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Illusory contour orientation discrimination in the cat

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We present the first evidence that a non-human species (the cat) is able to discriminate the orientation of illusory contours. Following Vogels and Orban[45], we used two types of illusory contours. In one type, the illusory contour was defined by a number of contour-inducing semicircles, of which the endpoints were separated by a gap. In the other pattern, the inducing semicircles were shifted in phase along their diameter and their endpoints were aligned along the contour. Just noticeable differences in orientation were measured (at the 73.5% correct level), using a Wetherill and Levitt[49] staircase procedure. Values in the order of 11 degrees were obtained when using the first type of illusory contour. Just noticeable differences with the second type were in the order of 17 degrees. Reducing the salience of the illusory contour, whether by scrambling the contour, or by decreasing the number or the contrast of inducing semicircles, systematically increased discrimination thresholds.

INTRODUCTION

Schumann[38] is usually considered to be the discoverer of stimulus patterns giving rise to the perception of boundaries in the absence of actual physical discontinuities, which are generally called illusory contours. Although Schumann was certainly not the first to report visual illusions (e.g. Hermann in 1870; see Spillmann et al.[40]), his study marked the beginning of a growing body of literature concerning the perception of illusory contours and the underlying neural processes. Since that time, an impressive number of figures have been devised generating the perception of illusory contours, of which the Kanisza figures are probably the best known[23]. Pritchard and Warms[33] and Parks[28] have provided excellent reviews.

A number of authors (e.g. refs. 1,19,29) have proposed that the processes which generate illusory contours 'actually prevent the emergence of illusions in normal visual environment'[47]. In other words, the processes generating illusory contours are essential in normal vision. This was fully confirmed in a fascinating study by von der Heydt et al.[46]. These authors reported that in monkey V2, a large number of cells are highly specialized for signalling the orientation of illusory contours. Some V2 cells even preferred the illusory contour stimuli over the classical solid bar. The high degree of specialization in monkey V2 for the processing of illusory contours may be linked to

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the vividness of many visual illusions reported in humans[31].

However, the behavioral relevance for human vision of animal units selective for the orientation of illusory contours critically depends upon the demonstration that non-human species are able to discriminate the orientation of such contours. Until now, this evidence has been lacking, although Bravo et al.[7] claimed that cats can detect a moving Kanisza square. However, the inference that cats actually perceive the illusory square is too strong a conclusion to be drawn from a detection task. A safer conclusion is that cats are able to detect the presence of an illusory contour. Furthermore, Bravo et al.[7] reported that 'performance of both cats remained consistently above chance and typically above 70%', which is a rather low performance for a detection task. Cats achieving a near 100% correct performance in detecting a solid square is not unusual (unpublished observations). Hence cats seem to have difficulties in detecting illusory contours, which suggests that further processing of parameters of such contours (e.g. its orientation) could be limited. This was initially confirmed by the extreme difficulties we encountered in training cats in orientation discrimination with illusory contours[12,26]. This is also in line with the neurophysiological study of Redies et al[34], showing that complex cells in cat areas 17 and 18 do respond to properly oriented illusory contours, but that the strength of this response never exceeds half of the response elicited by a solid bar of the same orientation.

The difficulty in detecting illusory contours, and the poor discrimination of its orientation in cats, is surprising in the light of theories which consider the processes underlying illusory contour extraction as essential for normal vision. Therefore, we decided to reinvestigate the abilities of cats in orientation discrimination with illusory contours. Contrary to our initial observations, the present study revealed that cats are able to discriminate relatively fine differences in orientation of illusory contours. Furthermore, the more salient the contour appeared to the human observer, the smaller the cat's just noticeable difference (JND) in orientation was. Salience of the contour was manipulated by scrambling the contour (Expt. 1), by reducing the number of inducing semicircles (Expts. 2 and 3) and by reducing contrast of the semicircles (Expt. 4).

MATERIALS AND METHODS

Apparatus and experimental set-up

Two cats, Barbarossa (cat 52) and Cleopatra (cat 54) were trained and tested in an apparatus designed after Berkley[2]. During training and testing sessions, the animals were enclosed in a box, and thrusted their head in a Plexiglas chamber with two nose keys through which the stimuli were viewed. The stimuli were back-projected onto a circular, semi-transparent screen of 75° diameter, positioned at 28.5 cm from the cat's eyes. Positive (S +) and negative (S −) stimuli were presented simultaneously, each stimulus behind a nose key. An occluder prevented the animals from seeing the stimuli together. This prevents discriminations based on configurational cues, which would arise if both stimuli were to be inspected simultaneously.

A standard discrimination trial (as used in the testing procedure) started after an intertrial interval (ITI) of 7 s. After the ITI, S + and S − were presented. During the first 0.35 s, all responses were ignored (response delay period, *RDP). Responses were taken into account only after expiration of the RDP. Pressing the nose key behind which the S + appeared was rewarded by a small amount of food. Errors were left unpunished. Upon a response, the stimuli disappeared. The S + was administered behind the left or right nose key in a pseudorandom order. The randomization was restricted in such a way that in each group of 6 consecutive trials, S + was presented on the left and the right side in an equal number. Position learning, defined as the occurrence of 6 consecutive responses with the same nose key, was controlled in the following way: when position learning developed, S + was presented on the non-preferred side until the number of left and right key responses were again equilibrated[14].

S + and S − were projected by 2 separate slide projectors. Orientation was manipulated by rotating a Dove prism mounted in front of the slide holder. The luminance of the stimuli was controlled by a variable neutral density filter, positioned in front of the Dove prism. Both manipulations were achieved by means of stepper motors. Exposure time of the stimuli was controlled with shutters, placed in front of the neutral density filters. Background luminance was maintained at 0.5 cd/m^2. The entire experimental set-up was incorporated in a large wooden box in order to control contrast (log [$\Delta l/l$]) rigorously. Luminances were measured by means of a Minolta luminance meter. Training and testing programs were controlled by a PDP-11 computer.

Stimuli

We used two types of illusory contours similar to those devised by Vogels and Orban[45]. The first stimulus (Fig. 1A) consisted of a number of inducing semicircles, separated by a gap (gap illusory contour, GIC). In the other stimulus (Fig. 1B), the illusory contour was induced by shifting each inducing semicircle along the contour (phase-shifted illusory contour, PSIC). All stimuli were presented from slides, reproduced from drawings plotted on a HP-plotter. Inducing semicircles were white, on a dark 0.5 cd/m^2 background. Width of the inducing semicircles was 0.2° (viewing distance 28.5 cm). Control experiments have shown that a variation of the width of the inducing semicircles in a 0.15–0.35° range does not affect thresholds in orientation discrimination[26]. Furthermore, in the same study it has been demonstrated that gap-width of a GIC and contrast of the inducing semicircles interact with each other (using a GIC with

