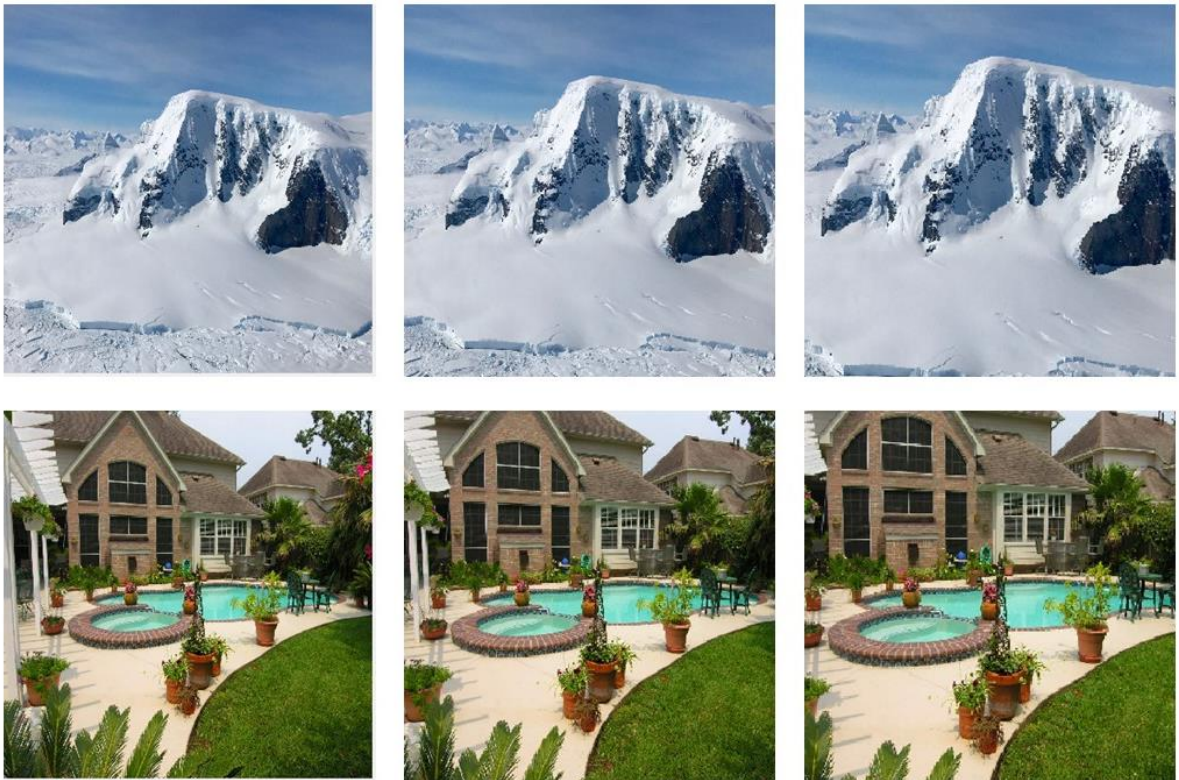


Figure 3.1 Example stimuli images of common human scenes. The wide-angle view (left) and the close-angle view (right) of each scene are also shown.

3.3 Design and Procedure

Participants first saw a start screen with task instructions. These instructions included a description of the task and directions for responding. To initiate each trial, participants clicked a “start” button located in the center of the computer screen. This resulted in immediate presentation of the sample image (400 pixels by 400 pixels) for either 500 or 750 ms, followed by a black and white mask image for 750 ms. Participants waited through a 2 s delay period

before seeing two same-size (400 pixels by 400 pixels) images as match options. One of these images was the sample image, while the foil image was either the zoomed in image of the same scene (called *wide* trials, because the sample image was the wider view) or the zoomed out image of the same scene (called *close* trials, because the sample image was the more close-up view). Left-right position of the sample image was randomized across trials. After choosing one of the match options by clicking on it, participants saw a green checkmark or a red “X” for 2 s in the bottom right corner of the computer screen, as well as heard either a brief melodic sound or a buzz tone, after correct or incorrect responses, respectively. Following incorrect responses, participants also experienced a 10 s timeout. See Figure 3.2 for a visual example of a trial.

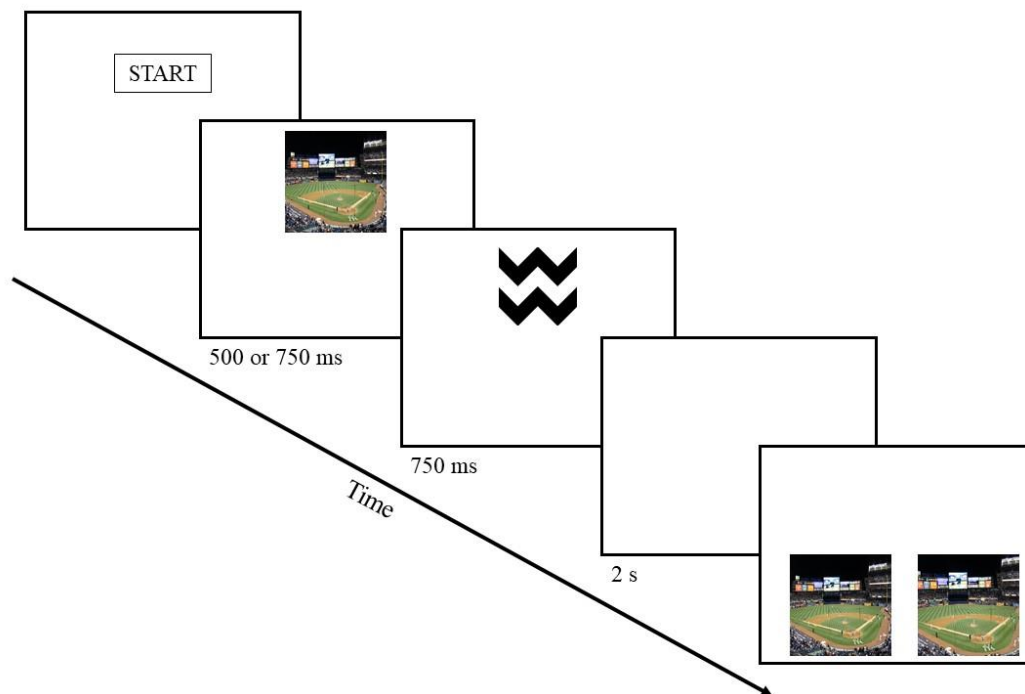


Figure 3.2 Example trial of the boundary extension task in the Pilot Study. Depending on the condition, the sample image was shown for either 500 ms or 750 ms. After a correct match response, participants saw a green checkmark for 2 s in the bottom right corner of the computer screen and heard a brief melodic sound. Following incorrect responses, participants saw a red “X,” heard a brief buzz tone, and experienced a 10 s timeout.

Participants completed a total of 240 trials, in four 60-trial blocks. Sample duration (500 or 750 ms) alternated by block, counterbalanced across participants. Per block, participants were presented with each of the 30 sample scenes once, in a random order, before any were repeated, during which each trial was randomly assigned to be a *close* or *wide* trial. For the remaining 30 trials of each block, sample images were presented in random order in the opposite trial type. As a result, each sample image was presented twice per block, once as a *wide* trial and once as a *close* trial. After testing, all participants were debriefed about the task.

3.4 Results

Participants' performance was similar with both presentation durations. When the sample image was presented for 500 ms, participants were correct on 77% of trials ($SD = 10.82$). When the sample image was shown for 750 ms, participants were correct on 78% of trials ($SD = 14.63$). Performance in both cases was significantly better than chance levels, 500 ms: $t(13) = 9.28, p < .001$; 750 ms: $t(13) = 7.09, p < .001$. There was no significant difference in participants' performance across conditions, $t(13) = -0.30, p = .77$.

3.5 Discussion

This pilot study with adult humans was needed to determine the testing parameters for the following experiments with humans and monkeys. Given that no significant differences in performance were seen between the two sample presentation durations, the longer sample presentation (750 ms) was chosen for the following experiments. Choosing the longer of the two sample durations would afford more time for nonhuman primates to view the sample image in Experiments 1 and 2, increasing the likelihood that they would be able to learn the DMTS task.

4 REPLICATION STUDY

Before testing with nonhuman primates, the present method was tested with human adults to determine whether a computerized DMTS two-alternative forced-choice task was sensitive enough to detect boundary extension. Considering the results of the pilot study, a 750 ms sample presentation duration was used.

4.1 Participants

Undergraduate students ($N = 63$, 59 females, 3 males, 1 participant chose to not provide their gender, M age = 19.51 years, $SD = 2.93$) were again recruited from the GSU psychology research pool and participated for course credit. All participants provided informed consent, and all research procedures were approved by the GSU Institutional Review Board. One participant did not complete the entire testing session, leaving a total of 62 participants for analysis.

4.2 Apparatus

The testing setup was the same as in the pilot study.

4.3 Design and Procedure

The task design was the same as in the pilot study, with the only exception being that the sample image was always presented for 750 ms. Participants completed a total of 180 trials, in three 60-trial blocks. Per block, participants were again presented with each of the 30 sample scenes once in a random order before any were repeated. For the first half of each block, each scene was randomly presented as either a *close* or *wide* trial. For the second half of each block, the sample images were shown again in a different random order, but in the other trial type. After testing, all participants were debriefed about the task.

4.4 Results

To test for boundary extension, the error rates in participants' responding as a function of trial type and block were examined (see Figure 4.1). Mauchly's test of sphericity indicated a violation of this assumption for block ($\chi^2(2) = 20.24, p < .001$) and the interaction term ($\chi^2(2) = 10.60, p < .01$), therefore degrees of freedom were corrected using the Greenhouse-Geisser estimations (block, $\epsilon = .78$; interaction, $\epsilon = .86$). There was a significant main effect of trial type, $F(1, 61) = 57.93, p < .001$, such that participants produced a significantly higher proportion of errors on *close* trials ($M = 0.27, SD = 0.11$) than on *wide* trials ($M = 0.18, SD = 0.12$). Correct performance patterns in both conditions were significantly above chance levels of responding, *close* trials: $t(61) = 16.05, p < .001$; *wide* trials: $t(61) = 21.37, p < .001$. There was also a significant main effect of block, $F(1.56, 94.84) = 110.54, p < .001$. Participants' proportion of errors significantly decreased across block (block 1, $M = 0.31$; block 2, $M = 0.22$; block 3, $M = 0.15$), with all pairwise comparisons significant after Bonferroni corrections ($p < .001$). There was not a significant interaction between block and trial type, $F(1.72, 104.99) = 0.97, p = .37$.

