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# Global visual processing in macaques studied using Kanizsa illusory shapes

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**Abstract**

The ability to extract form information from a visual scene, for object recognition or figure–ground segregation, is a fundamental visual system function. Many studies of nonhuman primates have addressed the neural mechanisms involved in global form processing, but few have sought to demonstrate this ability behaviorally. In this study, we probed global visual processing in macaque monkeys (*Macaca nemestrina*) using classical Kanizsa illusory shapes as an assay of global form perception. We trained three monkeys on a "similarity match-to-sample" form discrimination task, first with complete forms embedded in fields of noncontour-inducing "pacman" elements. We then tested them with classic Kanizsa illusory shapes embedded in fields of randomly oriented elements. Two of the three subjects reached our criterion performance level of 80% correct or better on four of five illusory test conditions, demonstrating clear evidence of Kanizsa illusory form perception; the third subject mastered three of five conditions. Performance limits for illusory form discrimination were obtained by manipulating support ratio and by measuring threshold for discriminating "fat" and "thin" illusory squares. Our results indicate that macaque monkeys are capable of global form processing similarly to humans and that the perceptual mechanisms for "filling-in" contour gaps exist in macaques as they do in humans.

**Keywords:** Kanizsa illusory contours, Macaque monkey, Global form perception, Perceptual completion, Contour integration

Object recognition and scene segmentation are among the most studied aspects of visual perception. The needed capacity to perceive partially occluded objects, complete contours, and extrapolate information about object boundaries further complicates the problem of recognizing objects. Perceptual grouping, filling in of gaps, and figure–ground segmentation are fundamental components of object recognition, yet the mechanisms underlying the ability of visually sophisticated mammals to form coherent images from ambiguous visual input remain an open question (see, e.g., Spillmann & Dresp, 1995; Halko et al., 2008). Among the best-documented and extensively investigated examples of perceptual grouping and boundary completion are Kanizsa illusory contours (KICs) (Kanizsa, 1979; see Fig. 1a). A KIC has been traditionally defined as the perception of an apparent edge, contour, or bounded form in an area of the visual field where no physical variation in light intensity exists (Kanizsa, 1979). The ability to appreciate KICs appears to be fundamentally rooted in an observer's ability to process visual information globally. That is, an observer must first identify and group the elements that belong together and then link them across space (Kanizsa, 1979). It is likely that a variety of neural and cognitive processes interact in the formation of the percept (Spillmann & Dresp, 1995).

The exact origins of illusory contour perception remain unclear despite numerous investigations of the neural correlates. Many recent studies have described specific activation patterns in human brain to illusory *versus* real contours using functional magnetic resonance imaging (fMRI), positron emission tomography (PET), magnetoencephalography (MEG) technology (e.g., Hirsch et al., 1995; Ffytche & Zeki, 1996; Larsson et al., 1999, Mendola et al., 1999; Halgren et al., 2003; Stanley & Rubin, 2003). While most studies report enhanced activity in V1 when viewing illusory forms that is similar to that seen with real forms, all studies reported distinctive activation in downstream areas, such as lateral occipital cortex (LOC) or V3/V4, and beyond in the ventral stream. Direct investigation of neural correlates of contour completion has been undertaken *via* electrophysiological recordings in nonhuman primates, under the presumption that they perceive such contours behaviorally (e.g., von der Heydt et al., 1984; Grosof et al., 1993; Baumann et al., 1997; Heider et al., 2000; Lee & Nguyen, 2001; Gillam & Nakayama, 2002; Sáry et al., 2007). However, there are only limited behavioral data available to support this presumption.

The first neurophysiological evidence for illusory contour processing by neurons in macaque brain was presented by von der Heydt et al. (1984). They used "abutting grating" type stimuli, which create an illusory boundary between the slightly offset parallel gratings, and found that approximately one third of the cells they studied in V2 of alert fixating macaques signaled the presence of the illusory boundary but no cells in V1 did. Peterhans and von der Heydt (1989, 1991) further demonstrated neuronal activation in area V2 in awake macaques in response to two dark notches that moved in synchrony across two parallel rectangles, resulting in the illusion—to a human observer—of a dark bar lying atop the rectangles. Similarly, Baumann et al. (1997) recorded from