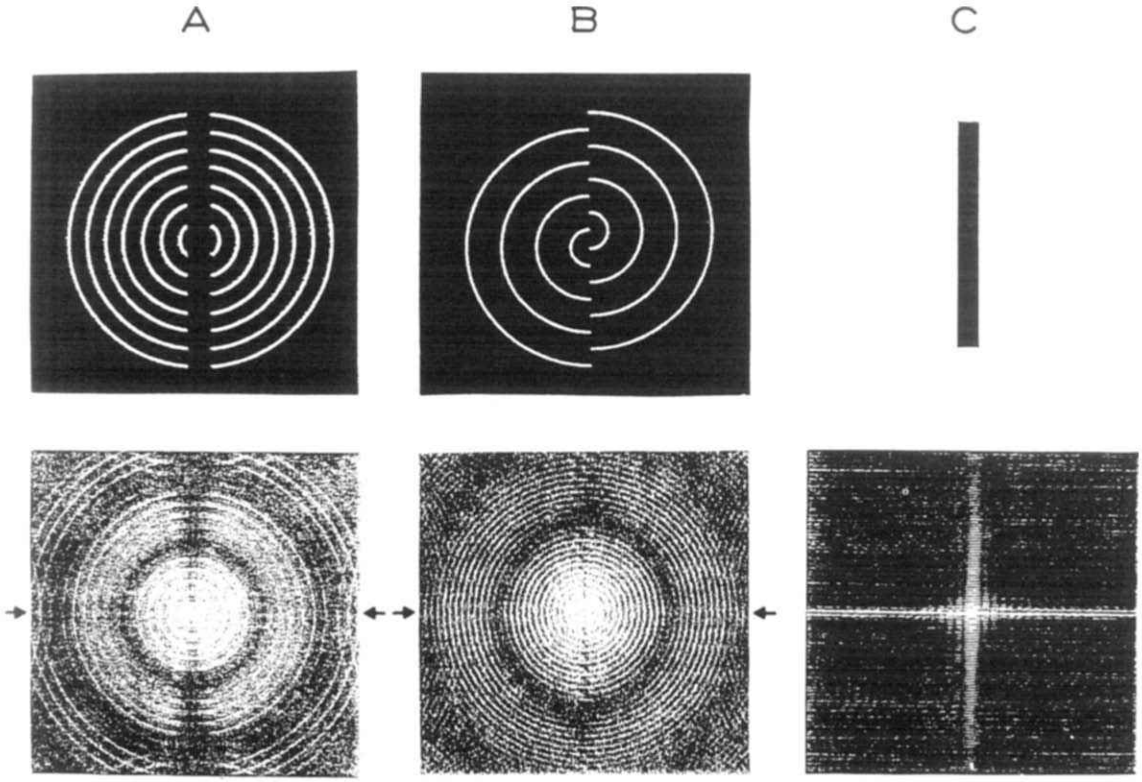

Fig. 1. GIC (A), PSIC, (B) and a black bar of dimensions equal to the dimensions of the gap in the GIC (C), with the corresponding Fourier spectra below. Elevated grey values indicate the power of a particular spatial frequency. The lowest spatial frequencies are represented in the middle of the spectra. The horizontal white line in the spectrum of the dark bar (C) represents the energy corresponding to the length orientation of the stimulus. Such an energy (indicated by arrows in A and B) is absent in both illusory contour types. Notice that the width orientation of the bar in C is represented by the vertical white line in the corresponding spectrum. The vertical dip in the spectra of the illusory contours (A and B) has mathematical underpinnings which go beyond the scope of this paper.

7 pairs of inducing semicircles). We used a 1.2° wide gap in our GIC, which is optimal for a large range of contrasts. Notice that the GIC induces a brightness effect, while the PSIC does not.

The illusory contour stimuli used are derived from the patterns used by von der Heydt et al.[46] in physiological recordings in monkeys. In one type of pattern the illusory contour was made of two line grids of which the line ends were separated by a gap (corresponding to our GIC). They also used a contour formed by two abutting line grids which were shifted in phase (corresponding to our PSIC). We have used circular inducing elements to ensure that the animals made use of the orientation of the contour in their discriminations, and not the orientation of the inducing elements.

Schumann[38] defined an illusory contour as a boundary which is perceived in the absence of physical discontinuities (see Introduction). This should not obscure the fact that the perception of illusory contours is always induced by a spatial arrangement of such discontinuities. In most illusory contour generating patterns, the physical discontinuities alone constitute a contour which, in addition, has illusory qualities. In the presently used patterns, the physical discontinuities are luminance changes along the contour. Hence, the question arises whether the animals did not discriminate the orientation of simple luminance-defined contours rather than the orientation of illusory contours. The simplest way to detect a luminance gradient in a pattern is by using a linear spatial filter. A 2-dimensional (2-D) Fourier analysis can be used to investigate how much orientation information could be provided by the output of such a linear mechanism. We refer to this information as linear orientation information. The spectrum obtained by 2-D Fourier analysis, represents the energy in the pattern at different spatial frequencies, along all orientation axes. The more the spectrum is isotropic, the less pronounced is the luminance gradient along the contour, and the higher the chance that the cats perceived the contour as illusory.

The results of the Fourier analysis of the stimuli used in this study are shown in Fig. 1. Since the nature of the spectra remains unchanged with parametric variations of the stimulus pattern, 2 typical spectra for GIC and PSIC stimuli are shown (Figs. 1A and 1B). The stimuli in Figs. 1A and 1B are those used for training the cats. Fourier analysis of the GIC and the PSIC results in Fourier spectra which are largely isotropic in the 2-D Fourier domain. In fact, these spectra strongly resemble the spectrum of a set of complete circles. This means that there is little linear orientation information about the contour in either pattern. On the other hand, a bar is a typical example of a boundary of which the orientation is linearly defined. The difference between the Fourier spectra of the illusory contours and a bar (Fig. 1C) is striking. The energy in the spectrum which runs orthogonal to the orientation of the bar, represents the orientation of the length axis of the stimulus. No such energy is demonstrable in the spectra of the illusory contours. In conclusion, little linear orientation information seems to be related to the illusory contour of GIC and PSIC patterns. Hence, the importance of the luminance gradient in both GIC and PSIC is minimal. Presumably, the GIC and PSIC patterns generated a similar percept of illusory contours in our cats as in humans.

Training methods

The cats were trained in real line orientation discrimination and orientation discrimination with illusory contours. In each of these discrimination tasks, the discriminanda were two contours of different orientation. The orientation of one of both discriminanda remained fixed throughout the task, and therefore will be referred to as the reference orientation. The reference orientation served as the S +. The other stimulus was of a variable orientation and served as S –. Hence, during the discriminations, the orientation difference was changed by manipulating the angle between S – and S +. To ensure the generality of our observations, the orientation discriminations were taught around two reference orientations, the horizontal (H) and the right oblique (RO). The order in which both references were trained was randomized between animals. To prevent confusion between S + of one reference and S – of the other, S – deviated clockwise from S + when the reference was H and anticlockwise when it was RO.

