

Cue-invariant shape recognition in rats as tested with second-order contours

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Nonhuman primates are the main animal model to investigate high-level properties of human cortical vision. For one property, transformation-invariant object recognition, recent studies have revealed interesting and unknown capabilities in rats. Here we report on the ability of rats to rely upon second-order cues that are important to structure the incoming visual images into figure and background. Rats performed a visual shape discrimination task in which the shapes were not only defined by first-order luminance information but also by a variety of second-order cues such as a change in texture properties. Once the rats were acquainted with a first set of second-order stimuli, they showed a surprising degree of generalization towards new second-order stimuli. The limits of these capabilities were tested in various ways, and the ability to extract the shapes broke down only in extreme cases where no local cues were available to solve the task. These results demonstrate how rats are able to make choices based on fairly complex strategies when necessary.

Introduction

Visual perception is one of the most intensely studied functions of the human brain, but despite all efforts, a full understanding of vision is still regarded as one of the biggest challenges today. Unlike in many other fields of brain research, dominated by mice and rat models, visual perception has been primarily investigated in monkeys. This choice has been motivated by several important reasons. First, there is ample

evidence for a similar hierarchical cortical organization of the visual areas between humans and monkeys (De Valois, 1965; Grill-Spector & Malach, 2004; Van Essen, Anderson, & Felleman, 1992; Van Essen & Gallant, 1994). While rodents also have multiple visual cortical areas and exhibit hierarchical processing in cortex (Vermaercke et al., 2014; Wang, Sporns, & Burkhalter, 2012), the homology with areas in the primate brain is still far from clear and will probably never be resolved. In fact, the list of differences in visual processing only becomes longer with time. Recent examples of these differences are orientation tuning in the mouse lateral geniculate nucleus and the lack of orientation columns in rodent primary visual cortex (Girman, Sauvé, & Lund, 1999; Hübener, 2003; Niell & Stryker, 2008; Ohki, Chung, Ch'ng, Kara, & Reid, 2005). Second, vision is the main sensory modality for most monkeys as well as for humans, whereas nocturnal rodents such as mice and rats largely rely on other senses (Burn, 2008), such as smell (Kepecs, Uchida, & Mainen, 2007; Uchida & Mainen, 2003) and touch (Krupa, Matell, Brisben, Oliveira, & Nicolelis, 2001). In particular, the limited relative size of the cortex involved in visual processing compared to primates has been a major argument that rodent vision is very simplistic (Baker, 2013).

However, recent advances in experimental techniques that benefit from genetic engineering, such as optogenetics (Deisseroth, 2011; Fenno, Yizhar, & Deisseroth, 2011; Lee et al., 2012; Pinto et al., 2013) and two-photon imaging, as well as practical considerations (cost, ethical discussions), have encouraged researchers

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to consider rodents as a complementary model to study visual perception. In fact, many popular experimental paradigms in rodents rely at least in part on visual cues, such as discrimination tasks (Markham, Butt, & Dougher, 1996) and spatial navigation tasks (Sutherland & Dyck, 1984; Whishaw & Mittleman, 1986), suggesting that rodents might be a useful model for some aspects of visual perception after all. A quick look in history shows that already in the late 1920s rodents were used in behavioral experiments to assess principles of visual perception (Fields, 1936; Higginson, 1926; Krechovsky, 1938; Lashley, 1912; Valentine, 1928; see Zoccolan, 2015, for a review). More recently, a renewed interest in rodent visual perception has shown that the rodent visual system is more advanced than previously thought. For example, Meier, Flister, and Reinagel (2011) showed that rats are sensitive to the collinearity of gratings, suggesting, as some of the older studies did, that the visual system in rats processes feature conjunctions. Other recent studies suggest that rats are capable to recognize and categorize objects irrespective of changes in location, size, lighting, and viewpoint (Alemi-Neissi, Rosselli, & Zoccolan, 2013; Simpson & Gaffan, 1999; Tafazoli, Di Filippo, & Zoccolan, 2012; Vermaercke & Op de Beeck, 2012; Vinken, Vermaercke, & Op de Beeck, 2014; Zoccolan, Oertelt, DiCarlo, & Cox, 2009).

These studies illustrate the capacity of rodents to use relatively complex recognition strategies that rely on conjunctions of visual features and lead to transformation-invariant object recognition. However, these results do not necessarily show that the visual features or the strategies used by rats are the same as those used by monkeys and humans. Humans and monkeys have the cortical machinery to allow them to use complex features to guide their perceptual decisions; for example, curved boundary elements and corners (De Winter & Wagemans, 2008; Pasupathy & Connor, 2001), whether lines are parallel (Jastorff, Popivanov, Vogels, Vanduffel, & Orban, 2012; Kayaert, Wagemans, & Vogels, 2011; Xu, Biederman, & Shah, 2014; Yue, Biederman, Mangini, Malsburg, & Amir, 2012), segmentation of inputs into figural and background regions (see Pasupathy, 2014, and Self & Roelfsema, 2014, for reviews), and so on. Nevertheless, differences in visual strategies already exist between humans and monkeys (Nielsen, Logothetis, & Rainer, 2006). This is also true for humans and rats. For example, by investigating rat discrimination of a square versus a rectangle, Vermaercke and Op de Beeck (2012) observed that the rats appeared to rely on relatively simple local contrast cues such as “a black region on top of two whiter regions” rather than the direct holistic comparison of a square versus a circle that humans might perform. While such local contrast cues might be relevant in some cases for primate vision as

well, as shown recently for face detection (Ohayon, Freiwald, & Tsao, 2012), the example by Vermaercke and Op de Beeck (2012) demonstrates that a great caution is necessary to conclude that rats do indeed construct more complex feature representations.

How could we determine if rats can truly detect simple feature conjunctions in a shape discrimination task? In a typical display, shapes are defined by a difference in luminance (referred to as the first-order boundaries), and thus successful shape discrimination can always be driven by luminance cues alone even if using higher level representations would appear a more intuitive way to solve the task, at least to a human observer. However, such first-order boundaries are not the only way to define shapes (Regan, 2000). As an extreme example, the primate visual system has been shown to be able to detect shapes even when no physical boundary is present, such as in the case of illusory boundaries (Shapley, Rubin, & Ringach, 2003; Von der Heydt, Peterhans, & Baumgartner, 1984). The underlying neuronal selectivity has been shown in monkeys and cats (Heitger, von der Heydt, Peterhans, Rosenthaler, & Kübler, 1998; Pan et al., 2012; Peterhans & von der Heydt, 1991; von der Heydt & Peterhans, 1989; von der Heydt et al., 1984), where some neurons respond to an illusory boundary as they would to a real boundary.