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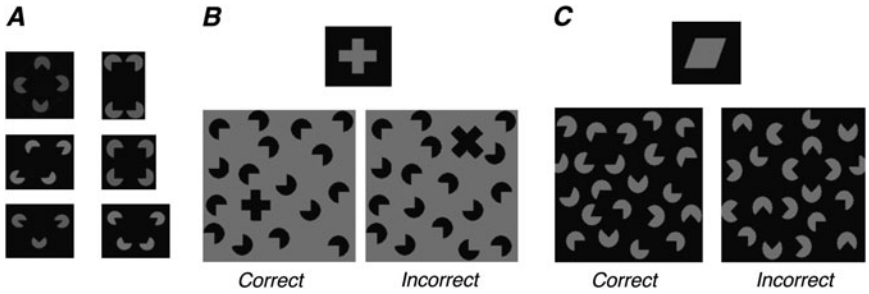



**Fig. 1.** (**A**) Schematic representations of the Kanizsa-type illusory shapes used in this study. (**B**) Schematic of a S-MTS trial with the added visual search component used in training. The isolated form (top of panel) was presented alone in the center of the screen followed by two comparison stimuli one of which contained a form similar in shape and orientation to the sample (left side) and one that differed on one or more dimensions (right side); both were embedded in a background of noise pacmen. (**C**) Schematic of a KIC test trial. The isolated bounded form was presented alone in the center of the screen, followed by two comparison stimuli, each containing an illusory shape; one was similar in shape and orientation to the sample (left side) and one differed on one or more dimensions (right side); both were embedded in a background of noncontour-inducing pacmen.

single neurons located in areas V1, V2, and V3/V3a in alert fixating macaque monkeys using stimuli that imply occluding contours. They showed that most of the neurons recorded in area V1 failed to respond to these stimuli; however, neurons from prestriate areas (V2, V3, and V3a) did show sensitivity to figure–ground segmentation cues. This study provided evidence for the detection of relative contrast differences and brightness as early as V1 but the ability to discern a figure as separate from background appeared to occur at higher areas in the visual system hierarchy (see also Heider et al., 2000). On the other hand, Grosof et al. (1993) reported that roughly half of V1 neurons they recorded, using a variety of illusory boundary configurations, signaled the presence of the boundary. Subsequent studies further highlighted response differences between V1 and V2 in nonhuman primates while viewing illusory stimuli.

Lee and Nguyen (2001) recorded from individual neurons in areas V1 and V2 of alert fixating monkeys while Kanizsa-type illusory form stimuli were presented. The monkeys were shown a series of real and illusory forms, although as in prior studies, no behavioral response was required. They found responses to static Kanizsa figures in both V1 and V2 neurons, although the responses were more numerous—twice as common—and more robust in V2 compared to V1. Importantly, they found a substantial delay in the V1 responses to illusory forms, both with respect to real forms and with respect to V2 responses. The authors proposed that these differences in response latency were likely due to feedback modulation from area V2 to area V1. An optical imaging study of primate V1 showed that the pattern of activation to abutting grating stimuli was quite different from that to standard grating patterns—the illusory boundaries evoked essentially an inverse pattern (Ramsden et al., 2001). At a higher neuronal level, Sáry et al. (2007, 2008) tested neurons in ventral-stream area inferior temporal cortex (IT) with real and illusory contours. Neuronal responses were similar to real and illusory versions of the same forms; however, again, the responses to illusory stimuli were of significantly longer latency. Taken together, these electrophysiological results show that neurons at various levels of the visual system can signal the presence of illusory contours and forms and that the responses are consistent with a feedback or top–down influence at the earlier stages of the system. These results are consistent with human imaging studies showing more robust responses to illusory boundaries and forms in areas downstream from V1 (e.g., Hirsch et al., 1995; Ffytche & Zeki, 1996; Mendola et al., 1999). Thus, it is likely that recognition of subjective illusory contours should be demonstrable behaviorally in macaques.

Several studies in a variety of species have shown evidence for illusory contour detection (see Nieder, 2002, for review); however, comparatively little is known about the nature of KIC perception in nonhuman primates. Two prior studies have investigated illusory contour perception in macaque monkeys using abutting grating and texture boundary stimuli. De Weerd et al. (1996) studied the effects of V4 lesions on a variety of types of contour and boundary discriminations. Using illusory boundaries defined by misaligned or differently oriented line segments, they demonstrated elevated thresholds for orientation discrimination based on illusory boundaries following V4 lesions. Orientation discrimination thresholds for the illusory stimuli in the control areas of the visual field were comparable to thresholds for discrimination of luminance-defined boundaries, suggesting that the animals perceived these boundary types similarly. Huxlin et al. (2000) also behaviorally demonstrated the ability of macaque monkeys to use illusory boundaries formed by differently oriented line segments as the basis for shape discrimination; this ability was disrupted by IT lesions, reinforcing the neurophysiological findings of Sáry et al. (2007, 2008) that IT cortex is important for perception of illusory forms. These behavioral data confirm that monkeys can use illusory boundaries to support perceptual discriminations, in these cases orientation and texture discriminations. However, to our knowledge, there is no prior demonstration of global form perception of the classical Kanizsa kind in macaque monkeys.