During the course of our experiments, we developed a number of training procedures for teaching the animals the different discrimination tasks[26]. Here, we only describe shortly the most efficient procedure. This procedure was coined the differential exposure method (DEM), since in this procedure, trials were administered in which a longer exposure of S + compared to S − provided the animal with a cue for an easy identification of S +. Each new orientation difference was introduced with discrimination trials in which S − disappeared shortly after stimulus onset, whereas S + remained in view until a response occurred. The shorter the exposure time of S −, the stronger the differential exposure cue. Each orientation discrimination training started at an orientation difference of 30°. This difference was presented during at least 60 trials. In the first 20 trials, the differential exposure cue was strong, in the next 20 trials, this cue was faded out and in the last 20 trials both discriminanda remained present until a response occurred (as in the standard discrimination trial). Only after the cat reached the 75% correct criterion within each separate block of 20 trials, was the orientation difference reduced. After each change in orientation difference, the same procedure was repeated until the threshold was reached. Further details about this procedure are given in De Weerd et al.[13]

The animals were trained with a GIC made of 7 pairs of inducing semicircles and a PSIC made of 4 such pairs (Figs. 1A and 1B). We failed in our attempt to train our cats with a PSIC made of 7 pairs of inducing semicircles. This can be explained by the elevated number of endpoints defining the contour, which might prevent the cat from detecting the contour. Indeed, in a PSIC with 7 pairs of inducing semicircles, 28 endpoints are aligned along the 12° long contour, which corresponds to a spacing of 2.33 points per degree. Despite the fact that this value falls within the average resolving power of the cat visual system (e.g. refs. 3,24,42), this might be near acuity limit for some cats (inspect the 75% correct performances in Berkley and Bush[4]). Alternatively, it is possible that acuity required for detecting the PSIC differs from grating acuity (see Discussion).

Both cats were first trained in bar orientation discrimination and afterwards in orientation discrimination with illusory contours (GIC and PSIC). With the DEM, some 30 daily 300-trial sessions sufficed to reach threshold, regardless of which stimulus pattern was used. It should be noted that the animals were trained with the PSIC only after the training and testing in Expt. 1 with the GIC. This order seems to be important, since 3 more animals which are not used in the present study, and which had only limited experience with the GIC, showed pronounced difficulties in the acquisition of orientation discrimination with the PSIC. This suggests that the training with the PSIC benefits from experience with scrambled GICs as used in Expt. 1.

Testing method

The animals were tested by means of a 73.5% Wetherill and Levitt staircase procedure[49]. We prefer this method over the commonly used constant stimuli method. In the cat, the choice of the stimulus differences used in the constant stimuli method can influence the magnitude of the JND (De Weerd, Vandenbussche and Orban, in preparation). Contrary to the method of constant stimuli, the staircase method is an adaptive procedure. Since we used a 73.5% correct Wetherill and Levitt staircase, the orientation difference was reduced after 3 consecutive correct responses or after two correct responses followed by an incorrect and a correct response. The orientation difference was increased after an incorrect response, a correct response followed by an incorrect one and after two correct responses followed two incorrect ones. One staircase measurement lasted 75 trials. This number of trials yields generally 12–16 reversal points. The orientation difference was adapted to performance by multiplying or dividing it by a factor 1.2. Since the staircase measurement started near threshold level, and because of the proportional rule for adapting the orientation difference, the geometrical mean of all pairs of reversal points was taken as the JND. Each threshold measurement started at the threshold level estimated from previous training or testing sessions. Two JNDs were measured daily for each reference orientation. The first JND of each reference orientation was preceded by a 20-trial introduction block, presenting a fixed orientation difference 1.5 times larger than the expected JND.

RESULTS

Both cats successfully discriminated the orientation of GIC and PSIC patterns. However, the possibility remains that the animals identified some local feature of the stimulus pattern at the beginning of a session, and simply discriminated its position instead of the orientation of contour. An obvious local cue would be an endpoint of an inducing semicircle. Technically, it was impossible to manipulate the strength of the local cue and to show that this did not affect the discrimination performance. Therefore, rather than manipulating the strength of the endpoint cue, we manipulated the salience of the illusory contour. If the cats used the orientation of the contour, one would expect JNDs in orientation to increase when the contour becomes less salient. Salience was manipulated first by scrambling the contour, second by reducing the density of semicircles at constant contour length as well as by reducing contour length at constant density, and finally by reducing contrast of the inducing semicircles.

Even if the cats used the orientation of the contour, it remains possible that they converted the contour into a bar by performing some sort of lowpass filtering of the incoming visual signals. In that case, the contour could hardly be considered illusory, since the alignment of the endpoints would not have to be used to extract the contour. In order to evaluate this possibility, we compared the discrimination behavior in the different experiments with the amount of linear orientation information present in the patterns. The amount of linear orientation information was evaluated by filtering each stimulus with a circular Gaussian filter having a high spatial frequency cutoff at 0.5 cycles per degree. Filters with much lower cutoffs (for example 0.1 or 0.2 cycles per degree) turn almost all GIC and PSIC patterns in homogeneous circular disks of light. Such filters do not differentiate between GICs and PSICs and there-

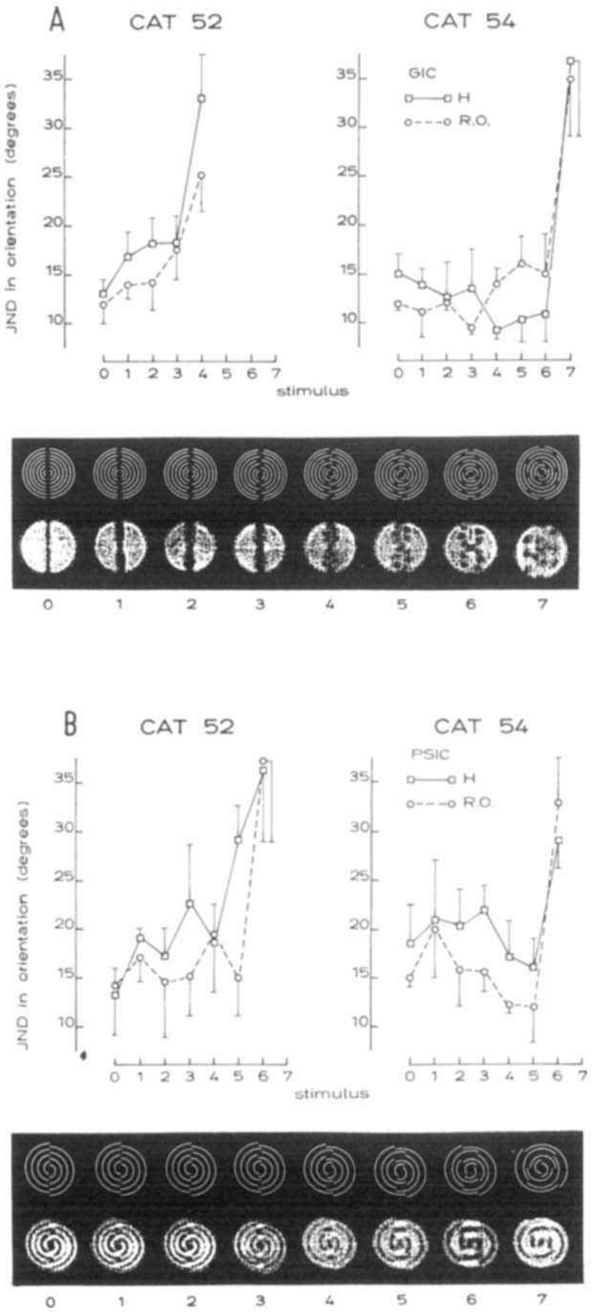

Fig. 2. JNDs in orientation plotted as a function of increasing scrambling of the illusory contour in cats 52 (Barbarossa) and 54 (Cleopatra) for GIC (A) and PSIC (B). The abscissa is an ordinal axis, with the numbers referring to the numbers of the stimuli represented at the bottom of A and B. Below each stimulus, the corresponding lowpass filtered version is represented. JNDs are measured for the horizontal (H) and right oblique (RO) reference orientation. Error bars represent standard deviations. The absence of data for one or more stimuli at one or both reference orientations means that no reliable JNDs could be determined.

fore are uninteresting. Filtering with an upper cutoff at 0.5 cycles per degree, however, gives different results in GICs and PSICs, which is relevant to the interpretation of our results (see Discussion). Furthermore, this cutoff is a behaviorally plausible choice, since in cats, contrast sensitivity at spatial frequencies below 0.5 cycles per degree is still considerable[5]. If the output of linear lowpass filtering mechanisms were used, the lowest thresholds would be expected for those stimuli in which such filtering reveals a bar-like pattern.

