The Perception of Illusory Contours By Rhesus Macaques (*Macaca mulatta*)

by

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Abstract

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A zero-delay matching-to-sample procedure (MTS) was used to determine whether rhesus macaque monkeys experience the illusory contours evident in human perception of the Kanizsa patterns. Prior to tests with an illusory square, parallelogram, and trapezoid, MTS training was given with patterns made of composites of grayscale squares or parallelograms. On some trials, a single square or parallelogram was used. Although prior to training with the composites, the monkeys readily learned to choose the matching one of two pictures only one of three monkeys met criterion, 80% correct, on the composite figures. Performance was particularly poor when the choice was between a single square and parallelogram where 7,500 trials were required to reach a criterion of 70% correct. When the square or parallelogram forms were presented as matches to their illusory forms on test trials selection of the match was at chance. However, the matching illusory trapezoid was chosen over one in another orientation on 69% of the trials, a percentage significantly above chance, $p < .05$. A test with three new illusory forms was done to determine whether failure to match the Kanizsa square and parallelogram was due to inattention resulting from exposure to these stimuli during training failed to provide clear evidence of the illusion. Weak evidence for the illusion was found when the spacing between the inducing contours was reduced to make the illusion more distinct. Further tests including training that was more similar to the test conditions (simpler stimuli, similarity matching) failed to yield evidence that the monkeys experienced the illusion.

It is possible that rhesus monkeys do see the illusory contours experienced by humans, however there is some evidence of anatomical differences from humans in layer 4A of primary visual cortex. Failure to obtain evidence for the illusion is more likely due to procedural variables used in these experiments such as failure to give sufficient training in similarity matching or requiring the monkeys to make fine discriminations between the choice stimuli.

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Chapter I: General Introduction

Perception of Illusory Contours by Rhesus Macaques (*Macaca mulatta*)

"When viewing a dangerous predator that is partly occluded by heavy foliage and shadow, a visually guided organism would do well to attend to the entire animal rather than mistake its parts for distinct perceptual objects"- (Moore, Yantis, & Vaughan, 1998 p. 109)

There are a number of visual phenomena that occur in normal adult human vision that do not necessarily occur in pre-linguistic children as well as non-human primates. Specifically, the development of contour integration is slow in childhood and the mechanisms involved in identifying object shape from discrete elements is unknown (Kaldy & Kovacs, 1999). It remains controversial whether the ability to resolve subjective (illusory) contours results from lower level processes of early vision or from higher processes involving feedback from other areas.

Although there is a host of physiological evidence in non-human primates to suggest they perceive illusory contours, to my knowledge there has been no clear behavioral evidence that non-verbal primates actually perceive such contours. Therefore the primary objective of this study was to behaviorally determine whether a rhesus macaque monkey (*Macaca mulatta*) perceives the illusory contours humans report when presented with illusions of the Kanizsa type.

Object Representations and Object Based Attention. In a typical visual scene multiple objects partially occlude one another, making object recognition a computationally complex task. Traditional information-processing theories of visual perception have suggested that prior to object representation and recognition, an earlier stage of perceptual organization occurs to determine which features, locations, or surfaces most likely belong together (Vecera & O'Reilly, 2000). Object representation, for the purpose of this discussion, is treated as a reflection of previous experience which affects later behavior in a fashion that allows for more efficient processing. In order to visually identify and recognize objects in our environment it is necessary, not only to pay attention to certain objects or features, but also to make the connection between a set of features and what has already been experienced and stored in memory (see Behrman, Mozer, & Zemel, 1998; Shipley & Kellman, 1992; Wallach & Slaughter, 1988).

Because our visual world is cluttered with arrays of objects occluding one another, it is possible that several visual mechanisms evolved to work synergistically or as back up mechanisms to one another, as a way to efficiently identify objects. It has been suggested that one way in which an organism can perceptually organize information is to selectively attend to specific locations (Akutsu & Levi, 1998; Wolfe, Butcher, Lee, & Hyle, 2003). Another source of attention to specific information is to selectively attend to individual objects and analyze them utilizing a top-down or bottom-up mechanism (e.g. Cavanagh, 1991; Chen, 1998; Deco & Lee, 2004; Vecera & O'Reilly, 1998). Top-down processing is based on the observer's explicit knowledge or expectations of a given stimulus, recognizing the whole image first and then "breaking down" that image into individual segments, whereas bottom-up processing is stimulus based requiring the observer to first delineate specific features within an image and "build-up" each segment until the final image is recognized (Wolfe et al., 2003). Finally, objects can also be identified utilizing global, attending to the entire visual array, or local based strategies, attending to individual components of the entire visual array (e.g. Navon, 1977).

Three-Dimensional Patterns and Depth Perception. The world in which we live is three-dimensional, however the way in which our environment is represented on our retina is two-dimensional. One of the most puzzling questions is how we convert a two-dimensional image on the retina into a three-dimensional percept. In order to recognize individual objects, we often rely on our ability to perceive variations in depth resulting from binocular integration between the visual fields of both eyes (De Valois & De Valois, 1988). In order to assign depth between two objects, one must first infer where one object boundary ends and the other begins. One could therefore theoretically solve the problem of occlusion by assigning boundaries to each object. Gibson (1966) postulated that the problem of visual perception is determining which aspects of the physical world are relevant features and which can be ignored. Gibson further speculated that the most important aspect necessary for object recognition is perception of object surfaces. By identifying which surfaces are salient (belonging to the same object) one could then extend the boundaries of that surface in order to classify that object. By systematically shifting one's attention to identify object surfaces or lines, we can establish relative depth based on the comparisons of orientation differences and binocular disparity (Gibson, 1966).

Language and Recognition. Does language provide an advantage on object recognition tasks? Is language required for an object to have meaning? Research has shown that pre-verbal infants use categories to discriminate what is familiar and what is novel (Meints, Plunkett, & Harris 1999). Deak, Ray, and Pick (2002) showed that 3 year old children typically classify objects by shape, whereas 4 year old children can recognize objects based on symbolic naming (object function) on object recognition tasks. In order to address the question of how objects are recognized (i.e. by object shape or by object function), 3 and 4 year old preschool children were instructed to sort objects either by shape or by function. A third group of 3 and 4 year olds were given no instruction on how to match the objects. The 3 year olds preferred matching by shape only. The 4 year olds could apply either rule when instructed to do so, however preferred to match objects based on shape when no instruction was given. These data provide evidence that explicit language cues are not necessary for object matching by form, however matching performance by function, improves with age as objects are named and given symbolic meaning.

Warrington and Taylor (1978) conducted a study using an object recognition task with human subjects who suffered lesions to the right or left side of their parietal lobes. The important finding was that patients that suffered lesions to the right side could identify the object presented before them, could name the object, and report details about its physical properties and function. On the other hand, subjects who sustained damage to the left hemisphere (the side associated with language comprehension and production) were not capable of naming or stating the purpose of the objects presented before them, although these subjects could perceive certain objects by recognizing basic geometric shapes. The results of this study imply that representations of geometric shapes may be stored in different locations than semantic information associated with a particular shape, and that human subjects who have suffered cortical damage to the left hemisphere can nonetheless recognize the overall geometric shape without naming it. Studies of patients who suffer from integrative visual agnosia (the inability to recognize the meaning of objects upon visual analysis) have provided evidence to suggest that persons afflicted with this condition fail to differentiate figure-ground displays as well as effectively perceive subjective contours (Behrmann & Kimchi, 2003).

Subjective Contour Perception. Humans are particularly good at extrapolating information about a continuous object from a set of visually distinct perceptual elements. In other words, we can fill in regions of our visual field when there is no physical stimulus available. The perception of an apparent edge in an area of the visual field where there is no physical variation in light intensity (i.e. subjective contour), was demonstrated by Kanizsa (1955). Theoretical accounts most frequently offered for subjective contour perception are the Gestalt principles of proximity, similarity, closure, symmetry, good continuation, and figure-ground separation. Many Gestalt theorists assert that there is an "optimal organization" strategy based on associative information held among individual parts. Coren (1972) suggested that subjective contours and perceived interposition emerge from depth cues allowing for a simplified organization of the visual field, e.g. the illusory figure may be seen as lying against a background. Gillam and Nakayama (2002) suggested that the depth relations between the pacmen elements observed in Kanizsa patterns will determine the extent of contour completion and the perceived shape of the illusory form.

Subjective Contour Perception in Human and Non-Human Infants. Several studies have investigated the development of subjective contour perception in human as well as non-human infants (see Condry, 2000; Curran, Braddick, Atkinson, Wattam-Bell, & Andrew, 1999; Kavsek, 2002; Zimmerman, 1962). Bertenthal, Campos, and Haith, (1980) provided evidence that 7-month old human infants could differentiate between illusory and non-illusory contours on an infant habituation procedure. To test this ability, 5 and 7-month old infants were shown a series of three patterns. One of the patterns did not form any contour, the second formed a partial contour, and the third pattern formed an illusory square of the Kanizsa type. The infants were repeatedly tested with each stimulus until looking time decreased. Following this habituation, a new stimulus was presented and the amount of time spent looking at the new stimulus (response recovery) was recorded to determine the degree to which the stimuli were discriminated. The results of this study indicate that the 7-month old but not the 5-month old infants exhibited consistent differential responding to the illusory vs. non-illusory conditions. Therefore, Bertenthal et. al, (1980) suggested that configural sensitivity to visual stimuli in human infants is refined with age. Csibra (2001) also showed evidence that 8-month old human infants perceived Kanizsa squares as evidenced by longer looking times on a familiarization task, whereas 5-month old infants could not. These data are consistent with previous work which suggest that the development of static depth perception emerges somewhere between 5 and 7 months of age, while the ability to complete illusory contours emerges after 7 months of age (Csibra, 2001). Otsuka, Kanazawa, and Yamaguchi (2004) investigated the effect of support ratio (the ratio of the specified contours to the total edge length) on the ability to perceive illusory contours in young human infants (3-8 months of age). To test this, infants were presented with illusions of the Kanizsa type with higher and lower support ratios. By recording preferential looking times it was determined that the 3-4 month old infants could perceive illusory contours but only when the support ratio was relatively high (66%), whereas the 7-8 month old infants showed evidenced of illusory contour perception when the ratio was decreased to 37%. Based on these results, Otsuka et al, (2004) suggested that the ability to perceive

illusory contours appears to emerge around 3 months of age. However this ability is extremely limited until the infant reaches approximately 7-months of age, which is consistent with previous research.

In addition, Kellman and Spelke (1983) showed that infants as young as 4-months old perceptually completed partially occluded rods when moving behind a horizontal rod. What is interesting is that adults and older infants can recognize a rod as being continuous (object unity) when partially occluded by another rod even in the absence of motion, but the ability to perceive static occluded objects as continuous does not seem to emerge until later in development.

In a similar study, Sato, Kanazawa, and Fujita (1997) reported evidence that an adult chimpanzee also perceived object unity of a rod that was partially occluded by a horizontal bar. That is, when the rods moved in unison they were perceived as a single rod occluded by a horizontal bar. When the rods moved out of synchrony with each other, they were perceived as two separate rods. Likewise, the chimpanzee also perceived a unitary rod when observing two static rods aligned properly. These data show that non-verbal primates are capable of the gestalt principle of good continuation when an object is partially occluded. Fujita (2001) showed evidence that rhesus monkeys appear to complete occluded images similar to humans (Kellman & Spelke, 1983) and chimpanzees (Sato et al., 1997) but pigeons fail to complete such images. During this study both monkeys and pigeons were trained to discriminate bars varying in length as short or long respectively. After this discrimination the subjects were tested with bars located alongside a gray box in different locations and distances from the box. Both the pigeons and monkeys could discriminate the bars as long or short when they were located some distance from the box with relative accuracy, however the pigeons tended to overestimate the length of the bar when it was located furthest from the gray box. On the other hand, when the bar touched the box the monkeys tended to overestimate the actual length of the bar providing evidence for perceptual completion extending behind an occluder similar to what has been demonstrated in human subjects (Kanizsa, 1979) as well as by capuchin monkeys (Fujita & Giersch, 2005). In a review article Nieder (2002) presented further evidence for illusory contour perception in monkeys (De Weerd, Desimone, & Ungerleider, 1996), in cats (Bravo, Blake, & Morrison, 1988; De Weerd, Vandenbussche, De Bruyn, & Orban 1990), in barn owls (Nieder & Wagner, 1999), and even honeybees (van Hateren, Srinivasan, & Wait, 1990). Further behavioral evidence supporting the susceptibility of a non-human primate to be "tricked" by visual illusions has been reported with the Ponzo illusion (Bayne & Davis, 1993; Fujita, 1997) and the corridor illusion (Barbet & Fagot, 2002; Barbet & Fagot, 2007). The ponzo and corridor illusion provide insight as to how a non-verbal primate might encode relative depth cues. Barbet and Fagot (2007) suggested that two of the reasons that contribute to these types of illusions in humans are gradient depth cues as well as perspective line cues (p.392). Based on the behavioral evidence obtained from monkeys that parallel what has been observed with humans when presented with the same types of illusions (i.e. ponzo and corridor illusion), it is therefore promising to consider that they would also behaviorally show evidence for the perception of Kanizsa illusory contours.

Modal vs. Amodal Completion. Two possible ways subjective contours are completed are modal completion and amodal completion. To say that an object is completed modally implies that subjects perceive areas of a visual stimulus that are physically present. Amodal completion on the other hand, occurs when an observer perceives parts of an object or display as being present, when in fact there is no physical stimulus present (as in illusory contour perception). In order for amodal completion to occur, a boundary of some kind must be completed (Kellman, Yin, & Shipley, 1998). Once amodal completion occurs, such as boundary extension, the subject's next task is to differentiate which of the objects is the figure and which is the ground (e.g. Peterson & Lampignano, 2003).

In figure-ground displays, there may exist more than one interpretation (bi-stability) as to which object is considered to be the figure, or foreground image. Stability of form perception requires detection of object borders. Identification of illusory contours may rely on mechanisms similar to those that underlie figure/ground perception, which has usually been explained in terms of basic sensory mechanisms either at the retina or in early cortical visual areas. Cortical representations of illusory contours have been reported in both animals and humans (e.g. Bauman, van der Zwan, & Peterhans, 1997; Gillam & Nakayama, 2002; Grosof, Shapley, & Hawken, 1993; Larsson, Amunts, Gulyas, Malikovic, Zilles & Roland, 1999; Von der Heydt, Peterhans, & Baumgartner, 2004).

Physiological Evidence for Contour Completion. Using fMRI with human participants, Hirsch, DeLaPaz, Relkin, Victor, Kim, Li, Borden, Rubin, and Shapley (1995) provided evidence of cortical representations of illusory contours in area V2 (also see, Edelman, Spector, Kushnir, & Malach, 1998; Halgren, Mendola, Chong & Anders, 2003). Ffytche and Zeki (1996) showed evidence of illusory contour representation in area V2 of humans using positron emission tomography (PET).

Evidence for lower-level mechanisms that may be responsible for contour completion have been identified in visual cortical areas 17 and 18 of the cat and areas V1 and V2 of the monkey (Hubel & Wiesel, 1959; Grosof, Shapley, & Hawken, 1993; Von der Heydt, Peterhans, & Baumgartner, 2004). These areas are reported as responding to changes in luminance, distinctions of lines and edges, as well as line orientation.

Baumann, van der Zwan, and Peterhans (1997) recorded from single neurons located in areas V1, V2, and V3 and V3a in monkeys trained on a visual fixation task. Subjects were required to view illusory images of artificial situations of spatial occlusion (e.g. light or dark rectangles lying atop line gratings of opposite contrast). They found that most of the neurons located in area V1 failed to respond to the direction of the occluding contour stimuli, but rather tended to be more sensitive to contrast polarity at the contour. On the other hand, recordings from pre-striate areas (V2, V3, V3a) showed sensitivity to figure-ground segmentation. These data provide evidence for the detection of contrast differences and brightness as early as V1 but that the ability to discern a figure as separate from background appears to occur at higher areas located outside of primary visual cortex. Lee and Nguyen (2001) recorded from individual neurons in areas V1 and V2 of conscious behaving monkeys. The monkeys were trained to fixate to a target area on the screen during stimulus presentation. The monkeys were shown a series of stimuli (e.g. 4 circular discs, 4 contour inducing pacmen, a white square on a gray background, a real contour- an outline of a square and rotated pacmen) over the course of a series of trials where the receptive field of the neuron being recorded was placed in different locations in relation to the stimuli. Of interest is that the onset to the illusory contour responses in both V1 (55ms) and V2 (30ms) were significantly delayed when compared to recordings in response to real contours. Lee and Nguyen (2001) proposed that the response differences were likely due to feedback modulation from area V2 to area V1 resulting from differences in the size of the receptive fields. Therefore, V2 neurons are likely to be involved in global computations that send feedback to area V1 where the final subjective contour is completed.

The results from the aforementioned research provide evidence that supports the hypothesis that figure-ground separation occurs at the lower-level stages of early visual processing prior to object recognition suggesting that subjective contour perception at the level of individual neurons depends on striate and pre-striate areas. However, completion of partly occluded contours and objects has sometimes been considered to be more cognitive in origin (Kellman, Yin, & Shipley, 1998). Lee (2002) showed physiological evidence of illusory contour perception at both early and later stages of visual perception, however the exact mechanism is still not known. They proposed the existence of multiple processing pathways that are simultaneously activated (in parallel), involving direct feed-forward integration as well as indirect feedback modulation to area V1 from area V2.