One study of chimpanzees suggests that they may be able to perceive illusory forms of the classical Kanizsa kind (Fagot & Tomanaga, 2001). The chimpanzees were trained to discriminate Kanizsa illusory squares from nonillusory squares. After initial training with the illusory squares, small line segments were added between the contour-inducing "pacmen" to determine whether the discrimination was weakened by the interruption of the induced contours. Although the chimpanzee's performance was hindered by the added line segments, the authors cautioned that they were not certain that the chimpanzees were making their discriminations based on actually "seeing" the illusion or whether the performance decrement was due to the change in the stimulus configuration (Fagot & Tomanaga, 2001). Thus, it remains an open question whether nonhuman primates perceive the classical Kanizsa illusions similarly to humans. An earlier study from our lab showed that macaques performed contour integration tasks similarly to humans, which lends further support to the hypothesis that they should be able to perceive Kanizsa forms (Kiorpes & Bassin, 2003).

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The purpose of this study was to behaviorally investigate the ability of macaque monkeys (*Macaca nemestrina*) to perceive Kanizsa illusory forms and provide further evidence that macaques and humans exhibit similar global form processing abilities. Prior behavioral and neurophysiological data suggest that this ability should be present. We present evidence showing that macaque monkeys can perform perceptual discriminations based on illusory forms, indicating that the underlying perceptual mechanisms for "filling-in" contour gaps to perceive global forms do exist in nonhuman primates.

## Materials and methods

### *Subjects*

Three visually mature and psychophysically experienced pig-tailed macaque monkeys (*M. nemestrina*) were used. Two juvenile monkeys aged 1.5 years [one male (S1) and one female (S2)] and a 3-year-old male (S3) were trained to perform visual discriminations. Subjects had previous experience making 2-alternative forced choice (2AFC) visual discriminations; however, they were naïve to the similarity matching-to-sample (S-MTS) paradigm used in this study. Subjects had no prior experience with illusory contour stimuli of any kind. They were rewarded for correct responses with a mixture of apple juice and water during testing; *ad lib* primate chow was available at all times. The home cage environment was enriched with food treats, toys, and regular interaction with peers and humans was provided. The testing procedures conformed with New York University's Institutional Animal Care and Use Committee approved protocols and were in compliance with the NIH Guide for the Care and Use of Laboratory Animals.

### *Apparatus*

The monkeys were trained and tested in a custom-made operant conditioning cage in which they were free to roam. A face mask, mounted on one wall, was used to view the display; the face mask was a plastic unit molded to the shape of the monkey's face. The mask served to position the animal correctly in front of the display and standardized the viewing distance at 100 cm. Viewing was binocular, and trials were initiated when the monkey placed his/her face in the face mask. Sensors in the mask detected the presence of the face and triggered the software to display the next trial. See Williams et al. (1981) for details of the operant methods.

The stimuli subtended 5.7 deg of visual angle and were presented on a 40-cm wide × 30-cm high display monitor (EIZO Flex Scan FX-E8 monitor, EIZO Nano Corporation, Shimokashiwano, Matto, Ishikawa, Japan). The space-average luminance of the display was 40 cd/m$^2$. The location of the correct choice stimulus varied randomly, left or right, across trials to avoid positioning biases. Responses were indicated by activating one of two grab bars (Micro Switch, Freeport IL) that corresponded to stimuli presented on the left and right sides of the monitor. The liquid reward for correct responses was delivered directly to the monkey's mouth *via* a tube attached to the face mask. Errors were signaled by a tone lasting 1–8 s, depending on each subject's level of motivation. Audible background masking noise (50–60 Hz) was provided by a noise generator. Stimulus generation and data collection were accomplished with a Dell computer *via* a VSG2/3 video card (Cambridge Research Systems, Rochester, Kent ME2 4BH, England).