In addition to manipulating the salience of the illusory contour, we will compare orientation discrimination performance measured with a real line and with the illusory contours. The data obtained in the different experiments will be presented for each cat separately, since in some experimental conditions, one cat was still able to achieve reasonable JNDs, whereas its 'colleague' had already given up.

Experiment 1: Influence of scrambling

The first way to reduce the salience of the contour was to disalign the endpoints defining the contour by increasingly scrambling the illusory contour (Fig. 2). To explain the way in which the illusory contours were scrambled, the term illusory contour component (ICC) will be introduced. An ICC is the 'illusory contour', defined by one pair of inducing semicircles. In the normal GIC or PSIC, all ICCs are aligned. As a consequence, the orientation of the illusory contour corresponds exactly to the mean orientation of the ICCs. The contour is degraded by changing the orientations of the individual ICCs, while keeping the mean orientation constant. The standard deviation on the orientation of the ICCs is used as 'scrambling measure' (SM). For both GIC and PSIC, stimulus patterns were devised having SMs of 3, 5, 8, 16, 26, 37 and 50°. The scrambling of the stimulus patterns reduces the salience of the illusory contours, which makes it more difficult to solve the discrimination task by comparing the orientations of the patterns. Hence, if the animals used the orientation of the illusory contours, JNDs in orientation would increase with increasing scrambling. On the other hand, if the cats isolated one local cue at the beginning of a testing session, and used the position of this cue to solve the discrimination task, JNDs would prove independent from the degree of scrambling. Indeed, using a local cue implies that the structure of the pattern is ignored; only the number of local cues in the pattern determines the difficulty to identify such a local cue. Since the number of local cues remains constant whatever the degree of scrambling may be, JNDs would remain constant in all scrambling conditions.

The experiment started with the standard stimulus (stimulus 0 in Figs. 2A and 2B). Subsequently, the other contours were presented in order of increasing scrambling, one stimulus per session. Going through all these stimuli will be referred to as a 'run'. Both animals first performed two runs in succession with the GIC, and much later two runs with the PSIC. The results are presented together in Figs. 2A and 2B. Thresholds in orientation discrimination are presented as a function of SM. The stimuli are ordered on an ordinal abscissa. At the bottom of the Figs. 2A and 2B, the stimuli viewed by the cats are represented with a filtered version of each stimulus below.

Firstly, notice the small thresholds the cats achieve when presented with the standard stimuli. This illustrates that cats discriminate the orientation of illusory contours relatively accurately. For the GIC (Fig. 2A, stimulus 0), JNDs (averaged over references) were 13.8° and 12.8°, whereas values of 16.8° and 13.7° were obtained when using the PSIC (Fig. 2B, stimulus 0), for cats 52 and 54 respectively.

An equally important feature of the results is the increase of the JNDs with increasing SM values, in both animals and for both stimulus types. This makes it highly unlikely that the cats used a local cue to solve the discrimination. On the contrary, the results suggest that JNDs start increasing when any global organization in the stimulus patterns becomes difficult to discern. Furthermore, the results obtained with the PSIC argue strongly against the lowpass filtering hypothesis. Indeed, the standard PSIC (stimulus 0 in Fig. 2B) is reduced to a nearly homogenous circular disk after lowpass filtering, and yet cats discriminate its orientation. It is also worthwhile mentioning that JNDs are not smaller for these scrambled PSICs in which peaks in the low frequency energy distribution are aligned along the contour (stimulus 3–6 in Fig. 2B) than for those in which this alignment is absent. On the other hand, JNDs for the GIC standard stimulus (stimulus 0 in Fig. 2A), are lower than those obtained with the PSIC standard stimulus (stimulus 0 in Fig. 3B). Clearly, an important difference between PSIC and GIC is the presence of a bar in the lowpass filtered version of the latter stimulus. In addition, JNDs in cat 52 increase strongly at GIC stimulus 4, where the bar in the filtered version of the stimulus becomes fuzzy. Both observations could indicate the involvement of lowpass filtering mechanisms in the results from cat 52. However, the other animal, cat 54, continues to discriminate the orientation of the GIC stimuli after the disappearance of any bar-like arrangement in the stimulus patterns. This is not too surprising, since even in stimulus 5 and 6, there is a global arrangement in the stimulus pattern, of which the orientation can be discriminated. It is only in stimulus 7, where any global arrangement is difficult to detect, that JNDs clearly rise. Hence, contrary to the PSIC results where both animals performed similarly, the GIC results which were obtained earlier in time, suggest differences in strategy between animals.

Experiment 2: Influence of density

In human vision, the strength of the illusion in stimulus patterns such as the PSIC and the GIC depends upon the density of endpoints aligned along the illusory contour. In the present experiment, we explicitly manipulated this factor by spacing a varying number of inducing semicircles along a contour of constant length (12°). We wanted to investigate whether degrading the illusion by manipulating density leads to increased thresholds in orientation discrimination. Density will be quantified by the fraction dividing the number (n) of pairs of inducing semicircles by the length (L) of the contour (n/L).

The cats started the experiment with the standard stimulus of the previous experiment. First, density was reduced until only one pair of