Higher Levels of Visual Processing in Contour Perception. We have seen physiological evidence that suggests that visual contour processing occurs even on the level of individual neurons, which clearly plays a large role in the detection and recognition of subjective contours. However, one must also consider the influences of higher cognitive functions, such as internal representations, that may act to facilitate performance on visual recognition tasks. Human, as well as non-human primates, rely on internal representations of three-dimensional objects in order to make sense of discontinuities in their visual field (Yantis, 1995). According to Peterson (1994), higher levels of cognition often guide how lower-level configural cues are organized. Many cognitive theorists have the notion that one must have previous experience with something in order to infer contextual organization among local components (Peterson & Lampignano, 2003; Peterson & Gibson 1993, 1994). Rubin, Nakayama, and Shapley (1997) required human subjects to perform a shape discrimination task involving the Kanizsa illusory contours. The contour inducing forms ("pacmen") were rotated at varying degree's to induce “fat” or “thin” illusory shapes. The subject's task was to discriminate between these shapes. The human subjects did not initially distinguish between the rotated illusory contours. Experience was necessary before they could perceive the contour. Moreover, the learning that took place was stimulus specific, that is, the learning did not generalize across stimulus types and was specific to training.

Further evidence of integration between lower and higher levels is provided by developmental data such as that of Burkhalter, Bernardo, and Charles (1993) who obtained evidence for delayed development of horizontal feedback connections in humans between areas V1 and V2. Kaldy and Kovacs (1999) reported that in humans the development of contour integration is slow and continues throughout childhood into adolescence (also see, Kovacs, Kozma, Feher, & Benedek, 1999; Kovacs, 2000).

Differences Between Human and Non-Human Primates in Global and Local Processing. It is likely that there are differences in contour completion in human and non-human primates. In addition to verbal coding strategies that are presumably not available to non-humans there are demonstrated differences in global and local processing. Fagot and Derulle (1997), using a delayed matching-to-sample paradigm, were interested in testing whether global advantages were influenced by purely perceptual mechanisms, or whether higher cognitive influences facilitated global adaptations in humans and baboons. To do this, they used large geometric shapes (e.g. circles and squares) made up of smaller geometric shapes (see Navon, 1977). Each species received two experimental conditions: local and global. The correct comparisons for the local matching condition were identical to the sample and the incorrect comparison had the same global shape but different local elements. The correct comparisons for the global matching condition were identical to the sample and the incorrect comparisons were composed of the same local elements but had a different global shape. Human subjects were told verbally to select the stimulus that was most identical to the sample as fast and accurate as possible. The baboons were trained to use a joystick and pay attention to a fixation point that remained on the screen during each trial. The subjects' task was to choose the best match for what had been observed on the sample presentation. Human performance on the local condition was 85% correct and 97% correct on the global condition. The baboons however performed slightly better on the local condition with accuracy of 68% correct, than on the global condition with accuracy of 60% correct. The results indicated that human subjects showed a pronounced global advantage (as evidenced by accuracy data and faster reaction times) while the baboons showed a dominant local processing advantage. In accordance with the study described above, Fagot and Tomanaga (1999) conducted a series of experiments using similiar stimuli as Fagot and Derulle (1997), using a visual search paradigm to test global and local advantages in chimpanzees. Their first experiment was nearly identical to that of Fagot and Derulle (1997) except the chimpanzees were trained to touch a warning stimulus that indicated the start of a new trial prior to the presentation of a visual search display. Once again, the subjects were required to make discriminations on local and global levels. Results indicate that both the humans and chimpanzees exhibited high performance for each condition (99 and 98% respectively). Response times however were faster for the local condition in chimpanzees but faster for the global condition in humans, providing evidence for a global processing precedence in humans. The global sizes of the stimuli were manipulated in Experiment 2 by increasing or decreasing the density of the local elements. Once again human performance across conditions was approximately 99% correct. The chimpanzee's performance was also exceptionally high (98-99% correct) when the local elements were densely packed versus 92-94% when the local elements were spaced farther apart. Based on this study, Fagot and Tomanaga concluded that humans exhibited an overall global processing advantage, while the chimpanzees showed an advantage for local processing when there was a low density of local items and no advantage when more local items were added to the display. As a final test, small line segments were introduced between the local elements when they were sparsely located during Experiment 3. It was only during this manipulation that the chimpanzees showed a global advantage, which was remarkably eliminated when the connector lines were eliminated.

These data are relevant because they provide insight into how a non-verbal primate discerns continuity, which appears to depend the density and alignment of local cue configurations. Spinozza, Delillo, and Truppa, (2003) extended these findings to capuchin monkeys. They used a simultaneous matching-to-sample task, in which the subjects had to move a sliding door to receive food reward. The correct door was baited with food on each trial. The stimuli used were similar to those used by Fagot and Derulle

(1997). The results of this study indicate that capuchin monkeys, like baboons and chimpanzees, on average tended to process local features more accurately than global features.

Evidence has shown that human children also show global preference when the local elements of a visual display are located close to one another (dense) and show a local preference when the elements are located at a distance from one another (sparse) (Dukette & Stiles, 1996). Neiworth, Gleichman, Olinick and Lamp (2006) compared adult humans, human children (ages 5-6), and adult tamarin monkeys on a global and local discrimination task. The human adults and children performed a category discrimination task while the adult tamarin monkeys performed a go/no-go task experiencing the same stimuli as the human subjects. The monkeys were trained to make discriminations between hierarchical stimuli. The stimuli were presented to the subjects on cards and were displayed in front of the subject. After the initial training with large circles composed of smaller circles and large squares composed of smaller squares, the monkeys were presented with novel conditions where the sample circle composed of circles was paired with two comparisons: a large circle composed of squares or a large square composed of circles. The subject's task was to choose the matching stimulus that most resembled what had been experienced on the sample session. The human subjects on the other hand, were split into two groups so that half were assigned to the densely packed element condition and the other half to the sparsely packed condition. Subjects were trained with larger circles composed of smaller circles, larger circles composed of smaller squares, larger squares composed of smaller squares, larger squares composed of smaller circles. The results of this study indicated that adult humans exhibit a global preference both when the local elements were densely packed as well as when they were spread out. The human children were capable of processing the displays locally and globally, but this was context specific. That is, when the elements were densely packed they developed an overall global preference and were better able to identify the overall contour of the larger geometric shape more efficiently. The adult monkeys interestingly processed the stimuli similar to the human children in that the density of the elements in the display guided the global or local preference. Based on the results of this study, it appears that the ability to process hierarchal stimuli globally is decreased when the local elements are spaced farther apart in both human children and adult tamarin monkeys. These data further provide evidence of developmentally different processing strategies between human children and adults.

The Macaque Monkey as a Model for Human Vision. The macaque visual system is one of the most widely understood and best models that exist for human vision in terms of basic structure, function, and physiology. Although the visual pathways of human and non-human primates share the same basic organization of cell layers in the retina, they appear to differ in both the number of cells in a given nuclear layer and also in the distribution of those cells across the retinal surface (i.e. number of macular ganglion cell layers: 6-7 in humans and 3-4 in macaques and fovea size: .66mm in humans, 1.9mm in macaques) (see Finlay & Sengelaub, 1989; Noback & Laemle, 1970). Some of the functions that appear to be similar include contrast sensitivity, visual acuity, visual field size, feature representation, and orientation sensitivity (Gazzaniga, Ivry, & Mangun 1998; Noback & Laemle 1970). There are however, a variety of visual phenomena that occur in human vision (e.g. closure, mental rotation, illusory contours, and subjective superimposition) that may not necessarily occur in non-verbal primates. More specifically, a number of visual phenomena share the property that boundaries and shape are perceived in locations where no local information is physically present (i.e. the subjective contour perception as described previously). Comparatively this is relevant because different sets of visual features may be emphasized in verbal but not in non-verbal primates. For example, as described earlier, Deak et al., (2002) showed that language cues were not necessary for object matching by form in 3-year old children, however matching performance by function is limited and appears to develop with age as objects are named and given symbolic meaning. These differences might also be explained by understanding the mechanisms of perception across species. Bottom-up processing theories tend to support lower level explanations of illusory contour perception, such as recordings from single neurons. There is no question that bottom-up, or feed-forward mechanisms are involved in the initial processing of contour integration, however it may not be solely responsible for the subjective contour phenomenon observed across species.

Lee and Nguyen (2001) provided evidence of delayed activation of neurons located in V1 in macaque monkeys in response to illusory contours versus real contours. Their results suggest an intermediate feedback loop, which is consistent with top-down theoretical accounts of visual perception, implying that more complex processing is required for completion of illusory contours. Differences in processing strategy are therefore likely to vary across species depending on each species' evolved ecological necessity to fill in missing attributes of visually incomplete images (see Nieder, 2002; Ramachandran, 1987). Kiorpes and Bassin (2003) reported evidence of delayed development of contour integration in macaque monkeys similar to the development of contour integration abilities in humans (Kovacs et al., 1999; Kovacs, 2000). Using Gabor ring stimuli, similar to that used by Kovacs (2000), Kiorpes and Bassin (2003) found that monkeys under 5-months of age were unable to perform the contour integration task when the contour was embedded with non-contour background noise, but they were however capable of detecting the location of the contour when the background noise was eliminated. The ability to discern the contours amongst the noise appeared to emerge at roughly 20 weeks of age. These data lend insight into the developmental similarities of global form perception in human and non-human primates, making the macaque monkey an excellent animal model for non-verbal visual perception.

Other Anatomical Differences in Human and Macaque Monkeys. Although the macaque monkey has been regarded as the best model for human vision, recent evidence has shown distinct differences in the cellular architecture of layer 4A of primary visual cortex. Preuss, Qi, and Kaas (1999), using microtubule associated protein – 2 (MAP-2) and non-phosphorylated neurofilament (NPNF) antibodies, obtained the first clear demonstration of distinctively different cortical architecture resulting from differences in magnocellular (responsible for detection of motion, luminance contrast, and coarse outlines) and parvocellular (responsible for detection of color and fine detail) inputs from the lateral geniculate nucleus (LGN) in human and non-human primates. Preuss et al., (1999) showed that layer 4A in the macaque monkey was characterized by a "honeycomb-like" appearance resulting from direct parvocellular inputs and indirect magnocellular inputs from layer 4B. Whereas layer 4A in humans, was characterized by direct magnocellular inputs that were distributed in a more complex, "mesh-like" arrangement. The use of cytochrome oxidase (CO) techniques further highlights these differences in layer 4A in that non-human primates exhibit a distinct band of stain, representative of parvocellular projections that is absent in humans (Preuss et al., 1999). It is not well known how these anatomical differences affect visual perception across species, however Pruess et al., (1999) suggested that the differences in the distribution of magnocellular and parvocellular projections could account for why the human visual system is more sensitive to variations in luminance contrast than that of monkeys (DeValois, Morgan, & Snodderly, 1974; Merigan, 1980).

The Present Research. The primary focus of this research was to investigate whether rhesus macaque monkeys (*Macaca mulatta*) experience the subjective illusory contours first described by Kanizsa (1955). It was hypothesized that the monkeys would provide behavioral evidence of illusory contour perception similar to what has been observed in adult humans when presented with illusory contours of the Kanizsa type. This was done by use of a matching-to-sample (MTS) paradigm. In this study, the MTS task proceeded as follows: a sample stimulus appeared in a designated region on a touch sensitive monitor. After a successful touch to the sample, the item typically disappeared and two comparison stimuli then appeared. A response to either of the comparison (match) stimuli ended the trial. More specifically, responses to the comparison stimulus that directly matched the original sample item allowed the animal access to a food pellet reward. Responses to the non-matching comparison stimulus were followed only by an inter-trial interval.

The MTS paradigm has been used to examine various areas of cognition in animals, especially abstract concept learning mechanisms (e.g. Fagot & Deruelle, 1997 by baboons; Spinozzi, De Lillo & Truppa, 2003 by capuchin monkeys; and Wright, Cook, Rivera, Sands, & Delius, 1988 by pigeons). In the procedure used here, the monkeys were trained to choose a matching picture when, after it disappears, it is shown again but in a different location and with a non-matching picture (Himmanen, 2000; Washburn, Hopkins, & Rumbaugh, 1989). The MTS procedure was used here to determine whether rhesus macaque monkeys perceive the illusory contour humans report when presented with the Kanizsa patterns (Ringach & Shapley, 1996; Rubin, Nakayama & Shapley, 1997; Shapley & Gordon, 1987). One of the more promising advantages of using the MTS procedure rather than alternative methods to studying non-verbal perception (such as go/no go and same/different) is that it is useful in examining relational learning between stimuli as well as study how animals perceive, code, and remember the stimuli. In addition, the decision to use an identity matching procedure was based on preliminary training, whereby neither monkey showed any evidence of learning on a 2-choice symbolic matching task.

Although, several studies have provided behavioral evidence of illusory contour perception over a variety of species (see Nieder, 2002), one of the earliest demonstrations of a non-human primate discriminating incomplete contours was a study by Zimmerman (1962). Zimmerman showed that infant monkeys could discriminate different geometric shapes even in situations where the contours were incomplete. One of the more recent indirect demonstrations of the Kanizsa illusion in a non-human primate was an experiment by Fagot and Tomanaga (2001) that examined perception of Kanizsa illusory squares in chimpanzees. The chimpanzees were trained on a two alternative forced choice task in which the subjects had to discriminate Kanizsa illusory squares and non-illusory squares. After the initial training with the illusory squares, small line segments were added between the contour inducing forms “pacmen” to determine whether the discrimination was weakened by the “interruption”. The chimpanzees’ performance was hindered by the line segments, however, the authors caution that they were not certain that the chimpanzees were making their discriminations based on actually “seeing” the illusion or whether performance was based on familiarity of the stimuli due to the extensive training with the illusory forms. Therefore, there are no definitive data on this quest in any non-human primate.

Why this Research is Important and Questions Raised. The purpose of this research was to determine whether rhesus macaque monkeys (*Macacca mulatta*) behaviorally perceived the illusory contours in Kanizsa patterns. The similarities and differences in how they and humans process such illusory images would expand our knowledge of the evolution of the mechanisms underlying visual perception, in particular extrapolation of whole forms from a set of individually configured features. Based on the physiological data and structural similarities between monkeys and humans, it was hypothesized that the monkeys would provide behavioral evidence of illusory contour perception similar to adult humans. Alternatively, if the monkeys did not show evidence for the illusion it might suggest different processing strategies that might be similar to what has been demonstrated in young children.

Chapter II: General Methods

Subjects

Three female rhesus monkeys (*Macaca mulatta*) were originally assigned as subjects. The three subjects (Samantha, Sophie, and Holly) were born in captivity and were approximately 4 years of age at the start of the experiments. They were housed at Lehman College Animal Care Facility in accordance with the NIH Guide for the Care and Use of Laboratory Animals. They lived socially in a group of three, and were kept on a 14-10 light/dark cycle. They were separated into individual units for feeding, transfer, and training. Each animal was weighed prior to each test session. Weights typically ranged from 90-100% of their normal weight. Based on a growth curve, the animals were fed approximately 110g-130g monkey chow (labdiet), one slice of bread, and one piece of fruit, once a day one hour after each test session. The monkeys did not receive additional food and were not fed again until after the following session. The monkeys were given one test session per day, 7 days a week.

***note:** Holly was discontinued from the study after failing to acquire the matching task.

PRELIMINARY TRAINING ON MATCHING-TO-SAMPLE (MTS)

Prior to the actual experiments, the monkeys were shaped using the method of successive approximation to touch images appearing on the touch sensitive monitor. This was followed by training on a 2-choice discrimination task where the subjects were trained to choose between two light blue discs located in the lower left and lower right regions of the monitor with one disk associated with a picture of flowers, the other a picture of a dolphin. The monkeys were required to respond to the left response disc when the picture of the flowers appeared and to the right response disc when the picture of the dolphin appeared. This training was discontinued when neither monkey showed evidence of acquiring the discrimination (50 sessions, 2,500 trials for Samantha, and after 30 sessions, 1,500 trials for Sophie). Prior to this training the subjects were experimentally naïve. This was followed by 4 experiments. The specifics of these experiments are described below.

Apparatus

The monkeys were trained and tested in an operant conditioning chamber that provided visual and acoustic isolation from potentially distracting external stimuli. The test area was a Plexiglass enclosure, 48.3 cm wide x 53.3 cm deep x 58.4 cm high, placed inside a sound-insulated BRS/LVE (Beltsville, MD) chamber. The test area was sufficient to allow free movement. The chamber was well ventilated and was housed in a room adjacent to the colony room. The temperature was maintained at the same level as in the colony room (75°F +/- 5°). This test area contained one opaque metal wall with a cutout to allow for a 13 inch color video touch screen monitor for stimulus presentation. The remaining walls of the operant chamber were transparent plexiglass. The walls of the sound-insulated outer chamber were off white with a video camera mounted on the adjacent wall to the left of the monitor. The monitor was covered by a clear plastic template with square openings 5.1 cm wide x 3.8 cm high for the nine possible stimulus locations (3 columns by 3 rows). Responses to these locations were sensed using a capacitance touch system (MicroTouch). The luminous intensity dark gray screen 6 inches from the monitor was 36 cd/m^2. The subjects were freely roaming and an averaged viewing distance of 6-12 inches from the display monitor was estimated. A small 40-watt house-light was located above the plexiglass enclosure. The illuminance provided by the house-light when recorded from the center of the operant enclosure measured 15 lx. Single food pellets (Noyes 190 mg, banana, grape, raspberry, and fruit punch-flavored, Research Diets, Inc., New Brunswick, NJ) were randomly delivered via two separate rotary feeders (Gerbrands Corporation, Model G5120) into cups located to the lower left and lower right of the computer monitor. Random delivery to either feeder was used to avoid the possibility of a location bias to either the left or right side of the monitor. A white noise generator provided masking noise (Model 15800 C, Lafayette Instrument Co., Lafayette, Indiana). A small video camera (Panasonic Digital, Model 5100) was used to observe the monkeys on a television monitor outside the chamber. Stimulus presentation and data collection were accomplished with a Pentium IV computer using custom-written software.