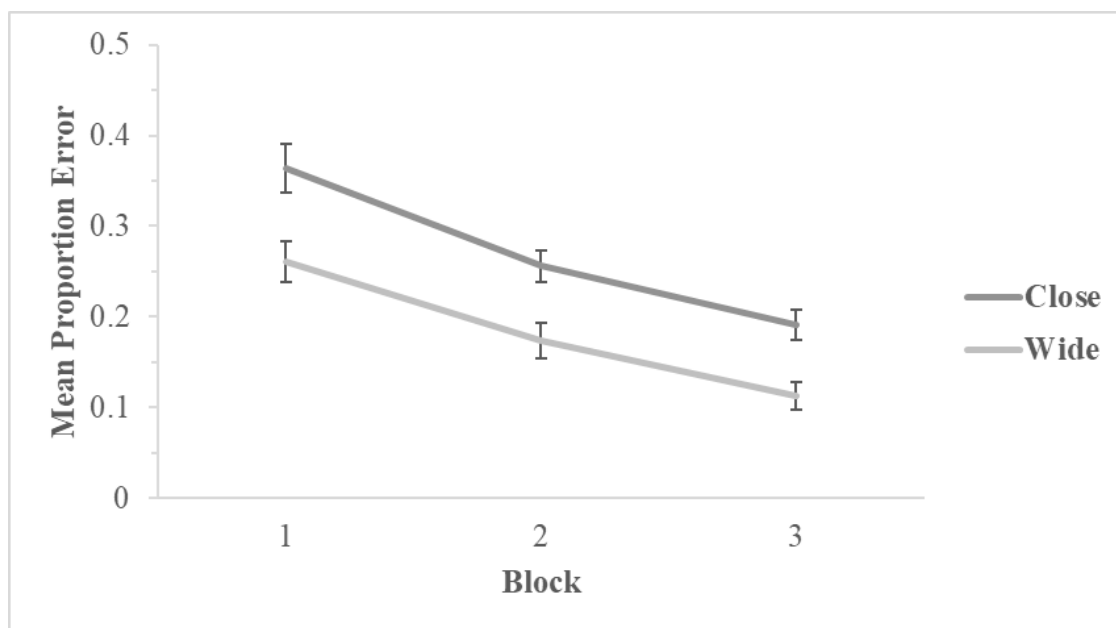


Figure 4.1 Mean proportion of errors, as a function of trial type and block, for human adults in the Replication Study.

Error bars show the 95% confidence intervals.

4.5 Discussion

The conceptual replication study with human adults using a new version of a DMTS paradigm replicated boundary extension with a task that could be used with nonhuman primates. Participants made a significantly higher proportion of errors on *close* trials than *wide* trials, demonstrating the error rate asymmetry indicative of boundary extension. Boundary extension leads participants to falsely remember the target image with more information just outside of the scene's boundaries than was originally presented. When the sample image was the wider view of the presented scene compared to the foil image participants were more easily able to identify the correct image, aiding their performance in the task. However, when the sample image was the closer view it appeared to show less of the original scene, resulting in more errors.

Across blocks, participants' performance significantly improved but boundary extension was not eliminated by experience. Feedback resulted in fewer errors as participants advanced through the task, presumably the result of a practice effect, with the magnitude of boundary

extension largest for block one, but boundary extension was still observed across all three blocks. The first block of trials was the most informative for boundary extension, as the sample images were not yet associated with rewards and penalties as was true in later blocks. This is an important issue to consider when giving this task to monkeys, as they require multiple sessions to complete the task. Evidence that feedback did not eliminate boundary extension indicated that the DMTS task used with human adults would be a suitable method for nonhuman primates. Overall, this DMTS design, which produces boundary extension in humans even with extended experience, proved to be a suitable method to study boundary extension in rhesus monkeys and capuchin monkeys in the following experiments.

5 EXPERIMENT 1

Given the successful replication of boundary extension in human adults, Experiment 1 was conducted to test for boundary extension in nonhuman primates with the same stimuli and methods as the previous experiment.

5.1 Participants

A total of six adult male rhesus macaques (*Macaca mulatta*, 13 to 34 years of age) and 23 adult capuchin monkeys (*Cebus apella*, 7 males and 16 females, 7 to 48 years of age) housed at the Georgia State University Language Research Center were tested. All monkeys had constant visual and auditory access to nearby monkeys during testing, as well as periods without testing with access to a compatible social partner or group and/or an outdoor play yard multiple times per week. All of the monkeys voluntarily chose to work for food rewards. Food and water deprivation were not used. The monkeys were fed a daily diet of primate chow biscuits and various fruits and vegetables regardless of their performance on the tasks, as well as provided with continuous access to water. All research procedures followed guidelines for working with

nonhuman primates and were approved by the GSU Institutional Animal Care and Use Committee. In addition, GSU is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care.

All of the monkeys were computer and joystick-trained, with extensive experience with a variety of computerized cognitive tasks, including DMTS tasks. Two capuchin monkeys and two rhesus macaques were used as pilot animals to determine the training parameters needed for testing. As a result of working with these animals, testing parameters were modified as needed for each species to learn the task. All four animals were included in the full testing procedure described below. After training (described below), nine capuchin monkeys were dropped from the experiment due to an inability to learn the task, lack of engagement with the task, or time constraints during testing. This left a total of 14 capuchin monkeys with data for analysis.

5.2 Apparatus

Each monkey was tested individually using the Language Research Center's Computerized Test System, which comprises a personal computer, digital joystick, color monitor, and pellet dispenser (Evans, Beran, Chan, Klein, & Menzel, 2008; Richardson, Washburn, Hopkins, Savage-Rumbaugh, & Rumbaugh, 1990). The monkeys used their hands to manipulate the joystick to control a small cursor on the computer screen. Contacting correct stimuli with the computer cursor resulted in a brief melodic chime and the delivery of a 45-mg banana-flavored chow pellet, while incorrect responses resulted in a brief buzz tone and a 30 s timeout period. All tasks were written in Visual Basic 6.0.

Experiment 1 used the same 90 scene stimuli images as the pilot and replication studies with human adults.

5.3 Design and Procedure

All monkeys were first trained on the present DMTS task until 75% correct performance was achieved for three consecutive 60-trial blocks. Monkeys indicated their readiness to work before each trial by contacting a “start” button through movement of the cursor. For rhesus monkeys, a training trial included presentation of one of the 90 scene images (selected randomly and shown as a 400 pixel by 400 pixel image in the center of the computer screen) for 750 ms, immediately followed by presentation of a black and white mask image for 750 ms, and a 2 s delay period. After the delay period, two match options (both 400 pixels by 400 pixels) were presented on the bottom half of the computer screen. One image was the previously seen sample image, while the foil image was a randomly selected image of a different scene (see Figure 5.1). Left-right position of the sample image was randomized across trials. After making a matching response by contacting one of the images with the cursor, monkeys saw either a green checkmark or a red “X” for 2 s in the bottom right corner of the computer screen, indicating a correct or incorrect response, respectively. After incorrect responses, monkeys also heard a brief buzz tone and experienced a 30 s timeout. After correct responses, monkeys heard a brief melodic chime and received a 45-mg banana-flavored food pellet.

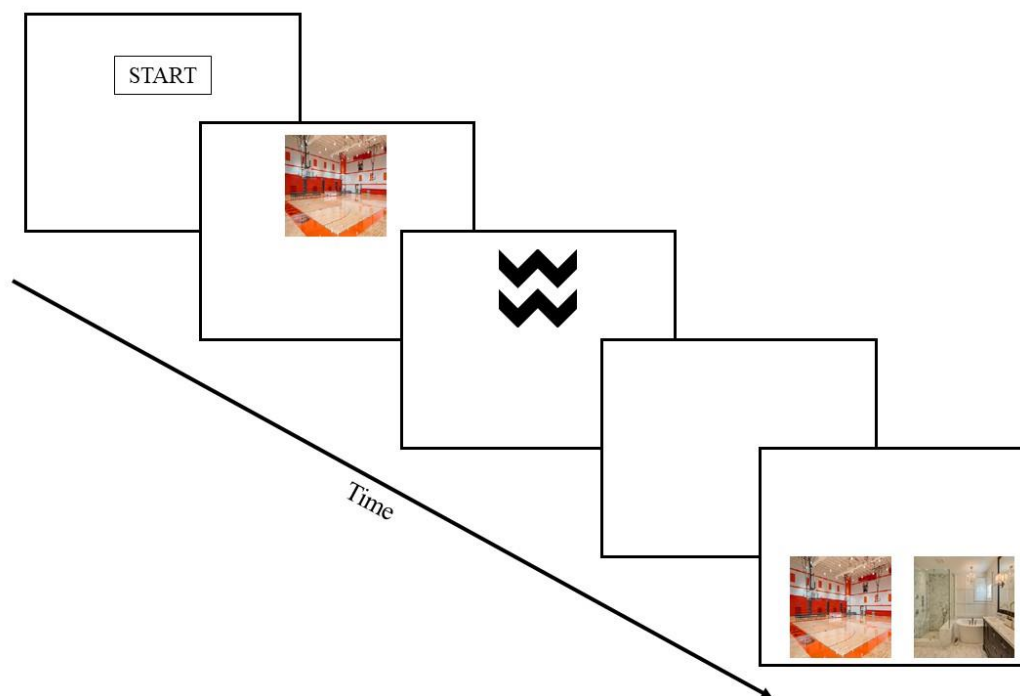


Figure 5.1 Example training trial of the boundary extension task in Experiment 1. Specific timing of each component depended on the monkey species being tested. After a correct match response, monkeys saw a green checkmark for 2 s in the bottom right corner of the computer screen, heard a brief melodic sound, and received a 45-mg food pellet. Following incorrect responses, monkeys saw a red “X,” heard a brief buzz tone, and experienced a 30 s timeout.

For capuchin monkeys, contacting the “start” button resulted in presentation of the randomly selected sample image (one of the 90 stimuli images, shown as a 400 pixels by 400 pixels image) until the monkey contacted it with the cursor, after which it was displayed for an additional 1.5 s. A black and white mask image was then displayed for 300 ms, followed by a 2 s delay period. After this delay, the sample image and an image of a different, randomly-selected scene were shown simultaneously on the bottom half of the computer screen as match options (400 pixels by 400 pixels, left-right position randomized across trials). The stimuli remained onscreen until the monkey contacted one image with the cursor. After correct match responses, monkeys saw a green checkmark for 2 s in the bottom right corner of the computer screen, heard a brief melodic chime, and received a 45-mg banana-flavored food pellet. After incorrect

responses, monkeys instead saw a red “X” for 2 s, heard a brief buzz tone, and were given a 30 s timeout.

Some capuchin monkeys ($N = 6$) were unable to pass training with this procedure, so they were given trials without the 300 ms mask image. All other aspects of the trial were the same. One capuchin monkey was unable to pass either type of training. As a result, she was given training trials without a mask image or a delay period. Therefore, after touching the sample image the match options were immediately presented. After passing this easier version of training, she was put back on training trials with a 2 s delay period but no mask image until training criterion was met.

Once each monkey met the training criterion, they were moved to the test phase. Each trial preceded the same way as described above for the training phase, except that 25% of the trials were now test trials and 75% of trials were baseline training trials identical to those just described. During test trials, match options included the sample image, which was always the central-view of a scene, and a foil image which was either the closer or wider view of that same scene (as shown in Figure 3.2). The test trials were intermixed among training trials and each of the 30 sample scenes were presented twice as *close* and *wide* trials before being repeated. For capuchin monkeys given training trials without mask images, test trials were also presented without a mask image. All monkeys worked until they completed at least 2,400 total trials in the test phase.