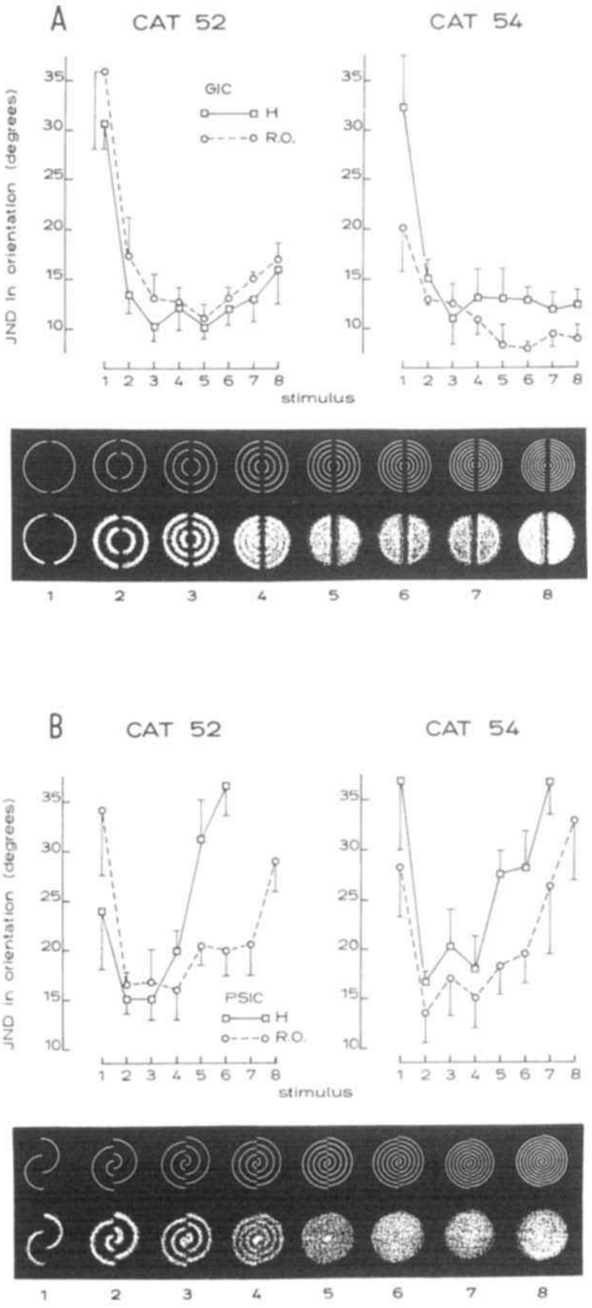

Fig. 3. JNDs in orientation plotted as a function of number of inducing circles in cats 52 (Barbarossa) and 54 (Cleopatra) for GIC (A) and PSIC (B). Since length of the contour is kept constant, this is a manipulation of density. The numbers at the abscissa refer to stimuli represented at the bottom of A and B. Lowpass filtered versions of the stimuli are shown below the original patterns. JNDs are measured for the horizontal (H) and right oblique (RO) reference orientation. Error bars represent standard deviations. The absence of data for one or more stimuli at one or both reference orientations means that no reliable JNDs could be determined.

inducing semicircles constituted the illusory contour. Afterwards, density was increased above the value of the control stimulus, always presenting one stimulus per session. This complete sequence constitutes a 'run'. For both GIC and PSIC, two runs were carried out. Unlike the previous experiment, the presentation of GIC and PSIC stimuli was interleaved, presenting each of them every other day.

The PSIC created difficulties for both animals during the first run. In particular, JNDs for the horizontal reference orientation remained above the normal level when the control stimulus was presented at the start of the second run. Therefore, we decided to retrain the animals. This was done for both reference orientations in order not to favour the horizontal reference. After this retraining, we restarted the complete experiment, the results of which are shown in Fig. 3. Thresholds in orientation discrimination are plotted as a function of density for GIC (Fig. 3A) and PSIC (Fig. 3B), for both cats separately. At the bottom of Figs. 3A and 3B, the stimuli and their filtered counterparts are represented.

A common feature of the results is the inaccurate performance of both cats when only one pair of inducing semicircles is present. JNDs are 30.0° for the GIC and 31.3 for the PSIC (averaged over cats and references). This result is in agreement with the previous experiment, in which thresholds in orientation discrimination increased for sufficiently scrambled contours. In both experiments, JNDs rise when no clear overall pattern is present in the stimulus.

With increasing density, however, differences between GIC and PSIC emerge. Whereas performance with the GIC remains largely unchanged when density increases from 2/12 to 8/12, this is not the case when using the PSIC. With the PSIC, thresholds in orientation discrimination increase for densities above 4/12.

This difference between GIC and PSIC is easy to understand. In the GIC, increasing density merely causes the contour to be defined more and more by linear orientation information. This is particularly clear in the filtered stimuli. The higher the density, the more the contour emerges as a dark bar in the lowpass filtered versions of the stimuli. Hence, in the GIC, increasing density causes no additional difficulty for the cat in discriminating the orientation of the contour. Notice that if the output of linear filtering mechanisms were to be used, one would even expect a clear improvement in orientation discrimination with increasing density. This clearly does not occur (Fig. 3A), which argues against a significant contribution of linear lowpass filtering in the present results. In the PSIC, however, increasing density will eventually cause the endpoints to fuse and the contour to disappear. JNDs increase strongly for PSICs defined by 7–8 pairs of inducing semicircles. This is in agreement with our unsuccessful attempt to train cats in orientation discrimination with a PSIC consisting of 7 pairs of inducing semicircles (see training methods).

Finally, the only stimuli for which systematic differences were observed between reference orientations were the PSICs at high densities. For these stimuli, orientation discrimination performance around the oblique reference orientation is superior to performance around the horizontal. It will be remembered that it was poor performance around the orientation at the start of the experiment that compelled us to retrain the animals. Since similar difficulties were absent with the GIC, this might point to differences in the processing of the two types of illusory contour. However, some peculiar behavioral difficulty cannot be excluded and therefore this phenomenon remains difficult to interpret.

Experiment 3: Influence of length

Orientation discrimination performance is dependent upon length of the contour. This has been demonstrated in humans[25,44] and in cats[14,43] using real lines as stimuli. In the present experiment, length of the illusory contour was manipulated by taking away the outermost pair of inducing semicircles, one by one. In this way, length of the contour decreased while maintaining a constant density. The experiment was carried out starting from a GIC of optimal density (5/12) and a PSIC of optimal density (3/12), as determined from the previous experiment. These stimuli served as standard stimuli. Length was then decreased until only the inner pair of inducing semi-