General Procedure

A zero delay matching-to-sample (MTS) procedure was used. Each session began with a programmed flicker of the house-light. The house-light remained on for the duration of each trial unless the subject failed to respond to the programmed sequence or unless an error was made. Two seconds later a black, gray, and white textured "marble rectangle" (5.3 cm wide by 4.24 cm high), the start stimulus, appeared in the center of the monitor. A touch to this stimulus was followed immediately by another stimulus, the sample stimulus, which appeared in one of the nine locations, with the sample stimulus occasionally appearing in the center. If this stimulus was touched within 5 s it disappeared and was replaced by a matching and non-matching comparison stimulus. The locations of these two stimuli were randomly determined with the restriction that neither was shown in the same location as the sample. The comparison stimuli remained on the monitor for 20 s or until touched. Two audibly different feedback tones were used, one (higher frequency) for correct responses and one (lower frequency) for incorrect responses, each 1 second in duration. A correct choice was followed by the higher sound and delivery of a food pellet into one of the cups, with left and right randomly determined, and a 3 s inter-trial interval. An incorrect choice was followed by the sound of lower frequency and a 20 s timeout during which the screen cleared, but remained illuminated, and the house-light extinguished. The house-light came on for 3 s after this timeout, flickered once after the 3 s to indicate the start of a new trial, and then remained illuminated throughout the trial. Following both correct and incorrect choices the next programmed stimulus sequence was presented. Trials such as these are referred to as feedback trials.

After performance on the task was reliably high, these informative feedback trials were gradually reduced and replaced by non-feedback trials to prepare the subjects for non-feedback probe trials on which the test stimuli were presented. The ratio of feedback trials to non-feedback trials was specific to each experiment, the details of which are described later. On non-feedback trials only the 3 s inter-trial interval followed the disappearance of the stimuli. Failure to touch a stimulus within 5 s during any phase of the trial resulted in the 20 s timeout during which the house light was off and followed by the 3 s inter-trial interval and the next programmed trial. One should take note that the only light illuminated between trials was from the monitor. In addition to the choices made, response times (the time between the disappearance of the sample and the comparison stimuli) were recorded. Latency differences were useful for identifying inconsistencies in performance, which might have resulted from the types of stimuli presented. For example, very short or very long latencies might be indicative of inattention or extinction behavior. The monkeys were given one 100-trial session on a minimum of five days each week.

Chapter III: Experiments

EXPERIMENT 1

In order to examine whether the monkeys could perceive illusory contours of the Kanizsa type, they were first given MTS training. At the start of MTS training it had not been determined that the monkeys would subsequently be required to make discriminations of grayscale stimuli. Color photographs were therefore initially used in accordance with standard laboratory protocol for MTS training (see Himmanen, 2000).

Subjects were initially trained on a program designed for list learning subjects where the stimuli could appear randomly in 16 possible locations. Following the initial MTS training however, the subjects were switched to a different program that only allowed for the stimuli to appear in 9 possible locations. Evidence has shown that moving the sample and comparison stimuli to different positions from trial to trial can actually facilitate learning, transfer, and matching (Washburn et al., 1989).

Method

Phase 1. MTS Training with Colored Pictures. In this initial MTS training, the screen was divided into 16 locations instead of the 9 used in all subsequent training and tests. The images were 5.3 cm wide by 4.24 cm high colored pictures of naturally occurring items, e.g. flowers, rocks, animals. The monkeys were trained to match a sample picture to one of two comparison pictures, one which was identical to the sample, but in a different location. Each monkey was first trained with one set of two pictures where the sample was presented first, followed by the two comparisons. Criterion for introducing a new pair of two pictures was at least 70% correct on two consecutive sessions. This was repeated until this criterion was reached on five different sets of three pictures.

Phase 2. Training with Sets of 32 Colored Pictures. Following criterion with the five sets of stimuli, using the 3x3 grid (9 locations), 32 new pictures from eight categories (4 each of amphibians, birds, mammals, fruits and vegetables, trees, scenery, sea life, rocks) were used. Different categories were used during training to ensure the monkeys could generalize their concept of matching. For each 100 trial session, scripts were created in which selection of samples and comparison stimuli was random with the restrictions that (1) the non-matching item was not from the same category as the matching item, (2) samples were not from the same category on successive trials, and (3) each stimulus appeared at least three times as the sample and as the non-matching stimulus. The criterion for moving to Phase 3 was at least 70% correct on two consecutive sessions.

Phase 3. Training with Non-Feedback Trials. The same 32 pictures used in Phase 2 were used during this phase. The proportion of trials on which feedback was given was gradually reduced from 100 to 90 to 80 to 70% with each reduction occurring following two sessions of 80% or better accuracy. At 70% feedback trials, the number of non-response trials (trials on which the monkey did not touch the start stimulus within 5 s) increased. In order to overcome this problem the monkeys were returned to 90% feedback trials. The criterion of 80% correct trials for two consecutive sessions was reached within one week.

Phase 4. Training with Grayscale Pictures with 90% Feedback Trials. Using the same procedure as described earlier, but with 90% feedback trials, the same stimuli as in Phase 3 were used with the exception that color was eliminated. Upon reaching criterion of 80% correct this set was replaced by a new set of 32 grayscale pictures. Following criterion of 80% correct Phase 5 began.

Phase 5. Training with Grayscale Pictures with Feedback Reduced to 80%. After criterion was reached on Phase 4, the percent of feedback trials was gradually reduced from 90 to 85 to 80%. The same 32 stimuli from the second set of grayscale pictures from Phase 4 were used during this phase of feedback reduction.

Phase 6. Transfer to the Second Novel Grayscale Stimulus Set. Once criterion was met, the monkeys were transferred to a new stimulus set of 32 stimuli with feedback remaining at 80%.

Table 1 is a summary of the number of sessions each of the monkeys required to complete the six phases of preliminary training. In some cases additional sessions were given after criterion was reached before introduction of the next phase. The number of such sessions is shown in parentheses. Figure 1 shows the percentage correct as a function of training session for the six phases of MTS training for the two subjects.

Table 1. Summary of MTS Training for Samantha and Sophie.

Phase	**Description of MTS Conditions**	**Sessions to Criterion**	
		Samantha	**Sophie**
1	Colored Picture Pairs	49	74
2	32 Colored Pictures 100% feedback – set 1	10 (5)	20 (3)
3	32 Colored Pictures – with non-feedback trials – set 1	24 (34)	15 (33)
4	32 Grayscale Pictures – 90% feedback – set 1	3 (35)	10 (37)
5	32 Grayscale Pictures – 80% feedback - set 2	2 (39)	9 (49)
6	32 Grayscale Pictures – 80% feedback – set 3	5	15

Phase 7. MTS with Geometric Forms and Non-Contour Forming Pacmen.

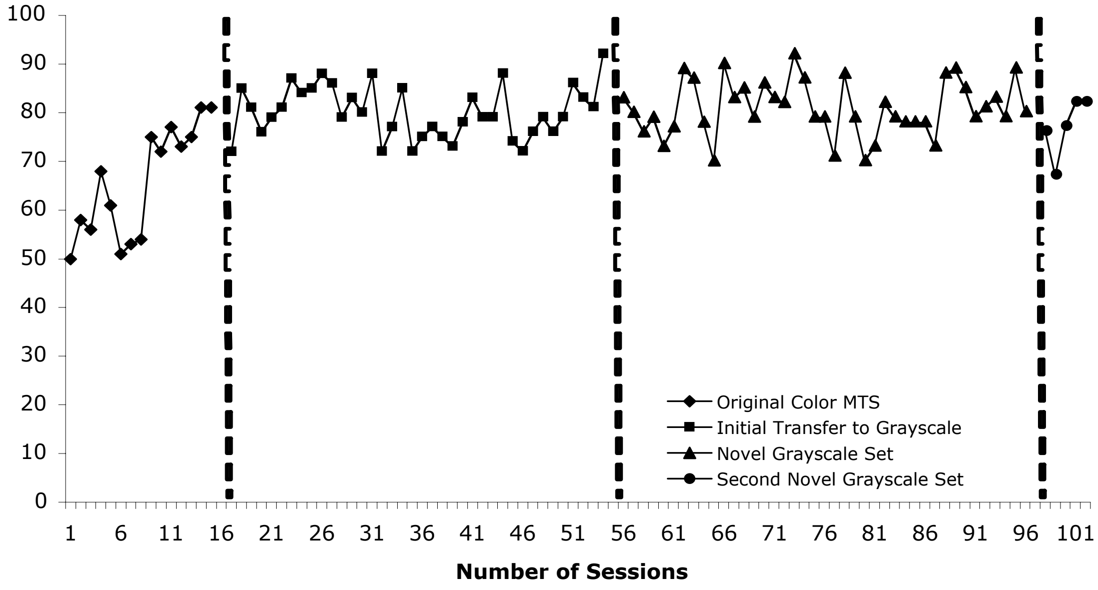
The same procedure as in the preliminary sessions was used. Sessions were 100 trials in length with feedback on 80% of the trials. However, in Experiment 1 the pictures were replaced by a combination of three different categories of abstract forms. As shown in Figure 2 the stimuli were abstract grayscale geometric figures composed of rectangles (top panel) or parallelograms (middle panel) surrounded by a uniform field. These geometric figures varied in size, shape, and brightness (i.e. the figure was lighter or darker than the background). The degree of contrast, the ratio between how light or dark the figure was from the background, was manipulated so as to highlight the figure as distinctly different from the background. Eight of these figures (bottom row) were accompanied by a disk with a segment removed, referred to here as a “pacman.” These forms were aligned so as to not produce the illusory contour reported by humans when pacmen are arranged to form a Kanizsa pattern. Each monkey received training with all three types of background stimuli. These three types of background stimuli were meant to prepare the subjects for the test using Kanizsa figures in Phase 9.

The distribution of non-feedback trials was random with the restriction that at least one geometric figure with an adjacent non-contour inducing pacman occurred on a non-feedback trial. This was done so that the monkeys received experience on trials for which pacmen elements appeared in the sample, a condition that was to be experienced on test trials, but for which no feedback was programmed. The criterion for advancement to the next stage of training was 80% or better on two consecutive training sessions.

Phase 8. MTS with Background PLUS Primes. Training with 80% feedback trials was continued with the same set of background stimuli and the addition of a square and a parallelogram. These patterns were similar to the background stimuli except that they were single rather than composite figures and in the test for the Kanizsa illusory contours the square and parallelogram were presented as comparison stimuli. It was expected that, experiencing an actual contour in the form of a parallelogram or a square during training would act as a *prime* when the pacmen were arranged to form the corresponding illusory figure. In Figure 3, these primes are shown as comparison stimuli in the illustration of the Kanizsa figures.

The plan was to train Samantha with the parallelogram and Sophie with the square as primes. The rationale for introducing the primes was to show that if the only test stimulus above chance was that for which the monkeys received as a prime, it would indicate that the monkeys were not “seeing” the illusion but were responding to the form that they had previously experienced. However, because Sophie did not reach criterion on Phase 7 only Samantha completed Experiment 1. For Samantha 14 sample parallelogram primes (10 feedback, 4 non-feedback) with the comparisons a parallelogram and a square were randomly interspersed among the background stimuli with the restriction that there were at least three non-prime stimuli between primes and that a prime did not appear in the first ten trials of a session. There were eight background forms with a pacman (7 with feedback and 1 non-feedback) and 88 geometric grayscale background stimuli (73 with feedback and 15 none-feedback). Criterion for completion of this phase was 80% correct on two consecutive sessions with at least 70% correct on each of the primes.

Samantha



Sophie

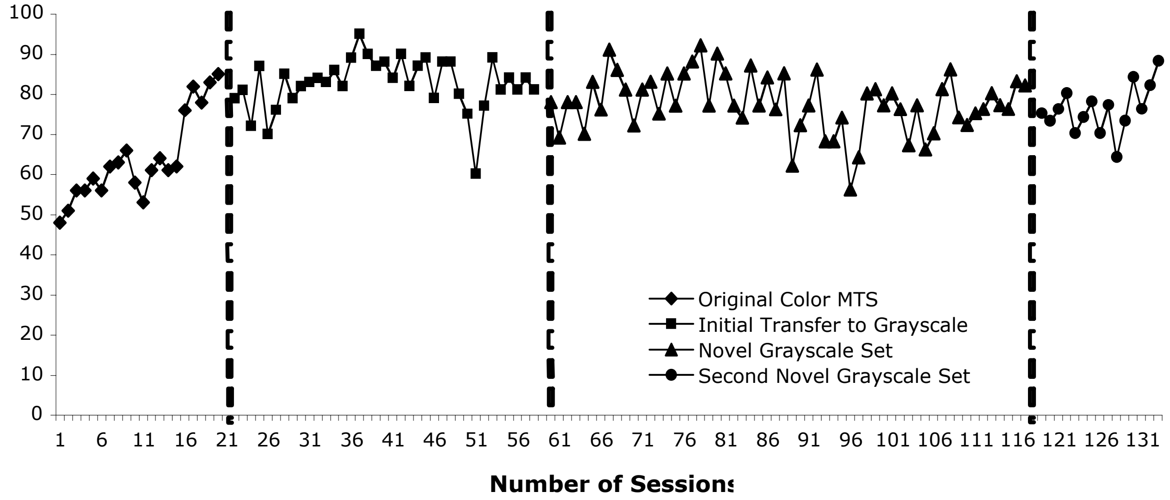


Figure 1. Percent correct as a function of Phases 3 to 6 of preliminary training. The top panel summarizes the data for Samantha. The bottom panel summarizes the data for Sophie.

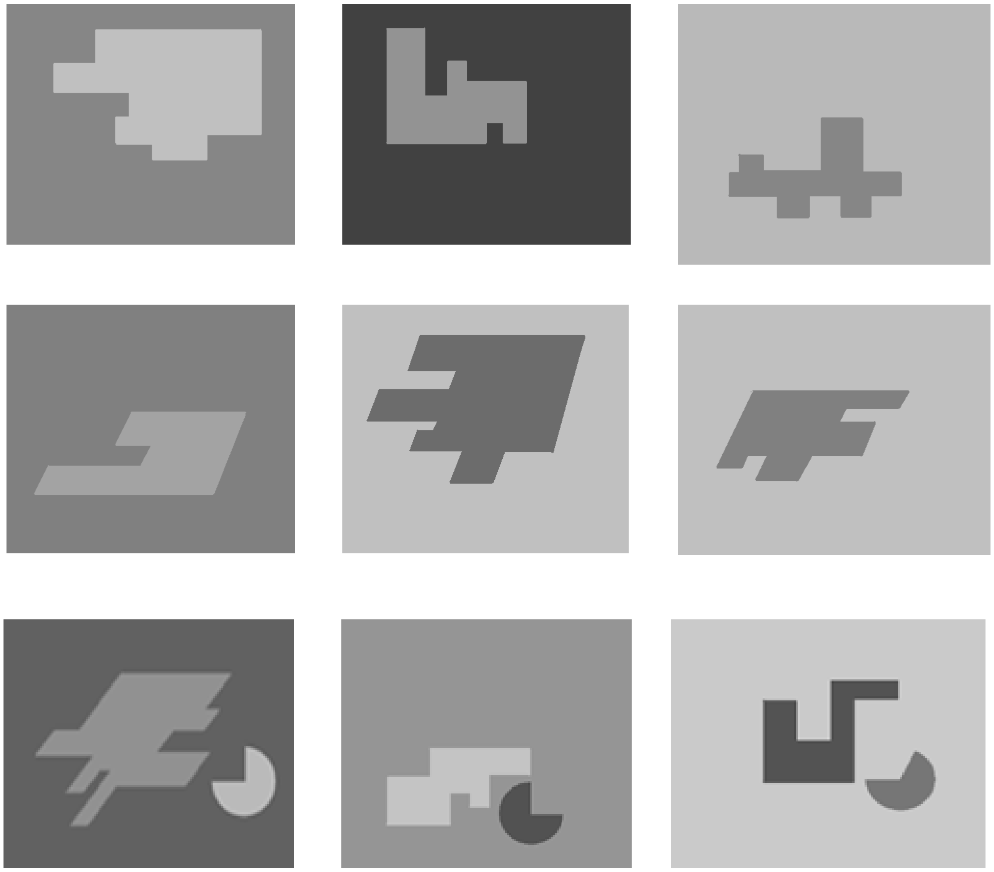


Figure 2. Examples of the figures used as background stimuli in Experiment 1.