5.4 Results

5.4.1 *Rhesus macaques*

By random chance, two blocks did not include all three conditions (*train*, *close*, and *wide* trials). Instead of excluding those blocks from analysis, each rhesus monkey’s performance was

binned into 20 120-trial blocks for analysis. Analysis of the monkeys' average proportion of errors, as a function of trial type and block, indicated a significant main effect of trial type, $F(2, 10) = 183.58, p < .001$ (see Figure 5.2). Performance was above chance levels for all trial types, train: $t(5) = 17.55, p < .001$; close: $t(5) = 2.81, p < .05$; wide: $t(5) = 2.69, p < .05$. Pairwise comparisons with Bonferroni corrections for multiple comparisons showed that rhesus monkeys made a significantly smaller proportion of errors on train trials ($M = 0.11, SD = 0.06$) compared to close trials ($M = 0.45, SD = 0.04$), $p < .001$, and wide trials ($M = 0.45, SD = 0.04$), $p < .001$, but that the proportion of errors made on close and wide trials were not significantly different from each other, $p = 1.00$. There was no main effect of block, $F(19, 95) = 0.62, p = .88$, or an interaction between block and trial type, $F(38, 190) = 0.43, p = .17$. Analysis of performance on critical trials during the first block also showed no difference in the rhesus monkeys' proportion of errors on close ($M = 0.47, SD = 0.19$) and wide ($M = 0.50, SD = 0.24$) trials, $t(5) = -0.27, p = .80$.

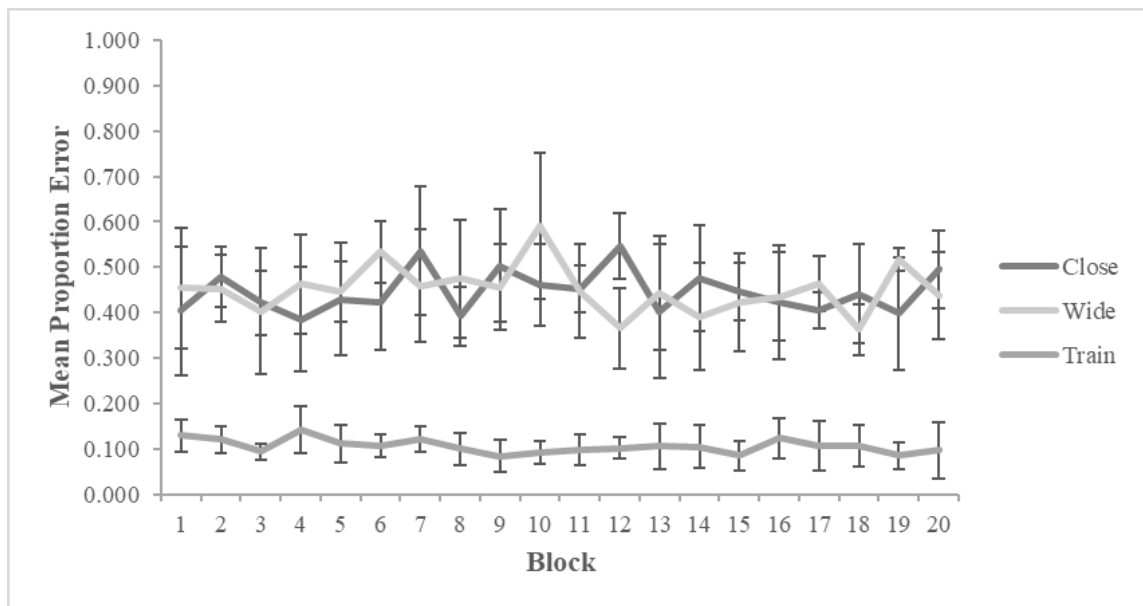


Figure 5.2 Mean proportion of errors, as a function of trial type and block, for rhesus macaques in Experiment 1.

Error bars show the 95% confidence intervals.

5.4.2 *Capuchin monkeys*

Capuchin monkeys' proportion of errors were analyzed across 40 60-trial blocks, as a function of trial type and block (see Figure 5.3). Overall, capuchins performed above chance in all trial types, train: $t(13) = 19.80, p < .001$; close: $t(13) = 4.11, p = .001$; wide: $t(13) = 3.91, p < .01$. There was a significant main effect of trial type, $F(2, 26) = 258.92, p < .001$. Pairwise comparisons, with Bonferroni corrections for multiple comparisons, showed that monkeys made a significantly smaller proportion of errors on train trials ($M = 0.20, SD = 0.06$) than on close ($M = 0.47, SD = 0.03$), $p < .001$, and wide trials ($M = 0.47, SD = 0.03$), $p < .001$. Performance on close and wide trials did not differ from each other, $p = 1.00$. There was no main effect of block, $F(39, 507) = 0.90, p = .65$, or an interaction between block and trial type, $F(78, 1014) = 1.03, p = .40$. The monkeys' performance on the critical close and wide trials during the first block showed a significant difference as a function of trial type, $t(13) = -2.72, p < .05$. Capuchin monkeys made a larger proportion of errors on wide trials ($M = 0.62, SD = 0.16$) than on close trials ($M = 0.47, SD = 0.14$)

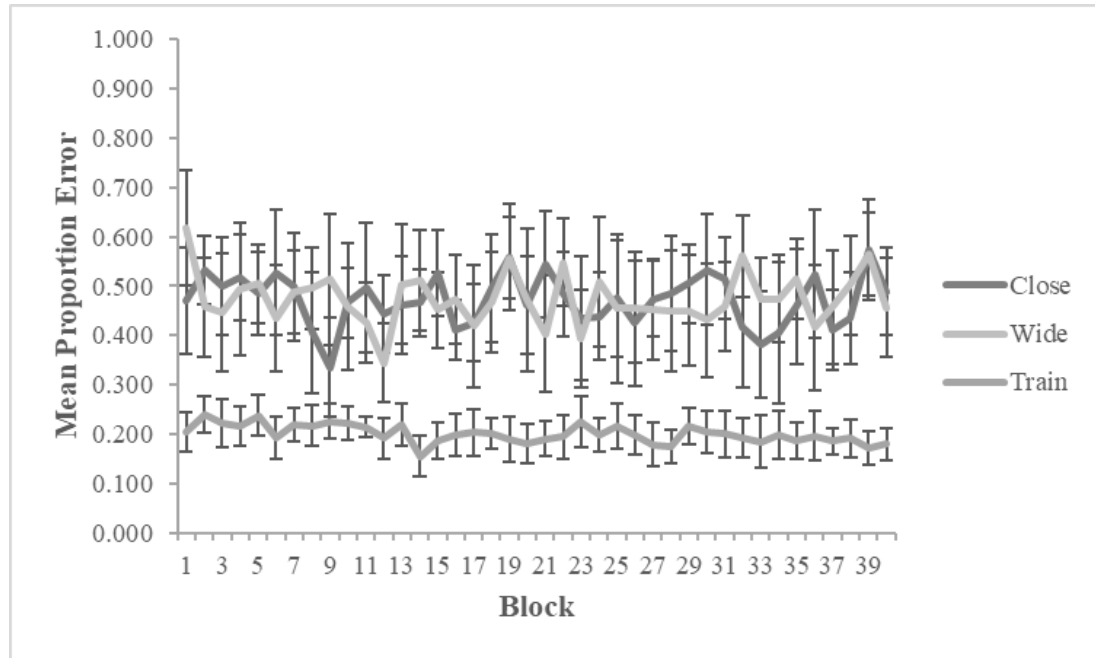


Figure 5.3 Mean proportion of errors, as a function of trial type and block, for capuchin monkeys in Experiment 1.

Error bars show the 95% confidence intervals.

5.5 Discussion

The multisource model predicts that either amodal perception or conceptual knowledge can result in boundary extension. However, the results of Experiment 1 suggest the contrary. Rhesus monkeys and capuchin monkeys did not show boundary extension when viewing scenes commonly encountered by humans but not nonhuman primates. Under these conditions, conceptual knowledge for categorization of the scene and contextual associations from objects were absent for the animals. However, based on research with fish (Sovrano & Bisazza, 2008), chicks (Regolin & Vallortigara, 1995), mice (Kanizsa, Renzi, Conte, Compostela, & Guerani, 1993), baboons (Deruelle, Barbet, Dépy, & Fagot, 2000; Fagot, Barbet, Parron, & Deruelle, 2006), rhesus monkeys (Fujita, 2001), and chimpanzees (Sato, Kanazawa, & Fujita, 1997) indicating that amodal completion is present in animal visual perception, it can be assumed that amodal perception would have been experienced by the monkeys.

The absence of boundary extension in the present experiment suggests that amodal perception may not be sufficient for boundary extension to occur in memory. Instead, object and conceptual knowledge of a scene may be a necessary mechanism of boundary extension. However, there is evidence that amodal perception is sufficient for boundary extension when abstract geometric shapes are the stimuli (see Hale, Brown, McDunn, & Siddiqui, 2015; McDunn, Siddiqui, & Brown, 2014). This would suggest that the failure of monkeys to show boundary extension in the present experiment is more likely a species difference, rather than the result of amodal perception not being sufficient to elicit boundary extension. However, it is important to withhold that conclusion until monkeys could be presented with relevant stimuli that would prompt conceptual knowledge, to see if this might induce boundary extension. By using scenes that are familiar to the monkeys, instead of human scenes that they have no knowledge of, the necessity of conceptual knowledge can be assessed, at least to the best extent possible with a nonverbal species. This hypothesis was tested further in the following experiments.

Unlike for human adults, the monkeys' performance did not benefit from experience. Error rates did not significantly improve or differ in any way for either species across 40 blocks of 60 trials. Capuchin monkeys did demonstrate a difference in performance on the critical test trials during the first block of Experiment 1. However, this outcome was unexpected, as it was in the opposite direction of boundary extension. Capuchin monkeys made fewer errors on *close* trials than *wide* trials. This result may have been because the monkeys were paying more attention to central features of the scene, as opposed to the overall scene. These central features would have been slightly more prominent in the closer view of the sample images, resulting in a bias for this view when making match responses during the task.

6 EXPERIMENT 2A

Given the absence of boundary extension in two species of nonhuman primates using images of human scenes, Experiment 2A was conducted to test for boundary extension with monkey-relevant stimuli. Showing the monkeys pictures of common human scenes (e.g., a restaurant) would not have activated any schemas in the animals, because they would not recognize what the image was a picture of. The rationale of the present experiment was that perhaps images of scenes that the monkeys would be familiar with would be more likely to induce boundary extension if this memory error requires conceptual knowledge and contextual associations evoked by the objects in the scene. This experiment was more species-fair if scene relevance matters for boundary extension, and I therefore was better able to investigate whether conceptual knowledge of familiar scenes was needed for boundary extension to occur.

6.1 Participants

The same six rhesus macaques and 14 capuchin monkeys that passed training in Experiment 1 participated in Experiment 2A.

6.2 Apparatus

The testing apparatus and computer task were the same as in Experiment 1. Experiment 2A used 90 images of common scenes encountered by the monkeys as stimuli. These images included 30 different scenes of the monkeys' inside and outside environments at the Language Research Center (e.g., play yards, inside home enclosures), as well as a closer and wider view of each scene (see Figure 6.1). The stimuli images were created using the same program previously described to create the stimuli images of human scenes and were cropped using the same dimensions.



Figure 6.1 Example stimuli images of common scenes encountered by the monkeys. The wide-angle view (left) and the close-angle view (right) of each scene are also shown.