### *General behavioral procedure*

A S-MTS paradigm, with no added delay between the sample and the presentation of the matching options, was used to train and test global form perception. On each trial, a sample stimulus was presented in the center of the display monitor and remained visible for 1 s. Thereafter, the sample disappeared and two comparison stimuli appeared, one on either side of the display monitor. The comparison stimuli remained on the screen for an unlimited duration, until a choice was made by the monkey *via* a bar pull. The subject's task was to choose the stimulus that best matched the shape and orientation of the sample stimulus. Correct responses were rewarded with 0.4 ml of dilute apple juice, while incorrect responses were signaled by a tone. An intertrial interval of 3 s elapsed before the monkey could trigger the next trial. Criterion performance on all discrimination problems was 80% correct over three consecutive runs of 25 trials each.

#### *Experiment 1. Testing for Kanizsa illusory form perception*

The subjects were initially trained on the S-MTS paradigm using simple forms. We then added a visual search component to the problem, to introduce the pacmen that would become inducers for the illusory forms during the test phase. The monkeys were trained to indicate the closest matching stimulus to encourage them to generalize and learn the global form rather than to choose the specific matching stimulus. Once performance on the combined S-MTS + visual search task was above 80% correct with real forms, they were tested with Kanizsa illusory forms. It is worthwhile to point out that the subjects were only actively trained on the S-MTS + visual search task with real forms. The illusory stimuli were only presented after each of the subjects demonstrated the ability discriminate real forms on each of the pretest discrimination training conditions. In addition, to ensure the novelty of the illusory shapes, the subjects were trained with real forms that were completely different than those used during testing. The training sequence was as follows.

Twenty simple shapes were used during initial similarity matching training. The correct matching stimulus was positioned in the same orientation as the sample, whereas the incorrect comparison (same shape) was positioned in a different orientation; we also used reverse contrast comparison stimuli. All stimuli were gray-scale and matched in overall luminance. A combined average over all 20 stimuli of 80% correct performance on three consecutive test runs was required before the visual search component was added. Using 9 of the initial 20 shapes, those that were the easiest for the monkey to differentiate, we trained the monkeys to perform the same task but in the presence of background "noise" pacmen (see Fig. 1b). The distributions of noise pacmen were randomly generated and the absolute locations of the embedded forms were not consistent from trial to trial, again to encourage the animals to generalize and encode the shapes and to guard against the possibility that the animals might learn individual stimulus comparisons. A combined average over all nine stimuli of 80% correct performance on three consecutive 25-trial test runs was required to advance to the KIC test.

For the KIC test, sample stimuli consisted of one of six novel real—bounded—forms (square, rectangle, triangle, trapezoid, parallelogram, or diamond); the comparison stimuli were both illusory forms (see Fig. 1a for sample shapes) embedded in arrays of noise pacmen. There were five different illusory test conditions: rectangle, triangle, trapezoid orientation discriminations, parallelogram *versus* diamond, and parallelogram *versus* square. Correct comparisons were identified as the field that contained the illusory contour whose orientation and/or shape matched that of the sample (e.g., Fig. 1c). Again, the locations of the comparison figures within each field of

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pacmen varied from trial to trial as did the locations of the noise pacmen. Our criterion for success was 80% correct performance or better over three consecutive test runs on at least four of five illusory test conditions to support the hypothesis that the monkeys perceived Kanizsa illusory forms behaviorally. We accepted four out of five because preliminary data showed individual variation in the difficulty of particular form discriminations. S1 and S2 were tested using a blocked method, with the five discriminations tested in sequence; S3 was tested with the five discriminations randomly intermixed.

*Experiment 2. Support ratio manipulation*

Support ratio is defined as the ratio of the length of the physical contour to the length of the total contour (real + illusory) (Shipley & Kellman, 1992; Singh et al., 1999). In adult humans, the ability to perceive Kanizsa illusory forms can vary with support ratio. We initially chose a large support ratio (60–75% in Experiment 1) to maximize the likelihood that our monkeys would be able to perceive the forms. In Experiment 2, we manipulated support ratio to see if the monkeys' performance was affected by this parameter, as it is in humans. Beginning with the support ratio that each subject used during Experiment 1, we gradually decreased the ratio in increments of 1–5% over blocks of trials until performance fell below 75% correct or until support ratio reached 25%—the lowest ratio we could produce. We took this point as our estimate of the minimum support ratio that would support KIC perception. We selected the illusory square *versus* parallelogram, upright *versus* inverted triangle, and the diamond *versus* parallelogram conditions for this investigation. Our rationale for using these conditions to assess support ratio was because each of the sides for these shapes was equivalent in length. To preserve the size of the original illusory form during this manipulation, the diameter of the inducing elements was reduced to change the support ratio (e.g., see Fig. 3a).