Phase 9. Test for Perception of Illusory Contours. During this phase, as before, 80% of the trials were followed by feedback. There were three types of trials. Eighty trials were background stimuli with feedback on 70 of these trials. There were 14 trials on which primes, the parallelograms, were shown with feedback on 10 trials. Six test trials without feedback were presented within each session as described below.

Test Trials. The three types of Kanizsa illusory contour patterns were presented during each session —a square, a parallelogram and a trapezoid as sample stimuli with the comparisons shown in Figure 3. The test patterns were the same size as the training stimuli. The diameter of each pacman element was 1 cm. The dimensions of the illusory square were 2.5 cm x 1.8 cm and 2.3 cm x 2 cm for the parallelogram. The dimensions of each of the horizontal lines of the trapezoid were 3 cm (top) and 1.5 cm (bottom) and each slanted contour measured 2 cm. One of the solid forms "matched" the sample if an illusory contour was perceived. The other was a non-match. That is, if the contour was experienced for pattern A in Figure 3 the monkey should have chosen the square.

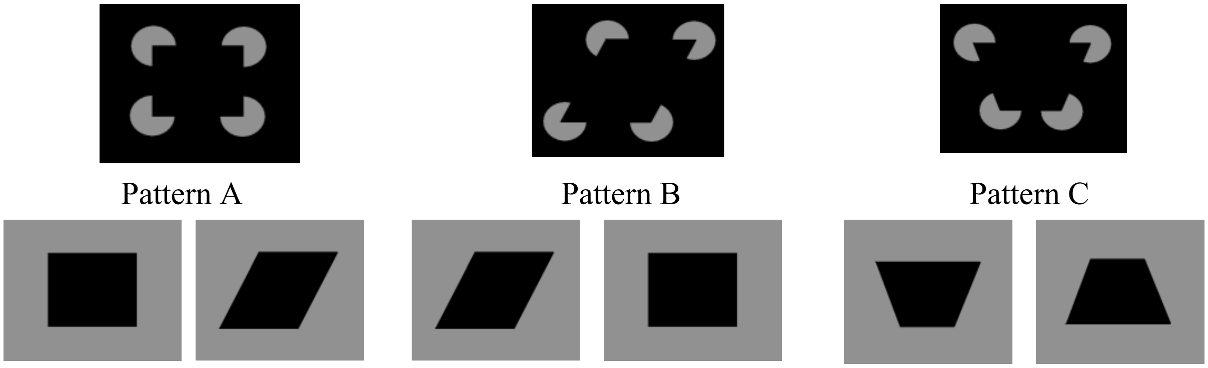


Figure 3. The three Kanizsa type test patterns and comparison stimuli.

These three Kanizsa patterns were presented as sample stimuli on test trials—two presentations of each during each 100 trial session. The six test trials were interspersed among the background and priming trials with the following restrictions: (1) A test trial did not occur during the first 10 trials of the session. (2) A test trial did not occur before the first prime (3) Test trials did not occur on successive trials. (4) Test trials did not appear immediately following a priming trial. (5) Each of the three types of test trials was presented once before it was repeated and (6) Test trials were separated by at least three background or priming trials. One additional session was given after 16 sessions so that there were 32 presentations of each of the three Kanizsa figures.

Evidence Required in Order to Demonstrate Existence of Perception of the Illusory Contours in the Kanizsa Figures. Of main interest were the choices made on the test trials – the 32 presentations of each of the three Kanizsa figures. The probability that the choices of the matching pattern were due to chance was to be rejected if on 21 or more trials the matching form was selected. That is, if the matching form was chosen on at least 21 out of 32 presentations, the probability that this would occur by chance is .034, the area in one tail of the normal curve for $z = 1.82$. In addition to the choices made, response latencies on correct and incorrect trials were also recorded in order to determine whether different strategies occurred when the response was or was not correct. The means of the median response latencies for each session were used for all t-tests.

Results and Discussion

Phase 7. Background. After approximately 98 sessions (9,800 trials) Samantha reached criterion of 80% or better on two consecutive sessions with set 1 and approximately 32 sessions (3,200 trials) on set 2. The mean of the median reaction times on the second background set (663 ms) were compared with those on the first background set (671 ms) to determine whether the task was getting easier. This difference was not significant, *t* (128) = .759, p > .05.

Sophie performed at chance for 85 sessions (8,500 trials) on the first set of background stimuli. Although she was returned to 100% feedback for 19 sessions (1,900 trials) she continued to perform at chance. She was then given 13 sessions (1,300 trials) in which the sample stimulus as well as the comparisons remained visible on the touch screen monitor. It was hypothesized that this simultaneous matching procedure would facilitate Sophie's performance. However, performance remained at chance. A correction procedure was then introduced. Following an incorrect response the same trial would repeat for up to five times or until the correct choice was made prior to advancing to the next scheduled trial. After 19 sessions (1,900 trials) Sophie was switched to a background set composed of less complex abstract forms than used previously. Complexity on the background forms was defined as the number of contours and the degree of contrast between the figure and background. Less complex background stimuli had fewer angles (closer to what appeared on test trials) as well as a greater degree of contrast so that the figure was clearly distinct from that of the background. The ratio of positive and negative contrast was manipulated by changing the brightness of either the figure or the background. After 17 sessions (1,700 trials) at chance with the new set of stimuli, Sophie's training was temporarily discontinued. Table 2 summarizes sessions of training and response latencies for Sophie.

Table 2. Sophie's Performance Background Set 1

Background Set 1 Modifications	**Number of Sessions at chance**	**Response Time (ms) Correct**	**Response Time (ms) Incorrect**
		Mean of the Medians	**Mean of the Medians**
Original background set 1 (80% feedback)	85	1503	1510
Background set 1 (100% feedback)	19	1290	1300
Simultaneous MTS (100% feedback)	13	3118	3202
Correction Procedure – Simultaneous MTS	19	2139	2155
Modified background set "less complex"	17	3165	3345

Phase 8. MTS with Background PLUS Primes. When the parallelogram match was introduced as a prime, Samantha continued to perform well above chance on the background stimuli (accuracy ranged from 69 to 93%) however, her performance on the primes was distinctly worse, ranging about a mean of 29 to 86% correct. Her performance on the background stimuli and the primes during this phase of training is shown in Figure 4.

This phase took 75 sessions (7,500 trials) for Samantha to reach a criterion of 70% accuracy on the primes for two consecutive sessions. Based on the number of sessions it took Samantha to reach criterion, it appeared that the parallelogram and square forms were more difficult to discriminate than the background stimuli. The mean of the median response latencies for the 75 sessions were significantly faster on the correct primes (583 ms) than on the correct background trials (630 ms), *t* (74) = 3.345, p < .001. The mean of the median response latencies were also significantly faster on the incorrect primes (568 ms) than on the incorrect background trials (623 ms), *t* (74) = 6.885, p < .001. It is likely that these differences in response time resulted from inattention on these trials. That is, it is likely that Samantha recognized these stimuli as being difficult and responded to them faster so as to advance to the next programmed trial where the stimuli were easier to discriminate.

Phase 9. Test for Perception of Illusory Contours. Samantha chose the matching illusory square on 17 of the 32 trials on which it was presented (z = .341, *p* = .366) and the parallelogram on 18 of the 32 trials on which it was presented (z = .681, *p* = .25). In both cases there was no evidence that she matched the solid figure to the illusory one. However, for the trapezoid, the comparison stimuli that had not been experienced prior to the test, she chose the matching trapezoid on 21 of 32 trials (z = 1.82, *p* = .034). That is, Samantha received the parallelogram prime as the sample, with the parallelogram and square as the comparisons. It is possible that because Samantha had such difficulty discriminating the parallelogram from the square that this hindered her ability to choose the correct match on the parallelogram and square test trials.

The mean of the median response latencies for the 17 sessions on correct priming stimuli (575 ms) were significantly faster than on correct background stimuli (656 ms), *t* (16) = 7.335, p< .001, as well as on the incorrect primes (605 ms) than on the incorrect background trials (672 ms), *t* (16) = 3.893, p< .001. These data again indicate inattention to the priming stimuli. Samantha’s response latencies during the test are summarized in Table 3.

Table 3. Samantha's Response Latencies During the Tests on the Different Stimulus Types.

Type of Trial	**Overall Percent Correct**	**Response Time (ms) Correct**	**Response Time (ms) Incorrect**
		Mean of the Medians	**Mean of the Medians**
Background	76%	656	672
Primes	53%	575	605
Test Square	53%	638	617
Test Parallelogram	56%	596	623
Test Trapezoid	69%	654	653

The abstract form background MTS task was acquired after many trials by Samantha and not at all by Sophie. This was true although both animals previously mastered the MTS task with colored and grayscale pictures. This could have resulted from several factors. Both color and grayscale photographs are visually more complex (e.g. greater variety of identifying attributes) than the abstract forms used here. It is possible that during the extensive training with the grayscale photographs the monkeys developed a strategy for solving the matching task that was specific to these stimuli and could not be readily generalized to more simple forms. That is, the strategy used in matching the pictures may have been ineffective with the abstract forms. There were multiple shades of gray in the pictures, but only two in the test forms, limiting the amount of information available for recognition. In addition, the abstract forms in this experiment had many more features in common as compared to those in the grayscale pictures. This could have changed the nature of the task. The monkeys could have solved the initial MTS tasks with the color and grayscale photographs by using a feature-based strategy, a strategy some investigators consider the basis of pattern recognition (e.g. Beiderman, 1987).

Samantha failed to show above chance criterion on the Square and Parallelogram test stimuli, the two comparisons she had previously experienced. Samantha's difficulty discriminating the square and parallelogram during training could have resulted from the similarity of the two comparison stimuli. It is worthwhile to mention that the square and parallelogram had almost identical areas and had the same color contrast. Of particular interest was that when shown the illusory trapezoid for the first time, during the test, Samantha more frequently chose the matching solid trapezoid than the non-matching, up-side-down comparison. These data suggest that experience with the parallelogram and square as primes detracted from her performance when these forms were presented as illusory forms on test trials. The finding that her latencies were significantly faster on the primes than on the background stimuli suggests that she did not attend to the forms on the trials on which the square or parallelogram appeared during the test.

Not only was the trapezoid a novel shape, it was also the only stimulus for which the slanted lines appeared in opposite directions. Although Samantha had received training with multiple angle stimuli on the background trials, they were always oriented in the same direction (i.e. slanted to the right). The trapezoid test added a novel element, a slanted line oriented to the left. As such the comparison stimuli that appeared with the trapezoid may have been easier to tell apart.

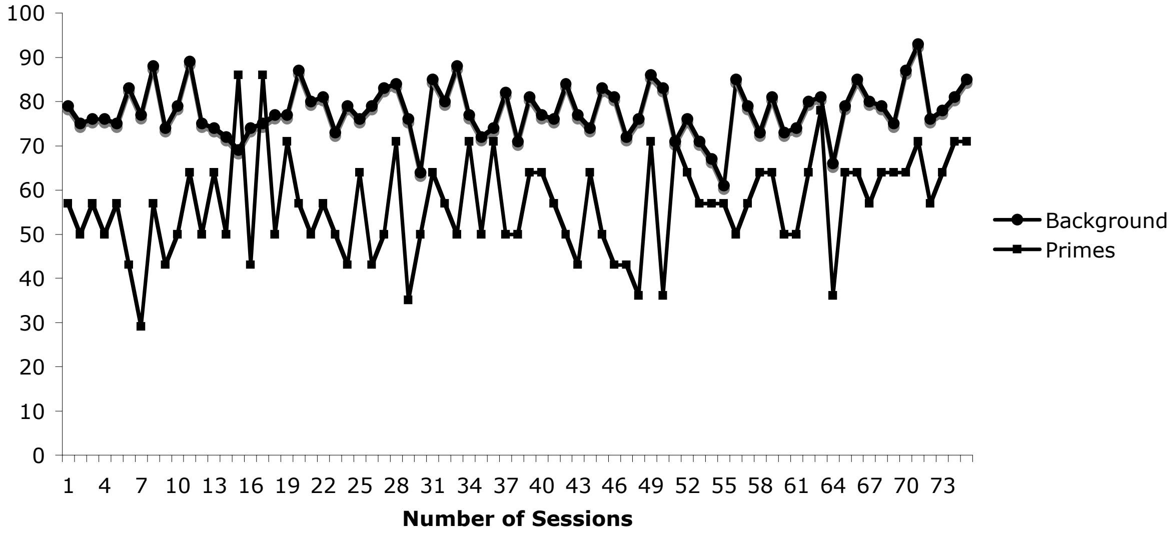


Figure 4. Shows Samantha’s performance on the background stimuli and primes for Phase 8 of Experiment 1.

EXPERIMENT 2A

Tests With Novel Kanizsa Patterns: Because Samantha's performance was best on the test type for which there was no prime, a follow-up test using the same procedure as Experiment 1 was done without the primes and with three novel Kanizsa figures as test stimuli—the inverted triangle, rectangle, and diamond patterns shown in Figure 5. This was done to determine whether her performance on the initial test was hindered by the use of the priming stimuli. The base of the illusory triangle measured 3 cm, with each side measuring 2.5 cm, and its height 1.5 cm. The dimensions of the illusory rectangle were 3.3 cm x 1.3 cm and each side of the diamond measured 2 cm in length.

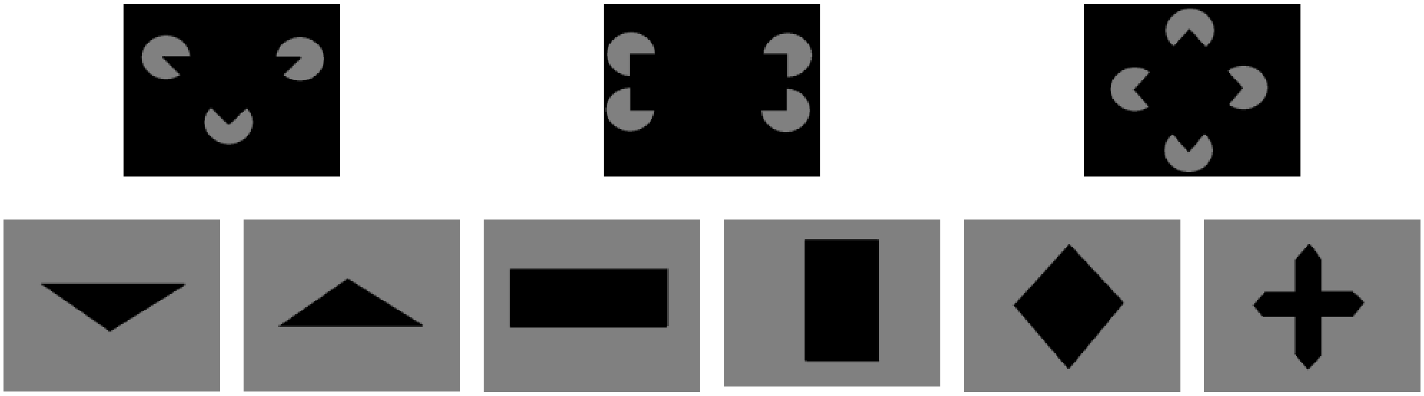


Figure 5: The three novel Kanizsa test stimuli (samples + comparisons).

Method

During this phase, as before, 80% of the trials were followed by feedback. There were eight background forms with a pacman (7 with feedback and 1 non-feedback) and 86 geometric grayscale background stimuli (73 with feedback and 13 non-feedback). The three Kanizsa patterns were presented on test trials—two presentations of each during each 100 trial session. Once again, one additional session to make up for trials on which a choice was not made was given after 16 sessions so that there were 32 presentations of each of the three Kanizsa figures.

Results and Discussion

Averaged across the 17 sessions in which the test stimuli were presented, Samantha chose the matching illusory triangle on 19 of the 32 trials on which it was presented (z = 1.065, *p* = .143) and the diamond on 14 of the 32 trials on which it was presented. In both cases less than 21 choices required to reject the hypothesis that selection of the form corresponding to the illusory form was due to chance. However, for the rectangle, she chose the matching rectangle on 22 of the 32 trials (z = 2.13, *p* = .016) suggesting that, for this stimulus, she may have based her choice on the pattern that appeared most similar to the illusory rectangle. Samantha's averaged performance for the 17 sessions on the background task was 78%. The mean of the median response times for correct background trials (666 ms) were not significantly different from the test stimuli (700 ms), *t* (16) = 1.805, p > .05. Latency data during this phase and are summarized in Table 4.

Table 4. Samantha's Response Latencies During the Test with Novel Test Stimuli.

Type of Trial	**Overall Percent Correct**	**Response Time (ms) Correct**	**Response Time (ms) Incorrect**
		Mean of the Medians	**Mean of the Medians**
Background	78%	666	681
Test Triangle	59%	701	638
Test Diamond	44%	697	722
Test Rectangle	69%	703	689

When shown the illusory rectangle, Samantha more frequently chose the matching solid horizontal rectangle than the non-matching vertical comparison. This was the only stimulus for which her choice may have been based on a match between the illusory and actual contour. One possibility as to why the rectangle was the only test that was chosen significantly more than chance could have been that Samantha was paying attention to the location of the pacmen rather than the illusory contours that emerge between the forms when properly aligned. Clearly, whatever strategy she used to resolve the illusory rectangle was not generalized to the triangle and diamond test.

It is interesting that Samantha's performance was below chance on the diamond test. Perhaps this was because the non-matching comparison differed substantially from patterns previously experienced, drawing her attention to it.