A less extreme example of luminance-independent shape processing is found by the ability to extract a shape based upon second-order boundaries. In such shapes, boundaries are defined by differences in texture (Kastner, Nothdurft, & Pigarev, 1999; Lamme, 1995), color (Saarela & Landy, 2012), motion direction (Marcar, Raiguel, Xiao, & Orban, 2000), and phase (Von der Heydt & Peterhans, 1989). Neural responses in monkeys (Sary, Vogels, & Orban, 1993) and humans (Grill-Spector et al., 1999) indicate that neurons that are selective for shapes defined by first-order boundaries can generalize this selectivity to second-order boundaries. This is referred to as cue-invariant shape processing.

If the flexible and transformation-invariant shape recognition of rodents would purely rely upon local contrast cues, then we would expect that their discrimination abilities would be very low when tested with shapes defined by second-order cues. Here we tested this prediction by training rats to discriminate two rectangular shapes defined by first-order or second-order cues, followed by a test of generalization to unseen second-order stimuli. The results showed that rats did not automatically generalize from first-order to second-order cues, but once trained with one set of second-order contours they showed a surprising amount of generalization to other second-order stimuli, indicating that more complex feature representations might be constructed in the rodent visual system.

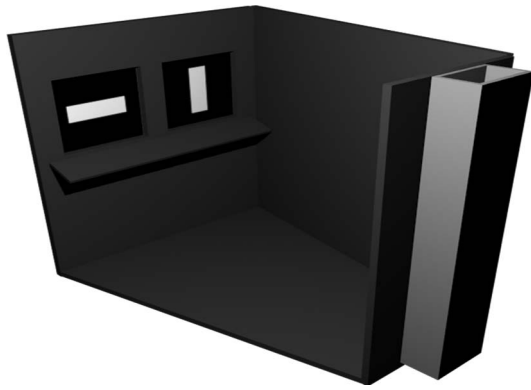


Figure 1. Schematic touch screen chamber. Two stimuli are shown on a touch-sensitive screen. A Perspex mask limits the area on the screen that rats can touch. Below the stimuli is a shelf. At the opposite side is a reward delivery system. Food pellets can be collected in a tray at the bottom (not visible from this perspective).

Methods

Subjects

We used Long Evans rats ($N = 6$), supplied by Janvier Labs (France). All animals were approximately three months old at the start of the experiment. They were housed in two Plexiglas cages containing three animals each. Each cage was enriched with a plastic toy item (Bio-Serv, Flemington, NJ). Before the start of the experiment, all animals were first handled for a few days to accustom them to the experimenters. During the actual experiment, animals received water ad libitum but received only a limited amount of food, which was always given after animals participated in a session. They were weighed on a daily basis before each session to make sure that their body weight did not drop below 85% of their free-feeding behavior.

Apparatus

Animals were trained in two automated touch screen operant chambers (Campden Instruments Ltd., Leicester, England). Each chamber was placed in a sound attenuating box. The operant chamber itself had the shape of a trapezoid measuring $30.5 \times 24.1 \times 8.25$ cm (Figure 1). There was a reward tray at one end of the chamber, in which food pellets (45-mg sucrose pellets, TestDiet) were delivered, and a touch screen at the opposite end of the chamber. The screen was divided into two adjacent displays by covering it with a Perspex mask with two apertures. Animals could respond to stimuli presented on these displays by touching either of the displays. Responses were

registered by arrays of infrared sensors so that animals did not have to exert any actual force on the screen to make a response. To reduce impulsive responses, the Perspex mask was equipped with an additional shelf in the front that forced the animals to rear on their hind legs before making a choice (Horner et al., 2013). The chamber was further equipped with a house light and a tone generator.

Stimuli

Static stimuli

For luminance stimuli, the target image consisted of a horizontal white rectangle at the center of the image against a black background. This target had to be discriminated from distractor image that contained a vertical white rectangle at the center of the image against a black background. Luminance position invariance was tested by displacing the rectangles from the luminance condition over a distance equal to the width of the bar (upward or downward for the horizontal rectangle, left or right for the vertical rectangle). For orientation-1 and orientation-2 stimuli, a vertical and horizontal grating was applied to the rectangle from the luminance stimuli. As background, a grating with an orthogonal orientation was used. Position invariance stimuli were constructed by applying the textures to the luminance position invariance stimuli. For orientation-3 and orientation-4 stimuli, we used a grating texture rotated by 233° and 116° for the rectangle. As background texture a grating rotated by 116° and 233° was used. Phase-horizontal stimuli were constructed by using the same horizontal grating, but by applying a 180° phase offset between background and the rectangle, and in a corresponding manner we constructed phase-vertical stimuli.

Each image measured 342×341 pixels on the screen. Both the horizontal and vertical rectangle measured 75×225 pixels. The spatial frequency of the gratings was always 0.05 cycles per pixel. Target and distractor images were always presented in pairs, but the position of the images (left or right) was chosen at random. Except in the unpaired stimulus condition, target and distractor properties were always matched (i.e., if the target image was defined as in orientation-1, so was the distractor image). How each stimulus is introduced in the experiment is described in the experimental procedures. An overview of the different stimuli is presented in Figure 2.