6.3 Design and Procedure

Due to a break in testing between experiments 1 and 2A, three rhesus macaques were re-trained on the boundary extension task using Experiment 1 training procedures and stimuli. All other monkeys moved directly from Experiment 1 to Experiment 2A without completing any additional training and without any substantial delay between test periods. Trials proceeded exactly as described in Experiment 1 for each species, with test trials occurring 25% of the time. Due to experimenter error, all capuchin monkeys were given trials with black and white visual masks, regardless of their training history with or without masks in Experiment 1. All monkeys worked until they completed at least 2,400 total trials.

6.4 Results

6.4.1 *Rhesus macaques*

Rhesus macaques' performance was divided into 40 60-trial blocks for analysis as a function of trial type and block (see Figure 6.2). Performance was above chance for all trial types, train: $t(5) = 5.95, p < .01$; close: $t(5) = 4.13, p < .01$; wide: $t(5) = 4.93, p < .01$. The monkeys' error rates showed a significant main effect of trial type, $F(2, 10) = 22.08, p < .001$. Pairwise comparisons (Bonferroni corrected for multiple comparisons) indicated that monkeys made a significantly smaller proportion of errors on train trials ($M = 0.24, SD = 0.11$) compared to close trials ($M = 0.45, SD = 0.03$), $p < .01$, and wide trials ($M = 0.45, SD = 0.02$), $p < .05$. Performance on close and wide trials did not differ from each other, $p = 1.00$. There was no main effect of block, $F(39, 195) = 1.00, p = .47$, or an interaction, $F(78, 390) = 0.98, p = .54$. Analysis of performance during the first block of testing also did not show any significant differences between close ($M = 0.44, SD = 0.31$) and wide ($M = 0.38, SD = 0.13$) trials, $t(5) = 0.57, p = .59$.

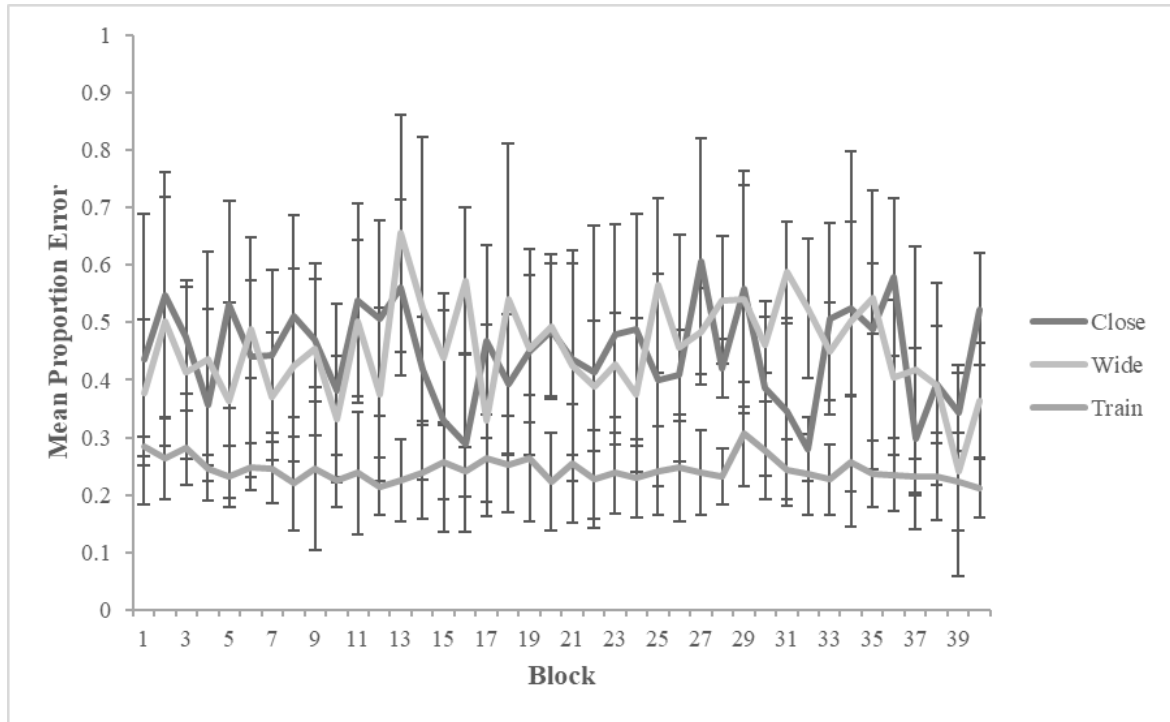


Figure 6.2 Mean proportion of errors, as a function of trial type and block, for rhesus macaques in Experiment 2A.

Error bars show the 95% confidence intervals.

6.4.2 Capuchin monkeys

Capuchin monkeys' performance was analyzed across 40 60-trial blocks, as a function of trial type and block (see Figure 6.3). Across all trial types, monkeys performed significantly above chance levels, train: $t(13) = 14.58, p < .001$; close: $t(13) = 2.92, p = .01$; wide: $t(13) = 4.23, p = .001$. There was a significant main effect of condition, $F(2, 26) = 123.66, p < .001$, such that monkeys made a significantly smaller proportion of errors on train trials ($M = 0.23, SD = 0.07$) than on close ($M = 0.46, SD = 0.05$) and wide ($M = 0.46, SD = 0.03$) trials, all pairwise comparisons with Bonferroni corrections $p < .001$. Performance on close and wide trials did not differ from each other, $p = 1.00$. There was no effect of block, $F(39, 507) = 1.01, p = .46$, or an interaction, $F(78, 1014) = 1.02, p = .43$. Monkeys' performance on close ($M = 0.47, SD = 0.21$)

and wide ($M = 0.44$, $SD = 0.23$) trials during the first block also did not show any significant differences in error rates, $t(13) = 0.42$, $p = .68$.

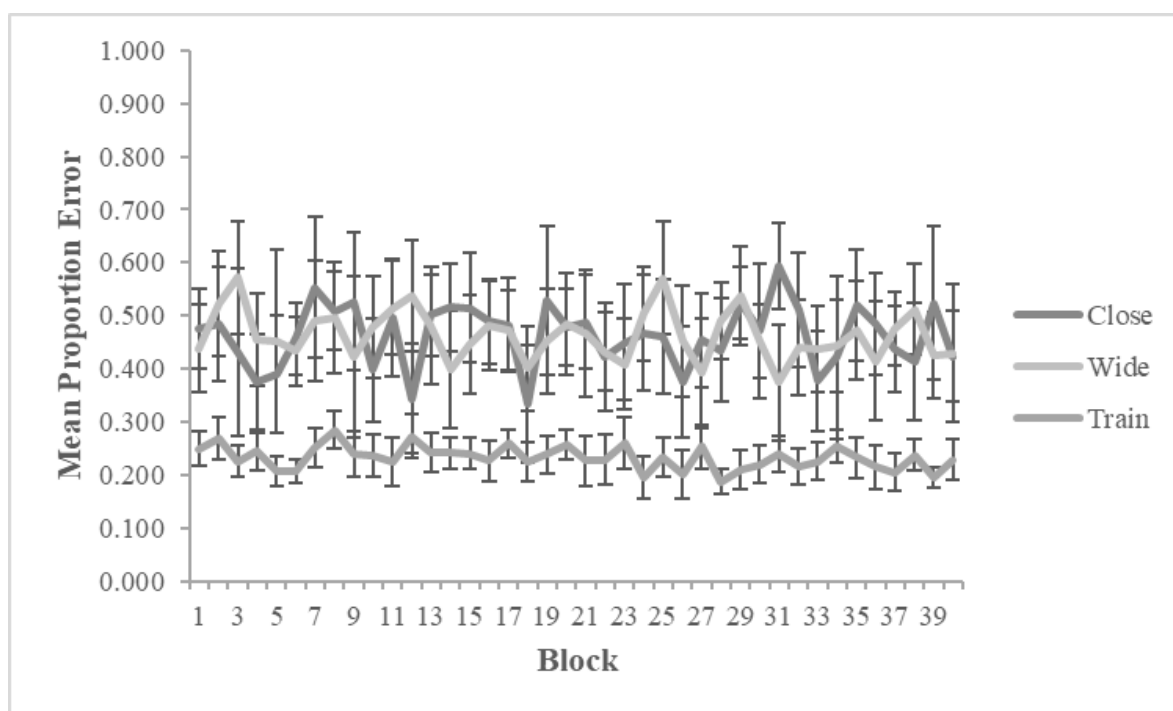


Figure 6.3 Mean proportion of errors, as a function of trial type and block, for capuchin monkeys in Experiment 2A.

Error bars show the 95% confidence intervals.

6.5 Discussion

Using images of relevant scenes for these monkeys (i.e., common scenes encountered by these specific animals) also did not lead to boundary extension. Neither species demonstrated a difference in performance on *close* and *wide* trials. This is contrary to predictions from both models of scene perception. Presumably, relevant scenes would have engaged the mental activities proposed by the traditional and multisource models to be present during scene perception (visual input, amodal perception, and schematic information of the scene). Despite the presence of an additional source of information compared to the previous experiment (i.e., categorization of the scene from conceptual knowledge and contextual associations), it seems that the monkeys were only relying on direct visual input during the DMTS task. This resulted in

an identical outcome as the previous experiment, with above chance performance when identifying the sample image from a foil image but no difference in performance based on the sample image's view relative to the foil image. This lack of boundary extension in rhesus monkeys and capuchin monkeys may represent a potential species difference between human and nonhuman primates for this memory error.

However, an additional explanation is that the monkeys were not motivated to perform well on critical trials compared to baseline trials given the much greater difficulty of those trials and the 50% chance level on what amounted to be a minority of the overall trials presented. This lack of motivation to attend carefully on these trials could have led to equal performance on *close* and *wide* trials. This possibility was investigated further in the following experiment by increasing the frequency of test trials experienced by the monkeys, so that they would have to try harder to perform well on those trials to keep the rate of reward that they had become accustomed to consistent.

7 EXPERIMENT 2B

Although all monkeys' performance in Experiments 1 and 2A were significantly above chance levels for all conditions, performance on the critical test trials did not differ greatly from chance unlike the baseline training trials. In Experiment 1, rhesus macaques' proportion of errors on training trials ($M = 0.11$) was much lower than their proportion of errors on close ($M = 0.45$) and wide trials ($M = 0.45$). The same pattern was observed for rhesus macaques in Experiment 2A: training trials ($M = 0.24$), close trials ($M = 0.45$), and wide trials ($M = 0.45$). Capuchin monkeys demonstrated the same trend in performance for Experiment 1 (train trials, $M = 0.20$; close trials, $M = 0.47$; wide trials, $M = 0.47$) and Experiment 2A (train trials, $M = 0.23$; close trials, $M = 0.46$; wide trials, $M = 0.46$). It was possible that the monkeys were not motivated to

do well on the critical test trials due to their infrequent occurrence (25% of the total trials), especially given the high levels of reward they received on baseline training trials.

Experiment 2B was done to increase monkeys' motivation to respond meaningfully on test trials by increasing the probability of *close* and *wide* trials occurring to 75%. To determine whether this made a difference in eliciting boundary extension, I tested macaques first to see whether additional tests with capuchin monkeys might be warranted by this manipulation.

7.1 Participants

The same six rhesus macaques from the previous experiments participated.

7.2 Apparatus

The testing apparatus was the same as in previous experiments with the monkeys. The computer task and stimuli were the same as in Experiment 2A.