Although performance on the trapezoid in Experiment 1 and the rectangle in Experiment 2 suggest that Samantha may have seen the illusory contour, the results of this experiment, an experiment in which the three patterns were novel weakens this conclusion.

EXPERIMENT 2B

In the previous tests the illusory form was shown as the sample. In order to examine whether this could have been responsible for her failure to obtain clear evidence for the Kanizsa illusions, a follow-up test (Experment 2B) was given for 8 sessions in which the sample stimulus for each test type was the whole form (i.e. the inverted triangle, rectangle, and diamond form) and the correct match was the stimulus with the pacmen, creating the illusory contour. The incorrect matches were the non-inducing pacmen in the same location (see Figure 6). During this phase, as before, 80% of the background trials were followed by feedback. There were eight background forms with a pacman (7 with feedback and 1 non-feedback) and 86 geometric grayscale background stimuli (73 feedback and 13 non-feedback). Each of the test stimuli were presented twice within a session, for 8 sessions, without feedback. Because there were only 16 test trials for each pattern the probability that the choices of the matching pattern was greater than chance was rejected if on 13 or more trials the matching form was selected. In addition to the choices made, response latencies on correct and incorrect trials were also recorded in order to determine whether different strategies occurred when the response was or was not correct.

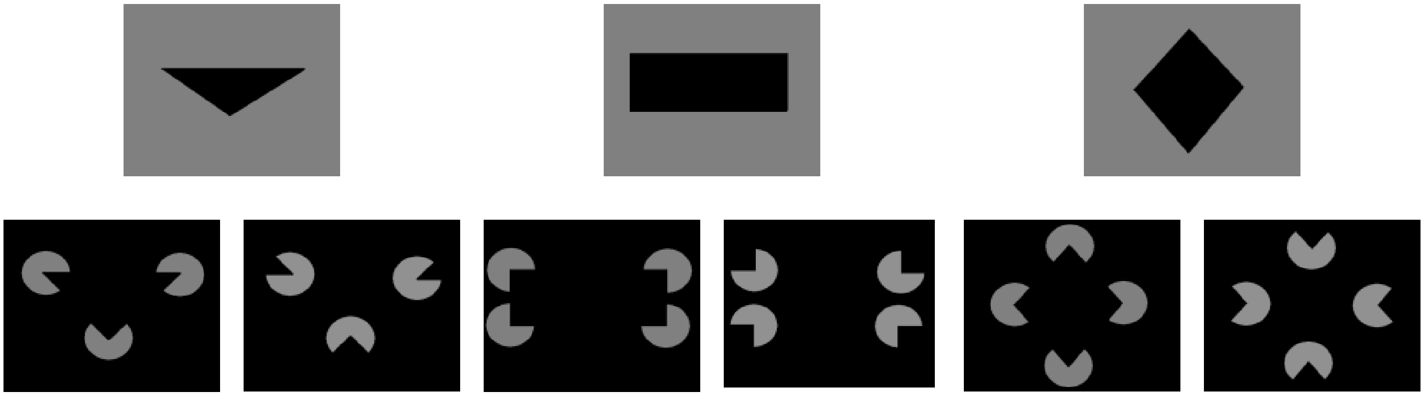


Figure 6: Follow up test for illusory contour perception.

Samantha failed to show above chance performance for each test type. She chose the matching illusory triangle and diamond on 7 of the 16 trials on which they were presented and the rectangle on 6 of the 16 trials on which it was presented. Her averaged performance after the 8 sessions was 78% on the background task. The mean of the median response times for the 8 sessions on correct background trials (686 ms) were significantly faster than on correct test stimuli (823 ms), *t* (7) = 3.986, p < .01. Longer latencies on the test stimuli suggest confusion or difficulty on these trials. Response latencies for background and test stimuli are summarized in Table 5.

Table 5. Response Latencies: Follow-Up Test

Type of Trial	**Overall Percent Correct**	**Response Time (ms) Correct**	**Response Time (ms) Incorrect**
		Mean of the Medians	**Mean of the Medians**
Background	78%	686	681
Test Triangle	44%	773	694
Test Diamond	44%	855	717
Test Rectangle	38%	843	788

If Samantha experienced the illusions we would have expected to see above chance performance for each test. In particular, we would have expected to see above chance performance on the rectangle test, the test for which she showed above chance performance when the illusory form was shown as the sample. By rearranging of the sample and comparison stimulus presentation (i.e. illusory form as sample to a solid form as sample) we may have diverted her attention away from the illusion and toward the general shape of the sample. That is, the pacmen for both comparisons occupied the same location, with the orientation of the correct matching illusory figure had the contours "facing in" while the incorrect matching figure had the contours "facing out". It is therefore possible that Samantha was attending to overall area, disregarding the contours established by the pacmen, and basing her choices either on the area outlined by the pacman or the position of the pacmen, rather than the relationship established between the pacmen forms when properly oriented. A strategy such as this would account for her chance performance for each test. In addition, by presenting the solid form first we set up a situation that was similar to what was experienced on background trials. In doing so, it is possible that Samantha's expectations of what the comparison stimuli should be were violated when she was presented with the pacmen displays rather than solid forms. This manipulation could have interfered with her short-term recall of what was experienced during the sample phase; therefore disrupting her ability to accurately choose the matching comparison. Finally, it is also possible that Samantha might have been avoiding the correct answer. That is, she could have been avoiding the correct orientation of the pacmen, if she had identified these stimuli as the patterns that were previously not rewarded, therefore choosing the more novel condition.

EXPERIMENT 3

The purpose of this experiment was to examine the possibility that the illusion was not experienced earlier because of the spacing between the pacmen. In work with human participants, Kovacs (2000) found that children had difficulty integrating elements that were spaced too far apart, while performance in adults did not depend on contour spacing but did depend on the density of elements. Similarly, in work with chimpanzees and humans, Fagot and Tomanaga (2001) found that chimpanzees were more sensitive to element spacing on a two alternative forced choice task in which the subjects had to discriminate Kanizsa illusory squares and non-illusory squares. They also found that human performance on this task was unaffected across spatial manipulations but tended to exhibit a global strategy overall. These experiments provide evidence that as the spacing between local elements gets closer, performance increases on global shape recognition tasks. Details for this experiment are described next.

Method

Increasing the Strength of the Illusion. In this experiment, an attempt was made to increase the strength of the illusion by increasing the size of the pacmen from 1 cm to 1.5 cm in diameter while maintaining the size of the original illusory contours and matching forms. Using this manipulation the degree of spacing between the pacmen elements was decreased. In other words, the support ratio, the ratio of the length of the physical contour to the length of the illusory contour, was increased by increasing the size of the pacmen (see Singh, Hoffman, & Albert, 1999; Shipley & Kellman, 1992). The ratio of the base of the triangle was increased from 40% to 57%, and each of the sides of the triangle was increased from 55% to 86%. The ratio of the length of the illusory rectangle was increased from 32% to 43% and the width from 88% to 95%. Finally, the ratio of the diamond was increased from 64% to 91%.

Re-Test for the Perception of Illusory Contours: The procedure and test stimuli were identical to those used during Experiment 2 (i.e. inverted triangle, rectangle, and diamond) except closer spacing of the pacmen as a result of their size enhancement as shown in Figure 7. During this phase, as before, 80% of the trials were followed by feedback. There were eight background forms with a pacman (7 with feedback and 1 non-feedback) and 86 geometric grayscale background stimuli (73 feedback and 13 non-feedback). The three Kanizsa patterns shown in Figure 7 were presented as sample stimuli on test trials—two presentations of each during each 100 trial session. As stated previously, the probability that the choices of the matching pattern were greater than chance was rejected if on 21 or more trials the matching form was selected.

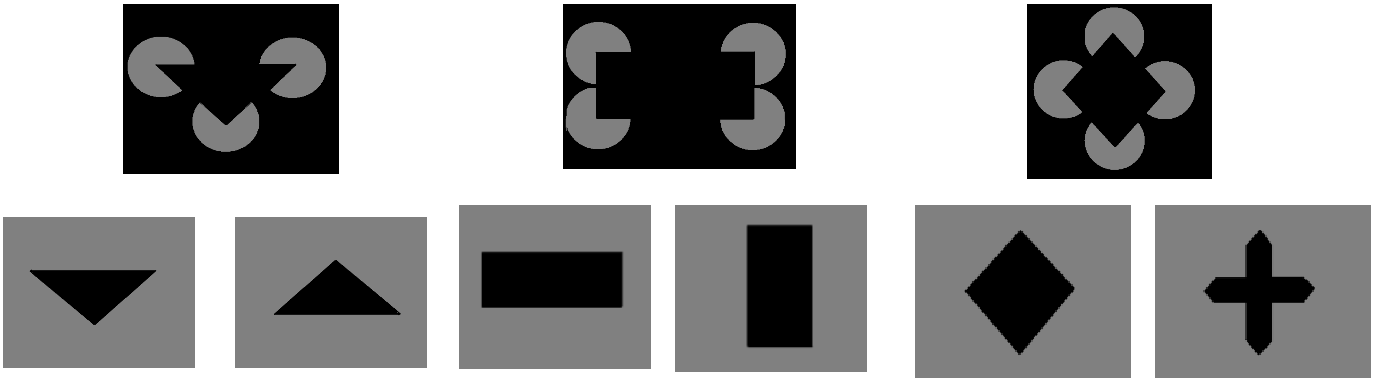


Figure 7: Test stimuli with increased pacmen size.

Results and Discussion

Samantha chose the matching illusory triangle on 19 of the 32 trials on which it was presented (z = 1.065, *p* = .143), the matching diamond on 19 of the 32 trials on which it was presented (z = 1.065, *p* = .143), and the matching rectangle on 19 of 32 trials on which it was presented (z = 1.065, *p* = .143). When the data were combined, Samantha chose the correct matching stimulus on 57 of the 96 trials (z = 1.84, *p* = .033). These data are consistent with what has been observed with chimpanzees (Fagot & Tomanaga, 2001). In addition, it appears that non-human primates are more sensitive to element spacing than human adults, and that the strength of perceived contours may depend largely on the spacing and alignment of pacmen (Shipley & Kellman, 1992). These data suggest that non-human primates perceive visual stimuli similar to what has been shown in young children (Kaldy & Kovacs, 1999; Kovacs, 2000; Kaldy & Kovacs, 2003).

After 16 sessions, Samantha's averaged performance on the background task was 79%. Latencies on test stimuli were recorded to determine whether performance across

16 sessions was more efficient for the correct test with larger pacmen (676 ms) versus the correct original forms (700 ms). This difference was not significant *t* (15) = 1.683, p > .05. The mean of the medians were also compared on correct background (693 ms) and correct test trials (676 ms), *t* (15) = 1.296, p > .05. This difference was also not significant. The latencies for this experiment are summarized in Table 6.

Table 6. Response Latencies on Background and Test with Larger Pacmen.

Type of Trial	**Overall Percent Correct**	**Response Time (ms) Correct**	**Response Time (ms) Incorrect**
		Mean of the Medians	**Mean of the Medians**
Background	79%	693	706
Test Triangle	59%	754	744
Test Diamond	59%	632	721
Test Rectangle	59%	643	694

Samantha’s performance on each of the test types was identical. There was some evidence that this manipulation made the illusory contours more pronounced when the data for each test type were combined. However, other factors could have been responsible for her failure to choose the form that most closely matched the sample. She had been trained to make an identity match. In tests for the illusion a “correct” response required that she choose the comparison stimulus that was most similar to the sample on the test trials.

EXPERIMENT 4
SIMILARITY MATCHING

Even if the contour was seen in the illusion, the matching solid form was not identical to the sample. In order to examine whether lack of similarity matching training was responsible for Samantha's failure to obtain clear evidence that she experienced the illusory contours, it was hypothesized that training on a similarity matching-to-sample task would remedy some of the confusion and/or difficulty that Samantha may have encountered on the test trials.

Phase 1: Training with Simple Forms (50% old, 50% new). Prior to introducing similarity matching, training with less complex background stimuli was introduced to increase Samantha's overall performance on the background task. Using the same procedure as in Experiment 1 (Phase 1), 50 new background forms replaced 50 of the original background stimuli for a total of 100 trials per session. The less complex stimuli consisted of stimuli with fewer angles and a larger color contrast between the background and the figure (see Figure 8). These forms were the same that were used for Sophie during Experiment 1. Criterion for this phase was 80% or better on two consecutive sessions.

Samantha reached criterion on this phase after 4 sessions (400 trials). Overall performance on the original background stimuli was 78% correct and on the less complex forms performance accuracy was 88%. The mean of the median response times were compared on all 4 sessions for the less complex correct trials (672 ms) and for the original more complex background forms (694 ms), a non-significant difference, *t* (3) =

1.734, p > .05, suggesting that whatever strategy she was using to recognize the more complex forms was also applied to the new forms.

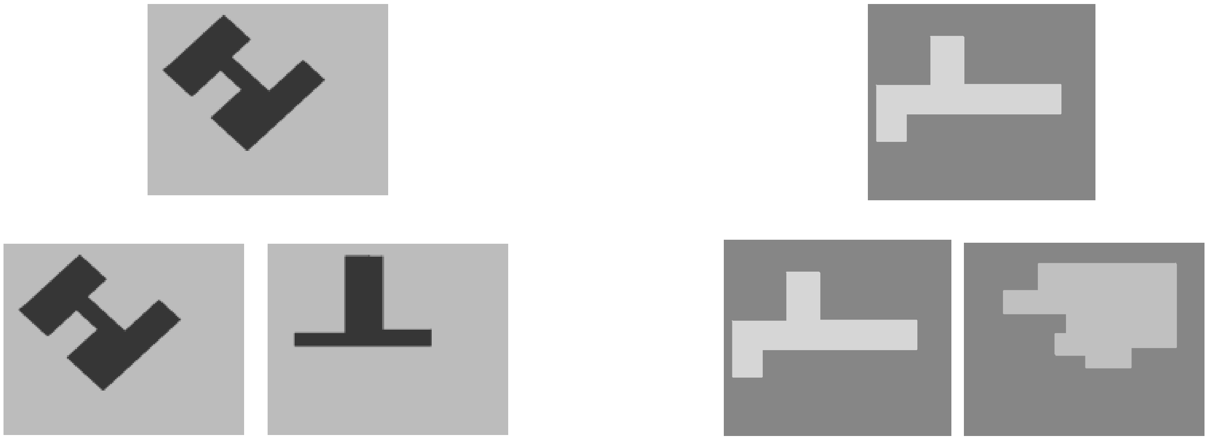


Figure 8: Examples of “simple” abstract grayscale forms.

Phase 2: Training with 100% Simple Background Stimuli. Following criterion on phase 1, the remaining original 50 background stimuli were replaced by a new set of 50 simple stimuli so that all 100 trials consisted of the less complex background stimuli. She was trained for seven sessions on these stimuli.

For the seven sessions (700 trials) of training on the simpler stimuli Samantha’s overall performance was 84% correct, exceeding the criterion of 80% correct on all sessions.

Phase 3: Similarity Matching with Pacman Elements. A possible reason for inconclusive evidence that Samantha saw the illusion when previously tested, was that even if the illusory contour was seen, the test for the illusion involved a similarity match. That is, the pacman did not appear in both the sample and the matching comparison form. In order to train Samantha to pay attention to the background form, rather than the pacmen, on 10% of the trials, one non-contour inducing pacman appeared in the sample but not in the comparisons. Once performance on this task was consistently above 70%, an additional 10 stimuli with one non-contour inducing pacman were added so that 20% of the stimuli consisted of samples with one simple abstract form and one non-contour inducing pacman form. Following criterion of 70% or better on two consecutive sessions, 10 more similarity matches were added for a total of 30. Except for these additional 10 stimuli, the samples consisted of one simple abstract form and 2 non-contour inducing pacmen forms (see Figure 9).

Samantha met criterion on all phases of similarity matching with pacmen elements (10, 20, and 30%) after a total of 12 sessions (1,200 trials). The latencies were recorded to determine whether there was a significant difference when responding correctly to stimuli with pacmen in the sample (662 ms) versus stimuli that did not contain pacmen (689 ms). After 12 sessions, this difference was significant t (11) = 2.115, $p < .05$.

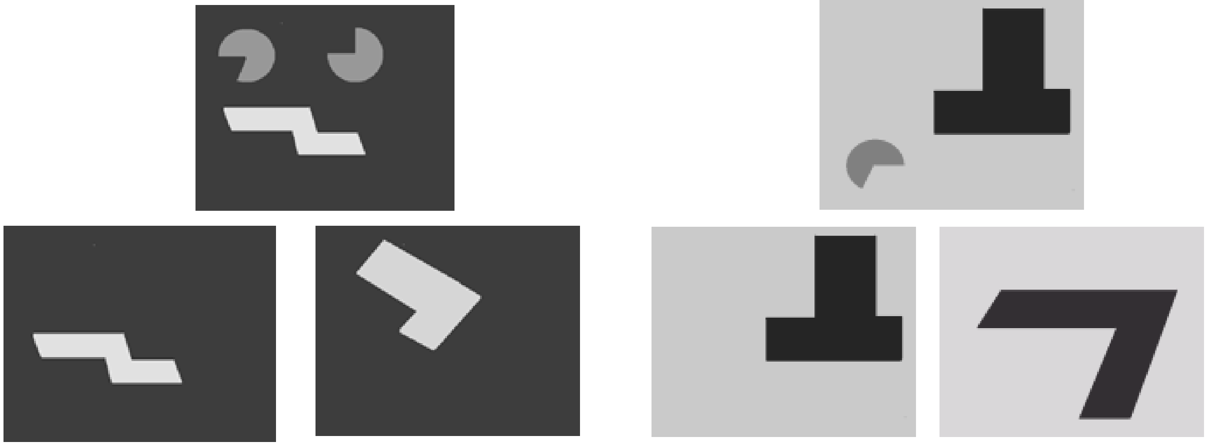


Figure 9: Examples of non-contour inducing pacmen in the sample stimulus and the matching and non-matching comparison forms.