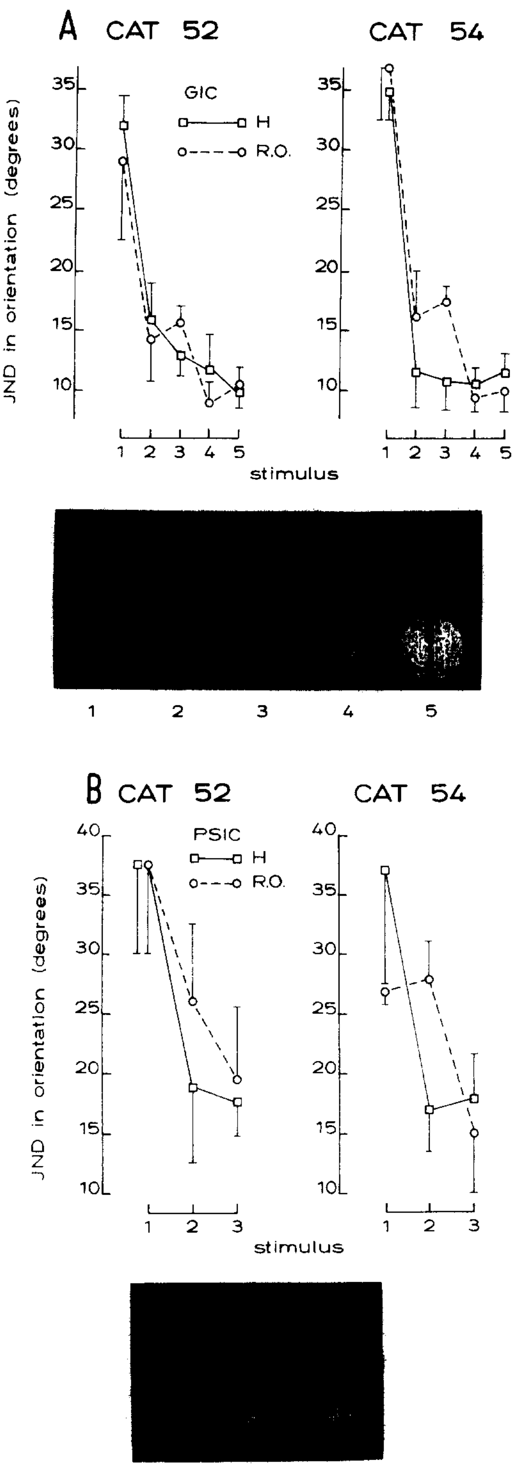

Fig. 4. JNDs in orientation plotted as a function of number of inducing circles in cats 52 (Barbarossa) and 54 (Cleopatra) for GIC (A) and PSIC (B). Since density of inducing circles is kept constant, this is a manipulation of length. The numbers at the abscissa refer to stimuli represented at the bottom of A and B. Lowpass filtered versions of the stimuli are shown below the original patterns. JNDs are measured for the horizontal (H) and right oblique (RO) reference orientation. Error bars represent standard deviations. The absence of data for one or more stimuli at one or both reference orientations means that no reliable JNDs could be determined.

circles was left, presenting one stimulus each session. This sequence will again be referred to as a 'run'. GIC and PSIC stimuli were interleaved, presenting each contour type every other day. Two runs were carried out in each animals for each stimulus type. The stimuli are represented at the bottom of Figs. 4A and 4B, together with the results of lowpass filtering.

Fig. 4 illustrates the effect of length upon orientation discrimination performance of GIC (Fig. 4A) and PSIC (Fig. 4B). Considering the GIC, performance is best for stimuli 4 and 5. (lengths 9.6° and 12°). JNDs (averaged over lengths and references) are 10.4° and 10.3° for cats 52 and 54 respectively. Performance changes little for stimuli 2 and 3 (lengths 4.8° and 7.2°), but when only one pair of inducing semicircles was left (length 2.4°) JNDs increase strongly. Considering the PSIC, performance is best for stimulus 3 (length 12°). JNDs are 20.2° and 16.7° for cats 52 and 54 respectively (averaged over references). At the oblique reference orientation, a reduction in length to 7.6° (stimulus 2) begins to affect performance in orientation discrimination. For stimulus 1 (length 3.3°), with only one pair of inducing semicircles defining the illusory contour, JNDs rise considerably, and certainly so in comparison to the standard stimuli. JNDs are more than 35.0° and 33.5° for cats 52 and 54 respectively (averaged over references). The inability of cats to discriminate the orientation of stimulus patterns made up of only one pair of inducing semicircles, is in line with the results of the previous experiments.

Experiment 4: Influence of contrast

Performance in orientation discrimination with long, real lines remains stable over a large range of contrasts[14]. Only for contrasts below −0.63 (log [Δl/l]), do JNDs start increasing. We investi-

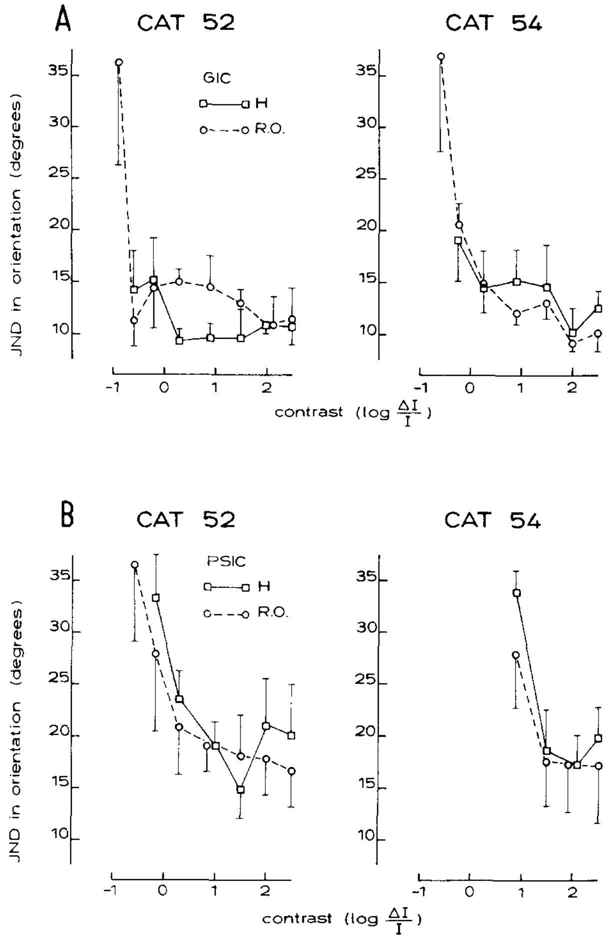

Fig. 5. JNDs in orientation plotted as a function of contrast of inducing circles in cats 52 (Barbarossa) and 54 (Cleopatra) for GIC (A) and PSIC (B). Error bars represent standard deviations. The absence of data for one or more stimuli at one or both reference orientations means that no reliable JNDs could be determined.

gated whether contrast has a similar effect upon orientation discrimination with illusory contours. Contrary to observations of Dumais and Bradley[15], subjective strength of the illusory contours in our stimulus patterns declines with decreasing contrast of the inducing semicircles. Hence, in this experiment, strength of the illusion was manipulated by varying the contrast of the inducing elements.

The GIC and PSIC of optimal density (5 and 3 pairs of inducing semicircles respectively) at a 1.46 contrast were used as control stimuli. First, contrast was reduced until no reliable JNDs could be determined any more. Afterwards, contrast was increased above 1.46, always presenting one contrast each session. This sequence, again referred to as a run, consisted of interleaved GIC and PSIC sessions. Each cat went through two runs for both GIC and PSIC.

Fig. 5 shows thresholds in orientation discrimination as a function of contrast for GIC (A) and PSIC (B). Contrast-dependency was clearly different for the two illusory contour types. Performance with the GIC remained unaffected over a broad range of contrasts and then suddenly increased at the − 0.8 contrast in cat 52 and a − 0.65 contrast in cat 54. With the PSIC, performance dropped much more rapidly, especially in cat 54.

Obviously, there was also a difference between animals, performance in orientation discrimination in cat 54 being less resistant to contrast reduction for both stimulus types.

Note finally that the 1.46 contrast used in training the animals was appropriate for both GIC and PSIC.