Dynamic stimuli

Moving orientation-1, orientation-2, orientation-3, and orientation-4 stimulus pairs were created by taking the static-orientation textured stimulus pairs and

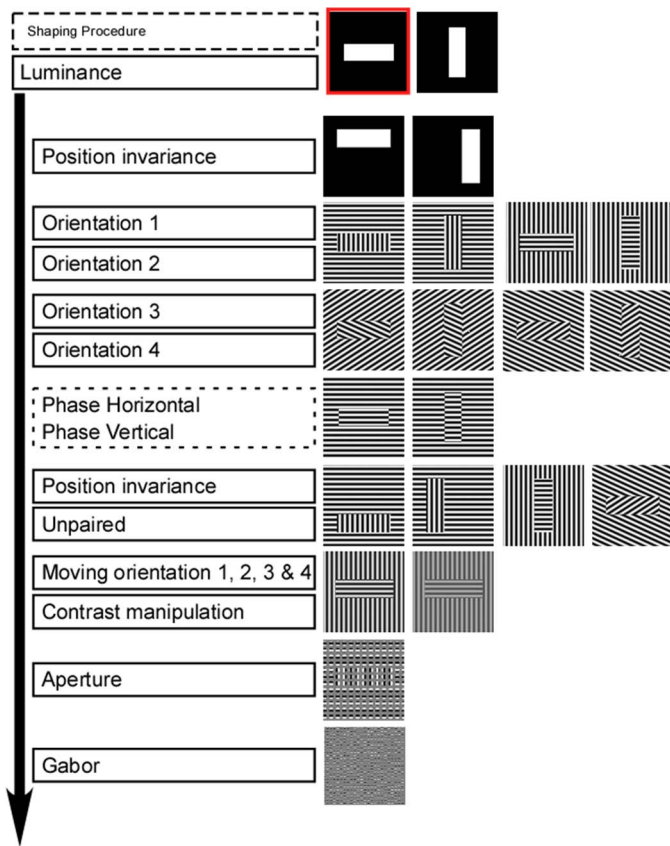


Figure 2. Overview of all the stimuli used, going from luminance-defined stimuli to Gabor-defined stimuli. The stimulus with the red border is the target stimulus during all phases. Phase-defined horizontal and phase-defined vertical were not completed by all animals. Movement was added from the moving orientation-defined 1 phase onwards and is necessary to perceive a shape in the Gabor-defined stimuli (see online materials).

adding positive phase offsets to the cosine term defining the texture pattern. These offsets were chosen such that the pattern shifted a full cycle per second.

Finally, we wanted to make sure that rats were not basing their decisions on any local luminance cues that could have remained along the texture discontinuity boundaries of our stimuli, and would have to integrate across multiple image regions. We therefore constructed two more types of stimuli where such integration would be necessary. Gabor-element stimuli were generated by the Grouping Elements Rendering Toolbox (Demeyer & Machilsen, 2012) by dividing the display into a 23×23 square grid and in each square placing a horizontal Gabor grating on a gray background. Each element had a random phase. In each frame, the phase was slightly shifted, creating a percept of a continuous motion. The rectangle area was defined by letting the corresponding elements shift their phase in an opposite direction than the background elements.



Figure 3. Construction of aperture stimuli: A mask with circular apertures (left) is applied to the stimulus (middle). In this example the mask is completely opaque, so that only parts that fall in the circular apertures remain visible (right).

After one full cycle, the direction of phase shift (or perceived motion) reversed.

As a simpler version of the Gabor stimuli, we also created aperture stimuli (Figure 3). They were created by taking moving orientation 1–4 and applying a mask with circular apertures. The mask was applied with different opacity levels. In the case of no opacity, this corresponded to the original stimulus. Increasing the opacity corresponds to a reduced contrast for the locations between the apertures. In the case of full opacity, only the aperture locations are informative as to the stimulus that is presented.

Procedure

Shaping

Animals performed a single session each day in the touch screen setup. First rats went through a shaping procedure in which they were gradually accustomed to our experimental protocol (see Horner et al., 2013, for a detailed description of this procedure). Briefly, animals were trained to initiate a trial by putting their head in the reward tray. At this point, a stimulus pair can be shown on the screen. The animal learned to touch one of the stimuli. If it touched the incorrect stimulus, the conditioning chamber illuminated for 5 s before the intertrial interval starts. If it touched the correct stimulus, a tone sounded and the animal received a single food pellet in the reward tray. Collection of the reward by the animal was detected by infrared sensors, after which the intertrial interval starts. The intertrial interval was 20 s, after which a light illuminated the reward tray and the animal could initiate the next trial by again putting its head in the reward tray. After an incorrect response, the same trial was always displayed again until the animal made a correct response. These trials are labeled as correction trials and are not taken into account for the analysis. Animals remained in the shaping procedure until they could perform 100 trials in 1 hr.

Condition	Stimulus added	Ratio old:new
Orientation-defined 1	Orientation-defined 1	1:4
Orientation-defined 2	Orientation-defined 2	1:1:4
Orientation-defined 3	Orientation-defined 3	1:1:1:7
Orientation-defined 4	Orientation-defined 4	1:1:1:1:6
Phase-defined H	Phase-defined H	1:1:1:1:1:5
Phase-defined V	Phase-defined V	1:1:1:1:1:1:4

Table 1. List of the different experimental conditions in the order in which they were introduced. *Note:* The middle column shows the new stimulus in that particular condition, and the right column shows the ratio of the old stimuli to the new stimulus. For example, ratio 1:1:4 means that of six presented trials, one was luminance defined, one was orientation-defined 1, and four were orientation-defined 2. *Notes:* H and V stand for horizontal and vertical, respectively.

Experimental procedure

Once animals mastered the protocol of the operant chambers, the actual experiment started. All animals started with the luminance stimuli only. After reaching criterion (described further) on these stimuli, we immediately tested for position invariance by including the luminance position invariance stimuli. Performance on these stimuli was assessed over a period of two consecutive sessions. After this test, we started introducing the different static textured stimuli as follows: Starting from a set that only contained the luminance stimulus pair (thus excluding the position invariance stimuli), we first added the orientation-defined 1 stimulus pair. After animals reached criterion performance on the newly introduced stimulus pair, which was tested after each session, we added orientation-defined 2 stimuli. This procedure was repeated for orientation-defined 3, orientation-4, phase-horizontal, and phase-vertical stimulus pairs. In each session there was therefore always a subset that contained all of the stimulus pairs already introduced (exact ratios are listed in Table 1). Unless otherwise noted, the performances mentioned and displayed in the Results section refer to the percentage correct on the new stimuli only, averaged across all rats that were tested in that phase.

At this point, we conducted two additional tests. For the first test we used luminance, orientation-defined 1, orientation-defined 2, orientation-defined 3, and orientation-defined 4 stimuli. Up to this point, target and distractor image features were correlated, such that if the target belonged to orientation-1, so did the distractor. Then we removed this correlation so that an orientation-defined 1 target image could be paired with each of the other distractor images, resulting in 25 possible pairwise combinations. In the second test, we used orientation-defined 1 stimuli to assess position invariance.

Threshold (%)	Number of sessions	Percentage during last session
80	2	80
75	4	75
70	8	70
65	12	65
60	16	60

Table 2. Performance criterion. *Note:* The threshold was lowered if the animals had an average performance below the threshold, during at least a determined number of sessions. Their performance during the last session had to be above threshold as well.