*Experiment 3. Category discriminations with illusory forms*

To determine whether macaques could not only discriminate illusory forms but also use them as a basis for perceptual categorization, we used a "fat/thin" discrimination task first described by Ringach and Shapley (1996). We manipulated the illusory form–inducing pacmen by rotating them about their centers, which created illusory squares that appeared to be either fat (convex) or thin (concave) (e.g., see Fig. 4a). We assessed the limits of the monkeys' illusory square discrimination capabilities by varying the angle of rotation, clockwise or counterclockwise, of the inducing pacmen. The degree of rotation of the elements corresponded to the amount of illusory curvature. Initially, the differences in rotation were 16 deg (high curvature) so that one illusory square was clearly "fat" and the other "thin." The degree of rotation on the comparisons was gradually reduced in 1–2 deg increments, again over blocks of trials, until performance fell to 75% correct. We fit the data using Probit analysis (Finney, 1971) and extracted the median of the fit as our estimate of threshold. For this experiment, support ratio was set at 60%. Note that, although it would have been desirable to randomly intermix different rotation angles and support ratios (Experiment 2), programming limitations necessitated our using the block design.

## Results

We tested the ability of three visually normal macaque monkeys to perceive classical Kanizsa illusory forms and use those illusory forms as a basis for categorical discriminations. Two of the three met our criterion for definitive demonstration of illusory form perception; one did not.

All three animals learned the S-MTS task and transferred comparatively easily to the addition of the visual search component. They achieved 80% correct performance across all stimuli and conditions with real forms as comparison choices. To test for illusory form perception, they viewed a real form as a sample and were required to choose the "matching" illusory form to the sample from a pair of illusory forms. Thus, the animals had to encode the sample shape and recognize the illusory version of that shape, as distinct from another illusory shape. The monkeys' performance with the illusory test stimuli is shown in Fig. 2. Number of trials to reach the 80% correct performance criterion for each of the five discriminations is plotted for each subject. As mentioned in the methods, S1 and S2 were tested on each of the discriminations sequentially (presentation sequence was that shown in Fig. 2, from left to right); their performance improved with subsequent discriminations, requiring fewer trials to reach criterion performance (e.g., compare Condition 1 with Condition 4). Interestingly, neither monkey mastered the illusory triangle *versus* its inverse, which was the last one tested. S3 was tested with the five discriminations randomly intermixed; his performance was consistent across all the tests and he mastered all the test conditions in comparatively few trials. S1 and S3 reached the criterion we set at the outset of 80% correct on four of the five discriminations, thus supporting the hypothesis that macaque monkeys perceive Kanizsa illusory forms. Alas, S2 reached criterion on only three of five illusory conditions; she failed to achieve 80% correct on the illusory trapezoid as well as the illusory triangle. These discriminations are similar in that the comparison stimuli are inversions of the same stimulus, which she may not have perceived as distinct.

The results of this experiment support the hypothesis that monkeys can use global processing strategies in form perception, "filling in" over gaps, and provide the first behavioral evidence that monkeys perceive illusory forms of the classical Kanizsa kind. In addition, the results show that monkeys can use illusory shapes as a basis for perceptual discriminations. Two additional experiments evaluated the limitations of their perception of illusory form.

### *Support ratio manipulation*

Previous studies have demonstrated that the ability to perceive KICs in humans depends on support ratio (Banton & Levi, 1992; Shipley & Kellman, 1992; Kojo et al., 1993; Ringach & Shapley, 1996; Liinasuo et al., 1997; Rubin et al., 1997; Danilova & Kojo, 2001; Otsuka et al., 2004; Hadad et al., 2009). Support ratio is defined as the ratio of the length of the physical contour to the length of the total contour (real + illusory) (Shipley & Kellman, 1992; Singh et al., 1999). We initially used a large support ratio to maximize the probability that the monkeys would appreciate the illusory shapes. To establish whether illusory form perception in macaque monkeys was subject to similar constraints as human subjects, we systematically manipulated support ratio (see Fig. 3a). Beginning with the support ratio used for each subject during Experiment 1, and following the same paradigm as in the test phase of Experiment 1, support ratio was gradually reduced to the point at which performance fell to 75% correct. We used the illusory square *versus* parallelogram, upright *versus* inverted triangle, and the diamond *versus* parallelogram conditions for S3 but did not include the triangle discrimination for S1 since he did not reach criterion for this condition in the main experiment; we do not report data for S2 since she did not reach our criterion for appreciation of KICs in Experiment 1.