Phase 4: Similarity matching – Grayscale Contrast Reversal Training. In addition to the presence of the pacmen in the sample but not the comparisons, the test trials differed in terms of contrast. On test trials the sample consisted of light gray pacmen on a black background, while the comparison stimuli consisted of a solid black form on a light gray background. Therefore, in addition to training with pacman forms in the sample but not in the comparison stimuli, Samantha was trained with stimuli where the contrast was reversed in the sample and comparison stimuli (see Figure 10). That is, if the sample was a dark gray figure on a light gray background then the correct match would be the same light gray figure on a dark gray background. The non-matching stimulus also had the same color contrast as the correct match so that correct responses were based on the form. That is, it was expected that reversing the contrast would require Samantha to focus on the form and not the difference in brightness of the figure and background. For this phase 15 contrast reversal stimuli were initially added to the stimuli used in the previous phase so that 20% of the trials had 1 pacman form in the sample, 10% of the trials with 2 pacmen in the sample, the contrast was reversed in 15% of the trials, and 5 of the reversal stimuli had 3 or 4 non-contour inducing pacmen in the sample. Again, the pacmen did not appear in the comparison stimuli.

Samantha met criterion on this phase after 44 sessions (4,400 trials). Accuracy and latencies were recorded to examine whether performance differed across similarity training manipulations. Samantha's overall performance was 82% on the background stimuli without pacmen, 68% on the reversal grayscale stimuli, 78% on the background stimuli with one pacman, and 65% on the background stimuli with two pacmen in the sample. The mean of the median response times for the 44 sessions were compared on the correct background without pacmen (659 ms) versus correct background with one pacman form (679 ms), *t* (43) = 1.460, p > .05, an nonsignificant difference. However, latencies significantly differed on correct background (659 ms) versus correct background with two pacmen (710 ms), *t* (43) = 4.000, p < .001, and for correct background (659 ms) versus correct reversal stimuli (713 ms), *t* (43) = 5.229, p < .001. These data indicate that the addition of pacmen and reversing the contrast made the task slightly more difficult. Samantha's chance performance of 68% correct on the reversal grayscale stimuli suggests that she might not have been matching on the basis of form on these trials. Instead, it is possible that Samantha was paying attention to the total amount of "lightness" or "darkness" of the sample stimuli. It is therefore reasonable to consider that when the contrast was reversed during the comparison phase of each of these trials, Samantha became confused and treated these trials as a novel, more difficult problem. A summary of the response latencies for this phase are summarized in Table 7 below.

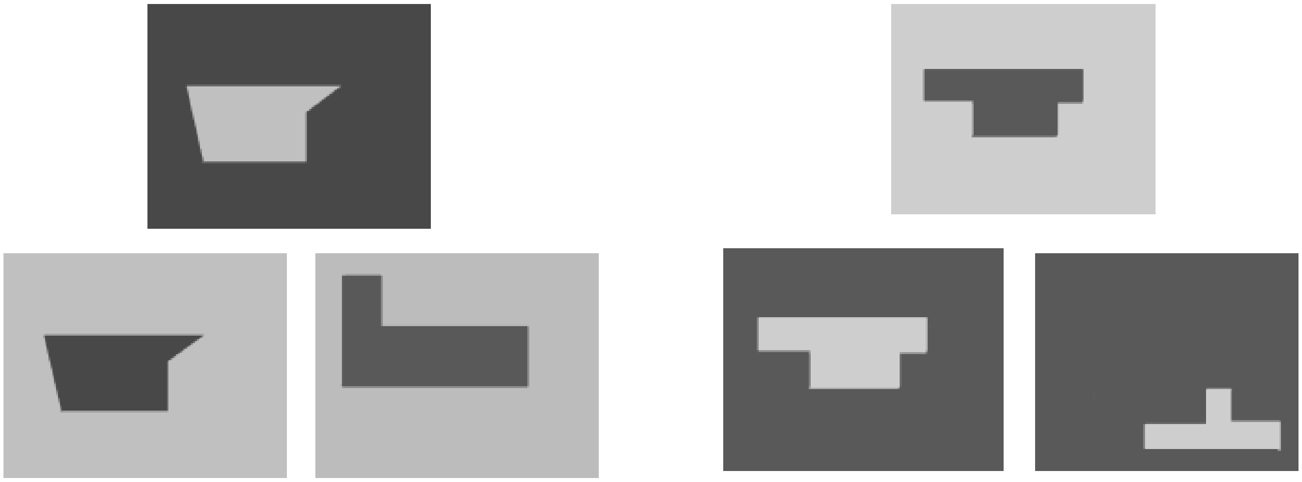


Figure 10: Examples of reversal stimuli.

Table 7: Latencies on Contrast Reversal Training Stimuli for Samantha.

Type of Trial	**Percent Correct**	**Response Time (ms) Correct**	**Response Time (ms) Incorrect**
		Mean of the Medians	**Mean of the Medians**
Background	82%	659	712
1 pacman	78%	679	681
2 pacmen	65%	710	703
Reversal stimuli	68%	713	701

Phase 5: Background Contrast to Match Test Contrast + 100% Feedback (Samantha). Once performance on phase 4 was consistently above chance the contrast of the background stimuli was manipulated to match that of the test stimuli. This manipulation was done so that Samantha could have training with contrast reversal that was identical to those that were experienced on test trials (see Figure 11). Due to the increased difficulty of this task, a correction procedure was used. That is, after incorrect responses the trial repeated up to ten times, or until a correct response for this trial was made, before advancing to the next programmed trial.

Samantha met criterion after 20 sessions (2,000 trials). Her averaged performance after the 20 sessions on reversal stimuli without pacmen was 68% and 66% on trials with pacmen. The mean of the median response times for the 20 sessions were compared to determine whether there was a significant difference when responding correctly to reversal stimuli with pacmen in the sample (702 ms) versus reversal stimuli that did not contain pacmen (715 ms). This difference was not significant t (19) = .595, p > .05. Once again, Samantha's chance performance on the reversal stimuli indicate lack of attention to form, which is essential for the discrimination of illusory contours.

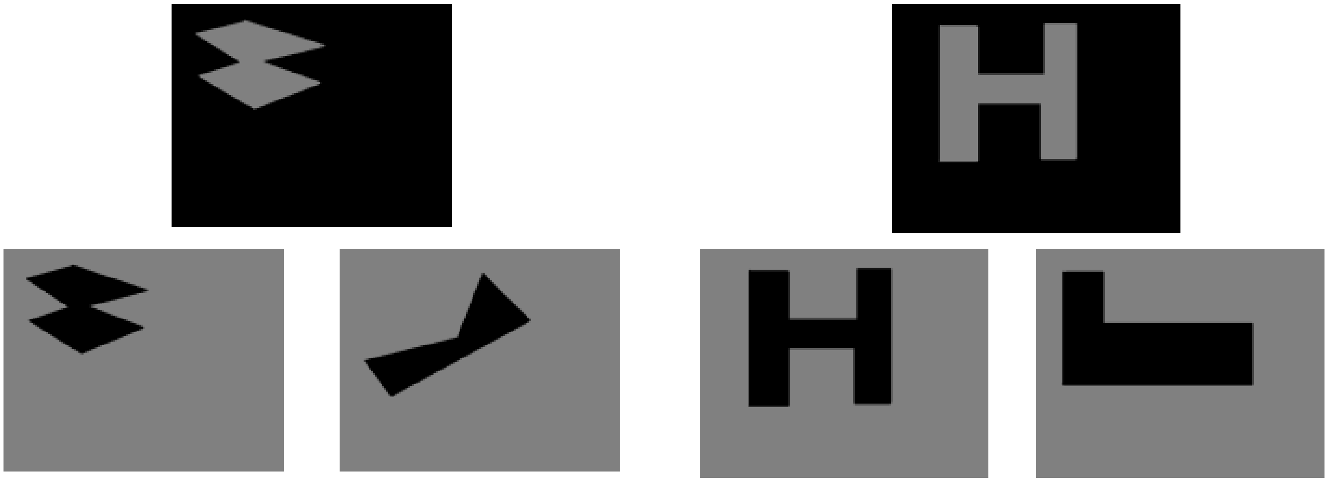


Figure 11: Examples of background stimuli with the same positive and negative contrast as the test stimuli.

Preliminary Investigation of Alternative Hypotheses

In Experiment 1 Samantha showed above chance performance with the illusory trapezoid and in Experiment 2 with the illusory rectangle test. In Experiment 3 Samantha showed significant evidence for the perception of the inverted triangle, rectangle, and diamond with the enlarged pacmen elements when the data for all three illusory forms were combined. When each of these forms was examined independently, performance was at chance. Looking beyond the support ratio effects observed during Experiment 3, it is possible that Samantha failed to show sufficient evidence for the perception of illusory contours with the original spacing because of differences between the training and testing conditions. For example: the background task required identity matching, while the test stimuli required similarity matching. Due to time constraints, it was not possible to train Samantha to criterion as had been done in the previous experiments. The following is a brief summary of the training and preliminary follow-up tests given to Samantha.

ALTERNATIVE 1

Method

Samantha was given 4 sessions with 80% feedback, using the same simple geometric background forms used during Phase 5 of similarity matching training. The six Kanizsa patterns (i.e. diamond, inverted triangle, rectangle, square, parallelogram, and trapezoid) were presented as sample stimuli twice per session, once where the pacmen were gray on a black background and once where the pacmen were black on a gray background. Along with the test stimuli, a corresponding control test was also administered within the same test session on days 1 and 3. For the control test, the sample stimulus consisted of black or gray pacmen facing out (non-contour inducing) on a gray or black background while the comparison stimuli consisted of the “correct” form versus a similar form. Chance performance was expected on these stimuli if the monkey was in fact responding to the illusion. That is, if the Samantha was simply responding to the location/spatial layout of the pacmen forms we would have expected her to choose the form that matched the physical location of the stimuli (for example choosing the horizontal rectangle over the vertical one when the location of the non-contour inducing pacmen were located horizontally). Chance performance on these control trials were indicative of confusion implying that the monkeys might have been seeing the contours rather than simply responding to the location of the pacmen elements.

Results

Samantha failed to show evidence of perception of the illusory contour choosing the illusory square, parallelogram and trapezoid on 3 of 8 trials of which each of these stimuli were presented. The inverted triangle and rectangle were chosen on 5 of the 8 trials and the diamond on 4 of the 8 trials. Samantha was correct on only 69% of the background task and 46% on the non-illusory test stimuli. These data are difficult to determine due to below criterion performance on the background task, which are indicative of confusion.

ALTERNATIVE 2

Method

Failure to show evidence of the illusion after being trained with similarity matching could have resulted from lack of training for which both comparison stimuli differed only in orientation. Therefore, Samantha was trained with the correct match in the same orientation as the sample and the incorrect comparison in a slightly different orientation. The new training stimuli used were an arrow, clover, fork, heart, oval, spade, and triangle Each of the new shapes was presented twice within a session, once as a gray shape on a black background and once as a black shape on a gray background. These are shown in Figure 12 along with the correct and incorrect comparison. Five 100 trial sessions were administered with the 14 new training stimuli randomly interspersed among the 86 simple geometric forms used previously followed. Samantha was returned to 100% feedback with correction only for this training. The trial was repeated up to 10 times following an error. This was followed by seven additional sessions in which 50 simple geometric background stimuli had at least 2 non-contour forming pacmen, either in the sample or in the comparison. The remaining 50 stimuli consisted of 22 older background similarity matching stimuli and 28 of the novel stimuli (each of which were presented twice within a session).

Results

Samantha was at 50% correct on the new stimuli and 71% correct on the older background stimuli. Samantha's overall performance after the additional sessions on the background forms with pacmen was 57%, background forms without pacmen was 72%, and performance on the 14 new stimuli was 58%.

ALTERNATIVE 3

For the final re-test for perception of the illusory contours each of the test types (square, parallelogram, trapezoid, inverted triangle, and diamond) were pseudo-randomly inserted into the previous background task. Each test was presented twice within a session. There were two different ways in which the test stimuli were administered on alternating days. The first condition consisted of gray contour-inducing pacmen as the sample on a black background and the comparison stimuli were black forms on a gray background and the second presentation within a session consisted of black contour-inducing pacmen on a gray background with gray forms on a black background for the comparisons (Figure 13). On test sessions 1, 3, and 5 a corresponding control test, as described earlier, was also administered within the same test session. On test sessions 2 and 4 one sample was a black form on a gray background and the two comparison stimuli consisted of properly oriented gray pacmen (forming the correct illusory contour) versus the pacmen facing out (non-contour inducing) on a black background, while the other sample was the same except the contrast was reversed.

Results

Evidence required to demonstrate existence of perception of the illusory contours for each test was choosing the correct matching form 8 out of the 10 trials for which it was presented. Samantha chose the matching square, parallelogram, rectangle, and diamond on 5 of the 10 trials on which they were presented, and the trapezoid and triangle on 3 of the 10 trials on which they were presented. Samantha was at 72% on the background task without pacmen, 56% on the background with pacmen, 62% on the 14 new shapes and 42% on the non-contour inducing test stimuli. Based on these results we do not have sufficient evidence to confirm that Samantha perceived the illusory contours similar to human subjects when presented with similar forms.

Because the monkeys did not have enough time to reach above chance criterion for these stimuli before they were switched to the final test it is not surprising that they did not perform as well when re-tested with the test stimuli. Furthermore, introducing a variety of changes to the task, without providing the monkeys sufficient time to acquire them appeared to have hindered their overall performance on the matching task.

FOLLOW-UP: SOPHIE

Sophie was reintroduced to the experiment, trained for 17 sessions on the original MTS task with grayscale pictures (i.e. trees, animals, insects, nature, etc). Then, she was trained for 32 sessions with the simple abstract forms experienced during Experiment 1. She was then trained for 13 sessions where 10 additional simple forms were introduced so that 20% of the stimuli consisted of the abstract grayscale forms. In addition, 5 of the abstract forms per session had 2 non-contour inducing pacman forms in the sample. The correct matching comparison was the same form that matched the form that was experienced during the sample phase minus the pacmen and the incorrect comparison stimulus was initially a gray dot. The single gray dot was only used as the incorrect comparison on the trials for which the pacmen forms appeared in the sample but not in the comparison, in an effort to make the two comparison's easier to differentiate. Following the 13 sessions, Sophie was given the same tests as Samantha (phase 5 of Similarity Training) and subsequently also showed no evidence of the illusion.

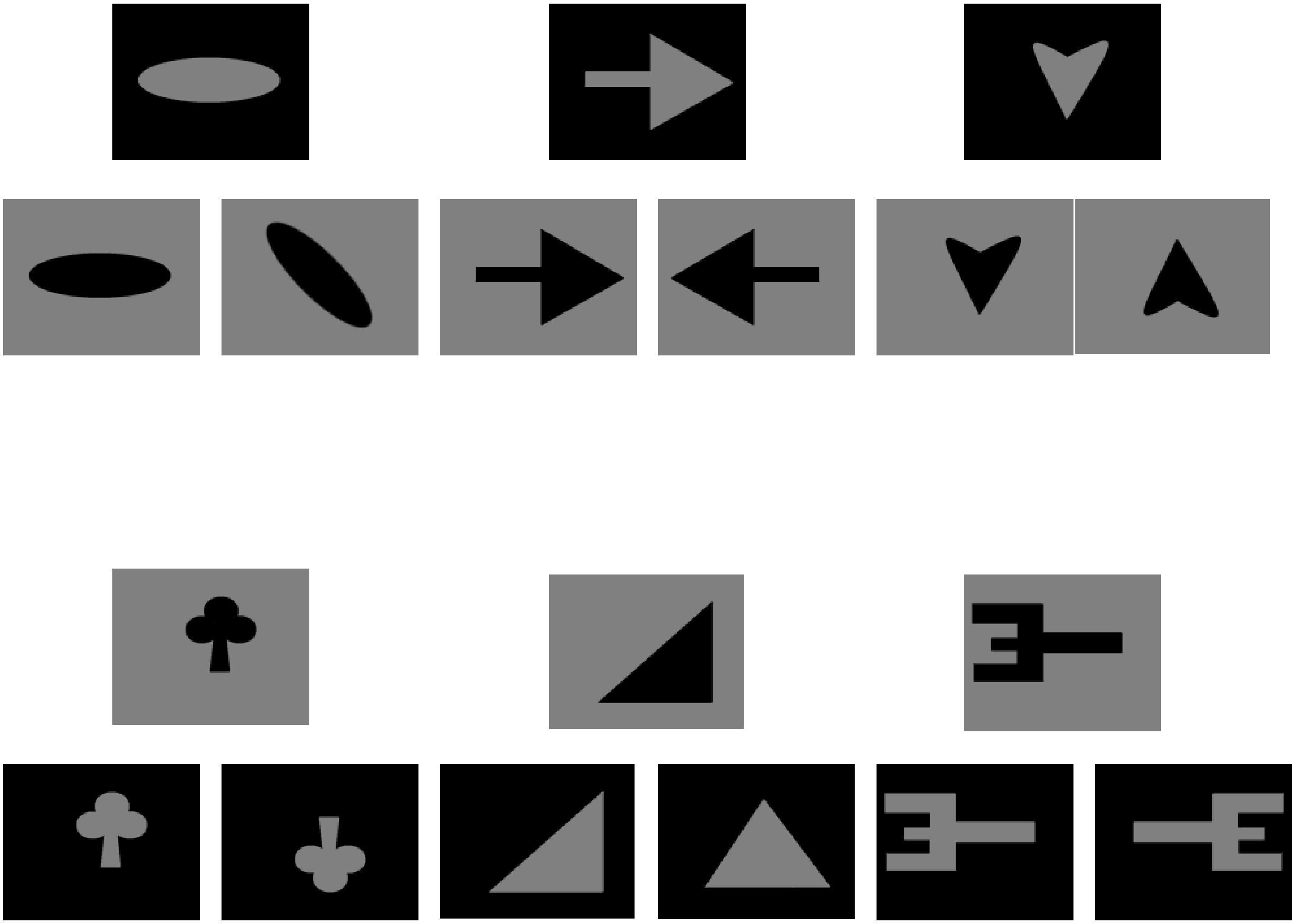


Figure 12: Examples of 6 of the 14 simple form reversal stimuli with comparisons.