Real line and illusory contour orientation discrimination compared

Fig. 6 compares performance in orientation

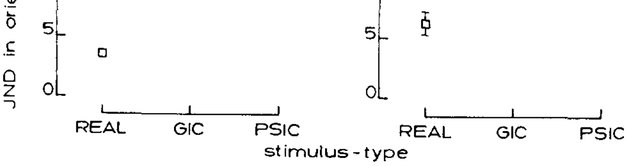

Fig. 6. JNDs in orientation plotted as a function of stimulus type in cats 52 (Barbarossa) and 54 (Cleopatra) for a real bar (R), GIC, and PSIC. GIC and PSIC JNDs are averages of the mean results obtained in the density, length and contrast experiments at both references with a GIC of 5 inducing circles and a PSIC of 3 inducing circles. Contrast of the inducing circles (log [$\Delta I/I$]) was 1.46. Error bars represent standard deviations. The absence of an error bar indicates that the standard deviation was smaller than the symbol size.

discrimination for real lines with performance for GIC and PSIC. The results for the real line were obtained after completing the training in orientation discrimination of real lines but before the training with illusory contours had begun. The real line was a 0.2° wide and 12° long light bar with a contrast of 1.46. These are optimal stimulus values for a real line[14]. The GIC and PSIC results were the average of the results obtained with the standard stimuli used in the length, density and contrast experiments (averaged over references). Contrast of the inducing semicircles was 1.46, which is optimal (see previous experiment).

The results are very similar in both cats. JNDs are lowest for the real line (3.9° and 6.5° in cat 52 and 54 respectively). JNDs determined with the GIC rise to 10.7° and 11.7° in cats 52 and 54 respectively. With the PSIC, JNDs increase further to 17.5° and 17.8° in cats 52 and 54 respectively. The average increase of the JNDs obtained with the GIC compared to the real line, is 2.3. For the PSIC this factor amounts to 3.7. This comparison between contour types shows that cats discriminate the orientation of real contours more easily than the orientation of illusory contours. Furthermore, discriminating the orientation of the PSIC is clearly a more difficult task than discriminating the orientation of the GIC.

DISCUSSION

One might ask why devote so much effort to demonstrate that animals can judge the orientation of illusory contours. Indeed, within a limited theoretical framework[8,11,16,18,21,22,32,36], visual illusions are no more than an artefact of visual processing. Recent computational theories suggest the contrary. According to Brady and Grimson[6], a major task of the visual system is to identify the different surfaces which constitute the visual scene. This implies the extraction of surface boundaries from local cues such as differences in colour, luminance, texture, as well as a number of depth cues such as perspective, shading and stereo. Importantly, in a correct interpretation of visual scenes, the visual system will ascribe depth values to differences in color, luminance and texture. Coren[10] catalogued those visual scenes in which one surface is closer to the observer as the other, and therefore occludes the most distant surface, as interposition-scenes. Since the GIC and PSIC are degraded images of interposition-scenes, it is possible that the visual system tries to give a 3-D interpretation to the discontinuities (luminance steps) in the patterns. However, since the discontinuities in fact belong to the same surface, the resulting boundaries are perceived as illusory. An alternative theory has been proposed by Grossberg[19,20]. In both instances however, the generation of illusory contours is the result of a basic visual processing (boundary completion).

If generation of illusory contours reflects a fundamental visual process, one would expect this to be present not only in the human brain but also in the brain of a number of other species. The demonstration of sensitivity to illusory contours in non-human species then adds further support to the view that perception of illusory contours reflects a fundamental aspect of visual processing. We have attempted to show that cats discriminate the orientation of illusory contours. In order to justify this claim, we must show that the animals used the orientation of the contour and not some covariant local cue. Furthermore, the possibility that the cats could extract the contour from the patterns by linear filtering must be excluded as much as possible.

Combining the evidence of the first 3 experiments, it is highly likely that the cats discriminated the orientation of a contour when it was available in the patterns. Indeed, reducing the salience of the contour through scrambling, density or length manipulations systematically resulted in increased JNDs in orientation. Notice that the patterns for which the cats discriminate the orientation best, are exactly those patterns in which the reader will also perceive the clearest contour. The fact that the performance varied with the salience of the contour, makes it unlikely that the cats used the position of a local cue to solve the discrimination task, since this cue was available in all stimulus patterns used. At least in the scrambling experiment, the local cue was equally present in all stimulus patterns. Furthermore, in absence of any contour, such as in a pattern with only one pair of inducing semicircles, or after extreme scrambling, the cats had severe discrimination difficulties. Hence, the local cue on its own cannot account for the relatively fine discriminations obtained with the standard illusory contour pattern.

When scrambling the contour, as well as when reducing the number of endpoints, the salience of the contours has to be reduced considerably before JNDs increase significantly. In the length and density experiments, JNDs remain at a relatively low level as long as more than 4 endpoints generate the contour. Similarly, in the scrambling experiment, cats perform relatively well when there is a configuration in the pattern in which more than 4 endpoints are more or less aligned (e.g. stimuli 5 and 6 in Fig. 2). It seems thus that in the scrambling experiment, the cat used the alignment of endpoints, even if no clear illusory contour was present.

Whether it is justified to claim that the cats discriminated the orientation of illusory contours, depends to a large extent upon the contribution of linear filtering mechanisms in the perception of the contours. Indeed, if a simple linear filter were sufficient to explain the data we collected, there would be no reason to accept that the animals used another contour than the luminance-defined contour detected by the linear mechanism.

Before evaluating to what degree eventual linear orientation information effectively is used, we will first discuss how much linear orientation information is *available* in illusory contour generating patterns. This question has been the subject of a debate which has been fully opened by Ginsburg[17] and Tyler[41] and which has produced interesting but conflicting evidence[9,15,16,27,35,37,39]. At first glance, Fig. 1 suggests that neither illusory contour used in the present study is linearly defined. However, the compression of the different spatial frequencies in this figure could mask any linearity present in a small range of spatial frequencies. Indeed, in the GIC, linear lowpass filtering is sufficient to extract the contour, whereas in the PSIC, it is not. In other words, by lowpass filtering of the GIC stimuli, a dark bar emerges in the GIC patterns but not in the PSIC patterns. Hence, in the very low spatial frequencies (too low to be represented adequately in the spectra in Fig. 1), the GIC spectrum must be anisotropic.

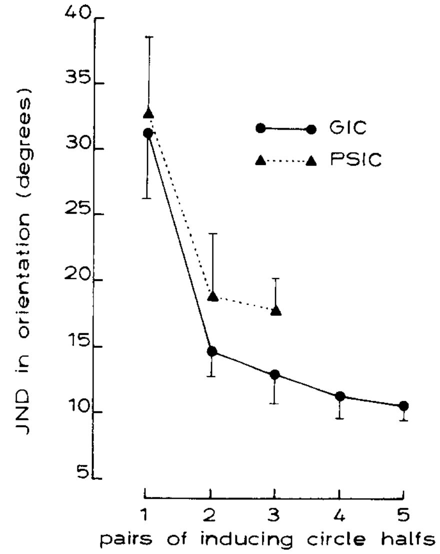

Fig. 7. JNDs in orientation plotted as a function of number of pairs of inducing semicircles for GIC and PSIC. JNDs are averages of the mean results obtained in the conditions of length and density experiment. Hence, for each number of a pair of inducing semicircles, an average was calculated over references ($n = 2$), experiments ($n = 2$) and cats ($n = 2$), which means that each data point refers to 8 values. Error bars represent standard deviations.