We then proceeded by adding the moving stimulus pairs. A single session contained luminance, orientation-defined 1, orientation-defined 2, orientation-defined 3, and orientation-defined 4 stimulus pairs. We started by adding the moving orientation-defined 1 stimulus pair to this set and proceeded with adding moving orientation-defined 2, moving orientation-3, and moving orientation-defined 4 stimulus pairs to the set as soon as criterion performance was reached on a newly introduced pair.

In the final two phases, we tested rats' performance with Gabor-defined stimuli and Aperture-defined stimuli (in separate sessions). In each session half of the trials included the new stimuli and the other half of the trials contained the horizontal/vertical textures and the diagonal textures.

Performance criterion

For most phase transitions, the time of transition from one phase to the next was contingent upon whether an individual animal reached the target performance in a particular number of sessions. For the first phases with luminance-defined shapes, an animal had to perform at or above 80% correct for two consecutive sessions. We noticed that some animals had problems reaching this criterion in later phases, despite consistent performance at levels well above chance level (50%). For this reason, we switched to a more gradual scheme to decide about completion of a phase (see Table 2). To accept a lower threshold, the animals' performance had to satisfy two conditions: First the animals had to maintain the (decreased) average performance over an increased number of sessions, and second, its performance during the last session had to exceed the thresholds' value.

Modeling

We employed a V1-like model to mimic the response properties of neurons in the rat primary visual cortex.

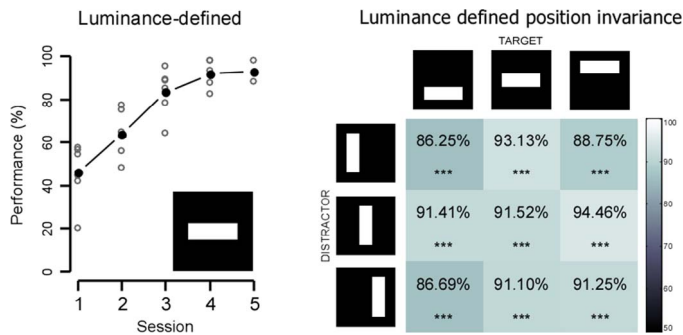


Figure 4. Behavioral performance for the luminance and position invariance phase. Left: Group performance (percent correct) in the luminance-defined stimuli. The black dots represent the group mean (average of individual performances) and the gray circles represent the individual performances. Note that in this and other figures, the number of animals decreases towards the last sessions because the other animals have already reached criterion and have proceeded to the next phase. Right: The mean performance matrix during the position invariance phase. Targets are shown on top of the figure while distractors are represented on the left side of the figure. All conditions differed significantly from chance according to a one-sided, one-sample t test ($***p < 0.001$).

The model consisted of a bank of Gabor filters with spatial frequencies of 0, 0.04, 0.08, 0.15, 0.3, and 0.6 cycles per degree, which is representative for the range of frequencies found in rat primary visual cortex (Girman et al., 1999). Each spatial filter had a corresponding receptive field size (37.31° , 37.31° , 18.52° , 10.13° , 5.19° , and 2.71°), and was modeled with 12 different orientations in steps of 15° . Model response was computed by convolving a given image with each of these filters at 120, 120, 200, 256, 256, and 256 steps (depending on the spatial frequency) in both the x and y direction. Responses of all filters to each stimulus were used as a feature vector for classification in a simple linear classifier.

We used the computed outputs as features for a linear classifier and tested on unseen examples in order to evaluate generalization performance. We tested four conditions in total. In the first condition, the classifier was trained on luminance stimuli only and tested for generalization to orientation-defined 1 stimuli. In the second condition, the classifier was trained on both luminance and orientation-defined 1 and tested for generalization to orientation-defined 2. In the third and fourth condition, orientation-defined 2 and orientation-defined 3 were added to the training set, and generalization was tested to orientation-defined 3 and orientation-defined 4, respectively. The training proceeded until classification on the training set was perfect, after which generalization was tested. The training procedure was repeated 100 times with a new random initialization of the weight vector.

Note that we only included a relatively simple model, which is already a simplification of V1, and which comes no way near the complexity of current state-of-the-art models of vision such as deep neural networks (e.g., Yamins, Hong, Cadieu, & DiCarlo, 2013). More complex models might be able to account for the rats' performance. We do not make any general statements about models in general, and we only use this computational approach to test whether there might be relatively simple luminance confounds that a simple linear filter bank could pick up.

Results

The rats were initially trained on luminance-defined shapes, after which we tested their performance with shapes defined by a second-order texture cue. Unless otherwise mentioned, reported analysis and group averages are for all six animals.

Luminance-defined

Mean group performance already reached 80% after only two training sessions (Figure 4, left). Four rats took four sessions to reach the criterion of 80% during two consecutive days. Two animals needed one extra session to reach the same criterion. Individual performances during the last session of each rat ranged from 88.17% to 97.94%.

Position invariance

Changing position did not have a marked influence on the ability to discriminate between a horizontal and vertical rectangle. All animals reached the criterion of 80% for two consecutive sessions after two sessions. As shown in Figure 4, right, the average performance was above 80% for each combination of positions. The performance averaged across the last two sessions of each animal was significantly higher than chance performance for each pair according to a one sample t test ($N = 6$).

Orientation-defined 1, 2, 3, and 4

Initially, group level performance dropped to chance on the first session of orientation-defined 1 ($M = 48.37\%$, $SD = 16.12$, $t[5] = -0.96$, $p = 0.81$). After a few sessions, rats learned to discriminate orientation-defined 1 stimuli. However, performance did not increase as fast anymore in the next sessions, and some

Session	<i>M</i>	<i>N</i> successes	<i>N</i> trials	<i>p</i> value	Lower bound	Upper bound
1	51.76	103	199	0.6707	0.45	0.59
2	45.45	65	143	0.3156	0.37	0.54
3	43.24	80	185	0.0774	0.36	0.51
4	46.99	78	166	0.4850	0.39	0.55
5	43.45	73	168	0.1049	0.36	0.51
6	44.38	75	169	0.1660	0.38	0.52

Table 3. Binomial test for each session in the Gabor-defined stimuli, with the mean, number of successes, the total number of trials made by the group, the *p* value associated, as well as the lower and upper bound of the 95% confidence interval.