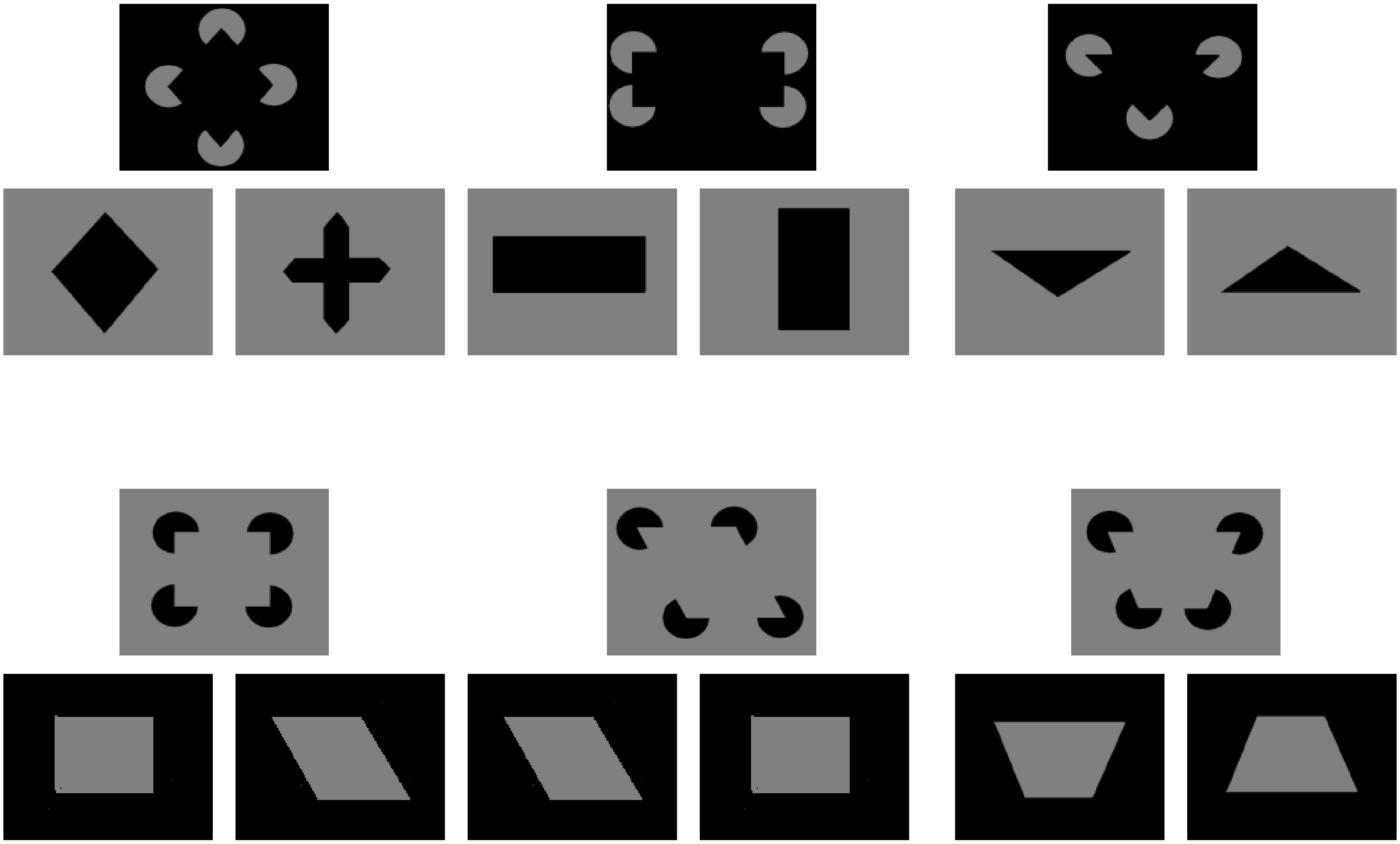


Figure 13: Examples of test stimuli.

Sophie chose the matching square on 6 of the 10 trials on which it was presented, the correct parallelogram, trapezoid, and triangle on 4 of 10 trials on which they were presented, and the rectangle and diamond on 3 of the 10 trials on which they were presented. Overall performance on the background task was 67% correct. Performance on the background with pacmen forms was 62%, on the background without pacmen was 84%, and on the background with 14 new shapes was 53%.

Chapter IV: General Discussion

There was some evidence early in the study that suggested that Samantha perceived the illusion on the trapezoid (first test) and on the rectangle (second test). On subsequent tests she failed to show sufficient evidence for each of the individual illusory shapes. However, there was a significant difference when the spacing between the pacmen forms was reduced (combined data from illusory triangle, rectangle, and diamond: $z = 1.84$, $p = .033$). These data are consistent with previous research on the effects of support ratio and illusory contour integration (Kellman & Shipley, 1991; Shipley & Kellman, 1992; Singh, Hoffman, & Albert, 1999; Fagot & Tomanaga, 2001). Looking at the data overall there were 444 trials on which the illusion could have been demonstrated. Of these the correct match was chosen 232 times ($z = .946$, $p = .171$). Samantha chose the correct matching square 25 of the 50 trials on which it was presented, the correct matching parallelogram on 26 of the 50 trials, the correct matching trapezoid on 27 of the 50 trials, the correct matching triangle on 53 of the 98 trials, the correct matching diamond on 49 of the 98 trials and she chose the correct matching rectangle on 56 of the 98 trials on which it was presented. Failure to find the sufficient evidence for the perception of illusory contours could have resulted from a variety of factors. These are discussed below.

The overall the findings of this study are inconclusive with respect to whether a rhesus macaque monkey can behaviorally perceive illusory contours of the Kanizsa type. Thus far there have been no definitive behavioral data on the perceptual ability to resolve contours of the *Kanizsa* type in any non-human primate (De Weerd, Desimone, Ungerleider, 1996; Fagot & Tomanaga, 2001; Fujita, 2001; Zimmerman, 1962). Several other studies have shown that non-humans primates are capable of detecting depth relations from 2-dimensional visual stimuli. For example, Bayne and Davis (1993) and Fujita (1997) have shown behavioral evidence that rhesus macaque monkeys are susceptible to the Ponzo illusion. Similarly, Barbet & Fagot (2002, 2007) have also shown behavioral evidence for the corridor illusion by baboons. These studies reveal the abilities of non-human primates to misperceive size relations based on perceived depth cues. Resolving illusory contours of the Kanizsa type also involves a subject's ability to discern depth relations between the illusory "occluder" (amodal completion) and the "occluded" pacmen elements (modal completion). In addition, several studies have investigated the ability of non-human primates to complete partially occluded objects, demonstrating the gestalt principle of good continuation (e.g. in rhesus monkeys: Fujita, 2001; Fujita & Geirsch, 2005; in chimpanzees: Sato et al., 1997). The results of the present study suggest that it is possible that Samantha was using either a feature-based strategy or a local processing strategy when the pacmen forms were spaced further apart and a global strategy when the spacing between the elements was decreased, which is consistent with previous studies on global and local processing in non-human primates (Fagot & Tomanaga, 1999; Fagot & Dereulle, 1997; Kiorpes & Bassin, 2003; Spinozzo et al., 2003) and young children (Dukette & Stiles, 1996; Neiworth et al., 2006; Kovacs 2000; Kaldy & Kovacs, 1999, 2003). Therefore, based on the results of this study we cannot definitively rule out the possibility that the monkeys perceived the illusory contours.

Possible Effects of Overtraining. As stated earlier, both monkeys had originally been trained with color photographs. Although the monkeys did not show a decrement in performance when transferred to grayscale photographs, there was a significant decrease in performance when the grayscale abstract forms were introduced. This raises the question as to the effects of the previous training and the possibility of negative effects of over-training. In a study by Beck, Warren, and Sterner (1966), the effects of overtraining were examined in naïve and experienced rhesus macaque monkeys on reversal discrimination problem sets. One finding provided evidence that the subjects' performance on the discrimination tasks improved overall with practice, however, the degree of overtraining was significantly correlated with the number of subsequent errors on the reversal task over the course of the experiment. They concluded that overtraining significantly hindered performance on reversal discrimination tasks and as a result, increased the number of trials necessary to solve discrimination problems following chance performance with novel sets. One must therefore consider the possibility that because the monkeys used in this study were initially trained with photographs; it is conceivable that the switch to distinctly different stimuli (abstract forms) was treated as a different task. One must keep in mind that although the abstract forms appeared "easier", it cannot be assumed that they were. Based on evidence from phase 1 of similarity matching training, Samantha's performance with the "simpler" stimuli was 88% correct compared to the more "complex" background stimuli (78%), indicating better performance with the less complex forms. In addition, we cannot be certain as to how the monkeys were solving the initial matching-to-sample problem. That is, there were many attributes in the photographs that could have been used to identify the correct match such as color, variation in grayscale, as well as variety of distinct visual features. The initial problem of transfer between grayscale photographs and grayscale abstract forms seems to lie in the nature of the stimuli. It is possible the transition from photograph to an abstract figure/ground problem was treated as a completely novel and more challenging task. Another factor that could have contributed to the difficulty transferring to the abstract forms is the number of possible stimulus combinations. The monkeys had originally been trained on smaller sample sets (i.e. 32 color or grayscale photographs) and although they appear to have demonstrated their ability to match, it is also possible that they were memorizing the individual stimuli, which could account for their difficulty with the abstract forms.

Abstract concept learning implies that certain rules are learned and can be generalized to novel situations allowing one to demonstrate and apply rule-based relationships. Katz, Wright, and Bachevalier (2002) were interested in how different species acquire abstract-concept learning. Of particular interest were the effects of sample size and role of attention on how quickly a rhesus macaque monkey could demonstrate abstract-concept learning on a same/different task. They had determined that the size of the training set had a significant impact on how well they transferred to novel stimulus pairings on the same/different task. Subjects who had only been trained initially with small sets were at chance performance upon transfer to novel stimuli. Of critical importance however, is that when the monkeys did not show evidence of learning with small sets, the same subjects were subsequently trained with gradually larger sets. It should come as no surprise that as the number of stimuli within training sets increased so did performance on transfer to novel stimuli. These data are consistent with other studies on sample size in monkeys and pigeons (e.g., Katz & Wright, 2006; Bhatt & Wright, 1992; D’Amato, Salmon, & Colombo, 1985). Another important finding by Katz et al.,

(2002) deals with rate of acquisition of abstract concepts and the role of attention. Using a multiple touch (to the sample) procedure, they found that subjects who had to touch the sample ten times prior to the discrimination phase learned and were capable of demonstrating the same/different concept faster than monkeys who were not required to have multiple touches to the sample. This finding is consistent with Wright's 2001 study with pigeons. These data are interesting and relevant to the present study in that once the monkeys demonstrated their knowledge of matching with a combination of 32 color and grayscale photographs, transfer performance to abstract forms became increasingly difficult. Based on the aforementioned studies, this could have been a direct result of the number of stimulus combinations given during training. When we consider the amount and duration of time spent on initial training, it seems reasonable that the monkeys may have learned specific stimuli and developed a preference for these photographs. It is worthwhile to mention, that once the monkeys were placed on the abstract form background task, they received thousands of possible combinations of stimuli, and this along with the dramatic change in physical appearance of the stimuli could also account for the difficulty and length of time with which it took each monkey to transfer their knowledge of matching to the abstract grayscale forms. Use of a multiple touch procedure would most likely have resulted in more efficient acquisition and transfer to novel stimuli, but due to programming issues this was not possible.

Identity-Matching versus Similarity-Matching. Although the monkeys were initially trained on an identity-matching task, they were required to perform a similarity-matching task when presented with the test stimuli. That is, the correct matching stimulus was an identical match to what was experienced during the sample presentation on background trials (Experiment 1). However, not only were the correct matches on test trials simple “whole” forms, but the contrast was also reversed. That is, during the sample the subject experienced gray pacmen on a black background, where as the correct match was a black form on a gray background. Despite the distinct differences between the background training and test stimuli, it was expected that the monkeys would respond appropriately on these trials. Failure to obtain sufficient evidence after re-testing Samantha with the 3 new test stimuli (Experiment 2) and with the individual (un-pooled) test stimuli with larger pacmen (Experiment 3) could have resulted from the lack of similarity training. During identity matching subjects are required to recognize an exact match for what has been previously experienced. During similarity matching however, subjects are required not only to recall what was observed during the sample presentation phase, but also relate and apply that information to what has been presented during the comparison phase. Similarity matching is often slightly more difficult initially for subjects to acquire because they must discern which comparison represents the best match for what was previously observed, taking into consideration how the comparisons are similar as well as how they differ from the sample. To complicate matters, once Samantha’s performance was consistently above chance on the similarity matching task with a variety of grayscale forms, the contrast was manipulated to match the contrast experienced on test trials (i.e. black and one shade of gray). In addition, up to this point each of the comparison stimuli on background trials were distinctly different abstract forms. These included differences in size, shape, orientation, and location. The only time the area of the stimuli was controlled for was on test comparisons, which could have contributed to confusion on these trials. Due to time constraints the monkeys unfortunately could not be trained to criterion on the background stimuli that would have accounted for this shortcoming. Failure to obtain evidence for the illusion after this similarity matching manipulation (follow-up tests) indicated that lack of this type of training was likely a major contributor for this failure. In addition, the latency data further suggest that the contrast reversal stimuli were significantly more difficult than the other background stimuli.

Stimulus Differences. Interestingly, Samantha's performance on the background task gradually decreased as the abstract forms became easier (i.e. fewer contours and larger contrast between figure and background). That is, as the background task became less complex and theoretically "easier", the more difficulty Samantha appeared to have. Performance also decreased when the contrast of the simple forms were manipulated to match the contrast of the test stimuli. These findings suggest that Samantha could have been using a feature-based strategy on the background task. Based on Biederman's (1987) recognition by components model, object shape is initially represented based on the identification of edges, contours, and boundaries. Biederman further suggested that as long as a few geons can be extracted from a visual image then that object will, in most cases, be recognized despite variations in orientation, occlusion, deletion, or rotation in space. But what happens when a feature-based strategy is attempted with stimuli that have several features in common? It is possible that as the abstract stimuli became less complex, limiting the total number of possibilities for distinct features, the more difficult it became to discriminate them. This hypothesis is supported by Samantha and Sophie's failure to reach above chance criterion on the 14 new shapes experienced during the follow-up training. Part of this failure is likely due to the limited amount of time they were exposed to these stimuli. But more notably, chance performance on this task is likely the result of the similarity of the comparisons. If the monkeys were ignoring the orientation cues, focusing on the contrast and/or shape of the simple form, then interference with the contrast reversal and orientation of the "incorrect" comparison could account for their inability to choose the correct match. In addition, our findings from the reverse contrast condition from phase 4 and 5 of similarity matching training indicate lack of attention to form information, which is what is needed for the discrimination of illusory contours.

The test stimuli were also profoundly different from all of the previous training stimuli in that they were the only images to contain pacmen that formed contours as well as being the only stimuli that did not contain an abstract form in the sample. That is, the subjects had experience with non-contour inducing pacmen located either in the sample or in the comparison stimuli during similarity training. The rationale for including the pacmen was (1) to train the monkeys to pay attention to the shape of the form and (2) to avoid extinction on the non-feedback test trials. In addition, the comparisons experienced during the test were single, rather than composite forms which, in most situations, closely resembled each other. The results from experiment 2B also shows that Samantha might have been ignoring the pacmen based on increased response latency data and chance performance on the test stimuli. These data suggest that she might have been confused by the reversed sequence or found the pacmen forms irrelevant. It is possible that training with the proper background stimuli, where the comparisons are the same form with the incorrect comparison in a slightly different orientation, could have facilitated performance on the test trials.