7.3 Design and Procedure

Experiment 2B used the same testing procedures as Experiment 2A, with one critical difference. Test trials now occurred 75% of the time during testing and baseline training trials occurred 25% of the time. No additional training was completed between this and the previous experiment. Halfway through testing, a procedure modification was made for one animal for husbandry reasons. Instead of being rewarded with one 45-mg food pellet for correct responses, he was rewarded with two 45-mg food pellets. All other procedures remained the same. Monkeys worked until they completed at least 1,200 total trials.

7.4 Results

Rhesus macaques' performance was analyzed across 20 60-trial blocks, as a function of trial type and block (see Figure 7.1). Fewer blocks were analyzed due to the higher percentage of test trials compared to previous experiments. Performance for all trial types was significantly

above chance levels, train: $t(5) = 6.32, p = .001$; close: $t(5) = 3.54, p < .05$; wide: $t(5) = 3.00, p < .05$. There was a significant main effect of trial type, $F(2, 10) = 27.87, p < .001$. Pairwise comparisons, corrected for multiple comparisons with the Bonferroni correction, indicated that monkeys made a significantly smaller proportion of errors on train trials ($M = 0.22, SD = 0.11$) than on close ($M = 0.46, SD = 0.03$), $p = .007$, and wide ($M = 0.46, SD = 0.04$) trials, $p = .01$. Performance on the critical close and wide trials did not differ from each other, $p = 1.00$. There was not a main effect of block, $F(19, 95) = 0.85, p = .64$, or a significant interaction, $F(38, 190) = 0.974, p = .52$. Performance during the first block of testing was not analyzed given that the stimuli and task design were no longer novel to the monkeys.

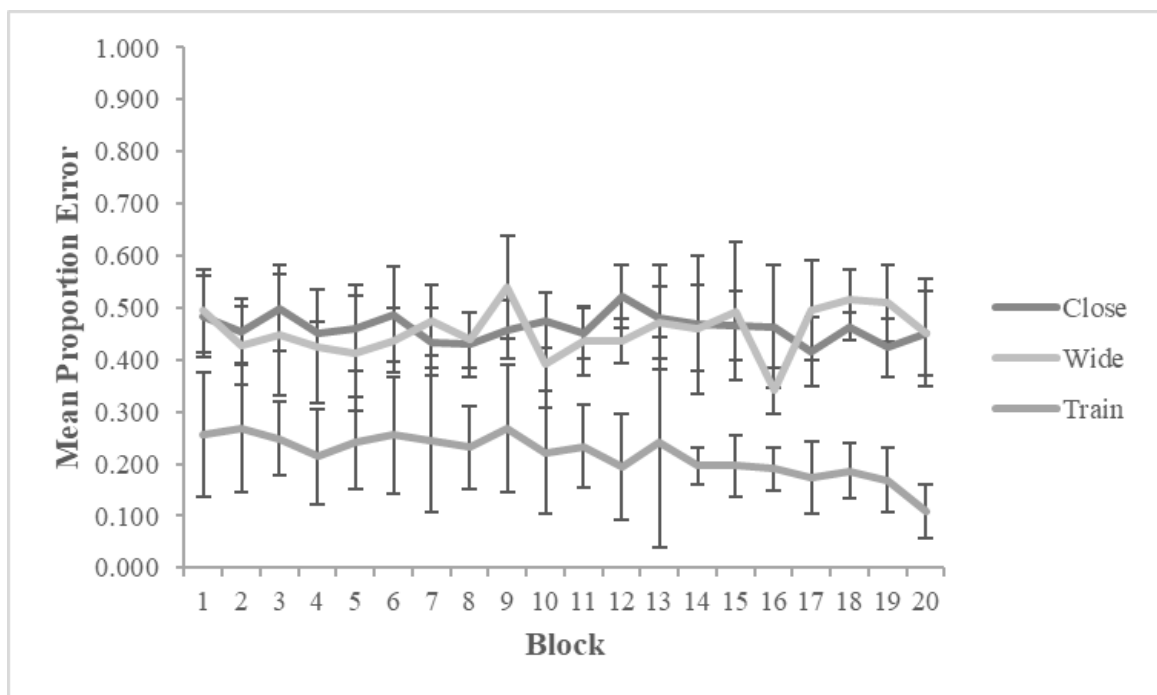


Figure 7.1 Mean proportion of errors, as a function of trial type and block, for rhesus macaques in Experiment 2B.

Error bars show the 95% confidence intervals.

7.5 Discussion

As in Experiment 2A, rhesus macaques did not demonstrate boundary extension or an effect of experience. Increasing the frequency of test trials to motivate the monkeys to perform

meaningfully on the critical *close* and *wide* trials did not elicit boundary extension. Rhesus monkeys' performance on the test trials did not differ, nor did their performance change across blocks. Monkeys performance on all trial types only differed slightly from previous experiments, suggesting that the monkeys were at their threshold of discriminative ability. Even when demonstrating their best performance, the monkeys were not affected by the scene's view relative to a foil image. Unlike humans, they did not misremember a sample image with a closer or wider view than was originally seen. Instead, rhesus monkeys and capuchin monkeys seemed to be "invulnerable" to boundary extension.

8 GENERAL DISCUSSION

Boundary extension, a memory error in which participants remember seeing details of a pictured scene that were not shown (e.g., Intraub & Richardson, 1989), has been observed in a variety of testing conditions in humans. To determine the underlying mechanisms of this phenomenon and whether it is better explained by the traditional visual-cognitive (Baddeley & Hitch, 1974; Irwin, 1991, 1993; Phillips, 1974; Potter, 1976; Sperling, 1960) or the multisource model (Intraub, 2010; Intraub & Dickinson, 2008), a series of experiments were conducted with humans and nonhuman primates (rhesus monkeys and capuchin monkeys) assessing boundary extension across species.

Consistent with previous research, human participants demonstrated boundary extension across three blocks of trials in a DMTS task with pictures of common scenes encountered by humans (e.g., beach, playground, backyard; Replication Study). These results provided a conceptual replication of boundary extension in human adults with a comparative method that could be given to nonhuman primates. When the same human-unique scenes and DMTS task were presented to the monkeys neither species demonstrated boundary extension in the absence

of conceptual knowledge and contextual associations (Experiment 1). Performance was above chance level in all conditions (baseline, close, and wide trials), indicating that the animals were able to remember and successfully discriminate between the sample image and a foil image. However, the error asymmetry between *close* and *wide* trials indicative of boundary extension was not observed. Images of monkey-relevant scenes (e.g., play yards, inside housing enclosures) also did not lead to boundary extension in rhesus monkeys and capuchin monkeys (Experiment 2A), even when the occurrence of test trials was increased to motivate the monkeys to perform well (Experiment 2B). Again, performance was above chance levels in all conditions for both experiments.

The magnitude of boundary extension can differ depending on the conditions under which it is studied (e.g., Beighley & Intraub, 2016; Hale et al., 2016; Intraub et al., 1996, 2008). Interestingly, the monkeys' performance was not impacted by the type of stimuli (relevant and non-relevant scenes) they were exposed to. There were no noticeable differences in the magnitude of the monkeys' error rates across Experiments 1, 2A, and 2B for either species. At their threshold of discrimination (error proportions ranged between 0.45 and 0.47 across experiments and species), monkeys were equally as good at discriminating the sample from closer and wider views of the same image. These results were seen even though the test trials were difficult trials that might have lended themselves to a bias on the basis of the match option's view angle (i.e., being the closer or wider view). No separation in performance (e.g., above and below chance level) for the critical test trials reflects no presence of boundary extension in a test in which humans did show a difference.

Unlike most studies of boundary extension, the present study also explored the effects of experience. Overall, monkeys did not show any differences in performance across blocks, except

capuchin monkeys who showed a significant difference in performance on close and wide trials during the first block of Experiment 1. However, this difference was in the opposite direction of the boundary extension effect, with the monkeys performing better on *close* trials (when the sample image was the closer view compared to the foil image) compared to *wide* trials (when the sample image was the wider view compared to the foil image), and the effect did not replicate in Experiment 2A with new stimuli. For humans, experience reduced the effect of boundary extension, but did not eliminate it. This again provides a strong contrast in performance among species, with humans showing a clear replication of the effect and monkeys instead showing limited or no evidence.

The present study demonstrated a thorough investigation of boundary extension in nonhuman primates. Monkeys' high performance on baseline training trials (which ranged from 76% to 89% correct, across species and experiments) clearly indicates that the monkeys were engaged and making meaningful responses throughout the DMTS task. Presenting the same stimuli to human adults, rhesus monkeys, and capuchin monkeys allowed for a direct comparison of recognition memory and possible boundary extension effects. The present study also included a species-fair investigation of boundary extension by exposing the monkeys to multiple pictures of scenes relevant to them. Seeing different pictures of outside play yards, for example, should have evoked the schema for "play yards" in the monkeys, just as seeing pictures of restaurants evokes schematic information (i.e., conceptual knowledge and contextual object associations) in human adults. Despite these manipulations, monkeys do not seem biased to interpret a wider-angle view as being more similar to the sample image, while humans are biased in this way.

While these null results do not provide evidence for the traditional visual-cognitive model or the multisource model of scene perception, they do suggest a possible species difference in

perception. Both models predict that amodal perception and conceptual knowledge of a scene would lead to boundary extension. The traditional model suggests that boundary extension would not occur in the absence of conceptual knowledge, while the multisource model predicts that boundary extension would occur both with and without conceptual knowledge due to amodal perception. Even though the mechanisms of boundary extension in human memory are still unclear, the present study suggests that capuchin monkeys and rhesus macaques are immune to this memory error, or at least that the present approach, which elicits boundary extension in humans, does not elicit this memory error in monkeys. The absence of boundary extension without conceptual knowledge (Experiment 1) and with conceptual knowledge (Experiment 2A and 2B) demonstrates that monkeys can rely on visual input alone to discriminate scenic stimuli, even in the presence of amodal perception, conceptual categorization, and contextual associations of the scene.

Rhesus monkeys and capuchin monkeys are primarily local processors (De Lillo, Spinozzi, Truppa, & Naylor, 2005; Hopkins & Washburn, 2002; Spinozzi, De Lillo, & Salvi, 2006; Spinozzi, De Lillo, & Truppa, 2003), unlike humans who show more frequent global-to-local precedence when assessing compound stimuli (e.g., Navon, 1977, 1981). This difference may have limited the monkeys' representation of the broader scene, making them unsusceptible to boundary extension effects. As local processors, the monkeys' ability to focus primarily on individual items of the scene through bottom-up processing (potentially resulting in a mental representation that was a collection of items, instead of a continuous scene) may have protected them from the interfering effects of conceptual knowledge and contextual associations from top-down processing. In contrast, due to the precedence for global processing, humans may not have been as easily able to overcome the interfering information from top-down processing during

scene perception, resulting in boundary extension in memory. This would be consistent with research demonstrating that boundary extension only occurs for views of scenes and does not occur for non-scenes (e.g., Gottesman & Intraub, 2002; Intraub et al., 1998; Legault & Standing, 1992; Park, Intraub, Yi, Widders, & Chun, 2007). Such a result demonstrates a sharp species discontinuity and may reflect a truly human-unique perceptual experience for boundary extension. However, future research with more species would be required to provide stronger support for such a contention.