animals failed to reach the 80% criterion altogether. Instead, they settled at a lower asymptote (see Table 2), showing the increasing difficulty of the discrimination task. The difficulty of learning the task was also noticeable in the number of sessions needed to reach the criterion. On average, the animals required 10.83

sessions (*SD* = 4.31) to reach criterion in orientation-defined 1, 18 sessions (*SD* = 1.26) in orientation-defined 2, 36.5 sessions (*SD* = 1.87) in orientation-defined 3, and 22.5 sessions (*SD* = 1.87) in orientation-defined 4. Nevertheless, after learning the discrimination in orientation-defined 1 stimuli, the animals were able to immediately generalize to other stimuli (orientation-defined 2, 3, and 4) above chance already from the first session (one-sided one-sample *t* test; orientation-defined 2: $t[5] = 5.00, p = 0.002$; orientation-defined 3: $t[5] = 10.55, p < 0.001$; orientation-defined 4: $t[5] = 14.89, p < 0.001$). Learning curves for each stimulus are shown in Figure 5.

How quickly did rats generalize from one stimulus type to another? To answer this question, we inspected their performance on the very first 20 trials of the first session where they saw the new stimulus type. Figure 6 depicts performance as a cumulative measure: The leftmost data point is the average performance on the very first trial (averaged across all six animals), the next data point is the average performance on the first two trials (averaged across all six animals), and so on.

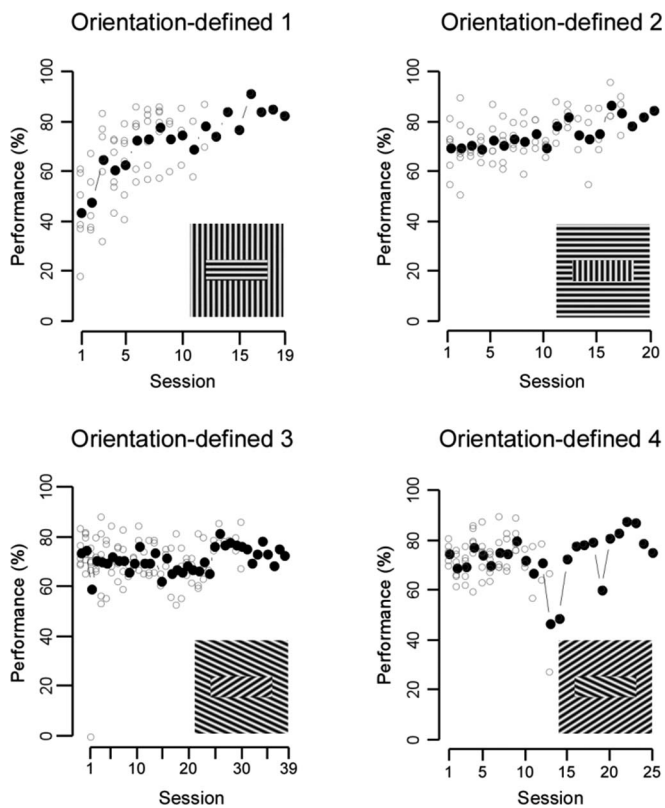


Figure 5. Behavioral performance for the first four texture phases. First row left: Average performance in orientation-defined 1. Performance is around 50% during the first session and slowly increases until all animals reach the criterion of two sessions in a row with a mean performance of 80%. First row right: Average performance for orientation-defined 2. Second row left and right show average performance for orientation-defined 3 and 4. Black dots represent the group average while gray circles represent individual scores. When no gray dot is visible, the data represents one animal, indicating that all other animals already passed criterion.

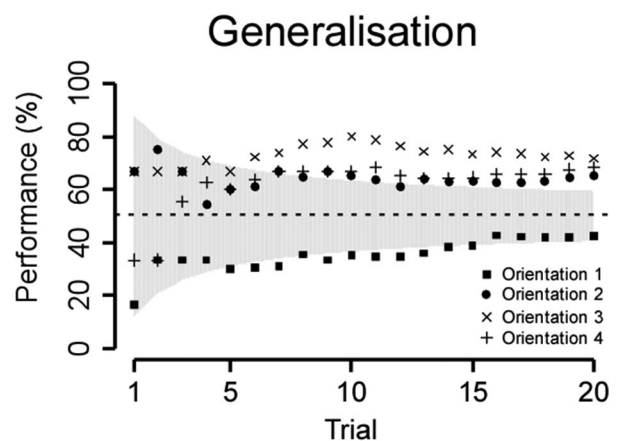


Figure 6. The evolution of the mean performance of all animals during the first 20 trials of the first session for orientations 1, 2, 3, and 4. The gray region represents the 95% confidence intervals around chance calculated over total number of trials, for example, six in trial 1, 12 in trial 2, and so on (binomial distribution).

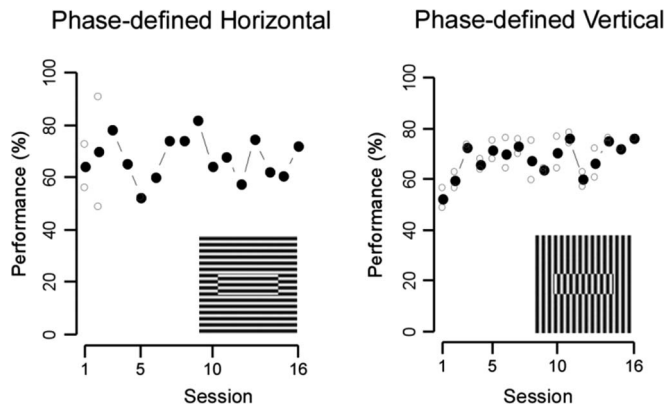


Figure 7. Behavioral performance for the two animals that did the phase-defined horizontal (left) and phase-defined vertical (right) stimuli. Gray circles represent individual performances, black circles represent group performances (or a single performance when no gray circles are shown).

Because the small number of trials, significance was assessed by using a binomial test on the pooled response data of all animals. As expected, in the orientation-defined 1 phase, performance started and remained around or even below chance level, indicating that rats could not generalize their strategy from luminance stimuli. In contrast, in the orientation-defined 2 phase, performance started above chance and stayed at a steady level across the 20 trials, reliably higher than chance from the seventh trial onward (binomial test: $p = 0.043$, 95% CI [0.504, 0.804]). Similarly, in the orientation-defined 3 phase, performance was significantly above chance after seven trials ($p = 0.043$, 95% CI [0.50, 0.80]), and the performance during the orientation-defined 4 phase was higher than chance from the sixth trial onward ($p = 0.0113$, 95% CI [0.55, 0.86]).