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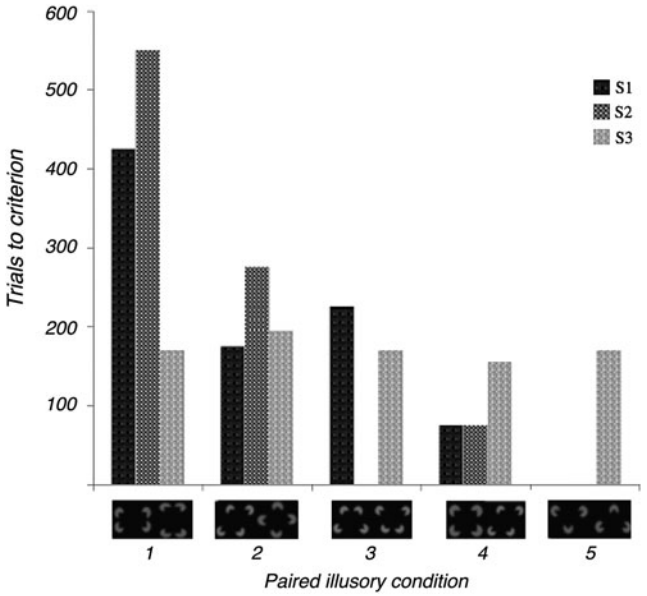



**Fig. 2.** The number of trials to reach criterion performance of 80% correct on each of the five illusory test conditions for each subject. Each subject is represented by a different bar pattern type; for instances where there is no bar shown, the subject did not meet criterion on that condition. S1 met criterion on each test condition except the illusory triangle (Condition 5). S2 met criterion on each test condition except the illusory trapezoid and triangle (Conditions 3 and 5). S3 met criterion on all test conditions. Note that a minimum of 75 trials was required for criterion performance on any given discrimination.

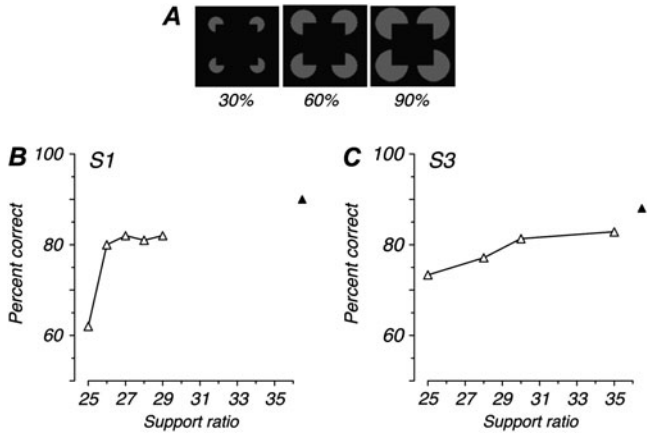



**Fig. 3.** (**A**) Schematic illustration of support ratio manipulation. Three different support ratio examples are shown for a Kanizsa illusory square: 30% (left), 60% (middle), and 90% (right). Note: manipulating the size of the pacmen serves to preserve the area of the central form. (**B** and **C**) Average performance across illusory contour conditions as a function of support ratio for S1 and S3; Discrimination Conditions 1, 2, 4, and 5 were included for S3; Discrimination Conditions 1, 2, and 4 were included for S1 since he did not master Condition 5. The isolated filled triangles show the percent correct for each subject at the starting support ratio of 60%.

Fig. 3b and 3c illustrates percent correct for S1 and S3, respectively, as a function of support ratio near the minimum support ratio we could produce; the filled symbol (upper right in each panel) indicates the percent correct shown by each subject at the starting point, support ratio (SR) of 60%. There was initially considerable variation in performance as the monkeys adapted to the changing stimulus configurations during the learning phase and then settled into stable performance. This was similar to the variability described by Rubin et al. (1997) while human subjects were practicing with small SR values. The data plotted in Fig. 3b and 3c show that, once a stable plateau was reached, performance fell off near a support ratio of 25, our minimum, for both monkeys. This limit is in the range that is considered challenging for human observers (Rubin et al., 1997). Thus, illusory form perception declines with support ratio in monkeys as well as in humans.