8.1 Implications

The present study highlights the processes necessary for scene perception. For boundary extension to occur a scene must be processed in its entirety and as a continuous view. This memory error was not seen in the monkeys perhaps because of their precedence for local features when viewing complex stimuli, limiting their interpretation of the sample images as scenes. It is humans' global-to-local processing of visual stimuli that allows for boundary extension to occur. This sharp contrast between humans and two species of nonhuman primates highlights the uniqueness of boundary extension in the human experience and the necessary role global processing plays in scene perception.

While no strong conclusions can be made about which of the former models best explains boundary extension based on the present comparative data, monkeys' ability to rely on visual input alone demonstrates that local processing can be protective against this memory error. While boundary extension plays an important role in scene perception by priming the next fixation, at times this memory error could be maladaptive. When accurate memory of a scene is essential, the present study suggests that local processing of the scene's features would lead to more accurate recall and recognition of that scene. Therefore, the present study's results suggest

that intentional local processing of scenes can be used to circumvent boundary extension when necessary.

8.2 Limitations

An unavoidable limitation of the present study is the assumption that the nonhuman primates interpreted the sample images as referents to real-world scenes. Several species of great apes, as well as capuchin monkeys, have been shown to be capable of referential understanding that can guide behavior in the real-world (e.g., Gardner, Gardner, & Van Cantfort, 1989; Itakura, 1994; Kuhlmeier & Boysen, 2001, 2002; Kuhlmeier, Boysen, & Mukobi, 1999; Menzel, Premack, & Woodruff, 1978; Poss & Rochat, 2003; Potì & Saporiti, 2010; Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rupert, 1986; Truppa, Spinozzi, Stegagno, & Fagot, 2009). These studies are encouraging results that the rhesus monkeys and capuchin monkeys interpreted the human-unique and monkey-relevant stimuli as images of the real-world, invoking top-down processes (conceptual and contextual associations) during perception. However, in several of the previous studies training was involved to teach the animals to learn the referential associations, so this assumption remains a concern for the present study.

Additionally, many of the monkeys advanced through the present study's experiments with different levels of experience. That is, while all monkeys completed at least 2,400 trials in Experiments 1 and 2A and 1,200 trials in Experiment 2B, some monkeys completed many more trials than that before moving on to the next experiment, while others did not (see Table 8.1 for the total number of trials completed by each monkey for each experiment). These differing numbers of trials determined each monkeys' experience and familiarity with the task as they advanced through the present study. However, the lack of a main effect for block in Experiments 1, 2A, and 2B make it less likely that these differences in experience affected the results.

Table 8.1 Total Number of Trials Completed by Each Monkey

	Exp 1*	Exp 2A*	Exp 2B**
Capuchin Monkeys			
Benny	3,539	3,509	-
Gonzo	2,663	4,262	-
Gretel	4,401	6,561	-
Griffin	5,750	4,632	-
Ira	2,845	2,976	-
Ivory	6,040	3,348	-
Lexi	2,696	4,525	-
Lily	5,844	2,462	-
Logan	2,760	13,373	-
Nala	6,049	2,413	-
Nkima	4,067	4,085	-
Paddy	4,764	3,450	-
Widget	2,608	3,092	-
Wren	3,342	6,100	-
Rhesus Monkeys			
Chewie	3,845	6,044	2,923
Hank	3,341	2,639	1,733
Lou	3,007	4,246	3,302
Luke	3,916	6,152	1,417
Murphy	2,437	2,458	1,994
Obi	5,385	3,133	2,563

Note. *Only the first 2,400 trials were analyzed **Only the first 1,200 trials were analyzed

8.3 Future Directions

One species that would be of interest to test for the presence of boundary extension would be pigeons (*Columba livia*). Pigeons are known to have visual systems with functionally equivalent properties to humans (Levenson, Krupinski, Navarro, & Wasserman, 2015) and, like

monkeys, are also local visual processors (e.g., Cerella, 1980). Additionally, like human and nonhuman primates, pigeons can learn to recognize and categorize objects into common and abstract categories using similar mechanisms (e.g., Bhatt, Wasserman, Reynolds, & Knauss, 1988; see Soto & Wasserman, 2014, for a review). For example, Bhatt et al. (1988) trained pigeons to classify images into four categories (cats, flowers, cars, and chairs). The pigeons were able to then generalize from exemplar images for each category and accurately categorize novel stimuli. Other pigeons were able to correctly classify stimuli in the absence of any exemplars. Given pigeons' ability to discriminate complex visual stimuli (e.g., color paintings by Monet and Picasso, Watanabe, Sakamoto, & Wakita, 1995; benign and malignant human breast tissue and cancer microcalcifications, Levenson et al., 2015) and presumably form concepts in order to categorize novel stimuli, they may offer interesting results in a study of boundary extension.

While there are similarities in pigeons' ability to visually discriminate stimuli, there are also differences between primate and pigeon learning. In a study of rule-based (RB) and information-integration (II) categorization, Smith et al. (2012a) found that humans, rhesus macaques, and capuchin monkeys learn a RB task quicker and more accurately than an II task. Pigeons, on the other hand, learned RR and II tasks with equal speed and performance. Given the high perceptual acuity of pigeons and the differences in learning, I would predict that they would not demonstrate boundary extension in memory. Most likely, discrimination of the sample image from a foil image would be even better than that by the rhesus monkeys and capuchin monkeys, with no effect of trial type on proportions of errors. If so, further evidence would be provided that boundary extension may be a human-unique experience.

Another study of interest would be a local-global training study with nonhuman primates. If the reason rhesus monkeys and capuchin monkeys did not demonstrate boundary extension is

because they are local processors, it would be expected that training them to allocate their attention to global features of a visual stimulus would lead to boundary extension during a subsequent test of scene recognition. Monkeys would have to be trained to be global processors, as well as demonstrate transference of this skill to novel complex stimuli, including images of scenes. Once monkeys can process stimuli with a global precedence, a test of boundary extension with the same DMTS task used in the present study might demonstrate boundary extension in the monkeys' performance. This would further demonstrate that local processing by the monkeys was the reason for the present study's results.

Overall, rhesus monkeys and capuchin monkeys do not seem to demonstrate boundary extension on a test for which humans clearly did demonstrate this memory error. This species discontinuity may be due to the difference in visual attention allocation between humans and two species of nonhuman animals, elucidating an important mechanism of scene perception and a potential means to prevent boundary extension from occurring in memory. Future studies with other species of nonhuman animals would further explain the mechanisms involved in boundary extension and the cognitive model that best describes this memory error.

REFERENCES

- Allen, G. L. (Ed.). (2004). *Human spatial memory: Remembering where*. Mahwah, NJ: Lawrence Erlbaum Associates.
- Aust, U. (2017). Perceptual and functional categorization in animals. In J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowdon, & T. Zentall (Eds.), *APA handbook of comparative psychology: Perception, learning, and cognition* (Vol. 2, pp. 89–116). Washington, DC: American Psychological Association.
- Baddeley, A. D., & Hitch, G. (1974). Working memory. In G. H. Bower (Ed.), *The psychology of learning and motivation* (Vol. 8, pp. 47-89). New York, NY: Academic Press.
- Bar, M. (2004). Visual objects in context. *Nature Reviews Neuroscience*, *5*, 617-629.
- Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, *22*, 577-660.
- Barsalou, L. W. (2010). Grounded cognition: Past, present, and future. *Topics in Cognitive Science*, *2*, 716-724.
- Beighley, S., & Intraub, H. (2016). Does inversion affect boundary extension for briefly-presented views? *Visual Cognition*, *24*, 252-259.
- Bertamini, M., Jones, L. A., Spooner, A., & Hecht, H. (2005). Boundary extension: The role of magnification, object size, context, and binocular information. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 1288-1307.
- Bhatt, R. S., Wasserman, E. A., Reynolds, W. F., Jr., & Knauss, K. S. (1988). Conceptual behavior in pigeons: Categorization of both familiar and novel examples from four classes of natural and artificial stimuli. *Journal of Experimental Psychology: Animal Behavior Processes*, *14*, 219-234.

- Biederman, I. (1972). Perceiving real-world scenes. *Science*, *177*, 77-80.
- Biederman, I., Mezzanotte, R. J., & Rabinowitz, J. C. (1982). Scene perception: Detecting and judging objects undergoing relational violations. *Cognitive Psychology*, *14*, 143-177.
- Blazhenkova, O. (2017). Boundary extension in face processing. *i-Perception*, *8*, 1-36.
- Bransford, J. D., & Franks, J. J. (1971). The abstraction of linguistic ideas. *Cognitive Psychology*, *2*, 331-350.
- Bryant, D. J., Tversky, B., & Franklin, N. (1992). Internal and external spatial frameworks for representing described scenes. *Journal of Memory and Language*, *31*, 74-98.
- Call, J. (2017). Introduction. In J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowdon, & T. Zentall (Eds.), *APA handbook of comparative psychology: Basic concepts, methods, neural substrate, and behavior* (Vol. 1, pp. xix–xxiii). Washington, DC: American Psychological Association.
- Call, J., Burghardt, G. M., Pepperberg, I. M., Snowdon, C. T., & Zentall, T. (2017). What is comparative psychology? In J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowdon, & T. Zentall (Eds.), *APA handbook of comparative psychology: Basic concepts, methods, neural substrate, and behavior* (Vol. 1, pp. 3–15). Washington, DC: American Psychological Association.
- Candel, I., Merckelback, H., Houben, K., & Vandyck, I. (2004). How children remember neutral and emotional pictures: Boundary extension in children's scene memories. *The American Journal of Psychology*, *117*, 249-257.
- Cerella, J. (1980). The pigeon's analysis of pictures. *Pattern Recognition*, *12*, 1-6.
- Chapman, P., Ropar, D., Mitchell, P., & Ackroyd, K. (2005). Understanding boundary extension:

- Normalization and extension errors in picture memory among adults and boys with and without Asperger's syndrome. *Visual Cognition*, *12*, 1265-1290.
- D'Amato, M. R., & Van Sant, P. (1988). The person concept in monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes*, *14*, 43-55.
- Davenport, J. L., & Potter, M. C. (2004). Scene consistency in object and background perception. *Psychological Science*, *15*, 559-564.
- Davidoff, J. B. (1975). *Differences in visual perception: The individual eye*. New York, NY: Academic Press, Inc.
- De Lillo, C., Spinozzi, G., Truppa, V., & Naylor, D. M. (2005). A comparative analysis of global and local processing of hierarchical visual stimuli in young children (*Homo sapiens*) and monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *119*, 155-165.
- DeLucia, P. R., & Maldia, M. M. (2006). Visual memory for moving scenes. *The Quarterly Journal of Experimental Psychology*, *59*, 340-360.
- Deruelle, C., Barbet, I., Dépy, D., & Fagot, J. (2000). Perception of partly occluded figures by baboons (*Papio papio*). *Perception*, *29*, 1483-1497.
- Dickinson, C. A., & Intraub, H. (2008). Transsaccadic representation of layout: What is the time course of boundary extension? *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 543-555.
- Dickinson, C. A., & Intraub, H. (2009). Spatial asymmetries in viewing and remembering scenes: Consequences of an attentional bias? *Attention, Perception, & Psychophysics*, *71*, 1251-1262.
- Dumay, N., & Gaskell, M., G. (2007). Sleep-associated changes in the mental representation of spoken words. *Psychological Science*, *18*, 35-39.