Phase-defined stimuli

Only the two rats that proceeded most quickly throughout the earlier phases were trained in this phase, because it proved to be relatively difficult (but not impossible) for the animals to learn and because we did not consider these specific textural properties as crucial for the experiment. Despite the fact that these two rats were the fastest animals to pick up the previous phases, the phase-defined stimuli were challenging to master. The first animal took only two sessions to master the horizontal phase, and ended with a performance of 90.7%, but the second animal took 16 sessions and a final performance of 72% with an average of 66.65% over the last 12 sessions to reach the criterion (Figure 7). Binomial tests also showed that performance during the first session of phase-defined horizontal phase for both

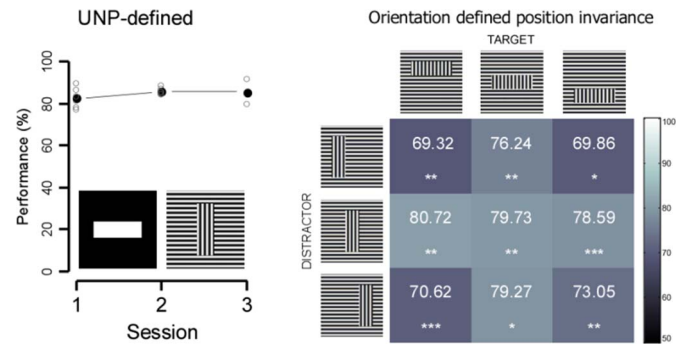


Figure 8. Behavioral performance for the discrimination and the position invariance with orientation-1 stimuli. Left: Group percentage correct in the discrimination phase. Black dots represent the group average while gray circles represent individual performances. Right: Group percentage correct for different combinations of target (columns) and distractor (rows) positions. All conditions differ significantly from chance (t test across animals; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

animals was significantly above chance ($M = 64.27$, $SD = 11.96$; 48 successes out of 76 trials, $p = 0.029$), while performance fell back to chance during the first session of the phase-defined vertical phase ($M = 52.37$, $SD = 5.49$; 43 successes out of 81 trials, $p = 0.66$).

Unpaired phase

In this phase we did not keep the original pairing of the orientation defined targets and distractors, and every target was paired with every distractor. Displaying the target with a varying distractor did not influence performances. The animals reached performances well over the 80%. Since all but two animals reached the criterion of two sessions above 80% in two sessions, two animals had three sessions of unpaired discrimination, after which they also reached the criterion of 80% during the last two sessions. Overall, these result show that the animals most probably do not directly compare both stimuli on local lower level features, but are more likely to evaluate the stimuli as a whole.

Position invariance for orientation-defined 1

Rats do not appear to have major difficulties in solving this task. Rats showed a position invariance to orientation-defined 1 stimulus (all p values < 0.05), albeit with varying degree of robustness across different positions (Figure 8). The animals were clearly able to cope with large changes in position that placed both target and distractor at screen positions that did not overlap with the original positions.

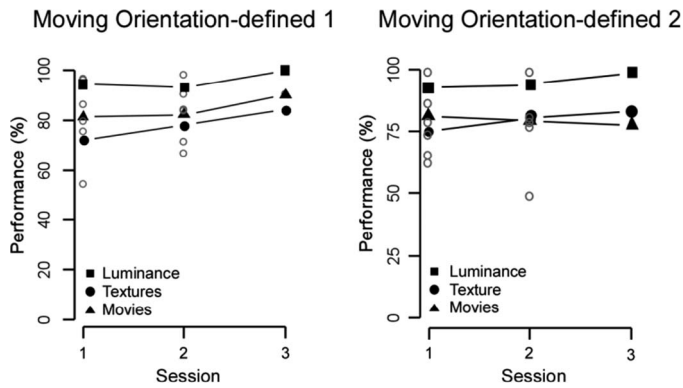


Figure 9. Behavioral performance for the movie phases. Left: Group performance (percent correct) in the first movie phase. Performances for moving stimulus are compared to texture-defined and luminance-defined stimuli. Right: Group performance (percent correct) in the movie II phase. Performances for moving stimuli are compared to texture-defined and luminance-defined stimuli. Filled markers represent group averages, open circles represent individual performances.

Moving orientation-defined 1 and moving orientation-defined 2, 3, and 4

We found that motion cues in the stimuli did not appear to affect performance, which fluctuated around 80% for both static and dynamic textures (Figure 9). When the first dynamic stimulus was introduced, performance for the moving stimulus was 83.03% correct during the first session ($SD = 15.9$, $t[5] = 4.79$, $p = 0.002$; one-sided, one-sample t test) and 82.3% during the second session ($SD = 11.61$, $t[5] = 6.79$, $p < 0.001$). In the second phase, when movement was added to all previously learned stimuli, animals reached a performance of 78.8% during the first session, which is significantly above chance ($SD = 13.5$, $t[5] = 5.21$, $p = 0.002$; one-sided, one-sample t test) and 78.56% during the second session, which is also above chance ($SD = 16.12$, $t[5] = 4.34$, $p = 0.004$).

Contrast manipulation

We included the contrast manipulation phase because the later phases would include stimuli with decreased contrast. Decreasing contrast caused a decreasing trend in performance (Figure 10, left). However, even at a contrast of 40, performance remained well above chance level. At a contrast of 80, performance was at 81.84% ($SD = 8$, $t[5] = 8.67$, $p < 0.001$, one-sided, one-sample t test). At a contrast of 40, the percentage correct was at 71.9% ($SD = 9.71$, $t[5] = 5.51$, $p = 0.001$). A single regression with contrast as regressor and individual performance as input shows