Brightness and Form Discrimination. The actual degree to which non-human primates can process visual information the same as humans is unclear. It is well known that other primates can perceive chromatic and achromatic visual information, but there may be differences in physical structure, acuity, preference, and salience. Weinstein and Grether (1940) conducted a study to compare the visual acuity in the rhesus macaque monkey and humans on a multiple choice delayed reaction experiment. What they concluded was that although rhesus monkeys seem to have very similar visual acuities as humans, they fail to reach the same precision as the human subjects. Similarly, De Haan (1925) conducted a study to determine the color sense of pig-tailed macaques (*Nemestrinus nemestrinus)* using a multiple-choice color apparatus. Interestingly, the monkey showed significant evidence for color gradation discriminations, however failed to distinguish between successive levels of gray that ranged on a continuum from white to black. In a more recent study, Jacobs and Blakeslee (1984) showed that squirrel monkeys of Peruvian origin show distinct variations in their color vision and visual sensitivity to different wavelengths, which are similar to what has been observed in humans with deficits in color vision. Using a forced-choice discrimination procedure, Jacobs and Blakeslee (1984) tested the visual sensitivity of squirrel monkeys originating from three different geographical regions (Guyana, Bolivia, and Colombia). The monkey's task was to choose a color stimulus that was different from two other illuminated colors. Interestingly, the data showed that monkeys originating from Guyana and Bolivia had dichromatic vision whereas some of the monkeys from Colombia had trichromatic vision. Based on this study, Jacobs and Blakeslee could identify five distinct color phenotypes within the dichromatic and trichromatic categories, revealing a wide range of variation of color sense within a single species. Much of the research on comparative visual perception has focused on the evolutionary trends of chromatic vision. However, contrary to De Haan's (1925) findings, several studies have also shown that many cells in V1 that respond to color information also respond to black and white luminance patterns (Boothe, 1984; Roe, Lu, & Hung, 2005; Shapley & Hawken, 2002). In addition, developmental studies with human infants (Atkinson, Braddick, & Braddick, 1974; Atkinson, Braddick, & Moar, 1977; Banks & Salapatek, 1978; Movshon & Kiorpes, 1988) and infant monkeys (Boothe, 1984; Boothe, Kiorpes, Williams, & Teller, 1988) have shown similar maturational time courses for normal visual development across species (at a ratio of 4:1 humans to monkeys), in particular the development of contrast sensitivity. Avidan, Harel, Hendler, Ben-Bashat, Zohary, and Malach (2002) using fMRI imaging in human subjects showed that contrast response functions decrease from lower level processing areas of visual perception such as V1 to higher levels located along the ventral processing stream. In this study human subjects were required to perform an object recognition task. The subjects were presented with line drawings of objects and faces with varying contrast levels. The results of this study showed a gradual declining trend of increasing contrast invariance moving from V1 (which showed the highest sensitivity to changes in contrast) to the lateral occipital complex which showed less sensitivity to contrast changes. These data suggest that performance on object recognition tasks do not necessarily depend solely on the degree of physical contrast of the visual stimulus but rather as a result of personal experience with a given object or form (Avidan et al, 2002). Similarly, fMRI contrast response trends have been correlated with results obtained from V1 single cell recordings in macaque monkeys (Heeger, Huk, Geisler, & Albrecht, 2000).

Perceived brightness often depends on a proportion of light and dark elements within the stimulus (Medin, Borkhius, & Davis, 1970). Brigner and Gallagher (1974) suggested that illusory contours are perceived because the pacmen elements have inducing fields, which increase the brightness contrast at each corner. Therefore, the differences in brightness contrast will be maximized within the corner elements producing apparent brightness differences to the observer, which ultimately results in the perception of an illusory contour (Brigner & Gallagher, 1974). Responses to differences in brightness (both real and illusory) from cells located in primary visual cortex (V1) of macaque monkeys indicate that initial computations of brightness and contrast sensitivity might occur in this region but are likely to extend well into V2 (see Huang, MacEvoy, & Paradiso, 2002; Hubel & Livingstone, 1990; Ramsden, Hung, & Roe, 2001; Shapley & Hawken, 2002). Roe, Lu, and Hung (2005), showed that the luminance ratio of border contrast influences the perception of surface brightness, suggesting different brightness processing capabilities of V1 and V2 in the macaque monkey.

It is often difficult to determine the role of attention in non-human primates, primarily because it is not clear what aspect of the visual stimulus the monkeys are attending to. Boucart and Humphreys (1991, 1994) provided evidence for independent processing pathways for different aspects of visual information. Specifically, they proposed that attention to color can interfere with access to the form-processing pathway. That is, the processing of form information can lead subjects to misperceive color information along specified contours. For example, Khurana (1998) showed that human subjects tend to misperceive color information when the color of a partially occluded form is inconsistent with the color of the occluding form. To test this, humans subjects were asked to view three versions of an occluded structure that share a common boundary but not necessarily the same color (two-color consistent, two-color inconsistent, and three-color inconsistent). The subjects were briefly shown the visual stimuli and were asked to report the color of the cued contour. The subjects in this study made more errors when the two and three colors of the forms were inconsistent with one another than when they were the same. These data indicate separate pathways for form and color information as well as evidence that form can interfere with the integration of color information, suggesting some type of inhibitory interaction between the two (Khurana, 1998). This is a logical suggestion for why the monkeys may have had trouble accessing the appropriate form/orientation during the match phase. If the monkeys were selectively attending to the grayscale color of the stimulus before attending to the form, interference could have occurred when the contrast was reversed. Because there were several stimulus attributes that the monkeys could have used when performing the matching task (form, size, orientation, contours, location of the form in space, and number of pacmen) it is difficult to determine to what aspect(s) of the stimuli they were allocating their attention. As mentioned earlier, one way in which this could have been controlled for was to incorporate a multiple touch procedure so that the monkeys had enough time to examine all aspects of the visual stimulus.

Developmental Processing Strategies. In humans, color and language are interconnected in that the recognition and identification of certain color or stimulus attributes are facilitated by the use of language. Color preference appears to emerge earlier during visual development. As cited in Staples (1931), Tobie (1927) conducted a color preference study with human infants and children to show whether color, form, or some combination would influence how children match objects. The results of this study indicated that prior to three years of age, children switch back and forth between color and form based on the actual stimulus. Children after three years of age to five years of age base their decisions on color alone, and after five years of age the ability to respond to both reappears. This is not so surprising when we think about the influences of language. It is during years 3-5 when children learn to associate the names of colors with the color itself, which may explain why we see this shift in processing during this age range. A similar pattern is observed during the development of global and local processing strategies in humans. It has been suggested that very young infants are born with the ability to process visual information on both local and global levels, but that global advantages tend to emerge over time with experience (Cassia, Simion, Milani, & Umitla, 2002 and Ghim & Eimas, 1988). In addition, several studies have shown that young children have the capability of processing local and global information when prompted to do so, however this ability tends to depend heavily on the magnitude of spacing between the local elements (De Lillo, Spinozzi, Truppa, & Naylor, 2005; Dukette & Stiles, 1996; and Ripoll, Fiere, & Pelissier, 2005). Dukette and Stiles (1996, 2001) have also shown that older children and adults exhibit a pronounced global precedence effect that is unaffected by the degree of spacing between local components indicating a processing strategy that is markedly different from that which is observed in young children. Similarly, Neiworth, Gleichman, Olinick, and Lamp (2006) in a study with humans and tamarin monkeys, showed that adult humans exhibited a global precedence with local and dense displays, whereas young children showed global advantages with dense displays but discriminated hierarchal stimuli locally and globally when the local components were spread further apart. Tamarin performance on these stimuli were similar to the young children and Neiworth et al., (2006) further suggested that this performance was also similar to what has been observed in adult humans with autism (see Brosnan, Scott, Fox, & Pye, 2004).

Several studies have also looked at the developmental abilities of young infants to detect illusory contours. The general consensus is that infants younger than 5-months of age do not seem to show evidence of identification of static illusory figures, however, by 7-8-months of age they have the capacity to complete static occluded objects whether they are real or illusory (Berenthal et al., 1980; Csibra, 2001; Curran et al., 1999; Kavsek, 2002; Kellman & Spelke, 1983; Otsuka, Kanazawa, & Yamaguchi, 2004). Interestingly, Curran et al., (1999), showed evidence of illusory contour perception in human infants as young as 2-months of age. Consistent with previous studies with infants, Curran et al., used a preferential looking task to measure infant responses to the visual stimuli. The stimuli consisted of randomly assigned black and white sinusoidal lines on a gray background. Creating areas where the lines abruptly terminated, where the alignment of the next phase of sinusoidal lines was shifted, generated the illusory contours. They found that 2-month old infants preferred to look more often when the illusory contour was present suggesting they saw the illusion. The aforementioned studies provide evidence that language is not necessary for the perception of illusory contours, suggesting that non-human primates might also experience similar phenomena.

Sophie and Samantha’s failure to show above chance criterion with the test stimuli as well as the 14 simple training stimuli throughout the preliminary investigation of alternative hypotheses, suggest that a local processing bias was being utilized. It is possible that the monkeys recognized both local and global properties, however if a feature-based strategy was used, a local precedence is likely to be more efficient. If this hypothesis is correct, the results of this study would support the claim that monkeys process illusory contours similarly to young children. However, based on the results of this study, the possibility that the monkeys could perceive the illusory contours similarly to adult humans cannot be ruled out.

Effects of Feedback Distribution: For these experiments feedback was operationally defined as an indication of being correct or incorrect. Feedback on correct trials was given in the form of a higher frequency sound accompanied by delivery of a food pellet in one of two feeders. Feedback on incorrect trials was signaled by a lower frequency sound followed by a 20s time out where the house lights extinguished but the monitor remained illuminated. During non-feedback trials the monkeys did not receive any indication of whether they answered correctly or incorrectly before advancing to the next trial. One of the problems with having non-feedback test trials is that one runs the risk of the monkeys learning that those are the trials for which they do not receive reward. If this happens, one runs the risk of extinguishing responding to those types of trials and one would expect to see either significantly longer latencies on these trials or very short latencies indicating that the monkey is arbitrarily touching in order to advance to a trials for which he/she will receive feedback. Based on the results of this study there was no indication that the monkeys were responding differently to the test stimuli.

The original matching-to-sample training was conducted with 100% feedback (correct responses = food reward, incorrect responses = no food reward) in order to maximize initial learning. Behar (1961) conducted a study that looked at the effects of partial reinforcement with naïve and experienced rhesus monkeys. When given a choice, naïve subjects exhibited no preference for the reinforcement condition whereas the experienced monkeys chose the condition where the object was rewarded 100%. This result was significant because it showed that more experienced monkeys are affected more by non-rewarded objects than naïve monkeys. Bowman (1963), conducted a similar study with rhesus monkeys where correct responses were rewarded on 100%, 75%, 50%, and 25% of the trials. Of importance were their results indicating that performance on a discrimination task was only effective for the 100% and 75% reward conditions. Anything below 75% reinforcement led to extinction. Based on this evidence, we decided to gradually reduce the amount of overall feedback to prepare the monkeys on trials for which they would receive zero feedback during test sessions. Consistent with Bowman's (1963) study, the monkeys that participated in this study showed a similar trend in that as the percentage of non-feedback trials increased, the number of non-response trials (trials on which the subject fails to initiate the start of a trial) also increased.

Of particular interest in this study, was whether the monkeys could generalize their knowledge of the matching task to novel stimuli and whether certain stimulus features interfered with performance on subsequent presentations of those stimuli. Typically, when monkeys perform a series of two-choice discriminations, performance on new problems gets better because the monkeys tend to approach novel stimuli (Medin, 1972 p.305). However, Medin (1972) also suggested that experienced monkeys also appear to investigate more familiar negative stimuli (those that have not been chosen or rewarded) than novel stimuli on generalization tasks. That is, even though a monkey has learned that the negative stimulus will not result in food reward, he is more likely to pick the incorrect answer as such simply because it is more familiar. Therefore, both novel and familiar cues play a role in how the monkeys learn to generalize their knowledge on discrimination tasks, further emphasizing the importance of training animal subjects with a variety of stimuli for successful generalization on discrimination tasks (Riopelle & Moon, 1968; Wright, 1988). Medin (1972) stated “choices are controlled by stimulus properties of cues (i.e. their salience) and by expected feedback from previous rewards…Rewards and non-rewards increase or decrease the expected feedback or anticipated reward value for the cue to which the animal responded” (p. 314). Moss and Harlow (1947) conducted a study to examine the effects of reward amount (always rewarded regardless of correct answer, never rewarded, or partial reinforcement) on a discrimination task in rhesus macaque monkeys. In order to test this, the monkeys were tested on paired discriminations for each reward condition for a total of 90-paired discriminations. The results of this study indicate that performance was best on the partial reinforcement condition. Of particular interest is that the monkeys learned to disregard stimuli for which they did not receive reward. Therefore, extreme precaution was taken with regard to the placement of the illusory test trials during this study. The latencies for all types of trials (background, tests, and control) were recorded so that detection of extinction to non-feedback trials could be assessed. We only found significant response differences to background and test stimuli during Experiment 1 phase 8 and Experiment 2B. Due to programming limitations, we were unable to set up a situation whereby either response would be considered “correct” for the test trials. It is hypothesized that the use of non-differential feedback on test trials would have allowed the monkeys to show evidence of illusory contour perception. Because neither response was rewarded on test trials it is possible that the monkeys became confused and began to arbitrarily choose either comparison on these trials.

Possible Effects of Anatomical Differences. Preuss et al., (1999) showed the first evidence of distinct differences in the organization of layer 4A in primary visual cortex between humans and non-human primates using MAP-2 and NPNF antibodies. This work was later supported by Preuss and Coleman (2002) utilizing a calbindin immunoreactivity (CAT-301) staining technique in human and non-human primates. These findings suggest an evolutionary modification to layer 4A of primary visual cortex. The dense staining evident in several non-human primate species in layer 4A indicate that several parvocellular inputs are vertically organized in this layer giving way to the “honeycomb-like” shape suggested by Preuss et al., (1999). The lack of this band in humans is indicative of some sort of evolutionary modification. Preuss et al., (1999) suggest that this modification most likely resulted in a reorganization of how the parvocellular inputs are distributed within layer 4A in humans rather than a complete loss of these inputs.

Staining methods were not used during the present study, however it is possible that the organizational differences of layer 4A described by Preuss et al., (1999) and Preuss and Coleman (2002) contribute to our failure to obtain sufficient evidence for the perception of Kanizsa illusory contours. As was described earlier, magnocellular inputs are critical for detection of contrast and boundary identification. It is possible that the ability to discern illusory contours relies on magnocellular inputs from layer 4A of primary visual cortex. This hypothesis does not negate the physiological evidence cited earlier that monkeys can perceive illusory contours, however it does suggest that due different distributions of magnocellular inputs to layer 4A in macaque monkeys, this ability is less pronounced. It is still likely that non-human primates perceive illusory contours, however the intermixing of magnocellular and parvocellular inputs in layer 4A might explain differences in contrast sensitivity in monkeys (Merigan & Maunsell, 1990; Merigan, Katz, & Maunsell, 1991). The perception of contrast and luminance differences have been reported to occur as early as V1, but the perception of form information has been regarded to take place along the ventral processing stream, beginning in area V1 and terminating in higher order areas such as the lateral occipital complex (LOC) and area V4 in primates (Avidan et al., 2002; Baumann et al., 1997; Livingstone & Hubel, 1988).

Limitations and Possible Confounds of this Study: Demolition in the animal care facility began approximately January, 2006 and construction continued through August 2006. Although the monkeys were isolated from the site of the construction and efforts were made to drown out as much sound as possible, it is possible that performance was hindered by this disturbance. In addition, there was a short period of time during the initial demolition when most of this work was conducted in the evening disrupting the monkey's sleep cycles, potentially increasing stress levels.

Anecdotal Evidence for Perception of Illusory Contours. Based on anecdotal evidence captured on videotape, we can observe specific trials in which the monkeys initiate a movement towards the incorrect matching stimulus, pause, and double back to make the correct choice. My interpretation of this evidence suggests that the monkeys are seeing the illusion, but that as time elapses during the matching phase, the monkeys appear to confuse the correct and incorrect match either because they are non-feedback trials or because in most situations the matches are similar to each other. Given the appropriate testing conditions and more time it is likely that the monkeys would definitively show evidence for the perception of illusory contours similar to adult humans.

Final Comments: The purpose of this research was to determine whether a rhesus macaque monkey (*Macaca mulatta*) could perceive the illusory contours adult human subjects experience when viewing illusory contours of the Kanisza type. We cannot however, at this time definitively confirm that they perceive the illusion similar to humans. We can only suggest that it is possible, but that the conditions of this study did not allow for proper analysis of this behavior and continued testing is necessary in order to obtain a more definitive conclusion. In the future, it would be beneficial to use an alternative strategy that allows one to make use of non-differential reinforcement on test trials. In other words, providing food reinforcement for either choice the monkey makes regardless of whether it is correct or incorrect. Although this method also has some drawbacks its major advantage is preventing extinction to specific trials. The future implications of this work are vast. Similarities and differences in how monkeys and humans process illusory images would expand our knowledge of the evolution of visual perception, in particular extrapolation of whole forms from a set of individually configured features. In addition, these data are useful in determining how non-verbal primates reconstruct and remember visual stimuli that are discontinuous and of greater interest, how primates “fill in” the blanks without the use of language. It is hypothesized that monkeys and young children have evolved alternate encoding strategies in establishing representational categories that facilitate perceptual completions of ambiguous stimuli.

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