### *Category discrimination*

Several studies have used a fat–thin illusory shape discrimination task designed by Ringach and Shapley (1996) to investigate various aspects of human global form processing abilities (Rubin et al., 1997; Kellman et al., 1998; Gold et al., 2000; Zhou et al., 2008). For example, Rubin et al. (1997) measured insight-like learning in human adults using the Kanizsa fat–thin shape discrimination task. They manipulated the inducing pacman stimuli by rotating them about their centers, which created illusory squares that appeared to be fat (convex) or thin (concave). We used this paradigm to assess the limits of the monkeys' illusory square discrimination capabilities. The sample stimulus was a real (bounded) square form that was clearly fat or clearly thin (see Fig. 4a). Fat and thin illusory square comparison stimuli were generated by counterclockwise and clockwise rotation of the inducing elements, respectively. The degree of rotation of the elements corresponded to the amount of illusory curvature. Initially, the differences in rotation were 16 deg (high curvature) so that one illusory square was clearly fat and the other thin. The degree of rotation on the comparisons was gradually reduced in 1–2 deg increments until performance fell to 75% correct.

Fig. 4b and 4c illustrates performance as a function of rotation angle on the fat/thin category discrimination for S1 and S3, respectively. The lines drawn through the data points are the Probit fits (see Materials and methods); the estimated thresholds (arrows) for the fat/thin discrimination are near 4 deg for both monkeys. These discrimination thresholds are similar to those found in adult human subjects prior to explicit training (Rubin et al., 1997; see also, Maertens & Pollmann, 2005), indicating that it is likely that the neural mechanisms underlying the ability to perceive illusory contours are similar in human and nonhuman primates. These results show that monkeys can use illusory forms to make a categorical discrimination and that their ability to do so is similar to that of humans.

## Discussion

This study provides the first direct evidence that macaque monkeys can perceive classical Kanizsa illusory forms. We further show that they can use the form information available in Kanizsa shapes to support perceptual discriminations and that their quantitative performance thresholds are similar to what has been shown in humans prior to explicit training. Our data help to bridge the gap between physiology and behavior and indicate that macaques have ready access to global processing strategies to utilize global form cues evident at several levels along the visual pathway (e.g., Lee & Nguyen, 2001; Sáry et al., 2008).

Prior behavioral studies with nonhuman primates suggested that illusory form discrimination should be demonstrable. These studies showed that illusory boundaries, created *via* the abutting grating

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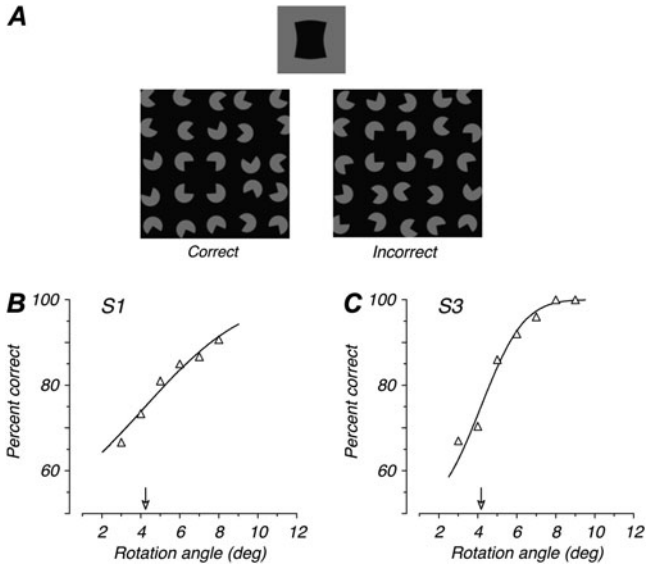



**Fig. 4.** (**A**) Schematic illustration of a fat/thin Kanizsa illusory square category discrimination trial. The sample (top), presented alone in the center of the screen, was a distorted square made to appear either fat or thin (illustrated). The comparison stimuli each contained an illusory square, one of which was thin (left panel) and one of which was fat (right panel). The degree of rotation in this example is 4 deg, near the monkeys' threshold. (**B** and **C**) Average performance for each subject as a function of the degree of inducing pacman rotation. Probit fits (smooth curves) and derived thresholds (arrows pointing to abscissa) for discriminating fat *versus* thin illusory squares are illustrated.