The question remains to what extent the cats *effectively* used the output of a linear filtering mechanism. In other words, this concerns the relative contribution of linear and non-linear filtering processes in the perception of the illusory contours. Using the PSIC, we showed that cats are able to extract and process contours which cannot be extracted by a linear mechanism. In these stimuli, non-linear mechanisms must be at work to construct a contour from the alignment of endpoints in the pattern. Concerning the GIC, a great deal of evidence also points to a significant involvement of non-linear processing. For example, in Expt. 1, cat 54 continued to discriminate the orientation of the GIC although no contour was available in the lowpass filtered version of the stimulus (Fig. 2A). Furthermore, in the GIC just as in the PSIC, performance in orientation discrimination is determined by the number of inducing semicircles, irrespective of the spacing of their endpoints. This is illustrated in Fig. 7, in which we calculated a JND for each number of pairs of inducing semicircles, averaged over cats, references and experiments (length and density experiment). The results of this figure are discussed in more detail below. Finally, in the density experiment with the GIC, JNDs do not decrease with increasing density, although the bar as extracted by lowpass filtering becomes increasingly clearer through this manipulation.

Three other findings would at first glance seem to point to the involvement of linear filtering. In cat 52, the increase of the JNDs in the scrambling experiment corresponded to the increasing fuzziness of the bar as extracted by lowpass filtering. Second, the GIC JNDs tend to be lower than the PSIC JNDs (Fig. 7). Finally, GIC JNDs are more resistant to contrast reduction than PSIC JNDs. However, for each of these findings an alternative explanation can be advanced. The lower endurance of cat 52 in the GIC control experiment compared to cat 54, could be explained by a lower degree of experience with the GIC at the time of the experiment. Indeed, for almost 3 years, cat 54 was involved in a number of preliminary studies with the GIC[26], whereas cat 52 participated in none of them. The differences in JNDs between GIC and PSIC, which become more pronounced at lower contrasts and higher densities, could be due to acuity constraints imposed by the latter pattern type. In PSIC patterns with small spacings between endpoints, resolution could limit detection of the contour, and therefore orientation discrimination. Furthermore, the mechanism which resolves the endpoints of the inducing semicircles in a PSIC pattern, must encode the phase information of the endpoints. Therefore, the type of resolution required for detecting the PSIC might well differ from ordinary grating acuity. The necessity of coding phase information also might cause the less efficient extraction of the contour at lower contrasts. In the GIC, there is no need to use phase information, which in itself already makes the detection (and discrimination) of the contour much easier, at all contrasts and densities.

In summary, our evidence strongly suggests that cats use contour orientation in solving the discrimination task. Furthermore, we excluded for either of the two stimulus patterns that only linear mechanisms contribute to the discrimination of the orientation of illusory contours in the cat, which significantly increases the possibility that cats perceive the presently used contours as illusory. Concerning the relative contribution of linear and non-linear processes in the GIC, some linear processing might contribute to the orientation discrimination of this pattern.

That linear mechanisms could contribute to the discrimination in case of the GIC is not surprising, if one considers the model proposed by Peterhans et al.[30] to account for their physiological observations. The circuit consists of a number of end-stopped units with a preferred orientation orthogonal to the contour and signalling the alignment of line ends. The end-stopped cells converge upon integrating units which are increasingly responsive as more end-stopped units are stimulated. AND-gating prevents the integrating units from being responsive if only one line end is present (non-linear processing). Since V2 cells were orientation-selective both for illusory contours and light bars, the authors postulated that the integrating units converge upon higher order units together with lower order end-free units, both of them having a similar preferred orientation (parallel to the contour). The lower order end-free units might be involved in linear processing. Thus, in the Peterhans et al.[30] model there are two pathways feeding into the higher order units corresponding to the V2 cells responsive to illusory contours: a non-linear pathway and a linear pathway. The PSIC would only drive the non-linear pathway while the GIC would drive both. This could account for the lower thresholds obtained with GICs compared to PSICs, even when parameters are optimized for each pattern. Furthermore, the special acuity constraints in the PSIC about which we have hypothesized, could correspond to the resolution of the integrating units of Peterhans et al.[30]. The vulnerability of orientation discrimination with the PSIC at low contrast could be related to a relatively high firing threshold in the integrating units. Such an elevated firing threshold naturally follows from the

AND-gating in these units proposed by Peterhans et al.[30].

The agreement between our behavioral data and the model of Peterhans et al.[30], is further supported by the similarity of length and density effects in our experiments and those of von der Heydt and Peterhans[48]. These authors showed that, in essence, the number of line ends which constitutes the illusory contour determines response strength. In general, increasing the number of line ends along the contour from 4 to 12 doubled response strength. We replotted the data of the length and density experiments for an easier comparison with von der Heydt and Peterhans'[48] data. In Fig. 7, we calculated a JND for each number of pairs of inducing semicircles, averaged over cats, references and experiments. For the GIC, as well as for the PSIC, 4 line ends were insufficient to obtain reasonable JNDs (one pair of inducing semicircles, Fig. 7). Adding one or two pairs of inducing semicircles brought the JNDs back to their normal level. Hence, the doubling in response strength with the increase from 4 to 12 line ends corresponds to the reduction by a factor 2 of the thresholds in orientation discrimination after a similar manipulation. The small standard deviations in Fig. 7 illustrate that in conditions in which the number of pairs of inducing semicircles is equal, JNDs are indeed very similar. The large standard deviation in condition 2 for the PSIC, points to the only exception: for the right oblique reference orientation, JNDs are 26.6° in the length experiment and only 15.1° in the density experiment. However, the difference was negligible for the horizontal reference (17.9° vs 16.1° respectively).

Performance in orientation discrimination with illusory contours is much better than could be expected from the poor detection performance described in Bravo et al.[7]. Indeed, when using optimal stimulus parameters (Fig. 6), thresholds in GIC orientation discrimination are 11.2°, and thresholds in PSIC orientation discrimination are 17.6° (averaged over references). It is worth mentioning that at orientation differences sufficiently larger than the JND (20–30°), our cats easily reached a 90% correct performance, which indicates that the detection of the illusory contour constituted no problem for these animals.

The only previous study which has been devoted to the response of cat visual neurones to illusory contours, is that of Redies et al.[34]. These authors have demonstrated that C-cells in areas 17 and 18 as well as cells in the corpus geniculatum laterale respond to borders formed by a phase-shift in a line pattern. The separation between line ends was manipulated in a 0.4–12° range. Interestingly, in the corpus geniculatum laterale, individual units preferred a spacing of 1.5°, which would correspond to a PSIC with a length of 12° and 2 pairs of inducing semicircles. This is an optimum spacing for the cat (see density experiment, Fig. 3B). In areas 17 and 18, however, optimal spacing for the C-cells was 3–6°, which is too large a spacing to account for the optimum in our behavioral data (Fig. 3B). S-cells in areas 17 and 18 responded only when a luminance gradient was added to the phase-shift in their pattern. Unfortunately, in Redies et al.'s[34] study, orientation tuning was not assessed, making it impossible to appreciate how well cat C-cells signal the orientation of illusory contours.

Assuming that illusory contours reflect a fundamental process of normal vision – the construction of boundaries –, the present study suggests that in the cat visual system, borders are extracted from visual input in a way similar to that of primates. We are currently making visual cortical lesions to identify the location of neural substrates critical in the processing of illusory contour orientation. The outcome of this study, we hope, could guide neurophysiologists searching for units turned to the orientation of illusory contours in the cat.

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