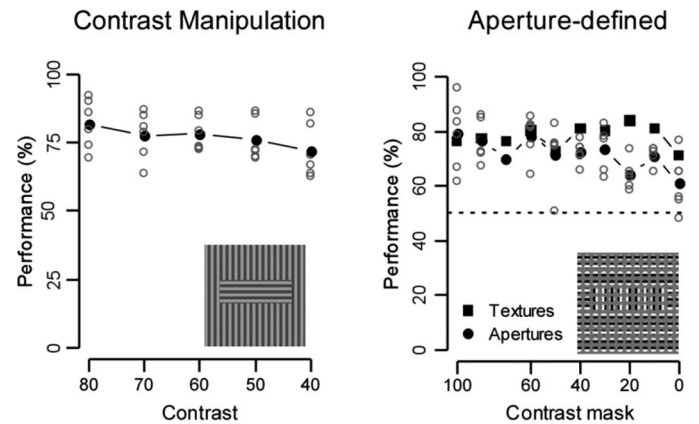


Figure 10. Behavioral performance in the contrast phase and in the aperture phase. Left: Group performance (percent correct) in the contrast phase. The contrast levels of the stimuli are represented on the x-axis, with 80 being the highest and 40 the lowest contrast tested. Right: Group performance (percent correct) in the aperture phase. The contrast of the aperture mask is displayed on the x-axis, ranging from 100 (high) to 0 (low). Black dots represent group averages, gray circles are the individual performances. The stimulus is an example of an aperture stimulus with a 0 contrast mask.

how level of contrast significantly predicts performance ($F[1, 28] = 4.43$, $p = 0.045$, $R^2 = 0.14$).

Apertures

The aperture stimuli represented a different manner to decrease the local information available to the animals and to increase the need to integrate across larger parts of the display in order to process the shape of the figure against the background. The transparency of the aperture mask had a clear effect on performance, and the lowest percentage correct of 64% was obtained for an aperture mask with 0% transparency (Figure 10, right). Still, this performance was significantly higher than chance performance ($SD = 10.21$, $t[5] = 2.637$, $p = 0.02$, one-sided, one-sample t test).

Gabor-defined stimuli, extended test

Finally, Gabor stimuli were tested in all animals for six sessions. Performance did not differ significantly from chance in any of the sessions and there was no sign of learning (see Table 3). In the last session, the performance was still only 45% correct ($SD = 14.33$, $t[5] = -0.8606$, $p = 0.78$, one-sided, one-sample t test) and not significantly different from chance (Figure 11). This failure is all the more striking given how many stimulus variations these animals had already learned before, and the persis-

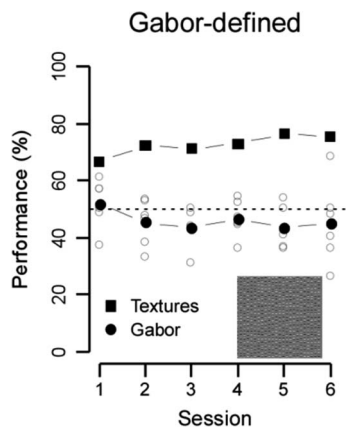


Figure 11. Group performance for the Gabor-defined stimulus phase (percent correct) and on the previously learned textures. Error bars represent the standard error of the mean across animals.

tency of it stands in sharp contrast with the relatively fast learning curves in most previous phases.

Modeling

We compared rat performance to a simple model of rat V1. As can be seen in Figure 12, a classifier trained on the V1 features generalized in some cases but not in other. There was an obvious discrepancy between the model and the behavioral data when

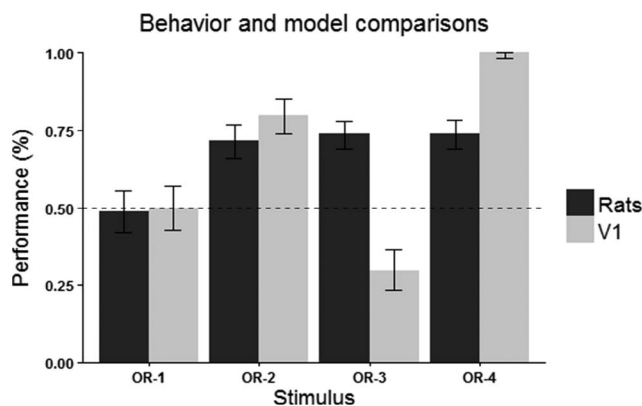


Figure 12. Comparison of the generalization performance between rats' behavioral data (Rat), and a simple model of rat V1 (V1). Behavioral performances were taken from the first session of the respective stimulus condition. The V1 performances were obtained by first training a linear classifier on the model's outputs to the luminance stimulus and all other stimuli preceding the stimulus on the x-axis, and then testing the performance on that stimulus. For example, performance on orientation-defined 3 (OR-3) is obtained by training each model on the luminance-defined, orientation-defined 1 (OR-1) and orientation-defined 2 (OR-2) stimulus. Error bars for the model represent 95% binomial confidence intervals.

generalizing to diagonal stimuli (orientation-defined 3). In that condition, rats do not show a drop in performance, while the model fails to generalize. In sum, the generalization of rats to new orientation-defined shapes cannot be fully explained by this model.

Discussion

Generalization across form-defining cues

In this study we demonstrated that rats can learn to discriminate between two rectangular shapes by making use of second-order cues. We started with an initial discrimination between a horizontal and vertical luminance-defined rectangle, which was solved easily by the animals. A subsequent immediately high performance in position-invariance test revealed that animals already developed a strategy that was not based on very local cues.

Rats did not immediately generalize to newly presented orientation-defined stimuli in which the shapes were defined by second-order cues, indicating that additional learning on second-order stimuli was required for animals to further develop a cue-invariant strategy. Notably, once they reached a stable performance on the initial orientation-defined stimulus pair, we found that performance no longer dropped back to chance level on new variants of stimuli where the figure and background contained textures with a different orientation compared to the initially learned pair. Although we cannot exclude the possibility that the animals learned the new stimulus in only a few trials, this dramatic difference in learning speed compared to earlier phases indicates that at least some form of generalization is taking place. Also, for these orientation-defined stimuli we observed robust tolerance for position changes.

Is this performance expected based on what we know about rodent visual system? In particular, could this task be solved by rat V1 alone? To answer these questions, we compared rat generalization performance to the performance of a simple V1 model (Figure 12). Interestingly, this simulation revealed that the observed pattern of generalization performance was to some extent still consistent with using local features. In particular, just like rats, after learning orientation-defined 1, this model could already correctly perform the task on orientation-defined 2 stimuli. Only when presented with diagonal stimuli (orientation-defined 3), this model failed to generalize and deviated from rat performance. This leads us to conclude that V1 is not sufficient to solve the task. In fact, studies of responses to second-order edges in monkey visual cortex impli-

cated the origin of these representations to be V2 or V4 but not V1 (Pan et al., 2012; Poort et al., 2012; von der Heydt & Peterhans, 1989; von der Heydt et al., 1984).