- Evans, T. A., Beran, M. J., Chan, B., Klein, E. D., & Menzel, C. R. (2008). An efficient computerized testing method for the capuchin monkey (*Cebus apella*): Adaption of the LRC-CTS to a socially housed nonhuman primate species. *Behavior Research Methods*, *40*, 590-596.
- Fabre-Thorpe, M., Richard, G., & Thorpe, S. J. (1998). Rapid categorization of natural images by rhesus monkeys. *NeuroReport*, *9*, 303-308.
- Fagot, J., Barbet, I., Parron, C., & Deruelle, C. (2006). Amodal completion by baboons (*Papio papio*): Contribution of background depth cues. *Primates*, *47*, 145-150.
- Fei-Fei, L., Iyer, A., Koch, C., & Perona, P. (2007). What do we perceive in a glance of a real-world scene? *Journal of Vision*, *7*:10, 1-29.
- Franklin, N., & Tversky, B. (1990). Searching imagined environments. *Journal of Experimental Psychology: General*, *119*, 63-76.
- Fujita, K. (2001). Perceptual completion in rhesus monkeys (*Macaca mulatta*) and pigeons (*Columbia livia*). *Perception & Psychophysics*, *63*, 115-125.
- Gagnier, K. M., Dickinson, C. A., & Intraub, H. (2013). Fixating picture boundaries does not eliminate boundary extension: Implications for scene representation. *The Quarterly Journal of Experimental Psychology*, *66*, 2161-2186.
- Gardner, R. A., Gardner, B. T., & Van Cantfort, T. E. (Eds.). (1989). *Teaching sign language to chimpanzees*. Albany, NY: State University of New York Press.
- Gibson, J. J. (1950). *The perception of the visual world*. Boston, MA: Houghton Mifflin Company.
- Gordon, I. E. (2004). *Theories of visual perception* (3rd ed.). New York, NY: Psychology Press.
- Gottesman, C. V., & Intraub, H. (2002). Surface construal and the mental representation of

- scenes. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 589-599.
- Gottesman, C. V., & Intraub, H. (2003). Constraints on spatial extrapolation in the mental representation of scenes: View-boundaries vs. object-boundaries. *Visual Cognition*, 10, 875-893.
- Greenberg, M. S., Westcott, D. R., & Bailey, S. E. (1998). When believing is seeing: The effect of scripts on eyewitness memory. *Law and Human Behavior*, 22, 685-694.
- Greene, M. R., & Oliva, A. (2009). Recognition of natural scenes from global properties: Seeing the forest without representing the trees. *Cognitive Psychology*, 58, 137-176.
- Hale, R. G., Brown, J. M., & McDunn, B. A. (2016). Increasing task demand by obstructing object recognition increases boundary extension. *Psychonomic Bulletin & Review*, 23, 1497-1503.
- Hale, R. G., Brown, J. M., McDunn, B. A., & Siddiqui, A. P. (2015). An influence of extremal edges on boundary extension. *Psychonomic Bulletin & Review*, 22, 961-966.
- Hering, E. (1977). *The theory of binocular vision*. (B. Bridgeman, Trans.). New York, NY: Plenum Press. (Original work published 1868)
- Hochberg, J. (1986). Representation of motion and space in video and cinematic displays. In K. R. Boff, L. Kaufman, & J. P. Thomas (Eds.), *Handbook of perception and human performance: Sensory processes and perception* (Vol 1., pp. 22-1–22-64). New York, NY: John Wiley.
- Hollingworth, A. (2006). Visual memory for natural scenes: Evidence from change detection and visual search. *Visual Cognition*, 14, 781-807.
- Hollingworth, A., & Henderson, J. M. (2002). Accurate visual memory for previously attended

- objects in natural scenes. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 113-136.
- Hopkins, W. D., & Washburn, D. A. (2002). Matching visual stimuli on the basis of global and local features by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). *Animal Cognition*, 5, 27-31.
- Hubbard, T. L., Hutchison, J. L., & Courtney, J. R. (2010). Boundary extension: Findings and theories. *The Quarterly Journal of Experimental Psychology*, 63, 1467-1494.
- Intraub, H. (1980). Presentation rate and the representation of briefly glimpsed pictures in memory. *Journal of Experimental Psychology: Human Learning and Memory*, 6, 1-12.
- Intraub, H. (1981). Rapid conceptual identification of sequentially presented pictures. *Journal of Experimental Psychology: Human Perception and Performance*, 7, 604-610.
- Intraub, H. (1984). Conceptual masking: The effects of subsequent visual events on memory for pictures. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 10, 115-125.
- Intraub, H. (1997). The representation of visual scenes. *Trends in Cognitive Sciences*, 1, 217-222.
- Intraub, H. (2002). Anticipatory spatial representation of natural scenes: Momentum without movement? *Visual Cognition*, 9, 93-119.
- Intraub, H. (2004). Anticipatory spatial representation of 3D regions explored by sighted observers and a deaf-and-blind-observer. *Cognition*, 94, 19-37.
- Intraub, H. (2010). Rethinking scene perception: A multisource model. *Psychology of Learning and Motivation*, 52, 231-264.
- Intraub, H. (2012). Rethinking visual scene perception. *WIREs Cognitive Science*, 3, 117-127.

- Intraub, H., Bender, R. S., & Mangels, J. A. (1992). Looking at pictures but remembering scenes. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *18*, 180-191.
- Intraub, H., & Berkowits, D. (1996). Beyond the edges of a picture. *The American Journal of Psychology*, *109*, 581-598.
- Intraub, H., & Bodamer, J. L. (1993). Boundary extension: Fundamental aspect of pictorial representation or encoding artifact? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *19*, 1387-1397.
- Intraub, H., Daniels, K. K., Horowitz, T. S., & Wolfe, J. M. (2008). Looking at scenes while searching for numbers: Dividing attention multiples space. *Perception & Psychophysics*, *70*, 1337-1349.
- Intraub, H., & Dickinson, C. A. (2008). False memory 1/20th of a second later: What the early onset of boundary extension reveals about perception. *Psychological Science*, *19*, 1007-1014.
- Intraub, H., Gottesman, C. V., & Bills, A. J. (1998) Effects of perceiving and imagining scenes on memory for pictures. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *24*, 186-201.
- Intraub, H., Gottesman, C. V., Willey, E. V., & Zuk, I. J. (1996). Boundary extension for briefly glimpsed photographs: Do common perceptual processes result in unexpected memory distortions? *Journal of Memory and Language*, *35*, 118-134.
- Intraub, H., Hoffman, J. E., Wetherhold, C. J., & Stoehs, S.A. (2006). More than meets the eye: The effect of planned fixations on scene representation. *Perception & Psychophysics*, *68*, 759-769.
- Intraub, H., & Richardson, M. (1989). Wide-angle memories of close-up scenes. *Journal of*

- Experimental Psychology: Learning, Memory, and Cognition*, 15, 179-187.
- Irwin, D. E. (1991). Information integration across saccadic eye movements. *Cognitive Psychology*, 23, 420-456.
- Irwin, D. E. (1993). Perceiving an integrated visual world. In D. E. Meyer & S. Kornblum (Eds.), *Attention and performance XIV: Synergies in experimental psychology, artificial intelligence, and cognitive neuroscience* (pp. 121-142). Cambridge, MA: MIT Press.
- Itakura, S. (1994). Recognition of line-drawing representations by a chimpanzee (*Pan troglodytes*). *The Journal of General Psychology*, 121, 189-197.
- Johnson, M. K., Hashtroudi, S., & Lindsay, D. S. (1993). Source monitoring. *Psychological Bulletin*, 114, 3-28.
- Johnson, M. K., & Raye, C. L. (1981). Reality monitoring. *Psychological Review*, 88, 67-85.
- Kanizsa, G. (1979). *Organization in vision*. New York: Praeger.
- Kanizsa, G., Renzi, P., Conte, S., Compostela, C., & Guerani, L. (1993). Amodal completion in mouse vision. *Perception*, 22, 713-721.
- Kellman, P. J., Yin, C., & Shipley, T. F. (1998). A common mechanism for illusory and occluded object completion. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 859-869.
- Konkle, T., Brady, T. F., Alvarez, G. A., & Oliva, A. (2010). Scene memory is more detailed than you think: The role of categories in visual long-term memory. *Psychological Science*, 21, 1551-1556.
- Koutstaal, W., Reddy, C., Jackson, E. M., Prince, S., Cendan, D. L., & Schacter, D. L. (2003).

- False recognition of abstract versus common objects in older and younger adults: Testing the semantic categorization account. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 29, 499-510.
- Koutstaal, W., & Schacter, D. L. (1997). Gist-based false recognition of pictures in older and younger adults. *Journal of Memory and Language*, 37, 555-583.
- Kreindel, E., & Intraub, H. (2017). Anticipatory scene representation in preschool children's recall and recognition memory. *Developmental Science*, 20, e12444.
- Kuhlmeier, V. A., & Boysen, S. T. (2001). The effect of response contingencies on scale model task performance by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 115, 300-306.
- Kuhlmeier, V. A., & Boysen, S. T. (2002). Chimpanzees (*Pan troglodytes*) recognize spatial and object correspondences between a scale model and its referent. *Psychological Science*, 13, 60-63.
- Kuhlmeier, V. A., Boysen, S. T., & Mukobi, K. L. (1999). Scale-model comprehension by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 113, 396-402.
- Kumaran, D., Summerfield, J. J., Hassabis, D., & Maguire, E. A. (2009). Tracking the emergence of conceptual knowledge during human decision making. *Neuron*, 63, 889-901.
- Lazareva, O. F. (2017). Comparative visual perception: An overview. In J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowdon, & T. Zentall (Eds.), *APA handbook of comparative psychology: Perception, learning, and cognition* (Vol. 2, pp. 49-68). Washington, DC: American Psychological Association.
- Lazareva, O. F., Shimizu, T., & Wasserman, E. A. (Eds.). (2012). *How animals see the world:*

Comparative behavior, biology, and evolution of vision. New York, NY: Oxford University Press.

Legault, E., & Standing, L. (1992). Memory for size of drawings and of photographs. *Perceptual and Motor Skills*, 75, 121.

Levenson, R. M., Krupinski, E. A., Navarro, V. M., & Wasserman, E. A. (2015). Pigeons (*Columba livia*) as trainable observers of pathology and radiology breast cancer images. *PLoS ONE*, 10, e0141357.

Lewis, P. A., & Durrant, S. J. (2011). Overlapping memory replay during sleep builds cognitive schemata. *Trends in Cognitive Sciences*, 15, 343-351.

Lin, J. Y., Pype, A. D., Murray, S. O., & Boynton, G. M. (2010). Enhanced memory for scenes presented at behaviorally relevant points in time. *PLoS Biology*, 8, e1000337.

Loftus, E. (1996). Memory distortion and false memory creation. *Bulletin of the American Academy of Psychiatry and the Law*, 24, 281-295.

Loftus, G. R., & Ginn, M. (1984). Perceptual and conceptual masking of pictures. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 10, 435-441.

Loftus, G. R., Johnson, C. A., & Shimamura, A. P. (1985). How much is an icon worth? *Journal of Experimental Psychology: Human Perception and Performance*, 11, 1-13.

Matin, E. (1974). Saccadic suppression: A review and an analysis. *Psychological Bulletin*, 81, 899-917.