illusion (Soriano et al., 1996) or a texture boundary, can be used by macaques to perform psychophysical discriminations (De Weerd et al., 1996; Huxlin et al., 2000). Fagot and Tomanaga (2001) showed that chimpanzees could discriminate isolated Kanizsa squares (i.e., in the absence of any background or masking pattern) from bounded squares, although they were explicitly trained to pick the Kanizsa square in a two alternative forced choice task. We did not explicitly train our monkeys with illusory forms; our monkeys only observed the illusory shape stimuli during the test phase, once the discrimination training with real forms was completed. Furthermore, we did not expose the monkeys to the particular shapes used for the illusory form discriminations during training, so they had no prior experience with those shapes. The ability of the monkeys to transfer to the novel, illusory, test conditions indicates that they understood the matching concept and, although the number of trials to criterion for each test condition varied, the number of trials to reach criterion on illusory contour conditions were much lower than those observed during the pretest discrimination training conditions. Quicker transfer has been observed in barn owls to subjective form recognition from completed forms (Nieder & Wagner, 1999); however, the owls were explicitly trained to recognize the two shape alternatives.

We used a combined S-MTS + visual search task that required subjects to (1) encode and remember the shape of the sample stimulus, (2) remember the orientation in which the shape was presented, (3) find the comparison objects located in both search fields, and (4) choose the correct comparison stimulus that most closely resembled the sample. During Experiment 1, S1 and S2 required several hundred trials to transfer the trained matching concept to the initial illusory contour condition (Fig. 2, illusory rectangle orientation discrimination). It is likely that this initial difficulty was due to the fact that the subjects were trained using real forms; the task became different, if not more difficult, when the comparison choice stimuli no longer contained complete physical boundaries. Thereafter, both monkeys showed good performance on the subsequent discriminations that they were able to master. Comparatively, S3's performance was better across all five illusory test conditions; he showed no difficulty transferring from the real comparison stimuli to the illusory ones and was the only one of the three monkeys to reach criterion performance on all five problems. Recall that S3 was tested with all the illusory conditions intermixed. Previous studies have shown that increasing the number of stimuli on MTS tasks (Wright et al., 1988, Wright et al., 2003) facilitates performance and also guards against learning individual visual discriminations. Thus, it is possible that the mixed design facilitated transfer in the test condition. It is also possible that S3 performed better because he was older than the other animals at the time of testing. However, preliminary data from our lab suggest that 1-year-old monkeys are able to perceive Kanizsa illusory shapes (Feltner & Kiorpes, 2009), so it seems unlikely that age was a significant factor.

S2 was the only one of the three monkeys tested that did not achieve criterion performance on four of the five discriminations. She reached criterion on three of the five but did not master the upright/inverted triangle or the upright/inverted trapezoid. She may have had particular difficulty with differently oriented versions of the same shape, although she was able to perform above 80% correct with the illusory rectangle discrimination and with inversion of real forms. Her failure on these discriminations, and S1's failure on the upright/inverted triangle, argues against the possibility that our monkeys were using a different strategy to solve the task: that of learning the physical locations and spatial relationships between individual pacmen. Our use of the randomly arranged and oriented noncontour-inducing pacmen as background noise was designed to guard against this possibility, as was the feature that the locations of the comparison stimuli varied across trials. If the monkeys were able to use that strategy, they could quite easily have learned all the particular discriminations given enough trials. Thus, we believe they were basing their choices on perceiving the contours rather than by extracting some local cue.

The limitations on perception of illusory forms shown by our monkeys, through variation of support ratio and fat/thin discrimination, are similar to the range of performance limits measured for human subjects. These demonstrations support our conclusion that monkeys can use illusory forms as a basis for psychophysical discriminations and are consistent with data from previous studies of this kind using illusory boundaries (De Weerd et al., 1996; Huxlin et al., 2000). Furthermore, they lend an additional dimension to a growing body of literature showing similarities between macaques and humans on a range of global form tasks, such as contour integration (Kiorpes & Bassin, 2003); Glass pattern integration (Kiorpes et al., 2003; Kiorpes, 2006); and, more generally, object recognition independently of orientation, occlusion, and other transformations (Kovacs et al., 1995; Schiller, 1995; Logothetis & Sheinberg, 1996; Sigala & Logothetis, 2002; Sigala et al., 2002; Matsuno & Fujita, 2009). Further reinforcing these similarities, Fujita (2001) showed that rhesus monkeys and humans observe similar perceptual biases on overestimation of length illusions, while other studies in a chimpanzee (Sato et al., 1997) and capuchin monkeys (Fujita & Giersch, 2005) provided evidence for perception of partly occluded figures when two rod halves shared the same alignment and/or direction of movement. While our data do not speak directly to the nature of the mechanisms underlying global form processing, they bridge the gap between neurophysiological studies investigating those mechanisms and behaviorally verified perception.

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