This finding raises the question of what kind of computations a model should be able to do to correctly learn the classification problem. Recently, by combining evidence from multiple studies, Kubilius, Wage-mans, and Op de Beeck (2014) proposed that a hierarchical computation of similarities between local image features followed by pooling of similar patches is sufficient to explain processing in midlevel vision. Within this framework, second-order edges emerge as the boundary between two dissimilar patches, and the classification problem could then be solved quite easily. More importantly, these computations require at least two layers of processing, and is thus consistent with the notion that V1 alone is not sufficient to solve the task.

We also ruled out the possibility that rather than solving the task in a generic way, the animals learned specific target and distractor combinations given the low overall number of stimuli pairs (that is, there were only four different pairs for the textured stimuli). In particular, even when we presented all pairwise combinations of target and distractor stimuli irrespective of cues defining them, task performance remained unchanged. Both the position invariance and the unpaired conditions show that the rats are not relying upon fixed local regions on the screen, which is in agreement with previous studies such as Alemi-Neissi et al. (2013).

Processing in the absence of local cues

All these data suggest that the animals are able to process shapes defined by second-order edges, independently from the local orientation of the textures defining these edges and with some generalization across position. Nevertheless, the stimuli do not exclude the possibility of a strategy based upon local detection of second-order contrast. An orientation-selective neuron in visual cortex that is able to process second-order edges would be able to perform the relevant computation to solve this task. The question remains whether the rats integrate information across multiple elements of stimuli when dealing with second-order edges, as has been shown before for luminance-defined stimuli (Dodwell et al., 1970; Kurylo, Van Nest, & Knepper, 1997; for a review see Zoccolan, 2015).

The aperture stimuli are an important challenge as the imposed aperture masks increases the need to integrate across multiple local elements. The animals were able to achieve above-chance performance on these stimuli. Nevertheless, this ability to integrate

across multiple elements is not very robust, as it was not found with the Gabor stimuli.

Given that the rats showed some evidence for integration across multiple elements with the aperture stimuli, what might be the causes for the failure to perform the task with the Gabor-defined stimuli? First of all, it might simply be an acuity problem, in which case the data do not inform us about higher processing stages. Stimuli were constructed assuming that rats had an acuity of one cycle per degree (which still allowed for sufficient Gabor patches and sufficient information per patch), which is the threshold where behavioral performance drops below 70% correct on a grating detection task (Prusky, Harker, Douglas, & Whishaw, 2002). It is possible that the mechanisms that allow a figure to pop out are not sufficiently activated with the chosen spatial frequency. Another explanation is that rats do not possess the cortical architecture that allows them to extract global shape from the combination of cues that define shape in these Gabor-defined stimuli. For example, experiments with random dot kinematograms indicate that rats do possess local motion detectors and some mechanism to extract global motion from a scene (Douglas, Neve, Quittenbaum, Alam, & Prusky, 2006). However, more is needed for the Gabor-defined stimuli, for which discrimination relies on attributing one motion direction to figure and the opposing motion direction to the background. Finally, our results do not rule out the possibility of learning Gabor-defined stimuli. We did not find generalization from the previous learned stimuli, and we did not find evidence for learning across six sessions. Still, it remains possible that if rats had been trained with more Gabor-like stimuli previously, had experienced more variation in stimuli, or had been trained for a longer time, we would have observed learning behavior of the Gabor-defined stimuli. Therefore, our null result suggests that complex perceptual organization might not be naturally present in rodents, but does not rule out the total possibility of complex perceptual organization.

Implications

Previous findings on visual object and shape recognition in rats do not determine to what extent rats are able to go beyond luminance contrast cues when solving such recognition tasks (for a review see Zoccolan, 2015). While studies were able to exclude simple luminance cues such as “go to the brighter stimulus,” some studies argued that rats might rely upon more complex contrast templates such as “go to the stimulus which contains a bright region on top of two black regions” (Vermaercke & Op de Beeck,

2012). Such contrast templates are also relevant for some aspects of human vision; for example, face detection is influenced by how much a face image contains the typical contrast features of a face (Gilad, Yovel, & Sinha, 2012). Nevertheless, despite this relevance of contrast templates, humans primarily rely upon oriented features such as edges. Models of object recognition also focus upon such shape features (e.g., Biederman, 1987; Riesenhuber & Poggio, 1999). Up to now it was not clear to what extent rats might use such oriented features on top of contrast templates. The current findings suggest that rats can move beyond luminance-based contrast templates and use oriented features that are no longer directly related to luminance differences.

The current study has additional minor implications for research on the rodent visual system. First, it is yet another demonstration of the phenomenon that rats will make use of a simple strategy, unless they are pushed to use more complex perceptual rules. This was illustrated by the fact that rats did not immediately generalize to stimuli with second-order edges, but only did so after some initial visual experience with these stimuli.

Second, the results show that the animals are able to process stimuli in a cue-invariant way to some extent. Even though there was no generalization between the luminance-defined and the orientation-defined stimuli, we have evidence for this cue-invariant processing from later phases. This implies some more complex shape processing than solely based on luminance differences.

Third, this study is an important contribution to the growing body of literature on the rodent visual system and its similarity to the primate visual system. Although rats have been demonstrated to be capable of transformation invariant object recognition (Zoccolan et al., 2009), this was always tested with stimuli on a homogeneous background. However, a real-life environment contains a lot of clutter, and then a prerequisite for object recognition is the ability to parse figures from their background. Ideally, this should involve some process that is invariant to the cues that signal the presence of a figure in some background. Here we showed that, once sufficiently trained, rats are able to do so, consistent with a large body of studies in monkeys documenting cue-invariant processing (e.g., Poort et al., 2012). Future studies might investigate if neurons sensitive to second-order cues are also present in the rodent visual system and whether this behavior performance is linked to the detection of the figure in the image (Poort et al., 2012).

Finally, our study also showed that perceptual organization in rodents failed when pushed very hard as we did with the Gabor-defined stimuli. Humans have

no problem to extract the figure shape in such a display. We are not aware of monkey research with these stimuli. Further research into the existence of species differences at the behavioral level and their potential causes at the neural level could reveal the necessary conditions for the superior human abilities.

Keywords: Perceptual organization, luminance cues, second-order cues, learning, shape discrimination

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