McDunn, B. A., Siddiqui, A. P., & Brown, J. M. (2014). Seeking the boundary of boundary extension. *Psychonomic Bulletin & Review*, 21, 370-375.

Mamus, E., & Boduroglu, A. (2018). The role of context on boundary extension. *Visual Cognition*, 26, 115-130.

- Mathews, A., & Mackintosh, B. (2004). Take a closer look: Emotion modifies the boundary extension effect. *Emotion, 4*, 36-45.
- Ménétrier, E., Didierjean, A., & Barbe, V. (2018). Effect of contextual knowledge on spatial layout extrapolation. *Attention, Perception, & Psychophysics*. doi:10.3758/s13414-018-1569-9
- Menzel, E. W., Jr., Premack, D., & Woodruff, G. (1978). Map reading by chimpanzees. *Folia Primatologica, 29*, 241-249.
- Miller, M. B., & Gazzaniga, M. S. (1998). Creating false memories for visual scenes. *Neuropsychologia, 36*, 513-520.
- Munger, M. P., & Multhaup, K. S. (2016). No imagination effect on boundary extension. *Memory & Cognition, 44*, 73–88.
- Munger, M. P., Owens, T. R., & Conway, J. E. (2005). Are boundary extension and representational momentum related? *Visual Cognition, 12*, 1041-1056
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology, 9*, 353-383.
- Navon, D. (1981). The forest revisited: More on global precedence. *Psychological Research, 43*, 1-32.
- O'Regan, J. K. (1992). Solving the “real” mysteries of visual perception: The world as an outside memory. *Canadian Journal of Psychology, 46*, 461-488.
- Park, S., Intraub, H., Yi, D.-J., Widders, D., & Chun, M. M. (2007). Beyond the edges of a view: Boundary extension in human scene-selective visual cortex. *Neuron, 54*, 335-342.
- Phillips, W. A. (1974). On the distinction between sensory storage and short-term visual memory. *Perception & Psychophysics, 16*, 283-290.

- Posner, M. I., & Keele, S. W. (1970). Retention of abstract ideas. *Journal of Experimental Psychology*, 83, 304-308.
- Poss, S. R., & Rochat, P. (2003). Referential understanding of videos in chimpanzees (*Pan troglodytes*), orangutans (*Pongo pygmaeus*), and children (*Homo sapiens*). *Journal of Comparative Psychology*, 117, 420-428.
- Potì, P., & Saporiti, M. (2010). A capuchin monkey (*Cebus apella*) uses video to find food. *Folia Primatologica*, 81, 16-30.
- Potter, M. C. (1976). Short-term conceptual memory for pictures. *Journal of Experimental Psychology: Human Learning and Memory*, 2, 509-522.
- Potter, M. C., Staub, A., Rado, J., & O'Conner, D. H. (2002). Recognition memory for briefly presented pictures: The time course of rapid forgetting. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 1163-1175.
- Quinn, P. C., & Intraub, H. (2007). Perceiving "outside the box" occurs early in development: Evidence for boundary extension in three- to seven-month-old infants. *Child Development*, 78, 324-334.
- Rayner, K. (2009). Eye movements and attention in reading, scene perception, and visual search. *The Quarterly Journal of Experimental Psychology*, 62, 1457-1506.
- Regolin, L., & Vallortigara, G. (1995). Perception of partly occluded objects by young chicks. *Perception & Psychophysics*, 57, 971-976.
- Rensink, R. A. (2000). The dynamic representation of scenes. *Visual Cognition*, 7, 17-42.
- Rensink, R. A., O'Regan, J. K., & Clark, J. J. (1997). To see or not to see: The need for attention to perceive changes in scenes. *Psychological Science*, 8, 368-373.
- Richardson, W. K., Washburn, D. A., Hopkins, W. D., Savage-Rumbaugh, E. S., & Rumbaugh,

- D. M. (1990). The NASA/LRC computerized test system. *Behavior Research Methods, Instruments, & Computers*, *22*, 127-131.
- Roberts, W. A., & Mazmanian, D. S. (1988). Concept learning at different levels of abstraction by pigeons, monkeys, and people. *Journal of Experimental Psychology: Animal Behavior Processes*, *14*, 247-260.
- Roediger, H. L., III, & McDermott, K. B. (1995). Creating false memories: Remembering words not presented in lists. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*, 803-814.
- Safer, M. A., Christianson, S.-A., Austry, M. W., & Österlund, K. (1998). Tunnel memory for traumatic events. *Applied Cognitive Psychology*, *12*, 99-117.
- Sanocki, T. (2003). Representation and perception of scenic layout. *Cognitive Psychology*, *47*, 43-86.
- Sato, A., & Kanazawa, S., & Fujita, K. (1997). Perception of object unity in a chimpanzee (*Pan troglodytes*). *Japanese Psychological Research*, *39*, 191-199.
- Savage-Rumbaugh, S., McDonald, K., Sevcik, R. A., Hopkins, W. D., & Rubert, E. (1986). Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *Journal of Experimental Psychology: General*, *115*, 211-235.
- Schacter, D. L., Verfaellie, M., & Anes, M. D. (1997). Illusory memories in amnesic patients: Conceptual and perceptual false recognition. *Neuropsychology*, *11*, 331-342.
- Schrier, A. M., Angarella, R., & Povar, M. L. (1984). Studies of concept formation by stumptailed monkeys: Concepts humans, monkeys, and letter A. *Journal of Experimental Psychology: Animal Behavior Processes*, *10*, 564-584.
- Seamon, J. G., Schlegel, S. E., Hiester, P. M., Landau, S. M., & Blumenthal, B. F. (2002).

- Misremembering pictured objects: People of all ages demonstrate the boundary extension illusion. *The American Journal of Psychology*, *115*, 151-167.
- Simons, D. J., & Levin, D. T. (1997). Change blindness. *Trends in Cognitive Sciences*, *1*, 261-267.
- Simons, D. J., & Rensink, R. A. (2005). Change blindness: Past, present, and future. *Trends in Cognitive Sciences*, *9*, 16-20.
- Smith, J. D., Beran, M. J., Crossley, M. J., Boomer, J., & Ashby, F. G. (2010). Implicit and explicit category learning by macaques (*Macaca mulatta*) and humans (*Homo sapiens*). *Journal of Experimental Psychology: Animal Behavior Processes*, *36*, 54-65.
- Smith, J. D., Berg, M. E., Cook, R. G., Murphy, M. S., Crossley, M. J., Boomer, J., Spiering, B., Beran, M. J., Church, B. A., Ashby, F. G., & Grace, R. C. (2012a). Implicit and explicit categorization: A tale of four species. *Neuroscience & Biobehavioral Reviews*, *36*, 2355-2369.
- Smith, J. D., Crossley, M. J., Boomer, J., Church, B. A., Beran, M. J., & Ashby, F. G. (2012b). Implicit and explicit category learning by capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *126*, 294-304.
- Smith, J. D., Zakrzewski, A. C., Johnston, J. J., Roeder, J. L., Boomer, J., Ashby, F. G., & Church, B. A. (2015). Generalization of category knowledge and dimensional categorization in humans (*Homo sapiens*) and nonhuman primates (*Macaca mulatta*). *Journal of Experimental Psychology: Animal Learning and Cognition*, *41*, 322-335.
- Soto, F. A., & Wasserman, E. A. (2014). Mechanisms of object recognition: What we have learned from pigeons. *Frontiers in Neural Circuits*, *8*, 122.
- Sovrano, V. A., & Bisazza, A. (2008). Recognition of partly occluded objects by fish. *Animal*

Cognition, 11, 161-166.

- Spanò, G., Intraub, H., & Edgin, J. O. (2017). Testing the “boundaries” of boundary extension: Anticipatory scene representation across development and disorder. *Hippocampus*, 27, 726-739.
- Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied*, 74, 1-29.
- Spinozzi, G., De Lillo, C., & Salvi, V. (2006). Local advantage in the visual processing of hierarchical stimuli following manipulations of stimulus size and element numerosity in monkeys (*Cebus apella*). *Behavioural Brain Research*, 166, 45-54.
- Spinozzi, G., De Lillo, C., & Truppa, V. (2003). Global and local processing of hierarchical visual stimuli in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 117, 15-23.
- Standing, L., Conezio, J., & Haber, R. N. (1970). Perception and memory for pictures: Single-trial learning of 2500 visual stimuli. *Psychonomic Science*, 19, 73-74.
- Tamminen, J., Payne, J. D., Stickgold, R., Wamsley, E. J., & Gaskell, M. G. (2010). Sleep spindle activity is associated with the integration of new memories and existing knowledge. *The Journal of Neuroscience*, 30, 14356-14360.
- Taylor, S. E., & Crocker, J. (1981). Schematic bases of social information processing. In T. E. Higgins, C. P. Herman, & M. P. Zanna (Eds.), *Social cognition: The Ontario symposium* (Vol. 1, pp. 84–134). Hillsdale, NJ: Erlbaum.
- Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature*, 381, 520-522.
- Truppa, V., Spinozzi, G., Stegagno, T., & Fagot, J. (2009). Picture processing in tufted capuchin

- monkeys (*Cebus apella*). *Behavioural Processes*, 82, 140-152.
- Tse, D., Langston, R. F., Kakeyama, M., Bethus, I., Spooner, P. A., Wood, E. R., Witter, M. P., & Morris, R. G. M. (2007). Schemas and memory consolidation. *Science*, 316, 76-82.
- Tuckey, M. R., & Brewer, N. (2003). The influence of schemas, stimulus ambiguity, and interview schedule on eyewitness memory over time. *Journal of Experimental Psychology: Applied*, 9, 101-118.
- Tversky, B., & Hemenway, K. (1983). Categories of environmental scenes. *Cognitive Psychology*, 15, 121-149.
- Võ, M. L.-H., & Henderson, J. M. (2010). The time course of initial scene processing for eye movement guidance in natural scene search. *Journal of Vision*, 10, 14, 1-14:13.
- Vogels, R. (1999). Categorization of complex visual images by rhesus monkeys. Part 1: Behavioral study. *European Journal of Neuroscience*, 11, 1223-1238.
- Vogels, R. (2012). Neural mechanisms of object recognition in nonhuman primates. In O. F. Lazareva, T. Shimizu, & E. A. Wasserman (Eds.), *How animals see the world: Comparative behavior, biology, and evolution of vision* (pp. 247-268). New York, NY: Oxford University Press.
- Watanabe, S., Sakamoto, J., & Wakita, M. (1995). Pigeons' discrimination of paintings by Monet and Picasso. *Journal of the Experimental Analysis of Behavior*, 63, 165-174.
- Yin, C., Kellman, P. J., & Shipley, T. F. (1997). Surface completion complements boundary interpolation in the visual integration of partly occluded objects. *Perception*, 26, 1459-1479.
- Yoshikubo, S. (1985). Species discrimination and concept formation by rhesus monkeys (*Macaca mulatta*). *Primates*, 26, 285-299.

Zakrzewski, A. C., Church, B. A., & Smith, J. D. (2018). The transfer of category knowledge by macaques (*Macaca mulatta*) and humans (*Homo sapiens*). *Journal of Comparative Psychology*, *132*, 58-74.

Zentall, T. R., Wasserman, E. A., Lazareva, O. F., Thompson, R. K. R., & Rattermann, M. J. (2008). Concept learning in animals. *Comparative Cognition & Behavior Reviews*, *3*, 13-45.